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DEEP UNDER THE SEA: UNRAVELING THE EVOLUTIONARY HISTORY OF THE DEEP-SEA SQUAT LOBSTER *PARAMUNIDA* (DECAPODA, MUNIDIDAE)

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The diversification of Indo-Pacific marine fauna has long captivated the attention of evolutionary biologists. Previous studies have mainly focused on coral reef or shallow water-associated taxa. Here, we present the first attempt to reconstruct the evolutionary history—phylogeny, diversification, and biogeography—of a deep-water lineage. We sequenced the molecular markers 16S, COI, ND1, 18S, and 28S for nearly 80% of the nominal species of the squat lobster genus *Paramunida*. Analyses of the molecular phylogeny revealed an accelerated diversification in the late Oligocene–Miocene followed by a slowdown in the rate of lineage accumulation over time. A parametric biogeographical reconstruction showed the importance of the southwest Pacific area, specifically the island arc of Fiji, Tonga, Vanuatu, Wallis, and Futuna, for diversification of squat lobsters, probably associated with the global warming, high tectonic activity, and changes in oceanic currents that took place in this region during the Oligocene–Miocene period. These results add strong evidence to the hypothesis that the Neogene was a period of major diversification for marine organisms in both shallow and deep waters.

KEY WORDS: **Biogeographic parametric methods, crustaceans, DEC model, divergence times, diversification, phylogenetics.**

Within the western Pacific, the Indo-Malayan triangle harbors the highest marine species diversity in the world, declining eastward across the Pacific and westward across the Indian Ocean (Paulay 1997; Bellwood and Hughes 2001). Much work conducted in the area has focused on ascertaining the origin and causes of this high diversity (Benzie and Williams 1997; Alfaro et al. 2007; Williams and Duda 2008; Malaquías and Reid 2009). These studies suggest that several factors, including changes in sea level and oceanic circulation, high tectonic activity, and varying temperature regimes, were likely involved in shaping the distribution and diversification of marine shallow fauna in this region (Barber and Bellwood 2005; Williams 2007; Williams and Duda 2008). All these studies, however, have focused on shallow-water or reef-associated species.

Examining the evolutionary history of deep-water organisms, such as those from slope and bathyal depths (200–2000 m), has been limited by the difficulties of sampling at such depths. In these habitats, some of the factors commonly invoked in influencing diversification in shallow waters, such as changes in sea level and temperature, are less likely to be influential (Williams and Duda 2008). Yet, in a recent study, Macpherson et al. (2010) suggests that both shallow- and deep-water fauna are likely to have

been driven by similar evolutionary and ecological processes. Previous molecular studies have identified a pattern of accelerated diversification in several Indo-Pacific shallow-water organisms in relation to palaeoclimatic and palaeogeological events that took place in the Late Oligocene–Miocene (e.g., Alfaro et al. 2007; Williams 2007; Williams and Duda 2008). If similar processes also influenced species distributed in deeper waters, we would expect to detect an increase in the rate of cladogenesis for the same period. In fact, Machordom and Macpherson (2004) found some evidence of a rapid radiation in the Indo-Pacific deep-sea lobster *Munida* during the Mid-Late Miocene, concurrent with the diversification peak in shallow-marine fauna. However, they did not test this hypothesis within a robust phylogenetic framework.

Time-calibrated molecular phylogenies contain information about the origin and temporal diversification of organisms, allowing us to explore the role of macroevolutionary processes, such as speciation and extinction, in shaping patterns of lineage diversification (Antonelli and Sanmartín 2011). When coupled with biogeographic information on distribution patterns of extant species, molecular phylogenies can also help us to understand how past events on Earth's history have influenced the spatiotemporal evolution of organisms. Compared with terrestrial organisms, there have been relatively few phylogeny-based biogeographic studies of marine taxa (e.g., Barber and Bellwood 2005). There are several reasons for this: (1) more difficult access to the range of marine habitats and areas, making taxon sampling challenging, especially in deep-water taxa; (2) the key role played by dispersal in shaping the spatiotemporal dynamics of marine biodiversity (Cowie and Holland 2006), which stands in contrast with traditional vicariance biogeography, a paradigm that has dominated terrestrial approaches early on (Platnick and Nelson 1978; Humphries and Parenti 1999); and (3) the difficulties to define areas of endemism in the marine realm, where boundaries can be more gradual, often vertically defined, and can change over time with varying sea levels and ocean currents. Recently, new methods have been developed in biogeography, which promise to be more powerful in inferring the distribution history of marine organisms (Ree et al. 2005; Sanmartín et al. 2008). These parametric methods can use branch length information to estimate rates of dispersal (and extinction) from time-calibrated phylogenies, and incorporate information on past geography and paleoclimates in the delimitation of area boundaries (Ree and Sanmartín 2009; Buerki et al. 2011). In these methods, spatially explicit area definition is less relevant than in classic cladistic biogeography, wherein the focus lies on finding patterns between areas of endemism (Humphries and Parenti 1999). Instead, areas are defined in relation to the hypotheses being tested, such as the relative frequency of speciation events or rates of movement between areas (Ree and Sanmartín 2009), making these methods more attractive for marine studies.

Taxon sampling of deep-water organisms is much more limited than for shallow-water fauna, which makes estimation of species ranges more difficult. However, decades of deep-sea surveys have led to a reasonable coverage in certain groups that can be used to effectively explore their evolutionary history. One of these groups is squat lobsters (family Munididae). Squat lobsters are abundant and diversified across all oceans and many marine habitats, although most species are restricted to the Pacific Ocean (Baba 2005). The group has been the focus of increasing taxonomic attention in recent years, but little is still known about its origin and diversification. Here, we focus on the genus *Paramunida*, comprised of 37 species distributed across the Indo-West Pacific (Baba et al. 2008; Cabezas et al. 2009; Macpherson and Baba 2009; Cabezas et al. 2010), typically recorded at continental slope depths (200–700 m). Most species are restricted to single islands or archipelagos, with the greatest diversity (more than 80% of species) found around the southwestern Pacific region. Morphologically, all species are very similar (Cabezas et al. 2010) and there are little data on the biology or ecology of the group (Poore et al. 2011). In this article, we present the first phylogeny of the genus, including 30 of the 37 recognized species (81% total species), plus two potential new species revealed by sequence data. Molecular phylogenetic hypotheses were reconstructed based on mitochondrial (COI, ND1, and 16S) and nuclear (18S and 28S) markers to explore: (1) phylogenetic relationships, (2) the timing and tempo of species diversification; and (3) the biogeographic history of the group using a parametric approach to ancestral area reconstruction that is used here for the first time in marine organisms. Comparing patterns of diversification in deep-water organisms with those reported for shallow-water species helps to understand the processes involved in shaping marine biodiversity at both levels in the Indo-Pacific.

Material and Methods

TAXON SAMPLING AND IDENTIFICATION

Samples were obtained from specimens deposited in the collections of the Muséum National d′Histoire Naturelle (MNHN) and the National Taiwan Ocean University (NTOU), collected during oceanographic expeditions in the Indo-Pacific during the last decades, representing 30 of the 37 nominal species of *Paramunida* (Table 1). Material of *P. spatula*, known from a single specimen in the French Polynesia, and *P. antipodes* known from a single collection in Australia, could not be obtained. Available specimens of *P. hawaiiensis* had been preserved in formalin and failed to amplify. Also, three additional species that were discovered in parallel to this work (Cabezas et al. 2010) were not included in the analysis.

In total 137 individuals were sequenced. Taxonomic identification was based on morphological characters following Baba

Table 1. Species and gene sequences included in the analysis. *Specimen PAR51 failed the amplification of the second fragment of the 18S, PAR75, PAR76, and PAR77 only could be amplified for the first fragment of the 16S, and specimen PAR123 failed to amplify the second fragment for both nuclear genes.

