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COMPARATIVE PHYLOGEOGRAPHY OF THREE CODISTRIBUTED STOMATOPODS: ORIGINS AND TIMING OF REGIONAL LINEAGE DIVERSIFICATION IN THE CORAL TRIANGLE

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Abstract.—The Indonesian-Australian Archipelago is the center of the world's marine biodiversity. Although many biogeographers have suggested that this region is a "center of origin," criticism of this theory has focused on the absence of processes promoting lineage diversification in the center. In this study we compare patterns of phylogeographic structure and gene flow in three codistributed, ecologically similar Indo-West Pacific stomatopod (mantis shrimp) species. All three taxa show evidence for limited gene flow across the Maluku Sea with deep genetic breaks between populations from Papua and Northern Indonesia, suggesting that limited water transport across the Maluku Sea may limit larval dispersal and gene flow across this region. All three taxa also show moderate to strong genetic structure between populations from Northern and Southern Indonesia, indicating limited gene flow across the Flores and Java Seas. Despite the similarities in phylogeographic structure, results indicate varied ages of the genetic discontinuities, ranging from the middle Pleistocene to the Pliocene. Concordance of genetic structure across multiple taxa combined with temporal discordance suggests that regional genetic structures have arisen from the action of common physical processes operating over extended time periods. The presence in all three species of both intraspecific genetic structure as well as deeply divergent lineages that likely represent cryptic species suggests that these processes may promote lineage diversification within the Indonesian-Australian Archipelago, providing a potential mechanism for the center of origin. Efforts to conserve biodiversity in the Coral Triangle should work to preserve both existing biodiversity as well as the processes creating the biodiversity.

Key words.—Allopatric speciation, biodiversity, center of origin, Coral Triangle, larval dispersal, marine phylogeography, stomatopod.

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The oceans of Indonesia are home to the highest marine biodiversity in the world (Myers et al. 2000; Veron 2000; Hughes et al. 2002; Roberts et al. 2002). Although a number of theories attempt to explain this pattern (for a review see Barber and Bellwood 2005), recent studies (Briggs 2000; Mora et al. 2003) support the hypothesis that this region is a center of origin (Ekman 1953), with increased biodiversity arising from speciation within the waters of Indonesia, Philippines, and Papua New Guinea, a region collectively known as the Coral Triangle (*sensu* Green and Mous 2004). A center of origin requires that mechanisms must be acting to promote lineage diversification within the Coral Triangle, and critics of this hypothesis have highlighted the lack of a convincing mechanism (Jokiel and Martinelli 1992). Although allopatric differentiation is the most common model of speciation invoked for terrestrial organisms (Mayr 1942; Bush 1975; Lynch 1989; Turelli et al. 2001) the pelagic larval dispersal common in marine species results in few clear boundaries to dispersal and should limit opportunities for allopatric divergence (Palumbi 1992, 1994). Thus, high biodiversity in the Indonesian-Australian Archipelago (IAA) seems paradoxical.

The dynamic geologic history of the IAA, however, suggests ample opportunity for vicariance. During Pleistocene glacial maxima, sea levels dropped 130 m below present levels (Porter 1989; Voris 2000), exposing the Sunda and Sahul continental shelves and constricting the waterways of

the IAA, potentially leading to increased isolation and allopatric differentiation between populations spanning the multiple ocean basins of the IAA. Support for Pleistocene vicariance in the IAA comes from biogeographic studies demonstrating patterns consistent with Pleistocene vicariance (McManus 1985; Potts 1985; Fleminger 1986; Woodland 1986; Springer and Williams 1990) and from genetic studies that indicate Pleistocene speciation (e.g., McMillan and Palumbi 1995). Further support comes from studies that demonstrate intraspecific genetic breaks on broad spatial scales (>1000 km) among populations of fish (Lacson and Clark 1995), crabs (Lavery et al. 1996), prawns (Duda and Palumbi 1999), sea stars (Williams and Benzie 1998; Benzie 1999) and mangroves (Duke et al. 1998) that span the IAA. These phylogeographic studies emphasize the IAA as a barrier between two oceans, resulting in allopatric diversification during the Pleistocene. However, the broad-scale geographic sampling employed in these studies is too coarse to determine whether phylogeographic patterns across species are truly concordant, limiting our ability to rigorously examine the specific processes promoting lineage diversification in the IAA.

