



Historical transoceanic dispersal of a freshwater shrimp: the colonization of the South Pacific by the genus *Paratya* (Atyidae)

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ABSTRACT

Aim To infer the phylogenetic relationships within the freshwater shrimp genus *Paratya* Miers, 1882 (Atyidae) and to use these data to answer biogeographical questions about the location, timing and form of evolution of this genus in the South Pacific.

Location *Paratya* are spread throughout various freshwater habitats in the western Pacific, with a disjunct northern range in the North Pacific (Japan, Korea, Ryukyu Islands, Siberia) and South Pacific (Australia, New Zealand, New Caledonia, Lord Howe, Norfolk Island).

Methods Specimens were obtained from throughout its range. Mitochondrial sequences of cytochrome oxidase subunit I and 16S ribosomal DNA were analysed using phylogenetic techniques to identify whether landmasses are monophyletic and what the relationships are between landmasses. Molecular clock dating methods were used to date divergences between taxa.

Results Each landmass was recovered as monophyletic. Japan/Ryukyu Islands is the most basal group, followed by New Zealand. Australian specimens form a sister group to a clade made up of two groups (New Caledonia and Lord Howe/Norfolk Island). The oldest divergence within the genus (between North and South Pacific) took place $12\frac{1}{2}$ –19 Ma.

Main conclusions The geographical origin of the genus (either Gondwana or Laurasia) is unclear. Dispersal occurred between the North and South Pacific long after the split up of Gondwana. Dispersal likely explains the presence of *Paratya* on each landmass in the South Pacific, from continent to isolated oceanic island. This dispersal is conjectured to have taken place through oceanic currents because of the amphidromous life cycle of some taxa of *Paratya*, given that amphidromy is plesiomorphic in atyid shrimp.

Keywords:

16S rDNA, amphidromy, COI, Crustacea, dispersal, Gondwana, molecular clock, mtDNA, *Paratya*, vicariance.

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INTRODUCTION

A classic conundrum of biogeography is the presence of related organisms in a landscape divided by substantial barriers to dispersal. Seemingly unfeasible dispersal routes, an increased knowledge of continental drift and the development of cladistics helped spawn ‘vicariance biogeography’ (Avice, 1994). This stresses the active role of landscape rather than organism in the formation of biogeographical patterns

(Rosen, 1976). In a vicariant event, the landscape moves, dividing a preexisting, stationary population of organisms, whereas in a dispersal event the organisms move across a static landscape.

Isolated, and yet related, populations of freshwater organisms can provide good examples of distributional puzzles, as both terrestrial and saltwater environments can prove effective barriers. This problem interested both Wallace (1881) and Darwin (1888). The combination of a freshwater-restricted

range and a disjunct distribution makes freshwater shrimps of the genus *Paratya* Miers, 1882 (Atyidae) a good model for the study of evolutionary and biogeographical processes at both the macro and micro scales.

Paratya are small freshwater shrimp, with a planktonic larval phase in their life history. They are found in varied environments from pure freshwater creeks and lakes to estuaries, and are distributed antitropically throughout the western Pacific (Fig. 1) (Carpenter, 1977a). Approximately 16 species of *Paratya* (depending on taxonomic authority consulted) are distributed on a range of landmasses, including continents (Australia), large and isolated remnant islands of Gondwana (New Zealand, New Caledonia, Chatham Islands), young volcanic islands (Lord Howe, Norfolk Island), as well as large continental Laurasian Islands (Japan) and small Laurasian islands (Ryukyu Islands) (Carpenter, 1977a; Walsh & Mitchell, 1995). They are also found on the Laurasian mainland in Korea and Siberia (Carpenter, 1977a; Walsh & Mitchell, 1995).

Paratya taxonomy has been discussed many times (Kemp, 1917; Roux, 1926; Riek, 1953; Williams & Smith, 1979; Choy & Marquet, 2002), but taxonomic characters used within the Atyidae can vary a great deal and make phylogenetic conclusions based on morphology challenging (Smith & Williams, 1980). The ecology and anatomy of *Paratya* has been most intensively

studied in Australia (Williams, 1977; Walsh & Mitchell, 1995; Hancock & Bunn, 1997; Hancock *et al.*, 1998; Fawcett *et al.*, in review), New Zealand (Carpenter, 1977b, 1983) and Japan (Suzuki & McLay, 1998; Ikeda, 1999). Earlier genetic studies have focused on only a single *Paratya* species each. In Australia, studies had been concentrated on restricted geographical areas (Hurwood *et al.*, 2003; Baker *et al.*, 2004a,b), but a recent study has considered the majority of the range of *Paratya australiensis* Kemp, 1917 in Australia (Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data). Genetic studies in Japan have used allozyme data to tackle taxonomic questions particular to Japan (Ikeda, 1999).

Genus-wide *Paratya* biogeography has been little studied, although it has been referred to in passing as part of larger distributional studies (Bishop, 1967; Carpenter, 1977a; Williams, 1981), but the lack of phylogenetic context makes biogeographical inferences from these studies difficult. Specific biogeographical hypotheses can be tested when phylogenetic relationships are considered, because these relationships between species from different landmasses can also reconstruct geographic, as well as taxonomic, relationships (Emerson, 2002). One way to differentiate the processes of vicariance and dispersal to infer biogeographical history is to overlay phylogenetic relationships with geographical distributions and geological data (Avice, 1994). Stock (1986) considered non-molecular phylogenies of atyid shrimps in assessing vicariant vs. dispersalist theories in the Caribbean. When the element of time is added to a phylogeny through the use of molecular clocks (Arbogast *et al.*, 2002; Burrige, 2002), specific competing biogeographical hypotheses can be assessed, as has been done for New Zealand cicadas (Arensburger *et al.*, 2004), Chatham Islands insects (Trewick, 2000) and freshwater fish in both Madagascar (Vences *et al.*, 2001) and the Pacific (McDowall, 2002, 2003).

Early descriptions of *Paratya* referred to taxonomic affinities between taxa (Kemp, 1917; Roux, 1926), which by extension may describe phylogenetic relationships. These range from deep relationships, reflected in Roux's (1926) division of the genus into subgenera (e.g. placing Japanese and New Zealand taxa together), to shallow relationships in which Roux proposed that Norfolk and Lord Howe Island taxa were both derived and very similar. Researchers have considered the ancient geographical origin of *Paratya*, which some have placed in the northern hemisphere, and so suggesting a southern dispersal (Bishop, 1967; Griffin & Yaldwyn, 1968; Williams, 1981). Others have postulated a Gondwanan homeland, sundered by tectonic activity (Walsh & Mitchell, 1995), and so suggesting a vicariant origin of South Pacific taxa, with a subsequent dispersal to Laurasia in the north. The present study will use the pattern and depth of phylogenetic relationships in comparison with geological data to assess the relative likelihoods of these hypotheses within the South Pacific. The genus-wide phylogeny of *Paratya* from this study will help tease apart the relative roles, timing and methods of dispersal and vicariance at a number of geographical, phylogenetic and temporal scales, and will also help explain the origin and formation of the freshwater biota of the South Pacific.