Species	Code	Specimen provenance	Survey	Depth (m)	COI	16S	ND1	18S	28S
Paramunida achernar	PAR17	Tonga	BORDAU 2	487	X	X	X	X	X
Paramunida amphitrita	PAR1	Wallis and Futuna	MUSORSTOM 7	233–235	X	X	X	X	X
	PAR3	New Caledonia	LIFOU	120–250	X	X	X	X	X
	PAR9	New Caledonia	LIFOU	120–250	X	X	X		
Paramunida antares	Fo35	New Caledonia	NORFOLK 1	400–440	X	X	X		
	Fo185	New Caledonia	NORFOLK 2	400–440	X	X	X	X	X
	PAR11	New Caledonia	LIFOU	120–250	X	X	X		
Paramunida belone	PAR71	Vanuatu	MUSORSTOM 8	400–440	X	X	X		
	PAR72	Vanuatu	MUSORSTOM 8	400–440	X	X	X		
	PAR73	Vanuatu	MUSORSTOM 8	400–440	X	X	X	X	X
	PAR74	Vanuatu	MUSORSTOM 8	400–440	X	X	X		
	PAR129	Tonga	BORDAU 2	384–402	X	X	X	X	X
	PAR130	Tonga	BORDAU 2	384–402	X	X	X		
	Fo196	New Caledonia	NORFOLK 2	245–437	X	X	X		
Paramunida cretata	PAR7	Wallis and Futuna	MUSORSTOM 7	300–305	X	X	X	X	X
	PAR99	Wallis and Futuna	MUSORSTOM 7	300–305	X	X	X		
	PAR20	Fiji	BORDAU 1	400–407	X	X	X		
	PAR21	Fiji	BORDAU 1	400–407	X	X	X	X	X
Paramunida crinita	PAR82	Philippines	MUSORSTOM 2	178–205	X	X	X	X	X
	PAR83	Philippines	MUSORSTOM 2	178–205	X	X	X		
	PAR84	Philippines	MUSORSTOM 2	178–205	X	X	X		
	PAR85	Philippines	MUSORSTOM 2	178–205	X	X	X		
	PAR100	Philippines	MUSORSTOM 3	195	X	X	X		
	PAR101	Philippines	MUSORSTOM 3	195	X	X	X		
	PAR102	Philippines	MUSORSTOM 3	195	X	X	X		
	PAR103	Philippines	MUSORSTOM 3	195	X	X	X		
Paramunida cristata	PAR6	Fiji	BORDAU 1	420–513	X	X	X		
	PAR156	Taiwan	TAIWAN (NTOU)	397–399	X	X	X	X	X
Paramunida curvata	PAR8	Fiji	MUSORSTOM 10	241–417	X	X	X	X	X
	PAR145	Vanuatu	BOA 0	260–313	X	X	X		
	PAR146	Vanuatu	BOA 0	260–313	X	X	X	X	X
	PAR147	Vanuatu	BOA 0	260–313	X	X	X		
Paramunida echinata	PAR52	Marquesas Islands	MUSORSTOM 9	200–260	X	X	X		
	PAR53	Marquesas Islands	MUSORSTOM 9	200–260	X	X	X		
	PAR54	Marquesas Islands	MUSORSTOM 9	200–260	X	X	X	X	X
Paramunida evexa	PAR49	Indonesia	KARUBAR	223–225	X	X	X		
	PAR50	Indonesia	KARUBAR	223–225	X	X	X		
	PAR51	Indonesia	KARUBAR	223–225	X	X	X	X*	X
Paramunida granulata	PAR27	New Caledonia	MUSORSTOM 6	600	X	X	X		
	Fo106	New Caledonia	NORFOLK 2	400–650	X	X	X	X	X
	PAR86	Vanuatu	MUSORSTOM 8	550–571	X	X	X		
	PAR88	Vanuatu	MUSORSTOM 8	550–571	X	X	X		
	PAR126	Tonga	BORDAU 2	564–569	X	X	X	X	X
	PAR127	Tonga	BORDAU 2	564–569	X	X	X		
Paramunida labis	PAR28	Vanuatu	MUSORSTOM 8	250–315	X	X	X		
	PAR29	Vanuatu	MUSORSTOM 8	250–315	X	X	X	X	X
	PAR30	Vanuatu	MUSORSTOM 8	250–315	X	X	X		
	PAR40	Vanuatu	MUSORSTOM 8	335–410		X	X		
	PAR41	Vanuatu	MUSORSTOM 8	335–410		X	X		

continued

Table 1. Continued

Species	Code	Specimen provenance	Survey	Depth (m)	COI	16S	ND1	18S	28S
	Fo64	New Caledonia	NORFOLK 1	245–440	X	X	X		
	Fo151	New Caledonia	NORFOLK 2	245–440	X	X	X		
Paramunida leptotes	PAR154	Taiwan	TAIWAN (NTOU)	329–456	X	X	X	X	X
Paramunida longior	PAR37	New Caledonia	HALIPRO 1	430	X	X	X		
	PAR38	New Caledonia	HALIPRO 1	430	X	X	X	X	X
	PAR46	New Caledonia	BATHUS 2	362–470	X	X	X	X	X
	PAR47	New Caledonia	BATHUS 2	362–470	X	X	X		
	PAR48	New Caledonia	BATHUS 2	362–470	X	X	X		
Paramunida lophia	S6	Solomon Islands	SALOMON 1	135–325	X	X	X		
	S23	Solomon Islands	SALOMON 2	135–325	X	X	X	X	X
	S24	Solomon Islands	SALOMON 1	135–325	X	X	X		
Paramunida luminata	PAR2	Wallis and Futuna	MUSORSTOM 7	550	X	X	X	X	X
Paramunida marionis	PAR75	Madagascar	MD 08	no record		X*			
	PAR76	Madagascar	MD 08	no record		X*			
	PAR77	Madagascar	MD 08	no record		X*			
Paramunida parvispina	PAR97	Chesterfield Islands	EBISCO	298-309	X	X	X	X	X
	PAR98	Chesterfield Islands	EBISCO	298-309	X	X	X		
Paramunida pictura	PAR121	Fiji	BORDAU 1	353	X	X	X		
	PAR122	Fiji	BORDAU 1	353	X	X	X	X	X
	Fo177	New Caledonia	NORFOLK 2	205-600	X	X	X	X	X
Paramunida polita	PAR4	Solomon Islands	SALOMON 2	399-427	X	X	X	X	X
	PAR5	Solomon Islands	SALOMON 2	399-427	X	X	X		
	PAR22	Indonesia	KARUBAR	390-502	X	X	X	X	X
	PAR23	Indonesia	KARUBAR	390-502	X	X	X		
	PAR65	Indonesia	KARUBAR	336-446	X	X	X		
	PAR66	Indonesia	KARUBAR	336-446	X	X	X	X	X
	PAR67	Indonesia	KARUBAR	287-298	X	X	X		
	PAR68	Indonesia	KARUBAR	287-298	X	X	X		
	PAR69	Indonesia	KARUBAR	287-298	X	X	X		
	PAR70	Indonesia	KARUBAR	287-298	X	X	X		
Paramunida poorei	Fo363	French Polynesia	BENTHAUS	212-450	X	X	X		
	Fo364	French Polynesia	BENTHAUS	200-350	X	X	X	X	X
Paramunida pronoe	PAR24	New Caledonia	NORFOLK 1	335-590	X	X	X	X	X
	PAR25	New Caledonia	NORFOLK 1	335-590	X	X	X		
Paramunida proxima	PAR18	Solomon Islands	SALOMON 1	135-325	X	X	X		
	S25	Solomon Islands	SALOMON 1	135-325	X	X	X	X	X
	PAR61	Vanuatu	MUSORSTOM 8	397-402	X	X	X		
	PAR62	Vanuatu	MUSORSTOM 8	397-402	X	X	X	X	X
Paramunida salai	S7	Solomon Islands	SALOMON 1	135-325	X	X	X	X	X
	S29	Solomon Islands	SALOMON 1	135-325	X	X	X		
Paramunida scabra	PAR55	Indonesia	KARUBAR	223-225	X	X	X	X	X
	PAR56	Indonesia	KARUBAR	223-225	X	X	X		
	PAR57	Indonesia	KARUBAR	223-225	X	X	X		
	PAR58	Indonesia	KARUBAR	223-225	X	X	X		
	PAR90	Indonesia	KARUBAR	215-219	X	X	X		
	PAR91	Indonesia	KARUBAR	215-219	X	X	X		
Paramunida setigera	PAR31	Philippines	MUSORSTOM 3	240-267	X	X	X	X	X
	PAR32	Philippines	MUSORSTOM 3	240-267	X	X	X		
	PAR33	Philippines	MUSORSTOM 3	240-267	X	X	X		
	PAR34	Philippines	MUSORSTOM 3	240-267	X	X	X		
Paramunida spica	PAR139	Vanuatu	SANTO	234-270	X	X	X		
	PAR140	Vanuatu	SANTO	234-270	X	X	X	X	X

Table 1. Continued

Species	Code	Specimen provenance	Survey	Depth (m)	COI	16S	ND1	18S	28S
Paramunida stichas	PAR12	New Caledonia	HALIPRO 1	464-480	X	X	X		
	PAR13	New Caledonia	HALIPRO 1	464-480	X	X	X		
	PAR14	New Caledonia	HALIPRO 1	464-480	X	X	X		
	PAR15	New Caledonia	HALIPRO 1	464-480	X	X	X	X	X
	PAR35	New Caledonia	MUSORSTOM 4	485	X	X	X		
	PAR36	New Caledonia	MUSORSTOM 4	485	X	X	X		
	Fo71	New Caledonia	NORFOLK 1	210-590	X	X	X		
	PAR19	Solomon Islands	SALOMON 1	135-325	X	X	X	X	X
	S27	Solomon Islands	SALOMON 1	135-325	X	X	X		
	S28	Solomon Islands	SALOMON 1	135-325	X	X	X		
Paramunida tenera	PAR42	New Caledonia	BATHUS 4	386-430	X	X	X		
	PAR43	New Caledonia	BATHUS 4	386-430	X	X	X		
	PAR44	New Caledonia	BATHUS 4	386-430	X	X	X	X	X
	PAR45	New Caledonia	BATHUS 4	386-430	X	X	X		
	PAR107	Fiji	MUSORSTOM 10	244-252	X	X	X		
	PAR108	Fiji	MUSORSTOM 10	244-252	X	X	X		
	PAR109	Fiji	MUSORSTOM 10	244-252	X	X	X	X	X
	PAR110	Fiji	MUSORSTOM 10	244-252	X	X	X		
	PAR149	Vanuatu	BOA 0	287-440	X	X	X		
	PAR150	Vanuatu	BOA 0	287-440	X	X	X	X	X
	PAR151	Vanuatu	BOA 0	287-440	X	X	X		
	PAR152	Vanuatu	BOA 0	287-440	X	X	X	X	X
	PAR153	Vanuatu	BOA 0	287-440	X	X	X		
Paramunida thalie	PAR10	New Caledonia	LIFOU	120-250	X	X	X	X	X
	Fo65	New Caledonia	NORFOLK 1	245-283	X	X	X		
	Fo28	New Caledonia	NORFOLK 1	245-283	X	X	X		
	PAR135	Tonga	BORDAU 2	327-360		X	X		
Paramunida tricarinata	PAR78	Philippines	MUSORSTOM 2	160-198	X	X	X		
	PAR79	Philippines	MUSORSTOM 2	160-198	X	X	X		
	PAR80	Philippines	MUSORSTOM 2	160-198	X	X	X		
	PAR155	Taiwan	TAIWAN (NTOU)	no record	X	X	X	X	X
	PAR157	Taiwan	TAIWAN (NTOU)	no record	X	X	X		
Paramunida aff. setigera	PAR148	Vanuatu	BOA 0	287-440	X	X	X	X	X
Paramunida aff. longior	PAR123	Fiji	BORDAU 1	420-450	X	X	X	X*	X*
	Outgroups								
Onconida alaini	Fo191	New Caledonia	NORFOLK 1	382-386	X	X	X	X	X
Plesionida concava	S8	Solomon Islands	SALOMON 2	399-427	X	X	X	X	X