A robust test of the processes promoting lineage diversification in the IAA requires comparative population genetic studies of multiple taxa on fine spatial scales throughout the region. Such comparative studies have been performed in the Caribbean (Shulman and Bermingham 1995), Great Barrier Reef (Doherty et al. 1995), Western Atlantic (Avise et al.

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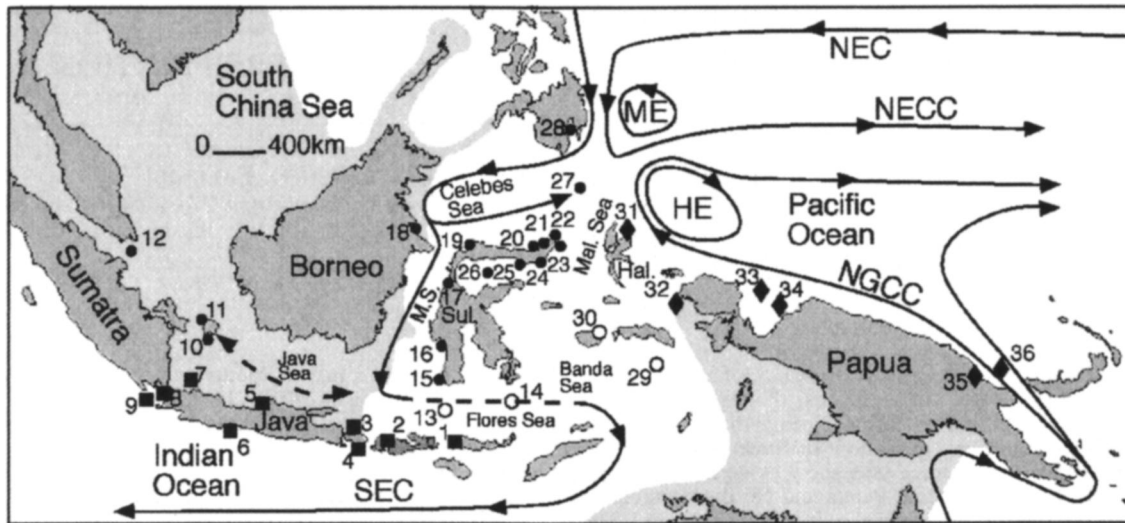


FIG. 1. Map of the Indo-West Pacific showing dominant (solid lines) and seasonally reversing currents (dashed lines), including the North Equatorial Current (NEC), North Equatorial Counter Current (NECC), New Guinea Coastal Current (NGCC), Mindanao Eddy (ME), Halmahera Eddy (HE), Makassar Strait (MS; the main passageway for the Indonesian Throughflow), and the South Equatorial Current (SEC). Squares indicate Southern Indonesia localities, closed circles indicate Northern Indonesia localities, and diamonds refer to Papua localities. Open circles indicate localities that could not be a priori assigned to one of the aforementioned regions. The islands of Halmahera and Sulawesi are identified by Hal. and Sul., respectively. Numbers identify localities described in Table 2. Light gray shading indicates coastal margins during Pleistocene low sea level stands, after Voris (2000).

1987), and French Polynesia (Fauvelot and Planes 2002), and Lourie et al. (2005) examined patterns of gene flow in brooding sea horses on the Sunda Shelf. However, there have been no comparative population genetic studies to date on species with pelagic larval dispersal on fine spatial scales in the center of the Coral Triangle. Such studies are critical to provide a robust test of the processes promoting lineage diversification in the IAA, improving our understanding of the origins of marine biodiversity in the IAA and of marine speciation in general.