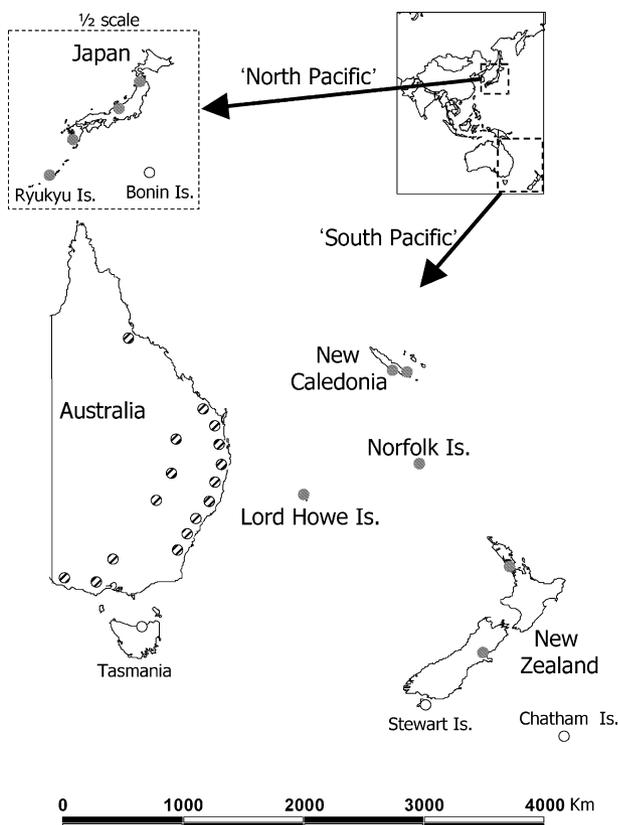


Figure 1 *Paratya* Miers, 1882 sampling locations. Filled in dots (●) = specimens from this study; striped dots (⊙) = specimens from Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data; empty dots (○) = landmass with confirmed *Paratya* population not included in this study.

MATERIALS AND METHODS

Collections and DNA sequencing

Australian *Paratya* were collected with dip or seine nets. *Paratya* from Lord Howe Island, Norfolk Island, New Caledonia, New Zealand, Japan and the Ryukyu Islands were provided by colleagues and preserved in 70–100% EtOH (Table 1). This includes specimens of described species from all major landmasses within the known geographical range of *Paratya* (Fig. 1) (except Siberia and Korea, which is the same taxon as southern Japan; Y. Cai, pers. comm.) and all groups of small, isolated islands except the Chatham Islands (same taxon as New Zealand main islands; Carpenter, 1977a).

Genomic DNA was extracted using a modified version of a CTAB-phenol/chloroform extraction (Doyle & Doyle, 1987). A fragment of the mitochondrial (mtDNA) cytochrome oxidase subunit I (COI) gene was amplified using the polymerase chain reaction (PCR). Specimens from Lord Howe Island, New Zealand, Japan and Ryukyu Islands were amplified using universal COI primers LCO-1490 and HCO-2198 (Folmer *et al.*, 1994) with the following cycling conditions: 15 cycles of 30 s at 94 °C, 30 s at 40 °C, 60 s at 72 °C; 25 cycles of 30 s at 94 °C, 30 s at 55 °C, 60 s at 72 °C. Specimens from Norfolk Island and New Caledonia were amplified using *Paratya*-specific primers ParaCOI-L and ParaCOI-H (Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data), which are internal to LCO-1490 and HCO-2198 (ParaCOI-L: 5'-CTG AAY TAG GTC AAC CAG GAA GAC-3'; ParaCOI-H: 5'-TCT GTR AGA AGT ATR GTA ATA GC-3') with the following cycling conditions: 30 cycles of 30 s at 94 °C, 30 s at 50 °C, 30 s at 72 °C. Exemplars from each area were also amplified for the more conserved mtDNA fragment, 16S ribosomal DNA (rDNA), using universal primers 16Sar and 16Sbr (Palumbi *et al.*, 1991) as per ParaCOI-L/ParaCOI-H.

Amplifications were 50 µL reactions on a Geneamp PCR System 9700 (Applied Biosystems, Foster City, CA, USA) of 1.25 µL template DNA, 0.4 µM primers, 0.2 µM dNTPs, 4 µM MgCl₂, 5 µL 10X PCR Buffer, 1.1 units of *Taq* polymerase (Bioline Pty Ltd, Alexandria, NSW, Australia) and the rest ddH₂O. All individuals were sequenced with the relevant forward COI primer (LCO-1490 or ParaCOI-L) and selected individuals from the major lineages were also sequenced with the reverse primer (HCO-2198 or ParaCOI-H) to check sequence accuracy. All individuals included in the 16S rDNA data set were sequenced in both directions with both primers. All sequencing reactions were carried out using BigDye v.1.1 Terminator (Applied Biosystems) and the sequences produced on an ABI Prism 377 Sequencer (Applied Biosystems) at Griffith University.

Phylogenetic analyses

In total, 53 *Paratya* specimens from outside continental Australia were sequenced for the COI gene. These were added

to existing sequences from representatives of 16 Australian *P. australiensis* lineages (see Table 1; Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data). Two sequences from another atyid shrimp genus, *Caridina* Milne-Edwards, 1837, which is often sympatric with *Paratya*, were added as an outgroup (*C. indistincta* Calman, 1926 from southeast Queensland, Australia and *C. cf. imitatrix* Holthius, 1969 from Grande Terre, New Caledonia). An aligned COI data set of 30 unique *Paratya* and two *Caridina* haplotypes (this study's new sequences lodged under GenBank accession numbers AY661487–AY661501) of 456 bp (Table 1) was produced with Sequencher 4.1.2 (Gene Codes, 2000) at default settings, corresponding to positions 1621–2076 of the decapod *Penaeus monodon* Fabricius, 1798 mtDNA genome (accession number AF217843; Wilson *et al.*, 2000).

For the 16S rDNA data set, a total of 22 *Paratya* specimens, representing each geographical area, were aligned as above with two outgroup Australian *Caridina* sequences (*C. indistincta* from south-east Queensland and *C. zebra* Short, 1993 from north Queensland) to produce an aligned 518 bp data set of 14 unique *Paratya* and two *Caridina* haplotypes (accession numbers AY661471–AY661486) (Table 1), corresponding to positions 12,817–13,329 of the *Penaeus monodon* mtDNA genome.

The two different data sets were included because of their ability to inform at different phylogenetic depths, with the highly conserved 16S data set valid for deep clade relationships between landmasses, and the more variable COI data set applicable to shallower divergences within smaller areas. Both data sets (COI and 16S) were analysed independently in the same manner. The best-fit model of nucleotide substitution was selected with Modeltest version 3.06 (Posada & Crandall, 1998). Maximum parsimony (MP), minimum evolution (ME) and maximum likelihood (ML) analyses were performed in PAUP* version 4.0 b10 (Swofford, 2002) using the suggested Modeltest parameters and bootstrapped 1000 times each (ME analysis does not use proportion of invariable sites or Γ -distributed rates parameters) (MP analyses displayed). Bremer decay indices were calculated for both MP analyses in TreeRot v.2 (Sorenson, 1999). A likelihood ratio test was used in PAUP* to test for non-clocklike molecular evolution (Arbogast *et al.*, 2002). A distance matrix was calculated in PAUP* using the suggested model of molecular evolution. Net divergence times between clades were calculated using a correction for within-clade polymorphism (Avice, 1994). For the COI data set, the sequence divergence rate used was 1.4% per million years (Caridean decapod; Knowlton & Weigt, 1998); and for 16S rDNA (both Pleocyematan decapods), 0.65% (Schubart *et al.*, 1998) and 0.9% (Sturmbauer *et al.*, 1996) per million years. Further, a rescaled COI divergence rate for some deeper COI nodes was calculated by multiplying the relevant 16S clade divergences by the COI/16S divergence ratio for the Lord Howe/Norfolk Island clades. The Lord Howe/Norfolk Island comparison was used because its shallow phylogenetic nature means sequence saturation is unlikely and so it may represent an accurate comparison between 16S and COI divergence rates.