(2005). Genetic variation of mitochondrial and nuclear markers was examined to confirm the taxonomic status of morphospecies. We included sequence data (COI and 16S) from previous studies (Machordom and Macpherson 2004; Cabezas et al. 2009, 2010). For these specimens, sequenced was extended to include an additional fragment of the 16S marker and the two nuclear genes. Two to ten individuals per species were included in the analysis to cover as much of the geographic range of the species as possible. For *P. leptotes*, *P. luminata*, *P. achernar*, and two potential new species (*P. aff. longior* and *P. aff. setigera*), only single specimens were available. Specimens of *P. tricarinata* from Madagascar were preserved in formalin and failed to amplify, except for a 436-bp fragment of 16S, and were not included in the final dataset. Nevertheless, independent analysis of the 16S fragment as well as morphological study revealed that these specimens from Madagascar represent an independent lineage from *P. tricarinata* (see Results). Therefore, the final dataset comprised 30 nominal plus two potential new species (*P. aff. longior* and *P. aff. setigera*). We generated phylogenetic trees for each mitochondrial gene, and on the basis of these trees we selected a subset of specimens for further sequencing of nuclear markers. *Onconida alaini* and *Plesionida concava* were selected as outgroup taxa, because previous work has shown that these two genera are part of the sister clade of *Paramunida* (Machordom and Macpherson 2004).

DNA AMPLIFICATION AND SEQUENCING

Total genomic DNA was isolated from abdominal muscle tissue or pereiopods using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen, Carlsbad, CA). Five markers were amplified: two nuclear (28S and the 18S) and three mitochondrial (16S, ND1, and COI) fragments. Amplification was accomplished using universal or newly designed primers; for the 16S, 28S, and 18S genes, two different fragments were amplified (see Table S1). PCR reactions were performed in a final volume of 50 μl. The PCR mix for mitochondrial markers contained 2 μl of DNA template, 0.16 μM of both primers, 0.2 mM of each dNTP, 5 μl of buffer (containing a final concentration of 2 mM $MgCl_2$), 0.5 μl of BSA (10 mg/mL), 1.5 U of Taq DNA polymerase (Biotools, Madrid, Spain), and ddH_2O. For the nuclear markers, PCR mix contained 2 μl of DNA template, 0.2 μM of both primers, 0.2 mM of each dNTP, 5μl of buffer without Mg^{++}, 6 μl of 25mM solution $MgCl_2$, 0.5 U of Jump Start Taq DNA polymerase (SIGMA, Sigma-Aldrich, St. Louis, MO), and ddH_2O. PCR conditions for mitochondrial markers consisted of an initial denaturation step of 94°C for 4 min followed by 39 cycles at 94°C for 30 sec, an annealing temperature of 45.5°C (16S), 40.5°C (ND1), and 45–50°C (COI) for 1 min, 72°C for 1 min, and a final extension at 72°C for 10 min. Conditions for nuclear markers included an initial step of 94°C for 3 min followed by 35 cycles at 94°C for 30 sec, 48–50°C (18S and 28S, respectively), 72°C for 1 min 30 sec, and a final extension at 72°C for 7 min. PCR products were purified using an ethanol/sodium acetate precipitation (mitochondrial markers) or cleaned with ExoSAP-IT (nuclear) (USB Corp., Cleveland, OH). Samples were cycle sequenced using the ABI Prism BigDye Terminator, and subsequently were run on an ABI 3730 Genetic Analyzer (Applied Biosystems, ABI, Foster City, CA). New sequences data are available in GenBank under accession numbers GU814634-GU815088, GU831576-GU831595 and HM060642-HM060644. Alignments are deposited on TreeBASE (http://www.treebase.org) (Submission ID 12200).

PHYLOGENETIC RECONSTRUCTION AND SPECIES BOUNDARIES

DNA sequences were edited using Sequencher 4.6 (Gene Codes, Ann Arbor, MI) and aligned manually in Se-Al version 2.0a11 (Rambaut 2002). The software GBLOCKS (Castresana 2000) was used to identify ambiguously aligned regions in 16S, 18S, and 28S. To examine the importance of these regions in phylogenetic reconstruction, we ran alternative analysis with and without the ambiguous nucleotides. The resulting topologies did not show substantial differences, and inclusion of these sites yielded stronger statistical support for several clades in some cases. Therefore, these positions were included in the final dataset. We inferred the best molecular evolutionary model for each marker using the Akaike Information Criterion (Akaike 1974) as implemented in the program ModelTest 3.07 (Posada and Crandall 1998). Phylogenetic relationships were estimated under maximum parsimony (MP), maximum likelihood (ML), and Bayesian Inference (BI) approaches. Parsimony analyses (MP) were performed through a heuristic search with the TBR swapping algorithm, 10 random stepwise additions, and treating indels as missing data using PAUP* v4.0 b10 (Swofford 2002). ML analyses were conducted in PHYML v2.4.4 (Guindon and Gascuel 2003) using the evolutionary model selected by ModelTest 3.07, and allowing the program to estimate model parameters. Clade support for the MP and ML phylogenies was assessed by nonparametric bootstrapping (Felsenstein 1985) using 1000 and 500 pseudoreplicates, respectively. Bayesian analyses were run using the software MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001), with two independent runs of four Metropolis-coupled chains with 5 million generations each. After assessing convergence between runs by monitoring the standard deviation of split frequencies in MrBayes 3.1.2 and using the effective sampling size criterion in Tracer version 1.4 (Rambaut and Drummond 2003), the initial 10% of the trees were discarded as burn-in. A 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities. Phylogenies were constructed for each marker and congruence among partitions was checked by looking for conflicting clades. Because there was no significant incongruence between the mitochondrial and nuclear datasets, that is, among clades that were strongly supported (>95 posterior probability [Pp] or >70% bootstrap value [Bv]), we combined all markers into a single concatenated dataset and analyzed it under the same settings given above.

ESTIMATING TIMES OF DIVERGENCE

We examined the data for evolutionary rate constancy using the relative rate test (Takezaki et al. 1995) implemented in PHYLTEST 2.0 (Kumar 1996). As rates did not conform to a molecular clock, a Bayesian relaxed phylogenetic approach, implemented in BEAST version 1.5.3 (Drummond and Rambaut 2007) was used to estimate lineage divergence times. Phylogeny and divergence times were estimated using the combined dataset (mitochondrial and nuclear partition). A GTR+I+G model with four rate categories was implemented for each partition, and all species were pruned to single specimens. An uncorrelated, normal, relaxed molecular clock, and the Yule process of speciation were selected as clock and tree prior, respectively. The fossil record of decapods, and in particular of squat lobsters, is too scarce and biased to allow a fossil-based calibration approach (De Grave et al. 2009). Therefore, to obtain absolute divergence times, we calibrated the relative-time chronogram obtained from BEAST using the average mitochondrial rate of molecular divergence proposed for other decapods, allowing the program to estimate the substitution rate

for the nuclear partition. For the 16S, a slow (0.53% per million years [my]; Stillman and Reeb 2001) and a fast (0.9% per my; Schubart et al. 2000) substitution rate have been proposed. For COI, a substitution rate between 1% and 2% has been reported (Knowlton and Weigt 1998; Lessios 2008). Thus, the BEAST chronogram was calibrated with the slowest (0.53% per my) and the fastest (2% per my) mitochondrial substitution rates to avoid placing too much confidence in just one estimate, using a normal distribution with a mean of 0.00625 substitutions per site per million years and a standard deviation of 0.0016. Two independent analyses were performed with MCMC chain lengths of 20×10^6 generations per run. Parameters were logged every 1000 generations. Log files were analyzed using Tracer v1.4 (Rambaut and Drummond 2003) to examine the effective sample size (ESSs) of each parameter and to determine the appropriate burn-in. After discarding the first 10% of the MCMC samples as burn-in, results of the two runs were combined with LogCombiner v1.5.3 to obtain the Pp distribution of each parameter. Consensus tree (maximum clade credibility tree with 95% confidence intervals) was compiled with Tree Annnotator version 1.5.3 (Drummond and Rambaut 2007).

DIVERSIFICATION RATES

Rapid diversification events can be explored using molecular phylogenies to estimate species birth–death rates without reference to the fossil record (Nee et al. 1994; Paradis 1997; Rabosky 2006a). Here, we used two different approaches. First, we investigated whether diversification rates varied among our lineages using the relative cladogenesis test (RC) implemented in the R package GEIGER (Harmon et al. 2008). This statistic represents the probability that a particular lineage, existing at time t, will have k extant tips under a constant rate birth–death model. Second, we identify temporal shifts in diversification rates using the gamma statistic (Pybus and Harvey 2000) and ML methods implemented in R (version 2.6.0) (Paradis et al. 2004; Rabosky 2006a,b). The gamma statistic γ indicates whether internal nodes are closer to the root or to the tips of the tree than expected under a constant-rate model ($\gamma = 0$). Negative values of γ that are significantly different from 0 indicate a decrease in diversification rate over time. To account for incomplete taxon sampling, which can bias the gamma test, we used the MCCR test (Pybus and Harvey 2000) implemented in the R package LASER 2.1 (Rabosky 2006b). We simulated 5000 phylogenies with 39 taxa (total species estimated) under the pure birth model, of which 32 were sampled, and then compared the gamma value of the original phylogeny against the distribution of values from the random phylogenies. Recently, Cusimano and Renner (2010) warned that the MCCR test can lead to wrongly rejecting the null hypothesis of constant rate diversification in favor of decreasing rates through time if taxon sampling within a study is phylogenetically overdispersed (as it often is). However, the effect is negligible if taxon sampling is greater than 80% of total richness. Because we have analyzed about 81% of the known *Paramunida* species, our diversification tests may be considered robust to this violation. Finally, we used survival analysis implemented in the R package APE (*Diversi* option, Paradis et al. 2004) to test three alternative models of lineage accumulation over time: Model A assumes a constant rate of speciation through time; Model B assumes a gradual change in the rate of lineage accumulation, with values of the slope parameter $\beta < 1$ indicating that diversification rates are increasing and values of $\beta > 1$ indicating a slow down over time; finally, Model C specifies a breakpoint in time with two different speciation rates before and after this point.