Although sea-level fluctuations may promote lineage diversification in the IAA, this isolation may be compounded or mitigated by the physical oceanography of this region because of the ability of oceanic currents to affect dispersal through the transport of larvae entrained therein. Indonesia's oceanography is dominated by the Indonesian Throughflow (Wyrski 1987), a movement of 20 million m^3/sec of water from the Pacific to the Indian Ocean (Godfrey 1996; Gordon and Fine 1996) through the waters of Indonesia (Fig. 1) with associated currents that exceed 1 m/sec (Wyrski 1961). The vast majority (~90%) of the Indonesian Throughflow water comes from the North Equatorial Current (Nof 1995; Morey et al. 1999), providing a dispersal corridor to potentially link populations throughout much of this region. The remaining fraction comes from the New Guinea Coastal Current that travels north and west along the northern coast of the island of Papua (Papua New Guinea and Indonesian Papua). The New Guinea Coastal Current is deflected in the proximity of the island of Halmahera, forming the Halmahera Eddy (Fig. 1) and greatly limiting transport of New Guinea Coastal Current waters into the Indonesian Throughflow (Nof 1995; Morey et al. 1999). A powerful graphical representation of this isolation is illustrated in Lukas et al. (1991, p. 7092) in which surface drifter buoys that enter the Halmahera Eddy do not

cross the Maluku Sea, but are instead retroflected and transported eastward. Thus, although marine larvae are often active swimmers (Stobutzki and Bellwood 1997; Leis and Carson-Ewart 1997; Wolanski et al. 1997; Armsworth 2001) and can engage in behaviors (Cronin and Forward 1986; Tankersley and Forward 1994; Forward et al. 1997) that may result in limited dispersal (Jones et al. 1999; Swearer et al. 1999; Thorrold et al. 2001), the physical oceanography of the IAA may have a profound impact on larval dispersal, which in turn will impact gene flow and genetic cohesion throughout this region.

Counter to predictions of genetic homogeneity resulting from larval transport within the Indonesian Throughflow, Barber et al. (2000) found pronounced patterns of genetic differentiation among populations of the mantis shrimp *Haptosquilla pulchella* (Crustacea: Stomatopoda) throughout the IAA. Sampling on a scale of hundreds of kilometers revealed that the genetic break between Pacific and Indian Ocean populations was more precisely a break between populations north and south of the Java and Flores Seas that are separated by only 300–400 km. The discovery of a similarly large genetic break between populations from Papua New Guinea and Indonesia led Barber et al. (2002a) to suggest that although Pleistocene vicariance may contribute to patterns of genetic structure in marine populations of the IAA, other processes such as limited water/larval transport across the Maluku Sea and ecologically limited larval dispersal across the Flores and Java Seas may be driving regional diversification in this taxon. However, the validity of these hypotheses can only be evaluated through a rigorous comparative study of multiple ecologically similar species spanning this region.

In this paper, we compare patterns of genetic structuring in three Indo-Pacific stomatopod species. The congeneric species *Haptosquilla pulchella* and *H. glyptocercus*, as well as

TABLE 1. Egg size and postlarval settlement size for *Haptosquilla pulchella*, *H. glyptocercus*, *Gonodactylellus viridis*, and the western Atlantic gonodactyloid *Neogonodactylus oerstedii*. We have previously estimated the larval period for *H. pulchella* at four to six weeks (Barber et al. 2000, 2002a) based on the established facts that stomatopod larval development is highly regular and hence size is an appropriate proxy for age, the larval duration of the related species *N. oerstedii* has been experimentally determined as 35 days, and the three species in question hatch at a slightly smaller size yet recruit at a slightly larger size than *N. oerstedii* and hence are expected to have a slightly longer larval period. Asterisk indicates estimated values.

Species	Egg size (mm)	Size at settlement (mm)	Larval period	Source
<i>H. pulchella</i>	0.73–0.85	9.5–10	4–6 weeks*	Erdmann 1997
<i>H. glyptocercus</i>	0.60–0.78	7–9.5	4–6 weeks*	Erdmann 1997
<i>G. viridis</i>	0.63–0.95	5–9	4–6 weeks*	Erdmann 1997
<i>N. oerstedii</i>	1.04–1.30	6	35 days	Manning 1963; Provenzano and Manning 1978