Table 1 *Paratya* specimens from this study listed by landmass, including COI and 16S rDNA GenBank accession numbers and provenance of specimens

Area/taxon	Location	Latitude–longitude	COI GenBank no.	16S GenBank no.	Specimen provider
Japan					
<i>Paratya compressa improvisa</i> Kemp, 1917	Honshu Island: Isawa River, Iwate prefecture	39° 58' N–141° 13' E	AY661489	AY661484	K. Nishi
<i>Paratya compressa improvisa</i>	Honshu Island: Lake Biwa, Shiga prefecture	35° 02' N–135° 53' E	AY661488	AY661483	K. Nishi
<i>Paratya compressa compressa</i> (De Haan, 1844)	Kyushu Island: Oda River, Kagoshima prefecture	31° 37' N–130° 32' E	AY661490		Raffles Museum
Ryukyu Islands					
<i>Paratya compressa compressa</i>	Okinawa: Okuma River	26° 20' N–127° 48' E	AY661491		Raffles Museum
New Zealand					
<i>Paratya curvirostris</i> (Heller, 1862)	North Island: Marawara Stream, Waitakere Ranges	36° 56' S–174° 32' E	AY661487	AY661475, AY661476	K. Collier
<i>Paratya curvirostris</i>	South Island: Cust River main drain, Christchurch	43° 22' S–172° 37' E		AY661475	A. McIntosh
New Caledonia					
<i>Paratya cf. caledonica</i> Roux, 1926	Grande Terre Island: Le Deversoir	22° 17' S–166° 53' E	AY661495, AY661496, AY661498	AY661479, AY661480, AY661481	C. Pöllabauer
<i>Paratya cf. intermedia</i> Roux, 1926	Grande Terre Island: Dumbéa River	22° 11' S–166° 26' E	AY661499, AY661500, AY661501		C. Pöllabauer
<i>Paratya cf. typa</i> Roux, 1926	Grande Terre Island: Dumbéa River	22° 11' S–166° 26' E	AY661497	AY661482	C. Pöllabauer
Lord Howe Island					
<i>Paratya howensis</i> Roux, 1926	Rocky Run	31° 31' S–159° 05' E	AY622605	AY661477	T. Moulton
Norfolk Island					
<i>Paratya norfolkensis</i> Kemp, 1917	Kingston	29° 03' S–167° 57' E	AY661492	AY661478	Australian Museum, A. Oosterman
Australia					
<i>Paratya australiensis</i> Kemp, 1917	Queensland, New South Wales and Victoria	Various*	AY308119, AY308122, AY308124, AY308126, AY308136, AY308141–AY308144, AY308147, AY308155, AY308163, AY308168, AY308172–AY308173, AY308175*	AY661471, AY661472, AY661473, AY661474	Authors
Outgroups					
<i>Caridina indistincta</i> Calman, 1926	Southeast Queensland, Australia	28° 09' S–153° 24' E	AY661493	AY661485	Authors
<i>Caridina zebra</i> Short, 1993	Northeast Queensland, Australia	18° 00' S–145° 37' E		AY661486	D. Hurwood
<i>Caridina cf. imitatrix</i> Holthius, 1969	Grande Terre Island, New Caledonia	22° 17' S–166° 53' E	AY661494		C. Pöllabauer

*These COI sequences from Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data.

RESULTS

Within the *Paratya* mtDNA COI sequences, 169 bases were variable, with 158 parsimony informative (16% in the first codon position, 0% in second, 84% in third). A chi-square test of homogeneity of base frequencies across taxa found no significant difference ($P = 1.00$). Modeltest selected the transversion model with a proportion of invariable sites and a Γ distribution of site-to-site variation (TVM + I + G, a submodel of the general time reversible model) as the best-fit (Γ distribution shape: 1.2754; proportion of invariable sites: 0.5878).

Within the *Paratya* 16S sequences, 93 bases were variable (80 parsimony informative, chi-square base frequencies not significant, $P = 0.99$). Modeltest selected the TVM + G model (Γ : 0.2275).

The likelihood ratio test could not reject clock-like evolution in either data set (COI: $P = 0.5660$, 16S: $P = 0.5381$).

Tree topologies

MP, ME and ML analyses for the COI data set all largely agreed in the monophyly of each landmass with respect to the others (Fig. 2: COI MP strict consensus of 112 cladograms of

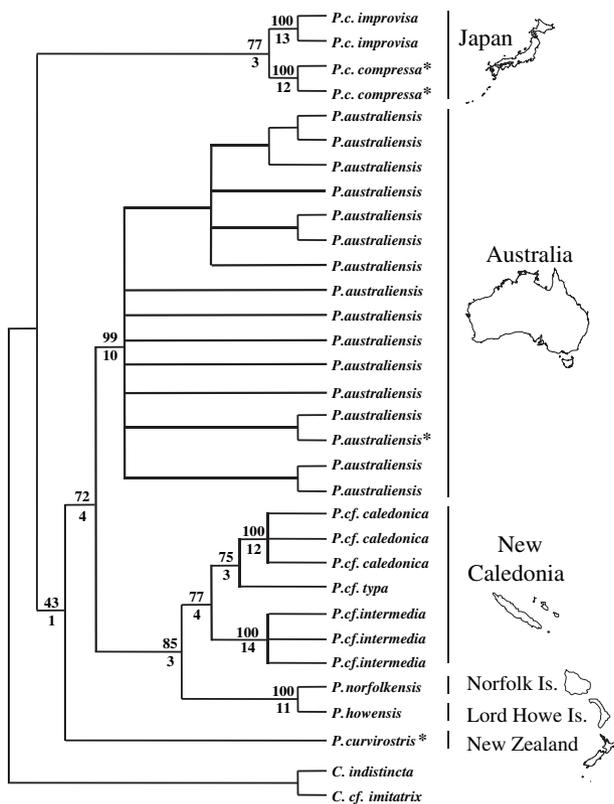


Figure 2 Maximum parsimony (MP) strict consensus cladogram of COI data set, showing landmass distributions. Selected bootstrap values displayed above node and Bremer decay indices below. **Paratya* taxa with known high salinity tolerance (Carpenter, 1977b; Walsh & Mitchell, 1995; Ikeda, 1999).

675 steps). Australian *Paratya* received bootstrap support of 99%, 74%, 35% (MP, ME, ML, respectively); North Pacific *Paratya* (Japan and Ryukyu Islands): 77%, 95%, 90%; New Caledonia: 77%, 62%, 40%. Relationships between landmasses were considerably more strongly supported nearer to the tips of the tree, and weakly in the deeper nodes: Lord Howe and Norfolk Island (Tasman Clade): 100%, 97%, 86%; New Caledonia, Lord Howe and Norfolk (the 'Island Clade'): 85%, 71%, 40%; the Island Clade and Australia (Western South Pacific Clade): 72%, 45%, 0%; the 'South Pacific' clade (i.e. also including New Zealand, but not Japan/Ryukyus): 43%, 0%, 0%.

Between landmass relationships are generally more strongly supported in the 16S than COI data set (Fig. 3: 16S MP majority rule consensus of 12 cladograms of 257 steps); Tasman Clade: 92%, 94%, 70%; the Island Clade: 97%, 91%, 67%; Western South Pacific Clade: 95%, 77%, 42%; South Pacific Clade: 92%, 92%, 59%.

North Pacific (Japan/Ryukyus) *P. compressa* (De Haan, 1844) was recovered as the most basal taxon in the appropriate deeper node analyses of the 16S data set (Fig. 3), with $c. 12\frac{1}{2}$ –19 Myr separating it from other *Paratya* (Table 2). Within the 'South Pacific' clade, New Zealand *P. curvirostris* (Heller, 1862) is the most basal (Fig. 3), diverging 12–18 Ma (Table 2). Within the 'Western South Pacific' clade, there is a split into two sister clades dated at $3\frac{1}{2}$ – $8\frac{1}{2}$ Ma (Table 2), one of which contains all the *Paratya* from Australia, and the other the 'Island Clade' of New Caledonia, Lord Howe and Norfolk Islands (Figs 2 & 3). *Paratya* from New Caledonia and Lord Howe/Norfolk Islands are sister taxa within the 'Island Clade' (Figs 2 & 3), diverging $2\frac{1}{2}$ –7 Ma (Table 2). Lord Howe and Norfolk Islands diverged from each other 2– $4\frac{1}{2}$ Ma (Table 2).