Both survival analysis and the gamma test assume as null model a constant-rate speciation or "pure birth" model (Yule 1924), which does not incorporate extinction ($\mu = 0$). However, a change in the rate of net diversification ($r = \lambda - \mu$) can be explained by a temporal shift in either the rate of speciation or the rate of extinction. To incorporate the effect of extinction, we used the ΔAIC_{RC} ML test (Rabosky 2006a) implemented in LASER to compare the fit of the original phylogeny to a constant-rate birth death model ($\mu > 0$) against several rate-variable models. The latter included the Yule-2-rate model, in which there is a point shift in the rate of speciation (Rabosky 2006a) and two models of exponentially decreasing rates through time characteristic of early evolutionary radiations (logistic density dependence model [DDL] and exponential density dependence model [DDX]), in which the rate of speciation decreases as ecological niches are filled (Rabosky and Lovette 2009). Critical values of the ΔAIC_{RC} test were assessed by simulating 100 phylogenies of 32 taxa under the pure birth model (using the birth rate estimated by LASER), and comparing the original value against the distribution of values from simulations. Simulated phylogenies were generated with the R package TreeSim (Stadler 2010) following Antonelli and Sanmartín (2011).

BIOGEOGRAPHICAL ANALYSES

Ancestral ranges and geographic speciation scenarios for *Paramunida* were inferred using the likelihood-based method "Dispersal-Extinction-Cladogenesis" (DEC, Ree et al. 2005) implemented in the program Lagrange version 2.0.1 (Ree and Smith 2008). Given a time-calibrated phylogeny and the distribution of extant species, Lagrange estimates rates of dispersal ("range expansion") and extinction ("range contraction") along branches and relative probabilities of range inheritance scenarios at cladogenetic events (Ree and Sanmartín 2009). Three alternative range inheritance scenarios are allowed at speciation nodes: within-area speciation for ancestors distributed in a single area (e.g., A); for ancestors distributed in more than one area (e.g., ABC), speciation can either take place via "broadly allopatric speciation" in which one descendant inherits one area and the other inherits the rest of

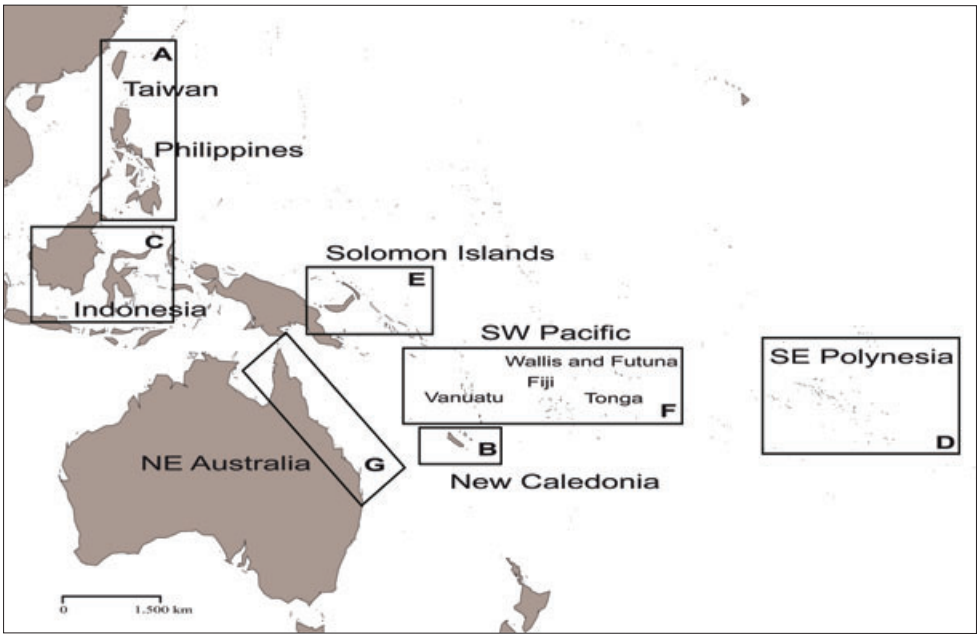

Figure 1. Operational biogeographical areas defined to perform biogeographical analyses.

the ancestral range (A/BC), or via "peripheral isolate speciation" (sensu Ree et al. 2005), in which one descendant inherits the area where the divergence occurred (A), whereas the other inherits the entire ancestral range (A/ABC). Inheritance of the entire widespread ancestral range by the two descendants (ABC/ABC) is not allowed (Ree and Sanmartín 2009).

Defining the areas of analysis is a critical step in many types of biogeographic analysis. In oceanic systems, this can be challenging because of the paucity and different nature of barriers. The vertical dimension (depth) usually provides a more limiting boundary than the horizontal dimension. For organisms living on the bathyal zone such as *Paramunida* adults, deep-water represents a barrier, isolating populations around continents and islands. We thus defined our operational areas around these landmasses. *Paramunida* species are distributed across the Indo-Pacific Ocean (between 200 and 700 m depth), with three widespread species extending north to Japan, two endemic to Madagascar and Mozambique, and three species occurring as far east as Hawaii and French Polynesia, respectively. However, some species from the Indian and Central Pacific oceans could not be included in our analysis (see above).

Thus, our biogeographic study focuses on the region where diversity is highest, the southwest Pacific. We defined seven operational areas based on the criteria of sympatry and level of endemism, geological history, and geographic distance between areas: (1) Taiwan + Philippines, (2) New Caledonia, (3) Indonesia, (4) southeast Polynesia, (5) Solomon Islands, (6) southwest Pacific (Vanuatu + Fiji + Tonga + Wallis and Futuna), and (7) northeast Australia (Fig. 1). To reduce the number of operational areas, small islands and archipelagos were grouped with the nearest area; for example, Chesterfield Islands were grouped with New Caledonia. Species distributions were coded according to the literature (Baba et al. 2008; 2009; Cabezas et al. 2010).

The size of the probability matrix specifying the rate of transition between geographic ranges in Lagrange increases exponentially with the number of areas, especially when there are widespread species, which results in a loss of resolution power (Ree and Sanmartín 2009). Most species of *Paramunida* are restricted to one or two areas, but there are several species that are distributed in three, four, or even five areas (e.g., *P. longior* or *P. granulata*). In our analysis, we constrained widespread ranges in the transition matrix to combinations of up to four areas (94 possible ranges), which were the minimum number of areas allowed by Lagrange without running into convergence problems (i.e., "reducible Markov chains", see Buerki et al. 2011). Unlike terrestrial systems where disjunct ranges are usually disallowed, we considered disjunct ranges as possible states in the analysis because area adjacency— the need for areas within ranges to share a physical edge or boundary— is not as relevant for marine organisms as for terrestrial animals. Finally, to examine the effect of geographic distance in ancestral area reconstruction, we run a second Lagrange analysis in which rates of dispersal in the transition matrix were scaled in relation to relative geographic distance between areas (Table 2). We then compared results from this analysis with those from the unconstrained DEC model in which dispersals rates were assumed equal. All analyses were performed on the maximum-clade-credibility tree with mean heights from the BEAST analysis.

Table 2. Probability transition matrix of dispersal between operation biogeographic areas. Area coding corresponds to that indicated in Figure 1.

Operational areas	A	B	C	D	E	F	G
A	1						
B	0.3	1					
C	0.7	0.5	1				
D	0.01	0.01	0.01	1			
E	0.6	0.7	0.6	0.01	1		
F	0.3	0.8	0.5	0.01	0.8	1	
G	0.5	0.8	0.7	0.01	0.8	0.7	1

Results

PHYLOGENETIC RELATIONSHIPS AND SPECIES BOUNDARIES

The mitochondrial dataset yielded a matrix with 137 taxa and 1947 characters (Table 3). The combined dataset (mitochondrial + nuclear, excluding most of the intraspecific variation) yielded a matrix with 48 taxa and 5527 base pairs. Of these, 1478 sites were variable and 1119 phylogenetically informative (192 informative sites among 575 bp for COI, 169/460 for ND1, 319/912 for 16S, 109/1797 for 18S, and 330/1783 for 28S). The mean base frequencies of the mitochondrial genes showed a clear AT bias (69.4% for COI, 78.2% for ND1, and 79.7% for 16S). Table 3 shows the best-fitting models selected by ModelTest and associated parameter estimates from MrBayes analyses (including 95% highest posterior density [HPD]). Intraspecific uncorrected "p" distances for mitochondrial genes ranged between 0% and 1.39% (COI), 0% and 1.53% (ND1), and 0% and 0.95% (16S), whereas interspecific divergence between sister species varied between 1.73% and 11.47% (COI), 2.17% and 12% (ND1), and 1.2% and 8.7% (16S).

The independent analysis of each mitochondrial and nuclear gene yielded similar topologies under the three methods of phylogenetic reconstruction (MP, ML, and BI), with a common lack of support for the basal nodes. The analysis of the three-gene mitochondrial dataset recovered *Paramunida* as monophyletic, but support values were not significant (<70% Bv or <95% Pp), and in general the backbone of the phylogeny received low support (Fig. 2). Eight clades (I–VIII) were well supported in all analyses (Fig. 2). Four of these clades (II, III, V, and VIII) contained only two species, and three additional species (*P. granulata, P. cristata,* and *P. polita*) were not strongly linked to any other species (Fig. 2). Relationships among species within the clades were usually well resolved, but relationships between clades were poorly resolved. The combined dataset (mitochondrial + nuclear) provided further resolution in the basal nodes and yielded better support for bootstrap and posterior probabilities values than the mitochondrial dataset. The monophyly of the genus received high support, as did the eight clades recovered in the mithocondrial analysis, but again support for the backbone of the phylogeny was low (Fig. 3). The main difference with the mtDNA dataset was in the position of Clade V, which grouped *P. amphitrita–P. thalie* with *P. curvata* (Fig. 3). The analysis of the nuclear loci

Table 3. Mitochondrial, nuclear, and combined datasets including informative sites and maximum likelihood (ML) models selected through AIC criterion as implemented in ModelTest. Base frequencies, rate matrix, gamma shape parameter, and proportion of invariable sites (including 95% HPD) resulting from MrBayes analyses are showed.