the more distantly related *Gonodactylellus viridis* (Barber and Erdmann 2000), are three of the most common coral reef flat stomatopods found in the IAA (Erdmann 1997). Larvae of each of these species hatch from similar-sized eggs and recruit as similar sized postlarvae (Table 1). Stomatopod larval development is highly regular such that larval size is good predictor of age (Hamano et al. 1995). Therefore, it can be assumed that the length of the larval period in these three species is roughly similar, previously estimated at four to six weeks (Barber et al. 2000, 2002a). Previous work has further confirmed that the larvae of both *H. pulchella* and *H. glyptocercus* are pelagic (Barber et al. 2002b). Ecologically, all three species inhabit the intertidal and subtidal zones of coral reef flats and are frequently found cohabitating in the same piece of coral rubble (P. H. Barber and M. V. Erdmann, pers. obs.). However, whereas *H. glyptocercus* and *G. viridis* occur in a wide range of habitats and are common inhabitants of both coastal and oceanic reefs, *H. pulchella* requires proximity to freshwater, excluding them from oceanic reefs systems, including those that span Flores Sea (Erdmann 1997; P. H. Barber and M. V. Erdmann, pers. obs.).

The comparison of these three taxa on fine spatial scales across the same geographic region permits an examination of how three ecologically similar species respond to the dynamic physical environment of the IAA, increasing our understanding of the processes promoting lineage diversification in this region. Because broadly acting physical processes produce similar patterns of regional genetic structure across taxa with similar ecologies and dispersal abilities (Avice et al. 1987; Avice 1992) this comparison will allow a robust test of previously hypothesized phylogeographic barriers. In particular, having similar larval durations, these three taxa should be similarly affected by previously hypothesized limited larval transport across the Maluku Sea between the islands of Papua and Indonesia (subsequently referred to as the Eastern Barrier), resulting in concordant genetic breaks across this region (Barber et al. 2002a). In contrast, we predict that the sharp genetic break seen in *H. pulchella* across the Flores and Java Seas (subsequently referred to as the Southern Barrier) should be absent or less pronounced in *H. glyptocercus* and *G. viridis*, given those two species' ability to inhabit oceanic reefs and hence use them as stepping-stones in dispersal.

MATERIALS AND METHODS

Sampling and Sequencing

From July 1994 until April 2005, over 800 juvenile and adult specimens of *H. pulchella*, *H. glyptocercus*, and *G. viridis* were collected from numerous localities throughout the IAA (Fig. 1, Table 2) and preserved in 70–95% ethanol. For both species of *Haptosquilla*, approximately 700 base pairs of the mitochondrial cytochrome *c* oxidase subunit-1 gene (CO1) was amplified from Chelex (Bio-rad, Hercules, CA) DNA extractions (Walsh et al. 1991) via polymerase chain reaction (PCR) using primers H1490 and L2198 (Folmer et al. 1994) following published protocols (Barber and Erdmann 2000). Primers internal to these were used for *G. viridis* (GV2LCO=GAGCATGATCAGGAATAGTAGG and GV5HCO=AAGTTGCGGTCTGTAAGAAGTA) with thermocycling parameters of 38 cycles of 94°C/30 sec, 50°C/30 sec, 72°C/30 sec. Five microliters of double-stranded PCR fragments were cleaned by adding 0.5 units of shrimp alkaline phosphatase and 5 units of exonuclease, then incubating at 37°C for 30 min and 80°C for 15 min. Cleaned PCR fragments were sequenced on an ABI 377 automated sequencer using BigDye (Applied Biosystems, Foster City, CA) terminator chemistry. Forward and reverse sequences were proofread in Sequencher (Gene Codes Corp., Ann Arbor, MI) and subsequently aligned by eye. Protein translations were confirmed in MacClade version 4.05 (Maddison and Maddison 2002).