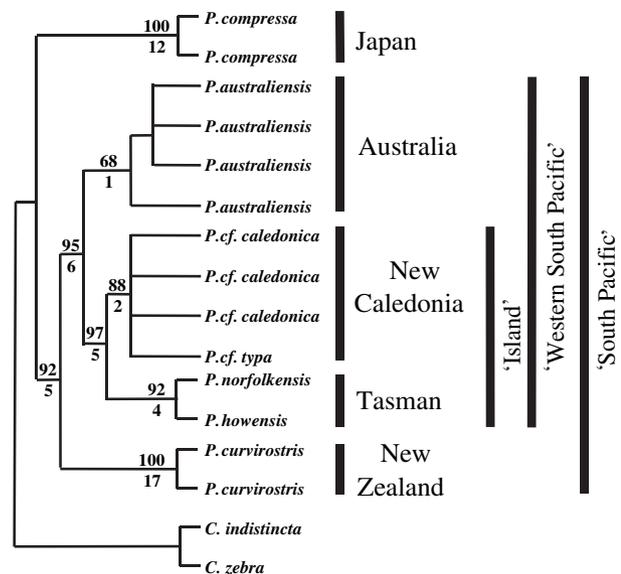


Figure 3 Maximum parsimony (MP) strict consensus cladogram of 16S rDNA data set, showing landmass distributions and between landmass clades (selected bootstrap values above and Bremer decay indices below).

	16S % divergence*	16S divergence†	16S divergence‡	COI rescaled divergence§
North vs. South Pacific	11.76 (0.45)	13.06 (0.49)	18.09 (0.68)	N/A
New Zealand vs. Western South Pacific	11.37 (0.33)	12.63 (0.37)	17.49 (0.51)	N/A
Australia vs. Island	3.25 (0.13)	3.61 (0.14)	5.00 (0.20)	8.62
New Caledonia vs. Tasman	2.60 (0.25)	2.89 (0.28)	4.00 (0.38)	6.91
Lord Howe vs. Norfolk Island	1.70 (0.00)	1.89 (0.00)	2.62 (0.00)	4.53

Standard error in parentheses. Divergence estimates in million years ago (Ma).

*Corrected net mean divergence using Modeltest-derived distance matrix.

†Estimate uses rate from Sturmbauer *et al.* (1996).

‡Estimate uses rate from Schubart *et al.* (1998).

§Estimate uses rate from Knowlton & Weigt (1998).

Sequence saturation and pseudogenes

The COI data set displayed a greater level of divergence between clades than 16S, as well as evidence of sequence saturation. Saturation occurs when multiple nucleotide substitutions occur in the same position over time (Arbogast *et al.*, 2002). This has the effect of masking the true level of divergence and obscuring deeper phylogenetic relationships to the point of making them unrecoverable (Avice *et al.*, 1987) even after a model of molecular evolution has been applied. Saturation is evident in the COI data set in all deep clade comparisons (North vs. South Pacific, New Zealand vs. Western South Pacific, Australia vs. Island). Saturation is revealed in a number of ways: (1) a plateau in the rate of accumulation of transversions plotted against transitions (not displayed); (2) the low ratio of transitions to transversions in the above mentioned three deep clade comparisons (0.90, 1.39, 1.17, respectively); (3) the extreme increase in genetic distance when the Modeltest molecular model distances are compared with uncorrected percentage differences in sequences from the same three comparisons (683%, 216%, 316%); (4) lower bootstrap support of deeper clades in COI MP compared with 16S MP analysis (South Pacific: 92% vs. 43%, Western South Pacific: 95% vs. 72%, Island: 97% vs. 85%); and (5) strongly supported COI clades in all analyses only being located near the tips for both bootstraps and Bremer support values. Only the shallow COI divergence between Lord Howe and Norfolk Islands is free of excessive saturation and appropriate for molecular clock analyses, given its transition/transversion ratio of 4.00, a modest increase of 16% between Modeltest and uncorrected distances and high bootstrap support in all six analyses (70–100%, average 90%).

The more slowly evolving 16S data set displayed much less evidence of saturation in transitions/transversions accumulation plots, and in the same three deep clade comparisons, e.g. ratio of transitions to transversions (1.12, 1.47, 3.76); much smaller increase in ML % differences (83%, 64%, 30%) and bootstrap support for deep clades. These differences highlight the differing phylogenetic levels at which the two data sets are appropriate, with the COI data set informative within each landmass and between very closely related ones, but noise due

Table 2 16S rDNA % sequence divergence between clades and calculated 16S and COI divergence times between clades

to sequence saturation in the data set makes it ineffective at deeper levels when uncorrected sequence differences approach 10–20%. The 16S data set is thus appropriate for the deep nodes, but is less effective in resolving shallower nodes due to insufficient time to reach reciprocal monophyly in more conserved sequences. When the appropriate strengths of the two data sets are considered together, it can provide the whole picture of *Paratya* phylogeny and biogeography from the global down to the local scale.

A further challenge to accurate biogeographical and phylogenetic inference is the unintentional use of nuclear mitochondrial pseudogene sequences (Numts) in a mitochondrial study (Williams & Knowlton, 2001). It was identified in this study as a probable pseudogene by its divergent nature from other *P. curvirostris* COI sequences, which contrasts strongly with the 16S sequences from the same individuals which were identical to the other *P. curvirostris* specimens. The presumed COI-like pseudogene displays many first and second codon position changes, which, if functional, would have lead to a large number of unique amino acid changes. This indicates it is likely to be a non-functional nuclear copy of a mitochondrial gene and thus is not under the strong selective pressure on amino acid integrity of a functional mitochondrial gene. Because this sequence appears not to be a legitimate mitochondrial COI sequence homologous to the others, it was excluded from all analyses. Interestingly from a biogeographical perspective, when this sequence is included in a phylogenetic analysis with actual *Paratya* mitochondrial COI sequences, it still clades with New Zealand *Paratya*. This, and its retention of a bias of high variation in the third codon position (Bensasson *et al.*, 2000), indicates that it has been integrated into the nuclear genome relatively recently in New Zealand, since its separation from other *Paratya* taxa.

DISCUSSION

Phylogenetic and taxonomic relationships

The North Pacific (Japan/Ryukyu) *P. compressa*, with two subspecies, is the most basal of the *Paratya*. The two

P. compressa subspecies, which are found on a number of different islands (Honshu, Kyushu, Okinawa), are recovered here as monophyletic. Their COI sequences are very divergent (this study) and they likely qualify as distinct species (based on allozymes; Ikeda, 1999). In fact, there is also strong evidence for the presence of two species within *P.c. improvisa*. This is due to genetic divergence (this study), clear differences in morphological characters (egg size, rostrum shape, body robustness; S. Choy, pers. comm.) and the demonstrated high level of variation in allozyme studies (Ikeda, 1999). Earlier morphological studies have highlighted similarities between *P. compressa* and *P. curvirostris* from New Zealand (Roux, 1926; Riek, 1953; Carpenter, 1977a; Suzuki & McLay, 1998) and placed them as the most primitive of the *Paratya* (Roux, 1926; Carpenter, 1977a). Roux (1926) placed both *P. compressa* from Japan and *P. curvirostris* from New Zealand in the nominal subgenus *Paratya* when he divided the genus into two subgenera. A basal clade composed of these two taxa (Carpenter, 1977a; Smith & Williams, 1980) does not agree with the conclusions of this study, but does agree with one analysis (COI ME, not displayed). This is not a likely scenario for two reasons; first, at this phylogenetic depth, the COI data set is heavily saturated, and so this basal clade is likely to have been caused by long-branch attraction (where two very divergent taxa are artificially forced together by phylogenetic algorithms; Felsenstein, 1978); second all the relevant 16S analyses strongly supported both species as independent basal clades, with the North Pacific the most basal.