Gene fragment	Mitochondrial	Nuclear	Combined
Total sites	1947	3580	5527
Informative sites	756 (38%)	439 (12%)	1119 (20%)
Model	GTR+I+G	GTR+I+G	GTR+I+G
Base frequency			
%A	36.9 (35.3–38.6)	25.9 (24.5–27.2)	29.2 (28.2–30.3)
%C	8.06 (7.25–8.97)	20.1 (18.8–21.3)	15.7 (14.8–16.6)
%G	14.6 (13.5–15.8)	26.1 (24.8–27.5)	22.5 (21.5–23.5)
%T	40.4 (38.8–42.2)	27.9 (26.6–29.3)	32.6 (31.5–33.7)
Rate matrix			
[A-C]	0.041 (0.029–0.054)	0.092 (0.072–0.113)	0.048 (0.039–0.057)
[A-G]	0.337 (0.294–0.381)	0.23 (0.198–0.26)	0.323 (0.299–0.347)
[A-T]	0.069 (0.06–0.08)	0.125 (0.105–0.145)	0.151 (0.139–0.163)
[C-G]	0.024 (0.0102–0.0387)	0.035 (0.228–0.484)	0.026 (0.018–0.034)
[C-T]	0.499 (0.451–0.545)	0.409 (0.369–0.448)	0.392 (0.365–0.42)
[G-T]	0.028 (0.02–0.36)	0.109 (0.091–0.128)	0.058 (0.05–0.067)
Shape parameter	0.651 (0.541–0.764)	0.649 (0.451–0.865)	0.512 (0.437–0.589)
Invariable sites	0.447 (0.417–0.478)	0.623 (0.568–0.675)	0.579 (0.548–0.608)

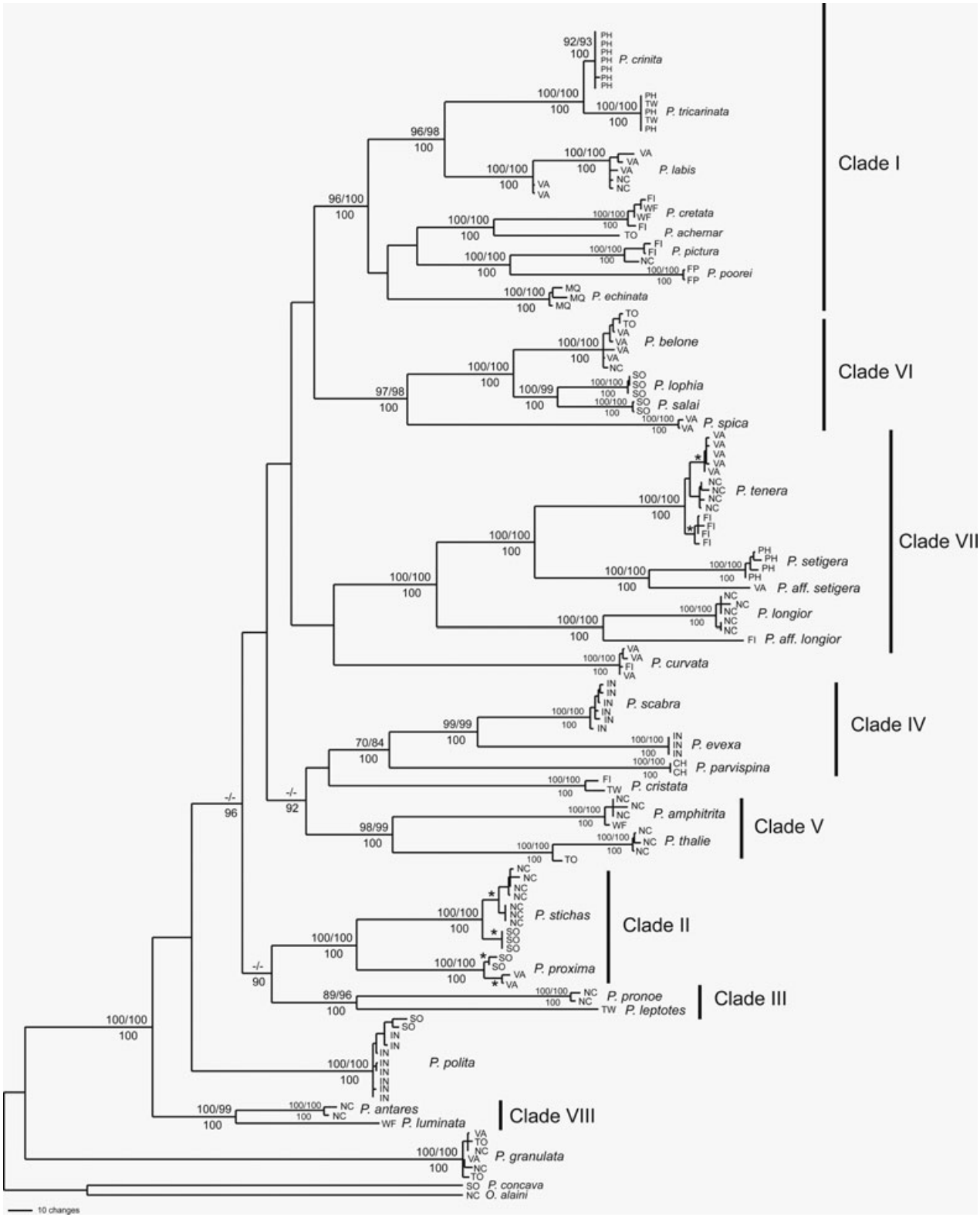

Figure 2. Majority-rule-consensus from a Bayesian analysis of the mitochondrial dataset. The values above the branches represent parsimony and maximum likelihood bootstraps (Bv > 70), respectively, and the values below the branches represent Bayesian posterior probabilities (Pp > 90). Asterisks represent well-supported clades within the same species. Codes in each species clade correspond to the sampled localities: CH, Chesterfield Islands; FI, Fiji; FP, French Polynesia; IN, Indonesia; MQ, Marquesas Islands; NC, New Caledonia; PH, Philippines; SO, Solomon Islands; TW, Taiwan; TO, Tonga; VA, Vanuatu; WF, Wallis and Futuna.

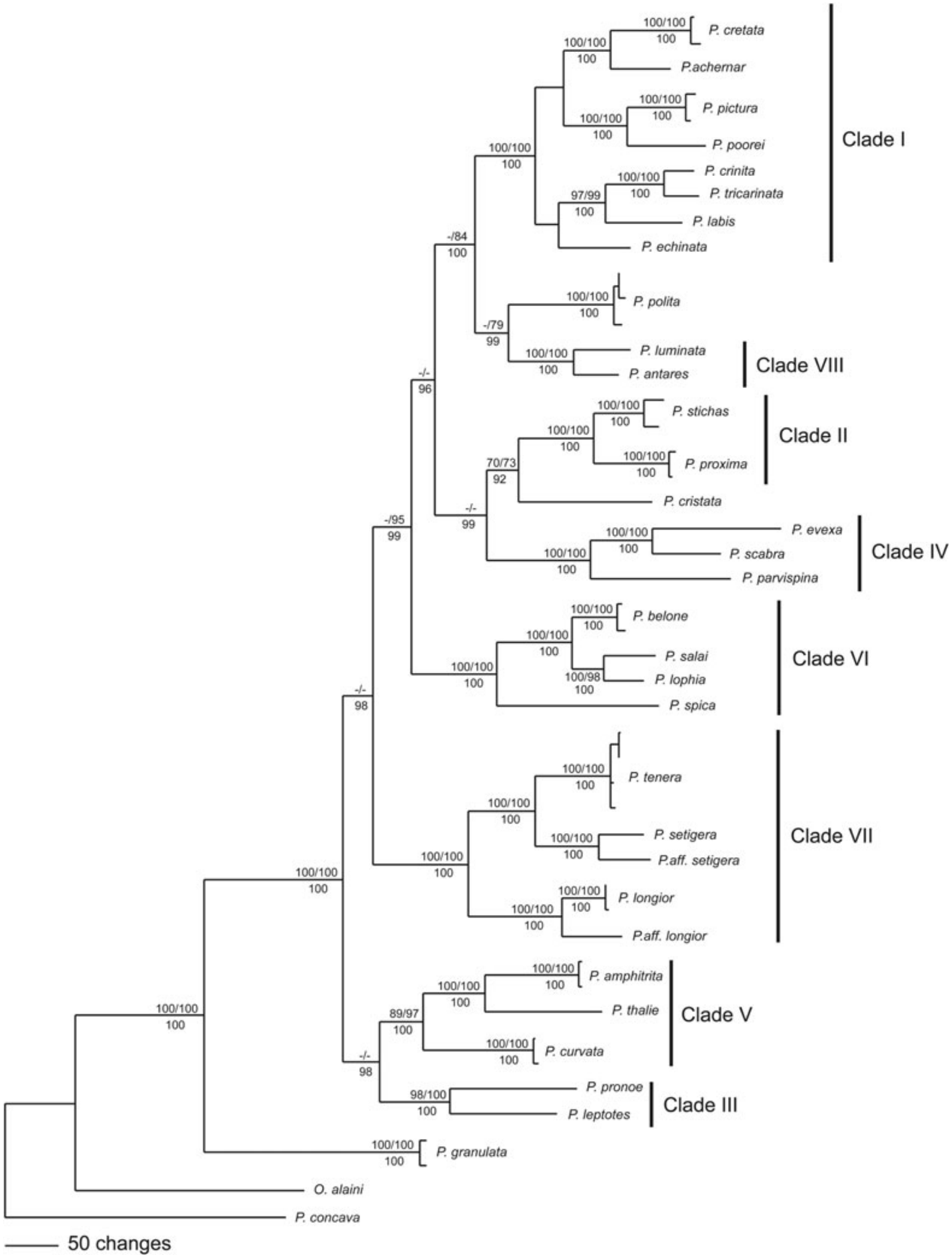

Figure 3. **Majority-rule-consensus from Bayesian analysis of the combined dataset. The values above the branches represent parsimony and maximum likelihood bootstraps (Bv > 70), respectively, and the values below the branches represent Bayesian posterior probabilities (Pp > 90).**

yielded a similar topology than the one from the combined dataset (see Fig. S1).