Phylogenetics, Population Structuring, and Gene Flow

Due to previously reported high levels of regional genetic variation (Barber et al. 2002a) and potentially polyphyletic lineages in stomatopods (Barber and Boyce 2006), sequence data from each individual species was initially screened to confirm that all sequences from a given species formed a monophyletic lineage and could therefore be reasonably assumed to be a single taxonomic unit. First, all sequences of *H. pulchella* and *H. glyptocercus* were compared to other Indo-Pacific Protosquillidae, and all *G. viridis* samples were compared to other Gonodactylidae from Barber and Erdmann (2000) using neighbor-joining as implemented in PAUP version 4.0b10 (Swofford 2002). Representative sequences from major clades identified through neighbor-joining analyses were then compared to all Protosquillidae and Gonodactylidae taxa from Barber and Erdmann (2000) via heuristic max-

TABLE 2. Collection localities and samples sizes of *Haptoquilla pulchella*, *H. glyptocercus*, and *Gonodactylellus viridis* examined in this study. Numbers correspond to Figure 1. South, North, and Papua refer to phylogeographic regions in Southern and Northern Indonesia and Papua New Guinea as discussed in the text. Flores and Banda populations could not be a priori assigned to a geographic region and were omitted from gene flow analyses.

Locality	Region	<i>H. pulchella</i>	<i>H. glyptocercus</i>	<i>G. viridis</i>
1 Komodo	South	6	9	12
2 Lombok	South	10	10	9
3 Lovina, Bali	South	48	5	
4 Sanur, Bali	South	16	11	
5 Jepara, Java	South			13
6 Pangandaran, Java	South		11	
7 Pulau Seribu	South	14	11	21
8 Carita, Java	South	16		
9 Krakatau	South	11	11	
10 Belitung, Batu Hitam	North	10		15
11 Belitung, Tanjung Pandan	North	10		
12 Riau	North	21		
13 Postiljons	Flores		10	10
14 Tukang Besi/Wakatobi	Flores		10	
15 Spermonde, Sulawesi	North	76	11	10
16 Pare Pare, Sulawesi	North	10		5
17 Pantaloan, Sulawesi	North	10	11	10
18 Derawan, Kalimantan	North		10	12
19 Toli Toli, Sulawesi	North	13		
20 Kwandang, Sulawesi	North	10	11	
21 Pulau Tiga, Sulawesi	North	14		
22 Malalayang, Sulawesi	North	10	11	
23 Lembeh, Sulawesi	North	10		
24 Tanjung Dodepo, Sulawesi	North		10	
25 Gorontalo, Sulawesi	North		10	
26 Togians	North	21	11	12
27 Talaud	North	20	11	9
28 Davao, Philippines	North	10	10	
29 Hatta, Banda	Banda		11	11
30 Obi	Banda	9		
31 Halmahera	Papua		11	9
32 Sorong, W. Papua	Papua	9		
33 Biak, W. Papua	Papua		11	16
34 Yapen, W. Papua	Papua	10		10
35 Long Island, Papua New Guinea	Papua	10	11	10
36 Madang, Papua New Guinea	Papua	8		
Total		403	238	204

imum likelihood with model parameters determined by ModelTest 3.0 (Posada and Crandall 1998), and 100 maximum likelihood bootstrap replicates were performed to assess node support. Sequences that fell outside monophyletic species groupings were assumed to be heterospecific and were omitted from all subsequent analyses. Furthermore, because highly divergent clades could likely represent cryptic species, all separations greater than 4.8% corrected sequence divergence (based on the maximum likelihood parameters from ModelTest) were also assumed to be heterospecific and were omitted from analyses of gene flow. This value was chosen based on Knowlton and Weigt (1998) in which the lowest corrected pairwise sequence divergence for CO1 between transisthmian sister species of alpheid shrimp was 4.8%. These divergent clades are, however, included in the phylogeography figures to show the geographic positions of these potentially cryptic species. Although defining taxonomic boundaries based on sequence divergence is inherently arbitrary, in the absence of detailed morphological studies, such a strategy was required for consistency among the analyses.

For each taxon, a minimum-spanning tree based on pairwise sequence differences was created via the MINSPNET

algorithm as employed in Arlequin 2.0 (Schneider et al. 2000). All alternative connections were examined to determine whether they resulted in fundamental changes in the tree topology. Clades separated by more than 10 mutational steps were color-coded, and the frequency of these divergent clades was plotted onto geography using pie diagrams.