Another possibility is that any common morphological characters are the result of evolutionary convergence due to common environmental factors. *Paratya compressa* and *P. curvirostris* are the furthest northern and southern representatives of the genus (Carpenter, 1977a), and thus neither may be 'primitive', but both merely responding to a common cool, temperate climate in a similar fashion. This evolutionary convergence explanation ignores the strong genetic data presented above, and does not explain the morphologically different Tasmanian *P. australiensis*, which is nevertheless found in a similar temperate climate. Thus, morphological characteristics of both basal taxa probably represent the ancient plesiomorphic character states of the genus.

The remaining taxa in the genus are all found in the South Pacific, where New Zealand is most basal. This agrees with the morphological findings of Carpenter (1977a), who found that the Australian and Norfolk Island *Paratya* are more similar to each other than either are to the New Zealand *Paratya*.

Within the Western South Pacific there are two clades, one of which contains all the *Paratya* from Australia, and the other the 'Island Clade' of New Caledonia, Lord Howe and Norfolk Islands. The taxonomic status of Australia's *Paratya* has been in a state of flux since its inception. The original and early descriptions of Australia's sole species, *P. australiensis* (Kemp, 1917; Roux, 1926), noted a great deal of intraspecific variation, to the extent that Riek (1953) split it into five taxa (three species and two subspecies). This was rejected by Williams & Smith (1979), who re-established *P. australiensis* as a single

species. Recent genetic work within Australia has uncovered many cryptic lineages within *P. australiensis* (Hurwood *et al.*, 2003; Baker *et al.*, 2004a,b; Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data), which have been shown through allozyme analysis (fixed allozyme differences of sympatric specimens) to represent a number of valid biological species (Baker *et al.*, 2004a; Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data). Despite the high level of Australian diversity, these divergent Australian lineage/species are recovered strongly as monophyletic with respect to all non-Australian *Paratya* in the relevant COI data set. The uncovering of cryptic species in other landmasses could potentially change colonization inferences.

The Island Clade of New Caledonia, Lord Howe and Norfolk Island from this study mirrors Roux's other subgenus, *Xiphatyoida* (Roux, 1926), which included the taxa from these areas. *Paratya* in New Caledonia is quite speciose (six species; Choy & Marquet, 2002), but a full reconsideration of their taxonomic status is warranted (S. Choy, pers. comm.). The three species that are included in this study are monophyletic, implying a single or closely spaced colonization (Emerson, 2002), at least for this half of the New Caledonian *Paratya* fauna. Roux considered these island taxa to be the most derived in terms of morphology, which is supported by the present study in the relatively shallow genetic differences between them. He described *P. norfolkensis* Kemp, 1917 as 'very nearly' related to *P. howensis* Roux, 1926, which agrees with this study's 'Tasman Clade', which displays the shallowest and strongest relationship between landmasses in both data sets. In the main, morphology-based groupings accord reasonably well with genetic-based ones, particularly in more recent, shallower relationships, but taxonomic groupings do not help much in defining the evolutionary relationships between these groups.

Origins of *Paratya*

The phylogenetic relationships detailed above can aid in unravelling the relative order in which different landmasses diverged from each other, but give no real clue as to the amount of real evolutionary time these divergences represent. The application of a 'molecular clock' to phylogenetic relationships can refine conclusions and resolve specific competing biogeographical hypotheses (BurrIDGE, 2002). There are certain caveats with molecular clocks, which can include large margins of error, inappropriate models of nucleotide evolution, differences between gene and species trees and the use of only a single locus (mtDNA) (Arbogast *et al.*, 2002). Notwithstanding these limitations, two different mtDNA genes and a number of methods were used to calculate the conservative divergence estimates presented here, which even if too large or small by a factor of four times, would have little effect on subsequent biogeographical conclusions.

The first biogeographical issue to consider is the geographical origin of the genus *Paratya*. Phylogenetic data presented

above places Japan and the Ryukyu Islands, in the North Pacific, as most basal. This does not suggest which of the two deepest sister clades (North and South Pacific), which by definition are the same age, represent the geographical point of origin. The internode distance between the North Pacific and deep clades within the South Pacific (e.g. New Zealand) is short, which means these clades are nearly as old as each other and thus an inference of origin is unclear. The geographical origin is likely to remain uncertain because of the limited availability of specimens from outside the South Pacific. A non-phylogenetic method to infer an origin is to assume that it is located at the point of highest current diversity, because more evolutionary time allows for more potential diversity. If diversity were measured by a simple taxonomic species count, then the origin would be in the South Pacific. This is unsurprising as it is an unbalanced comparison between a relatively small area (Japan and Ryukyu Islands) and a huge one (South Pacific). There are many reasons the South Pacific would be inclined to host many species that have little to do with long stretches of evolutionary time, including (1) isolation due to enforced allopatry over large distances (Grant, 1998); (2) a profusion of ecological niches in a heterogeneous environment (Holt, 1997); (3) a large area (MacArthur & Wilson, 1967); (4) or, as the neutral theory of biodiversity and biogeography would predict, simply due to a potentially large number of individuals increasing the rate of new species arising (Hubbell, 2001). Importantly, these South Pacific speciation events would not necessarily be ancient ones. However, if diversity were instead assessed in terms of genetic variation, then the North Pacific would instead be the geographical origin, as *P. compressa* alone displays more COI nucleotide polymorphism than all other *Paratya* combined.

Irrespective of whether the origin of *Paratya* lies in the North or South Pacific, their disjuncture could suggest a seemingly unlikely 10,000 km oceanic dispersal in either direction between Japan and New Zealand 12½–19 Ma. A more likely scenario would be a series of intervening 'stepping stones' between north and south; a theory tested by Gillespie (2002) for Pacific island spiders. This begs the question of the location of these stepping stones. The ability of *Paratya* to disperse across significant tracts of open ocean is evident in its presence on isolated oceanic islands, some over 800 km from major landmasses, e.g. *Paratya curvirostris* on the Chatham Islands east of New Zealand (Carpenter, 1977a) and *Paratya boninesis* sp. nov. on the Bonin Islands (Ogasawara Archipelago) south of Japan (Y. Cai, pers. comm.). This implies that long distance oceanic dispersal by *Paratya* is possible, which was also the conclusion for the Pacific island spider study (Gillespie, 2002).

Another potential dispersal route between north and south is via a series of small distance dispersals along the coast of Asia. During times of lower sea levels, ancestral shrimp could have moved along an unbroken coastline from Japan to the edge of the Sunda Shelf near Australia (Sahul Shelf) (Voris, 2000). This may also explain the possible presence of a number of unsampled and taxonomically uncertain specimens of

Paratya described from Vietnam, Indonesia and India (Carpenter, 1977a; Walsh & Mitchell, 1995). These were described early in the twentieth century, but their taxonomic status and affiliations is unclear as they are known only from their original descriptions (Y. Cai, pers. comm.; T. Komai, pers. comm.; D. Pham, pers. comm.). While the Indian description is potentially mistaken (Carpenter, 1977a), any future *Paratya* specimens discovered in mainland and insular Southeast Asia may provide a link between north and south, especially given that Roux (1926) grouped his Indonesian specimens with both Japan and New Zealand, and might make possible more definite conclusions about the geographical origin of the genus.