Because the mitochondrial analysis included more individuals and covered more geographic locations, results from these analyses were used for species delimitation. Our analysis focuses on genetically distinct evolutionary significant units (ESUs, Moritz 1994). Here, we defined ESUs as populations that are reciprocally monophyletic for the three mitochondrial loci investigated and can also be distinguished morphologically, thus satisfying the phylogenetic species concept (Wheeler and Meier 2000). All species, for which multiple individuals were sequenced, were recovered as monophyletic units with high support, representing a total of 27 ESUs. For *P. achernar*, *P. luminata,* and *P. leptotes*, only one specimen could be sequenced, limiting the reconstruction of reciprocal monophyly. However, these species have clear morphological distinctiveness and they are not nested among sequences from other ESUs, revealing independent evolutionary trajectories. For *P. aff. setigera* and *P. aff. longior*, a detailed morphological study could not be performed because only one damaged specimen was available for each (see Cabezas et al. 2010). However, sequence data for both specimens revealed high genetic divergence values with respect to their sister group (4.8% and 8.6%, respectively), which substantially exceeds the intraspecific divergence range reported for all species (see above). Therefore, *P. aff. setigera* and *P. aff. longior* were treated as potential new ESUs.

Our results also revealed that several presumed widely distributed taxa are actually species complexes, with component species exhibiting more restricted, single-area distributions (Fig. 2). Molecular data, as well as subtle morphological differences associated to the spinulation of the caparace, antennal and antennule peduncle, and walking legs, confirm that specimens originally identified as *P.* "*pictura*" from French Polynesia represent a divergent form (*P. poorei*) from the nominal species distributed in New Caledonia and adjacent waters (Cabezas et al. 2010). Specimens of *P. setigera* from Vanuatu, New Caledonia, and Fiji were also confirmed as different taxa (*P. tenera* and *P. aff. setigera*, Fig. 2), in agreement with the morphological study of Cabezas et al. (2010). Specimens of *P. "tricarinata"* from Madagascar were considered to be a different lineage (*P. marionis*) on the basis of deep divergence split (14.6%), reciprocal monophyly in the sole fragment of 16S that we could amplify (data not shown), and morphological differences (Cabezas et al. 2010). Finally, we recovered well-supported monophyletic clades at the population level within several species that received more extensive sampling, such as *P. tenera*, *P. stichas,* and *P. proxima* (Fig. 2).

TIMING AND TEMPO OF DIVERSIFICATION

Genus *Paramunida* is estimated to have originated around the Early Oligocene, with *P. granulata* representing the earliest offshoot within the genus (Fig. 4). All diversification analyses rejected a model of constant-rate diversification in favor of a model with an early rapid diversification followed by a slow down in the rate of lineage accumulation over time. The RC test identified an increase in diversification rate within the first four nodes after the divergence of *P. granulata*, between 21 and 17 Ma—the Oligocene–Miocene period if the 95% confidence intervals are considered (Fig. 4). The lineage-through-time plot (LTT) for the phylogeny of *Paramunida* was convex (Fig. 5) and differed significantly from a model of constant rate diversification, supporting decreasing speciation rates through time ($\gamma = -2.85$; critical value for $\gamma = -1.72$, $P < 0.01$.). Survival analyses indicated that Model B (gradual change in the rate of lineage accumulation) with a β value of 1.73 fitted the data better than a constant rate model or a model with two distinct rates of diversification. Also, the ΔAIC_{RC} test in LASER indicated a significant departure of the lineage cumulative curve of *Paramunida* from a constant-rate birth–death model ($\Delta AIC_{RC} = 8.44$; $P < 0.01$). The model with the lowest AIC score was the density-dependent cladogenesis (DDL, $k = 35.39$, AIC $= 50.54$), which supports a burst of speciation followed by a decrease in diversification rates over time as ecological niches are filled. Rabosky and Lovette (2009) showed that increasing extinction rates with constant speciation can produce a pattern of decreasing diversification rates through time. To test this possibility, we compared the fit of the LTT plot of *Paramunida* to two time-varying speciation and extinction models: a model of exponentially increasing extinction but constant speciation (EXVAR function in LASER) against a model with constant extinction and exponentially declining speciation rate through time (SPVAR). The AIC score was better for the SPVAR model (58.73) than for the EXVAR model (68.07), and both showed a worse fit to the LTT plot than that of the density-dependent cladogenesis model DDL.

BIOGEOGRAPHICAL RECONSTRUCTION

The Lagrange unconstrained (Fig. 6) and the geographically constrained analysis (see Fig. S2) yielded very similar results for reconstructed ancestral area ranges and estimates of dispersal and extinction rates. There were not significant differences in the global likelihood of these two models (unconstrained $-\ln L = 127.7$; constrained $-\ln L = 128$). In general, relative likelihoods for ancestral areas were low and there were not significant differences (two log-likelihood units) among them, indicating considerable uncertainty in ancestral area reconstruction (Fig. 6).

Speciation within area F (southwest Pacific) was the most frequently inferred range inheritance scenario (19 events, Fig. 6), especially at basal nodes. Yet, there are few cases of monophyletic endemic clades within this area (e.g., *P. cretata–P. achernar*), as speciation within F is often accompanied in our reconstruction by range expansion to nearby areas, such as New Caledonia (area B)

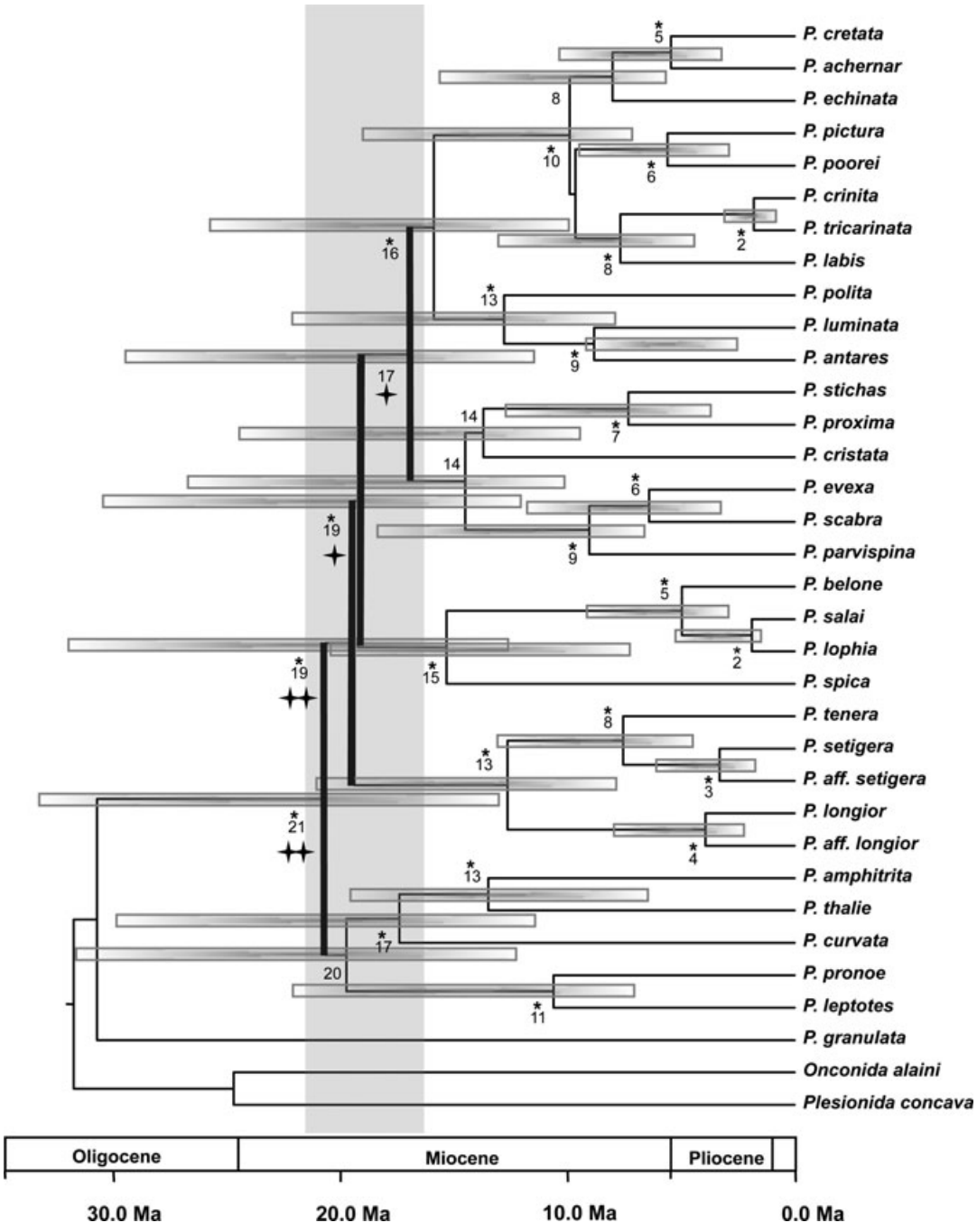

Figure 4. **Maximum clade credibility tree with branch lengths proportional to time (million years ago [Mya]) estimated with a Bayesian relaxed clock approach (BEAST) on the combined dataset and calibrated with the average mitochondrial molecular rate. Clades with significantly increased rates of diversification are indicated by thick black lines and symbols indicate levels of significance using the relative cladogenesis test (++ $P < 0.005$ and + $P = 0.01$). Asterisks in branches represents clades supported by Bayesian analysis (Pp > 95), gray bars represent 95% highest posterior density intervals (HPD) and numbers correspond with mean age estimate.**

or northeast Australia (area G) that give rise to more widespread species (e.g., *P. pronoe*, *P. thalie*). There were eight cases of Lagrange "allopatric" speciation, in which dispersal to a new region is followed by a widespread ancestral state, divided at cladogenesis by allopatry, for example, *P. cretata–P. achernar*/*P. echinata* (F/D), *P. luminata*/*P. antares* (F/B). In contrast, only one case of peripheral isolate speciation was reconstructed: the ancestor of *P. longior* and *P. aff. longior* in the widespread range ABCEF, within which *P. aff. longior* diversified (area F). However, this result requires further investigation because specimens of *P. longior* from Fiji (area F) could not be sequenced, so we cannot conclude if they belong to the same ESU as *P. aff. longior*. Two