Patterns of genetic structuring were estimated using the AMOVA algorithm as implemented in Arlequin 2.0 (Schneider et al. 2000). Analyses were run with regional subdivisions of Papua (populations east of the Maluku Sea and north of the Banda Sea), Northern Indonesia (populations west of the Maluku Sea and north of the Java and Flores Seas) and Southern Indonesia (populations south of the Java and Flores Sea) except for *H. pulchella* where additional groupings defined by phylogeographic structure were also included. Significance levels were determined through 10,000 randomization replicates. To examine levels of gene flow among defined regions, pairwise Φ_{ST} , an analog of F_{ST} (Michalakis and Excoffier 1996), among regions were calculated in AMOVA from both pairwise and Kimura two-parameter distance. For these analyses, populations from distinct phylogeographic regions were grouped into single regional populations (e.g.,

Papua, Northern Indonesia, Southern Indonesia) to be comparable with other migration estimates (see below). To standardize regional comparisons, samples from the Tukang Besi (Wakatobi), Banda, and Postiljons were omitted from gene flow analyses because their geographic positions in the Flores or Banda Seas precluded clear a priori assignment to Papua, Northern Indonesian, or Southern Indonesian populations. Gene flow was then estimated using the formula $Nm = 0.5 \times [(1/F_{ST}) - 1]$ (Hudson et al. 1992).

Gene flow and divergence time among geographic regions across the Southern and Eastern Barriers were simultaneously examined with Mdiv (Nielsen and Wakeley 2001), a program that can account for existing polymorphism prior to vicariance through simultaneously estimating θ , Nm , and divergence time, and can give effective estimates of these parameters with single nonrecombining loci such as mtDNA. Analyses were run using a finite-sites model, a Markov chain length of 2×10^6 , burn-in time of 50,000, maximum migration rate and divergence time of 10. Scaled divergence time was converted to years following Smith and Farrell (2005) where $T_{div} = T\theta/(2\mu)$, with T and θ being estimated from Mdiv, and μ being calculated by multiplying a 1.4%/million year rate of COI divergence (Knowlton and Weigt 1998) by the length of the COI sequence data for each of the three species. Because Mdiv reports results in terms of generations, the resulting value was converted into years by assuming a minimum generation time of two years in gonodactylid stomatopods (R. Caldwell, pers. comm.). As with AMOVA, analyses were run excluding clades in excess of 4.8% divergence. Although Nm values were estimated from mtDNA and hence only represent female dispersal, sex-biased dispersal of pelagic crustacean larvae is highly unlikely, suggesting that mtDNA derived dispersal estimates are likely representative of males as well.

RESULTS

A total of 625 bp of mitochondrial cytochrome oxidase I was sequenced from 403 individuals of *H. pulchella* and 227 individuals of *H. glyptocercus*, and 491 bp of COI was sequenced from 213 individuals of *G. viridis*. All sequences aligned easily and translated into protein. A total of 14 amino acid substitutions were recorded for *H. pulchella*, three for *H. glyptocercus*, and five for *G. viridis*; the remainder of nucleotide variation was silent.

Neighbor-joining analyses of all haplotypes of *H. pulchella* and *H. glyptocercus* with seven Protosquillid taxa from Barber and Erdmann (2000) showed these two taxa to be monophyletic. This result was confirmed with maximum likelihood analyses (Fig. 2) of representative sequences from the unique clades identified in neighbor-joining analyses. However, while the *H. glyptocercus* clades received 93% bootstrap support, there was no bootstrap support for the *H. pulchella* clades with the exception of the unity of Northern Indonesia and Yapen haplotypes receiving 74% bootstrap support. In contrast, phylogenetic analysis of *G. viridis* haplotypes with 20 other gonodactylids from Barber and Erdmann (2000) indicated two small clades that fell outside of the otherwise monophyletic *G. viridis* sequences. Maximum likelihood analysis confirmed (Fig. 2) that instead these sequences close-

ly allied (88% bootstrap support) with a recently described species *G. erdmanni* (Ahyong 2001) although their specific taxonomic status is uncertain (S. Ahyong, pers. comm.). As such, these samples were omitted from analyses of genetic structure and gene flow of *G. viridis*. However, the remainder of *G. viridis* *sensu stricto* received 99% bootstrap support.