A further possibility is that *Paratya* once had a continuous distribution throughout the North and South Pacific, including the now apparently empty intervening tropical areas. Subsequent extinctions may have confused the biogeographical patterns inferred from present distributions, as noted by Wallace (1881) while discussing camelid distributions. White (1986) put forward the hypothesis that antitropically distributed taxa were the result of climatic vicariance due to a rise in sea temperature in the mid Miocene. Previously widespread taxa were sundered into northern and southern hemisphere representatives because of an intolerance to the new high tropical temperatures. This fits both the pattern and timing of *Paratya* distributions and divergences between the North and South Pacific from this study. Temperature has been put forward as a possible determining factor in *Paratya* distributions at both micro-scales (within a single Australian creek; Fawcett *et al.*, in review) and at landmass scales (New Zealand, Carpenter, 1977a; eastern Australia, Cook, B.D., Baker, A.M., Page, T.J., Fawcett, J.H., Hurwood, D.A. & Hughes, J.M., unpubl. data), and thus may also apply at the hemispheric scale. A review of molecular studies dealing with antitropicality in Pacific fish (Burrige, 2002) found only limited evidence for Miocene divergences, and so any Miocene climate change appears not to have been the key factor in antitropicality, at least for the taxa considered in that study.

Briggs (1987) has questioned the interpretation and extent of this Miocene climate change event, and instead considered continuous competition from younger tropical species a better explanation for antitropicality. Competition and predation could both play a role in *Paratya* distributions, as Carpenter (1977a, 1983) has suggested that New Zealand *Paratya* might have been forced upstream into freshwaters by predation from palaemonid shrimps. Another possibility is successful competition from other similar atyid shrimps, especially the tropically speciose and abundant genus *Caridina*.

Any extinctions could have been caused by climate change, predation, competition, and/or stochastic events (MacArthur, 1972; Stock, 1986). All explanations may play a role, as does the nature of the intervening land, which is mostly composed of small islands. Populations on small, isolated islands have a higher risk of extinction, given that slight or random fluctuations in predation, competition or climate will lead to a much steeper extinction curve (MacArthur, 1972). The

presence of *Paratya* in some of these places may have been transitory, and long-term persistence may be limited to large, complex landmasses where large population sizes and refugia from predation, competition and climate are located.

South pacific colonization routes and timing

Our data indicate that New Zealand *Paratya* are the oldest in the South Pacific, possibly arriving from the north between 12½ and 19 Ma, during the abovementioned warming of the Miocene, when other subtropical taxa, such as mangroves, reef corals and marine molluscs, were also colonizing from the Indo-Pacific (Cooper & Millener, 1993). The split between New Zealand and the other South Pacific taxa is within a similar time frame (12–18 Ma), leading to the possibility that Australia and the islands may not have been colonized directly from New Zealand, but from a third unsampled or no longer existing population (potentially Southeast Asia) which also sourced the New Zealand colonists.

The *Paratya* found on the remnants of Gondwana (Australia, New Zealand, New Caledonia) were apparently not separated by the breakup of Gondwana as suggested by Walsh & Mitchell (1995), as this would require a divergence time in the order of 82 Myr (Cooper & Millener, 1993). Dispersal is the likely explanation, which is in line with McDowall (2002) and Arensburger *et al.* (2004), who found dispersal rather than vicariance best explains the biogeographical patterns of freshwater fish and cicadas (respectively) in former Gondwanan landmasses (New Zealand in particular).

Our data suggest that Australia was colonized by *Paratya* 3½–8½ Ma, either from the east or north. Bishop (1967) pointed out that Australian caridean shrimp differed from Asian ones at the specific and not generic level and considered atyids and palaemonids to have come from the north, as did Williams (1981). Despite Australia being the landmass with by far the largest geographical range of *Paratya*, its strong COI monophyly suggests a single colonization, or possibly a number of colonizations from the same source population over a relatively short period of time.

Initially, the continent of Australia would appear to be a likely source for the Island populations, but our data does not support this. Rather, the New Caledonian and other island populations are sister clades, and not derived from Australian *Paratya*. This means that the islands may have been colonized contemporaneously with Australia 3½–8½ Ma. Lord Howe/Norfolk Island *Paratya* diverged from New Caledonia 2½–7 and 2–4½ Ma from each other. This accords well with geological estimates of the ages of these two volcanic islands (3–7 Myr; McDougall *et al.*, 1981).

Potential methods of dispersal

Although the inference of a process from a pattern can be fraught with danger, the method of dispersal of a freshwater animal across vast stretches of inhospitable, saltwater ocean must be considered. A frequently invoked explanation for disjunct distributions that do not fit a vicariant explanation is

the medium of Darwin's 'ducks feet' (or gut) (Darwin, 1888). A review by Bilton *et al.* (2001) has shown that crustacean eggs have survived the digestive tracts of birds and that migrating birds may act as vectors of dispersal for some freshwater invertebrates.

While this can not be excluded, a more parsimonious explanation for the dispersal of an obligate aquatic animal is likely to be found in some form of water-borne dispersal. One possibility is that *Paratya* is polyphyletic due to multiple independent incursions into freshwater by a number of separate *Paratya* ancestors, as has been shown for a copepod (Lee, 1999) and may be the case for Australian palaemonid shrimps (Williams, 1981). However this scenario is unlikely given there are no known close marine relatives to *Paratya*, nor in fact to the whole family Atyidae. Further, a great deal of evidence points to atyids being ancient freshwater denizens, such as well-developed osmoregulation (Carpenter, 1977b), a profusion of cave species (Carpenter, 1977a), wide distribution of taxa (Fièvet & Eppe, 2002), fossils in freshwater deposits (Fièvet & Eppe, 2002) and a complex morphology adapted to running water (Suzuki & McLay, 1998; Fièvet & Eppe, 2002).

The aforementioned points notwithstanding, it is also plain that many atyid species are associated with saline environments for at least part of their life cycles. The larvae and/or adults of species of many atyid genera survive naturally in saline estuarine and anchialine (inland saline habitat) environments, including species of *Antecaridina*, *Atya*, *Atyoida*, *Atyopsis*, *Caridina*, *Halocaridina*, *Micratya*, *Typhlatya* and *Troglocaris* (Carpenter, 1977b; Hayashi & Hamano, 1984; Stock, 1986; Benstead *et al.*, 2000; Shy *et al.*, 2001; Fièvet & Eppe, 2002).

Of the three *Paratya* taxa that have been studied ecologically, all have shown some level of tolerance for saline conditions. Adult *P. curvirostris* survived 7 days in a laboratory at salinities up to 18.8‰ (c. 50% seawater), while first stage larvae survived over 12 days in 100% seawater (Carpenter, 1977b). Another basal taxon, the *P.c. compressa* Kemp, 1917, survives naturally in a saline environment, particularly its larval stage (Ikeda, 1999). Walsh & Mitchell (1995) found all life stages of *P. australiensis* (eight larval stages, juveniles, adults) thriving naturally in high salinities (larvae to 33.6‰, juveniles to 33.8‰, adults to 28.9‰) in coastal southern Australia.

A continuum of salinity tolerances is thus evident within the family Atyidae, within numerous atyid genera (including *Paratya*) and even within some members of a species complex (*P. australiensis* Lineage C *sensu* Baker *et al.*, 2004b). Salt tolerant larvae of *P. curvirostris*, *P.c. compressa* and *P. australiensis* Lineage C float downstream from fresh upstream waters to brackish estuarine waters, to grow and then migrate back upstream. This amphidromous pattern of reproduction is ancestral in atyids (Vernberg & Vernberg, 1983; Hancock & Bunn, 1997) and is likely the plesiomorphic state within *Paratya* (Carpenter, 1977a).

Different taxa within Atyidae display three different modes of reproduction: (1) few, large eggs, short larval development,

inhabiting upstream freshwaters; (2) an intermediate number of medium sized eggs with medium number of larval stages in many freshwater habitats; (3) large numbers of small eggs, many larval stages, found in lowland and saline estuarine environments (Hayashi & Hamano, 1984; Hancock *et al.*, 1998; Shy *et al.*, 2001; Fièvet & Eppe, 2002). Both of the basal taxa, *P. curvirostris* (Carpenter, 1983) and *P.c. compressa* (Ikeda, 1999), conform to the third type. New Zealand *Paratya* display no divergence in 16S sequences between North and South Island specimens, which is surprising given the barrier of the Cook Strait and long history of *Paratya* in New Zealand. This may be explained by *P. curvirostris*'s tolerance for salinity and so presumed high dispersal ability. Interestingly, the other North Pacific taxon, *P.c. improvisa* Kemp, 1917, conforms to the first type and also displays a much higher level of intra-taxon diversity (Ikeda, 1999), likely due to a much reduced dispersal ability (Ikeda, 1999). This change in reproduction has happened since cladogenesis and reflects a microcosm of the Atyidae as a whole. A similar situation is reported in New Zealand freshwater fish, where obligately freshwater species display more within-species diversity than those with diadromous life stages (McDowall, 2002).