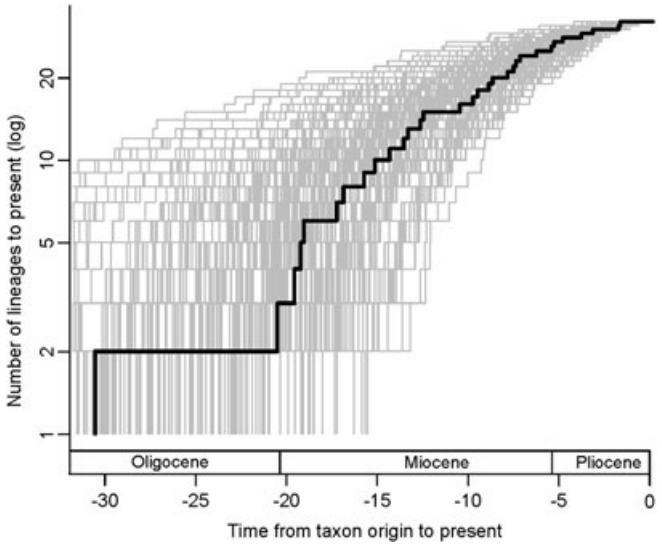

Figure 5. Lineage-through-time-plot (LTT) of the maximum clade credibility tree represented in Figure 4. Gray lines represent the 95% confidence interval for the observed LTT plot, as estimated from 180 dated trees randomly sampled from the posterior distribution of the Markov chain Monte Carlo (MCMC) BEAST analysis.

speciation cases involve "direct dispersal" from one region to another region without going through a widespread ancestral state: the ancestor of species *P. evexa–P. scabra* and *P. parvispina*, distributed in areas C, B, and ACG, is reconstructed as originating in area CB. However, its immediate ancestor is reconstructed as having diversified within F, which implies direct movement from F to CB along the branch leading to the *P. evexa–P. parvispina* clade. A similar example can be found in the ancestor of *P. polita* (F/F), a species that occurs only in areas A, C, and E.

The likelihood-based DEC reconstruction indicates that the ancestral lineage of genus *Paramunida* most likely lived in the southwest Pacific area, along the island arc formed by Fiji, Tonga, Vanuatu, Wallis and Futuna. From this area, *Paramunida* ancestors would have dispersed to the north and east, colonizing New Caledonia, South East Asia, and other Pacific Islands. The model suggest that dispersal to Taiwan and Philippines (area "A") have occurred independently several times from the southwest Pacific region, except for the clade (*P.–evexa–P.-scabra*), where dispersal seems to have occurred from Indonesia to Taiwan–Philipinnes (Fig. 6). The model also suggests several independent dispersal events from the southwest Pacific to New Caledonia (area B), but unlike the dispersals above, these events have ended in range expansion and widespread species, (i.e., only one endemic in "B": *P. antares*). Indonesia (area C) was mainly colonized via the southwest Pacific (e.g., *P. belone*), and occasionally from the Solomon Islands (e.g., *P. salai*). There were also several independent colonization events of the Solomon Islands (area E) and southeast Polynesia (area D) (e.g., *P. echinata* and *P. poorei*). Finally, northeast Australia has been colonized at least three times, from the southwest Pacific (e.g., *P. thalie*) or from the Indonesian region (e.g., *P. scabra*) (Fig. 6, inset).

Discussion

CLASSIFICATION AND PHYLOGENY OF *PARAMUNIDA*

The extensive application of molecular tools in systematic studies has revealed that the number of described morphospecies tends to be an underestimation of the real biological diversity in marine taxa (Meyer 2003; Malay and Paulay 2009). Much of this incongruence reflects the lack of taxonomic studies, but also the difficulty in identifying diagnostic characters and determining the intraspecific variability in groups where morphological homoplasy is high. Convergence or stasis in morphological evolution appears to be common in decapods (Knowlton 1986). It has been proposed that extreme environmental conditions can lead to stabilizing selection on morphology, reducing or even eliminating morphological change that can accompany cladogenesis (Bickford et al. 2007). Cryptic speciation has been described for both shallow- and deep-water squat lobsters (Jones and Macpherson 2007; Cabezas et al. 2011), suggesting that high morphological conservatism may be typical within the group, rather than reflecting limitations imposed by the habitat.

Both the mitochondrial and combined dataset showed *P. granulata* as the most basally diverging lineage within the genus, separated by a long branch from the remaining species (Fig. 4). This species can be clearly distinguished within *Paramunida* by the length of the distomesial spine of the second article of the antennal peduncle (Baba 1988). This conspicuous morphological difference in combination to high genetic divergence suggests that this species may represent a separate monotypic genus or a relict representative of a more diversified lineage. Taxonomic studies to reconsider the generic adscription of this species are thus needed. Our study has also validated the taxonomic status of several species recently described (Cabezas et al. 2010) and highlights the importance of subtle morphological differences to delimit species within this marine group.

In addition, we recovered well-supported monophyletic clades within species *P. tenera*, *P. stichas,* and *P. proxima* that correspond to endemic populations in different archipelagos (Fig. 2). Although morphological examination did not reveal morphological differences to support the split of these specimens in a different lineage, this genetic differentiation between Fiji and Vanuatu, Solomon and New Caledonia, and Solomon and Vanuatu points to the existence of restricted gene flow among these islands. Interestingly, we did not find a phylogeographic division between Solomon and New Caledonia populations of other coranging species such as *P. polita* and *P. granulata*. Although our limited taxon sampling does not allow any inference about the processes generating these differences, it stimulates future