Haplotypes of *H. pulchella* formed four distinct clades: a black clade separated by a genetic break of 18 mutational steps (2.9% corrected sequence divergence) from a red clade that itself was separated by 30 mutational steps from a white clade (5.5% corrected sequence divergence), which in turn was separated by 34 mutational steps (6.6% uncorrected sequence divergence) from a blue clade (Fig. 3A). As such, the blue and white clades were omitted from AMOVA and Mdiv analyses. Haplotypes from *H. glyptocercus* also fell into multiple groups: a black clade separated by 27 mutational steps (4.7% corrected sequence divergence) from a blue clade which was separated by 50 mutational steps (11.7% corrected sequence divergence) from a group of two rare haplotypes (white and red) that were 30 mutational steps (5.3% corrected sequence divergence) different from each other (Fig. 3B). The highly divergent red and white clades were omitted from AMOVA and Mdiv analyses, but the blue clade was included despite being close to the 4.8% cutoff. This decision was made because although the red and white clades could be morphologically distinguished from the blue and black, the latter could not be distinguished even with the aid of knowing their genetic identity (S. Ahyong, pers. comm.). Haplotypes of *G. viridis* had four divisions: a black clade separated by 17 mutational steps (3.53% corrected sequence divergence) from a white clade which was 15 mutational steps (3.0%) from a light blue clade which in turn was 38 mutational steps (10.6% corrected sequence divergence) from a dark blue clade (Fig. 3C). Because of the deep divergence, the dark blue clade was omitted from AMOVA and Mdiv analyses. However, the remaining clades were included because no clear morphological differences could be found among them, even when separated genetically (S. Ahyong, pers. comm.). Although all minimum-spanning trees had alternate connections, none affected the results reported herein.

Geographic distribution of the genetic variation was highly concordant with geography. Previous results from *H. pulchella* (Barber et al. 2002a) showed that the Papua New Guinea populations had only blue clade haplotypes, Northern Indonesia populations had only black clade haplotypes and the white clade was exclusive to Southern Indonesia (Fig. 4A). However, new results obtained by including additional populations in the analysis show black clade haplotypes spanning the Eastern Barrier, extending across the Maluku Sea to western Papua (population 32, Fig. 1), whereas a fourth less divergent clade was found only in northwestern Papua on the island of Yapen. Results from *H. glyptocercus* show that blue clade haplotypes dominate in Papua and decrease dramatically in frequency west of the Eastern Barrier. Black clade haplotypes span the Southern Barrier, dominating in both Northern and Southern Indonesia, although the two rare highly divergent white and red haplotypes are only encountered in Bali (Fig. 4B). Similarly, in *G. viridis*, light blue haplotypes are only seen in Papua, black clade haplotypes dominate Northern Indonesia, and white clade haplotypes are predom-