The estuarine habitat of ancestral *Paratya* thus provides a feasible means for its historic dispersal. Larvae floating downstream are passive and unable to move upstream (Hancock & Bunn, 1999). This suggests the occasional flushing of salt tolerant larvae out to sea (Walsh & Mitchell, 1995; Bilton *et al.*, 2002), where ocean currents would serve as dispersal corridors (McDowall, 2002). Carpenter (1977a) suggested that this would explain the presence of *P. curvirostris* on the Chatham Islands 800 km east of the South Island of New Zealand, possibly aided by freshwater plumes at sea resulting from rivers in flood. Bishop (1967) considered that the presence of atyids in Australia could be explained by dispersal due to their planktonic larvae. Saltwater dispersal of atyids, however, is not merely a historical process, since a successful colonization by *P. australiensis* of a previously dry coastal creek in southern Australia likely occurred through the sea within the last 770 years (Walsh & Mitchell, 1995). Specimens of atyid shrimp, including *Paratya*, have recently been reported from a saltwater environment (seagrass beds) in north-eastern Australia (Kwak & Klumpp, 2004), although the taxonomy of these specimens is still unclear. Stock (1986) found the dispersal of amphidromous atyid larvae at sea a more likely explanation than vicariance to explain Caribbean biogeography, as did McDowall (2002, 2003) in studies of diadromous freshwater fish of New Zealand and Hawaii. Those individuals surviving this form of 'sweepstake' dispersal at sea and arriving at an estuary would already be pre-adapted to that environment, and so the historic colonization of the South Pacific by *Paratya* may be seen more as an estuary-to-estuary dispersal than a freshwater to freshwater one. The level of subsequent genetic divergence and speciation in each case is likely to be tied to how far along the continuum from the ancestral amphidromy to an obligate freshwater life style the taxon has moved.

ACKNOWLEDGEMENTS

Specimens were kindly provided by Penny Berents (Australian Museum), Christine Pöllabauer (Etudes et Recherches Biologiques, Nouvelle-Calédonie), Tim Moulton (Universidade do Estado do Rio de Janeiro), Kevin Collier (National Institute of Water and Atmospheric Research), Angus McIntosh (Canterbury University), Koji Nishi (Ecology and Civil Engineering Society), Cai Yixiong (Raffles Museum), Stuart Bunn (Griffith University) and Adrian Oosterman. Tomoyuki Komai (Natural History Museum, Chiba) and Pham Anh Duc (Institute of Tropical Biology) answered taxonomic questions, and Satish Choy (Queensland Department of Natural Resources, Mines) helped with species identifications. Jing Ma and Jemma Somerville helped considerably with laboratory work and David Gopurenko and Cai Yixiong made useful comments on a number of drafts. Two anonymous reviewers improved the manuscript. Miharuru Mori (Imperial College) did the Japanese translations. Funding was provided by the CRC for Freshwater Ecology, Australian Postgraduate Award (TJP) and Land and Water Australia (BDC).

REFERENCES

- Arbogast, B.S., Edwards, S.V., Wakeley, J., Beerli, P. & Slowinski, J.B. (2002) Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, **33**, 707–740.
- Arensburger, P., Buckley, T.R., Simon, C., Moulds, M. & Holsinger, K.E. (2004) Biogeography and phylogeny of the New Zealand cicada genera (Hemiptera: Cicadidae) based on nuclear and mitochondrial DNA data. *Journal of Biogeography*, **31**, 557–569.
- Avise, J.C. (1994) *Molecular markers, natural history and evolution*. Chapman & Hall, New York.
- Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. & Saunders, N.C. (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.
- Baker, A.M., Hughes, J.M., Dean, J.C. & Bunn, S.E. (2004a) Mitochondrial DNA reveals phylogenetic structuring and cryptic diversity in Australian freshwater macro-invertebrate assemblages. *Marine and Freshwater Research*, **55**, 629–640.
- Baker, A.M., Hurwood, D.A., Krogh, M. & Hughes, J.M. (2004b) Mitochondrial DNA signatures of restricted gene flow within divergent lineages of an atyid shrimp (*Paratya australiensis*). *Heredity*, **93**, 196–207.
- Bensasson, D., Zhang, D.-X. & Hewitt, G.M. (2000) Frequent assimilation of mitochondrial DNA by grasshopper nuclear genomes. *Molecular Biology and Evolution*, **17**, 406–415.
- Benstead, J.P., March, J.G. & Pringle, C.M. (2000) Estuarine larval development and upstream post-larval migration of