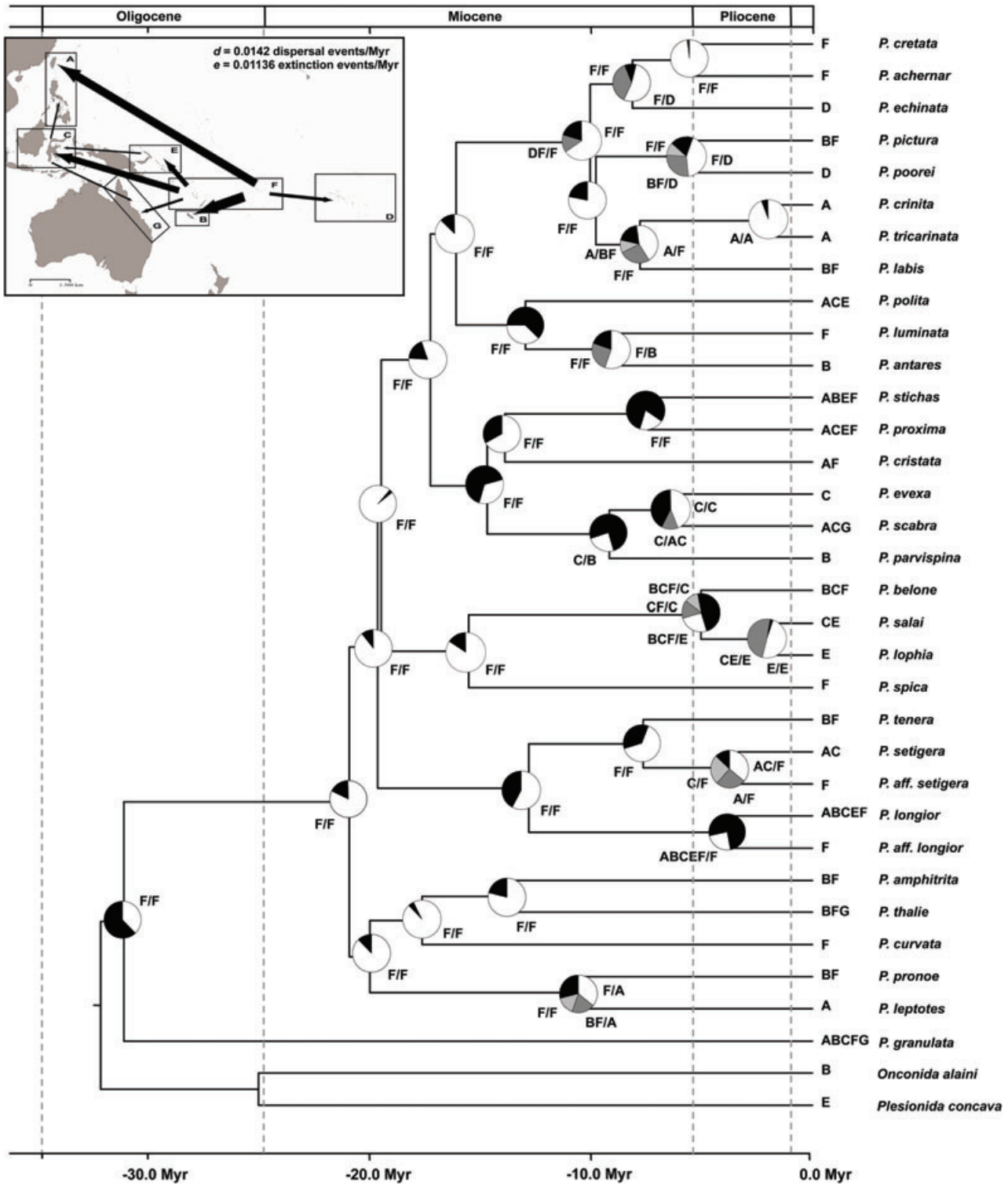

Figure 6. Reconstruction of the biogeographic history of *Paramunida* inferred using the Dispersal-Extinction-Cladogenesis model (DEC) implemented in Lagrange. The tree is the maximum-clade-credibility tree from BEAST. Letters in pie charts represent ML relative probabilities for range inheritance scenarios. The white color represents the reconstruction with the highest relative probability; gray and shady ones represent, respectively, the second and third most likely inferred reconstructions. Alternative reconstructions with a relative probability below 0.1 are represented by the black color. Current distributions are listed before each species. Inset: Biogeographical scenario depicted as frequencies of dispersal (range expansion) events between areas estimated following conventions in Buerki et al. 2011 (i.e., transition events that involve three or more events of range expansion and for which there is uncertainty in the direction of dispersal were not mapped).

comparative phylogeographic studies to elucidate scales of connectivity and the role of biotic/abiotic factors responsible for generating breaks at population species level.

TIMING AND CAUSES OF DIVERSIFICATION

The dynamics and mechanisms of marine diversification in Indo-Pacific waters have been extensively debated (Barber 2009 and references cited herein). Early studies argued for sea level changes and climatic oscillation during the Pliocene–Pleistocene glacial eustatic cycles as the driving force responsible for the high species diversity peak observed in the Indo-Malayan triangle (Benzie and Williams 1997). However, recent works using more accurate fossil-calibrated molecular phylogenies did not show evidence for species-level radiations during the last 3 million years ago (Ma) (Williams and Reid 2004; Barber and Bellwood 2005). Instead, an older diversification from the Oligocene onwards is now supported (Williams 2007; Williams and Duda 2008; Malaquías and Reid 2009). Our diversification tests support an early radiation in *Paramunida* coincident with the late Oligocene–Miocene period, suggesting that similar evolutionary and ecological processes may have affected both shallow and deep-water faunas.

The intense tectonic activity along the Asian, Australian, and Pacific plate margins during the Oligocene–Miocene period has been invoked as an important factor promoting rapid speciation in marine organisms (Renema et al. 2008; Williams and Duda 2008), by means of providing greater geological and habitat complexity, which in turn create opportunities for isolation and diversification of marine species (Wilson and Rosen 1998). The collision of the Australian and Pacific plates in the early Oligocene increased volcanism, resulting in the formation of new island-arc systems (i.e., the Melanesian archipielago of Fiji, Tonga, and Vanuatu [McLoughlin 2001]), the formation of new seamounts, and the uplift (and subduction) of existing seamounts and islands (Neall and Trewick 2008). These processes likely provided new habitats for colonization and stepping stone dispersal (Renema et al. 2008; Williams and Duda 2008), and also disrupted connectivity in other areas by loss of habitat at various water depths. These tectonic events triggered a major shift in the dynamics of the global climate system, with the onset of a period of global warming in the Early Oligocene that peaked in the Mid-Miocene Climatic Optimum (Zachos et al. 2001). Furthermore, temperature has been shown to have a significant impact on rates of genetic divergence and speciation (Gillooly et al. 2005; Allen et al. 2006), as evidenced by accelerated rates of turnover and speciation during the Late Eocene–Oligocene reported in some biotas (Prothero and Berggren 1992).

The absence of a fossil record of *Paramunida* (De Grave et al. 2009) makes it difficult to examine the role of extinction in the diversification of this group (Rabosky 2009). Nevertheless, our results suggest a period of initial diversification during the Late Oligocene–Miocene marked by high speciation relative to extinction rates. Although correlation does not necessarily mean causation, the rapid diversification observed in deep marine Indo-Pacific squat lobsters during this period (Machordom and Mapherson 2004; this study) could be linked with the high tectonic activity, changes in oceanic currents, and climatic shifts that took place in this region from the Late Oligocene onwards. These results represent the first evidence for a common period of diversification in both shallow- and deep-water environments. Additional data from other deep-water taxa would be needed to confirm the generality of this pattern.

BIOGEOGRAPHICAL RECONSTRUCTION

High dispersal abilities and the exceptional broad ranges of marine organisms make historical biogeographic reconstruction from present-day distributions particularly difficult (Barber and Bellwood 2005). To date, the DEC model (Ree and Smith 2008) has been used for reconstructing biogeographic patterns in terrestrial ecosystems in both continental and insular settings (Clark et al. 2008; Buerki et al. 2011). Here, we explore for the first time its efficacy in reconstructing biogeographic patterns in the marine realm, a system characterized by range-limiting vertical zonation and more permeable boundaries between biogeographic units. Although it is important to keep in mind the limitations imposed by our taxon sampling, which was much more extensive in New Caledonia and adjacent waters than in other western Pacific regions (see Table 1), our study points out several interesting patterns. The southwest Pacific region, here defined as the island arcs of Fiji, Tonga, Vanuatu, and Wallis and Futuna, is here identified as a major center for diversification of *Paramunida*. Most basal speciation events in the phylogeny are inferred to occur within this area. The importance of this region for squat lobsters was recently highlighted by Macpherson et al. (2010), who identified three different areas of high diversity in the Pacific—the Coral Sea, the Indo-Malay-Philippines archipelago (IMPA), and southeast Polynesia—based on the species richness and degree of endemicity in 22 deep-sea squat lobster genera. The fact that several endemic species have their sister group in a different area and that there are no monophyletic clades of three or more species endemic to this (or any) area, suggest that these areas of high diversity did not represent centers of diversification for the genus *Paramunida*. Instead, the analysis suggests a long-term role of the southwest Pacific region in the diversification of the genus, with periodic dispersal and speciation events to the nearby north and east Pacific regions. It is possible that this result is biased by recent higher sampling effort in this region. However, New Caledonia has been equally or even more intensively sampled than the southwest Pacific and yet this area is not identified as an important region of ancestral diversification in our analysis; in fact, few species seem to be endemic to this area (Fig. 6). Notice,

however, that area F is a composite of several islands, some of which harbor their own endemics.

So, it is possible that some of this speciation is actually allopatric speciation between the islands that form area F. The southwest Pacific archipelagos of Fiji, Tonga, Vanuatu, Wallis and Futuna are part of a continuous island arc formed after the collision of the Pacific and Australian plates in the Oligocene, and it is likely that the islands have had a long history of biotic connection.

Most species of *Paramunida*, and squat lobsters in general, show reduced geographic ranges confined to a single archipelago or a single biogeographic area (Cabezas et al. 2010). Even widespread species such as *P. stichas* are likely to be complexes of species with more restricted distributions. This high level of single-archipelago endemism is much higher than typical for most shallow faunas (Paulay and Meyer 2002), and has been also reported in other deep-water organisms (Richer de Forges et al. 2000; Bouchet et al. 2002). Interestingly, the distribution of the genus *Paramunida* extends from French Polynesia to Madagascar, suggesting that geographic distance is not a limiting factor in its current distribution. The geographically constrained model did not fit the data better than the unconstrained model, and our ancestral area reconstruction showed several independent colonization events from the southwest Pacific region to distantly located regions, such as Taiwan-Philippines—although this could be an artifact of incomplete taxon sampling, because several intermediate areas have been poorly sampled (e.g., New Guinea).

Knowledge on larval development of squat lobsters is very limited and unfortunately there are no data for *Paramunida*. Other genera of the family Munididae, however, are characterized by small eggs developing into planktrotophic larvae (Guerao et al. 2006; Baba et al. 2011). A similar developmental mode would imply a high power of dispersal for larvae of *Paramunida*. In contrast, adult stages are restricted to continental slope depths between 200 and 700 m, and their distribution is limited to shelves around islands and continents at these depths, with the deep ocean forming a barrier to dispersal. Thus, it is possible that sporadic long-distance events by larvae together with dispersal limitations in adult's stages could have generated the often narrow-ranging distributions of species but widerange distribution of the genus as a whole.

Conclusions

Here, we presented the first attempt to unravel the evolutionary history—phylogeny, diversification, and biogeography—of a deep-water lineage. The multidisciplinary approach used supports the hypothesis that the late Oligocene–Miocene was a period of rapid diversification for both shallow- and deep-water marine organisms in the Indo-Pacific region. This diversification was probably related to concurrent high regional tectonic activity, corresponding with changes in the distribution of habitats and of ocean currents, and the onset of a period of global warming. Our results suggest that the southwest Pacific region has acted as a major center of diversification in squat lobsters, from where species dispersed to other Pacific regions, rapidly building species richness. Finally, our study confirms the taxonomic value of subtle morphological differences to delimit species boundaries within genus *Paramunida*. Further comparative research including additional taxa along with more accurate divergence time estimates, will allow us to refine inferences about the origin and processes involved in generating the high marine diversity of the Indo-Pacific region.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Majority-rule-consensus from Bayesian analysis of the nuclear dataset.

Figure S2. Biogeographical reconstruction of *Paramunida* inferred using Lagrange with a constrained model in which dispersal rates are scaled by geographic distance according to Table 2.

Table S1. Loci and primers used in this study to amplify and sequence mitochondrial and nuclear genes.

Supporting Information may be found in the online version of this article.

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