- freshwater shrimps in two tropical rivers of Puerto Rico. *Biotropica*, **32**, 545–548.
- Bilton, D.T., Freeland, J.R. & Okamura, B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.
- Bilton, D.T., Paula, J. & Bishop, J.D.D. (2002) Dispersal, genetic differentiation and speciation in estuarine organisms. *Estuarine Coastal and Shelf Science*, **55**, 937–952.
- Bishop, J.A. (1967) The zoogeography of the Australian freshwater decapod Crustacea. *Australian inland waters and their fauna* (ed. by A.H. Weatherly), pp. 107–122. Australian National University, Canberra.
- Briggs, J.C. (1987) Antitropicality and vicariance. *Systematic Zoology*, **36**, 206–207.
- Burridge, C.P. (2002) Antitropicality of Pacific fishes: molecular insights. *Environmental Biology of Fishes*, **65**, 151–164.
- Carpenter, A. (1977a) Zoogeography of the New Zealand freshwater decapoda: a review. *Tuatara*, **23**, 41–48.
- Carpenter, A. (1977b) Salinity tolerance of *Paratya curvirostris* (Heller, 1862) (Decapoda: Atyidae). *Mauri Ora*, **5**, 53–57.
- Carpenter, A. (1983) Population biology of the freshwater shrimp *Paratya curvirostris* (Heller, 1862) (Decapoda: Atyidae). *New Zealand Journal of Marine and Freshwater Research*, **17**, 147–158.
- Choy, S. & Marquet, G. (2002) Biodiversity and zoogeography of Atyid Shrimps (Crustacea: Decapoda: Natantia) of New Caledonia. *Zoologia Neocaledonica 5. Systematique et endemisme en Nouvelle-Caledonie* (ed. by J. Najt and P. Grandcolas), pp. 207–222. Museum national d'Histoire naturelle, Paris.
- Cooper, R.A. & Millener, P.R. (1993) The New Zealand biota: historical background and new research. *Trends in Ecology and Evolution*, **8**, 429–433.
- Darwin, C. (1888) *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, 6th edn. John Murray, London.
- Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure for small quantities of leaf tissue. *Phytochemistry Bulletin*, **19**, 11–15.
- Emerson, B.C. (2002) Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology*, **11**, 951–966.
- Fawcett, J.H., Hughes, J.M. & Hurwood, D.A. (in review) Consequences of a translocation between two populations of the glass shrimp *Paratya australiensis*: the relative importance of dispersal, hybrid inviability and selection. *Biological Journal of the Linnean Society*.
- Felsenstein, J. (1978) Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology*, **27**, 401–410.
- Fièvet, E. & Eppe, R. (2002) Genetic differentiation among populations of the amphidromous shrimp *Atya innocua* (Herbst) and obstacles to their upstream migration. *Archiv für Hydrobiologie*, **153**, 287–300.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**, 294–299.
- Gene Codes (2000) *Sequencher version 4.1.1 b1*. Gene Codes Corporation, Ann Arbor, MI.
- Gillespie, R.G. (2002) Biogeography of spiders on remote oceanic islands of the Pacific: archipelagos as stepping stones? *Journal of Biogeography*, **29**, 655–662.
- Grant, P.R. (1998) Speciation. *Evolution on islands* (ed. by P.R. Grant), pp. 83–101. Oxford University Press, Oxford.
- Griffin, D.J.G. & Yaldwyn, J.C. (1968) The constitution, distribution and relationships of the Australian decapod Crustacea. *Proceedings of the Linnean Society of New South Wales*, **93**, 164–183.
- Hancock, M.A. & Bunn, S.E. (1997) Population dynamics and life history of *Paratya australiensis* Kemp, 1917 (Decapoda: Atyidae) in upland rainforest streams, south-eastern Queensland, Australia. *Marine and Freshwater Research*, **48**, 361–369.
- Hancock, M.A. & Bunn, S.E. (1999) Swimming response to water current in *Paratya australiensis* Kemp, 1917 (Decapoda, Atyidae) under laboratory conditions. *Crustaceana*, **72**, 313–323.
- Hancock, M.A., Hughes, J.M. & Bunn, S.E. (1998) Influence of genetic and environmental factors on egg and clutch sizes among populations of *Paratya australiensis* Kemp (Decapoda: Atyidae) in upland rainforest streams, south-east Queensland. *Oecologia*, **115**, 483–491.
- Hayashi, K.I. & Hamano, T. (1984) The complete larval development of *Caridina japonica* (Decapoda, Caridea, Atyidae) reared in the laboratory. *Zoological Science*, **1**, 571–589.
- Holt, R.D. (1997) From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. *Metapopulation biology: ecology, genetics, and evolution* (ed. by I.A. Hanski and M.E. Gilpin), pp. 149–164. Academic Press, San Diego, CA.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Hurwood, D.A., Hughes, J.M., Bunn, S.E. & Cleary, C. (2003) Population structure in the freshwater shrimp (*Paratya australiensis*) inferred from allozymes and mitochondrial DNA. *Heredity*, **90**, 64–70.
- Ikeda, M. (1999) Genetic analyses for the problem of species *Paratya compressa* (Decapoda: Atyidae). *Aquabiology*, **21**, 299–307.
- Kemp, S.K. (1917) XVII. Notes on the Crustacea Decapoda in the Indian Museum: XI. Atyidae of the genus *Paratya* (=Xiphocaridina). *Records of the Indian Museum*, **8**, 293–306.
- Knowlton, N. & Weigt, L.A. (1998) New dates and new rates for divergence across the Isthmus of Panama. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **265**, 2257–2263.
- Kwak, S.N. & Klumpp, D.W. (2004) Temporal variation in species composition and abundance of fish and decapods of

- a tropical seagrass bed in Cockle Bay, North Queensland, Australia. *Aquatic Botany*, **78**, 119–134.
- Lee, C.E. (1999) Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution*, **53**, 1423–1434.
- MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- McDougall, I., Embelton, B.J.J. & Stone, D.B. (1981) Origin and evolution of Lord Howe Island, Southwest Pacific. *Journal of Geological Society Australia*, **28**, 155–176.
- McDowall, R.M. (2002) Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *Journal of Biogeography*, **29**, 207–219.
- McDowall, R.M. (2003) Hawaiian biogeography and the islands' freshwater fish fauna. *Journal of Biogeography*, **30**, 703–710.
- Palumbi, S.R., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *A simple fool's guide to PCR*. University of Hawaii Press, Honolulu.
- Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.
- Riek, E.F. (1953) The Australian freshwater prawns of the family Atyidae. *Records of the Australian Museum*, **23**, 111–121.
- Rosen, D.E. (1976) A vicariance model of Caribbean biogeography. *Systematic Zoology*, **24**, 431–464.
- Roux, J. (1926) An account of the Australian Atyidae. *Records of the Australian Museum*, **15**, 237–254.
- Schubart, C.D., Diesel, R. & Hedges, S.B. (1998) Rapid evolution to terrestrial life in Jamaican crabs. *Nature*, **393**, 363–365.
- Shy, J.Y., Lai, H.T. & Yu, H.P. (2001) On the larval development of *Caridina formosae* (Decapoda, Atyidae) reared in the laboratory. *Crustaceana*, **74**, 1159–1168.
- Smith, M.J. & Williams, W.D. (1980) Intraspecific variation within the Atyidae: a study of morphological variation within a population of *Paratya australiensis* (Crustacea: Decapoda). *Australian Journal of Marine and Freshwater Research*, **31**, 397–407.
- Sorenson, M.D. (1999) *TreeRot version 2*. Boston University, Boston, MA.
- Stock, J.H. (1986) Caribbean biogeography and a biological calendar for geological events. *Crustacean biogeography: Crustacean issues 3* (ed. by R.H. Gore and K.L. Heck), pp. 195–203. A. A. Balkema, Rotterdam.
- Sturmbauer, C., Levinton, J.S. & Christy, J. (1996) Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 10855–10857.
- Suzuki, H. & McLay, C.L. (1998) Gill-cleaning mechanisms of *Paratya curvirostris* (Caridea: Atyidae) and comparisons with seven species of Japanese atyid shrimps. *Journal of Crustacean Biology*, **18**, 253–270.
- Swofford, D.L. (2002) *PAUP* version 4.0b5 – phylogenetic analysis using parsimony (* and other methods)*. Sinauer Associates, Sunderland, MA.
- Trewick, S.A. (2000) Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography*, **27**, 1189–1200.
- Vences, M., Freyhof, J., Sonnenberg, R., Kosuch, J. & Veith, M. (2001) Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *Journal of Biogeography*, **28**, 1091–1099.
- Vernberg, W.B. & Vernberg, F.J. (1983) Freshwater adaptations. *The biology of Crustacea. Vol. 8: Environmental adaptations* (ed. by W.B. Vernberg and F.J. Vernberg), pp. 109–177. Academic Press, New York.
- Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27**, 1153–1167.
- Wallace, A.R. (1881) *Island life*. Harper & Bros, New York.
- Walsh, C.J. & Mitchell, B.D. (1995) The freshwater shrimp *Paratya australiensis* (Kemp, 1917) (Decapoda: Atyidae) in estuaries of south-western Victoria, Australia. *Marine and Freshwater Research*, **46**, 959–965.
- White, B.N. (1986) The isthmian link, antitropicality and American biogeography: distributional history of the Atherinopsinae (Pisces: Atherinidae). *Systematic Zoology*, **35**, 176–194.
- Williams, W.D. (1977) Some aspects of the ecology of *Paratya australiensis* (Crustacea: Decapoda: Atyidae). *Australian Journal of Marine and Freshwater Research*, **28**, 403–415.
- Williams, W.D. (1981) The Crustacea of Australian inland waters. *Ecological biogeography of Australia, Vol. 3 – The inland fresh waters* (ed. by A. Keast), pp. 1103–1138. Dr W. Junk, The Hague.
- Williams, S.T. & Knowlton, N. (2001) Mitochondrial pseudogenes are pervasive and often insidious in the snapping shrimp genus *Alpheus*. *Molecular Biology and Evolution*, **18**, 1484–1493.
- Williams, W.D. & Smith, M.J. (1979) A taxonomic revision of Australian species of *Paratya* (Crustacea: Atyidae). *Australian Journal of Marine and Freshwater Research*, **30**, 815–832.
- Wilson, K., Cahill, V., Ballment, E. & Benzie, J. (2000) The complete sequence of the mitochondrial genome of the crustacean *Penaeus monodon*: are malacostracan crustaceans more closely related to insects than to branchiopods? *Molecular Biology and Evolution*, **17**, 863–874.

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