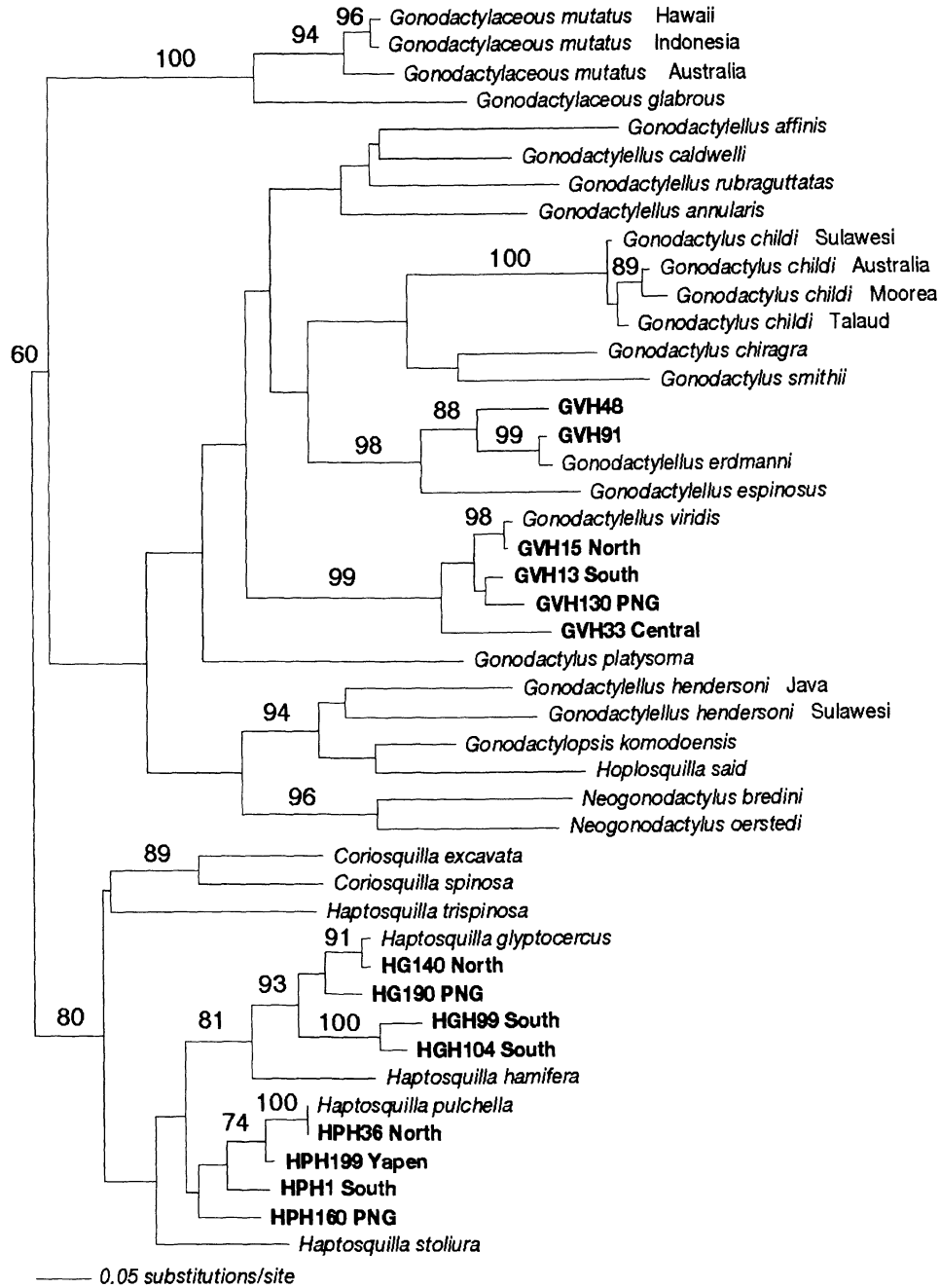


FIG. 2. Maximum likelihood tree of representative haplotypes from divergent clades of *Haptosquilla pulchella*, *H. glyptocercus*, and *Gonodactylellus viridis* (in bold) with gonodactylid and protosquillid stomatopods from Barber and Erdmann (2000). Numbers at nodes indicate support from 100 maximum likelihood bootstrap replicates.

inant in Southern Indonesia. Haplotypes from the dark blue clade were distributed sparsely throughout central Indonesia, and are subsequently referred to as the central clade (Fig. 4C).

AMOVA results calculated from pairwise distance indicated that populations of *H. pulchella* were highly structured. Excluding the highly divergent blue clade from Papua New Guinea and white clade from Southern Indonesia, $\Phi_{ST} = 0.800$ ($P < 0.00001$) and a total of 77.2% of the observed variance was the result of differences between Papua, South-

ern Indonesian, and Northern Indonesia populations. Variance among populations within groups and variance within populations accounted for 2.9% and 19.9%, respectively. Even excluding all but the black clade haplotypes, genetic structure was strong in *H. pulchella* ($\Phi_{ST} = 0.16$, $P < 0.00001$). Similarly, *H. glyptocercus* was highly structured, but less structured than *H. pulchella*, with $\Phi_{ST} = 0.527$ ($P < 0.00001$), excluding the highly divergent southern haplotypes. Again, even when only black clade haplotypes are considered, $\Phi_{ST} = 0.113$ ($P < 0.00001$) for *H. glyptocercus*.

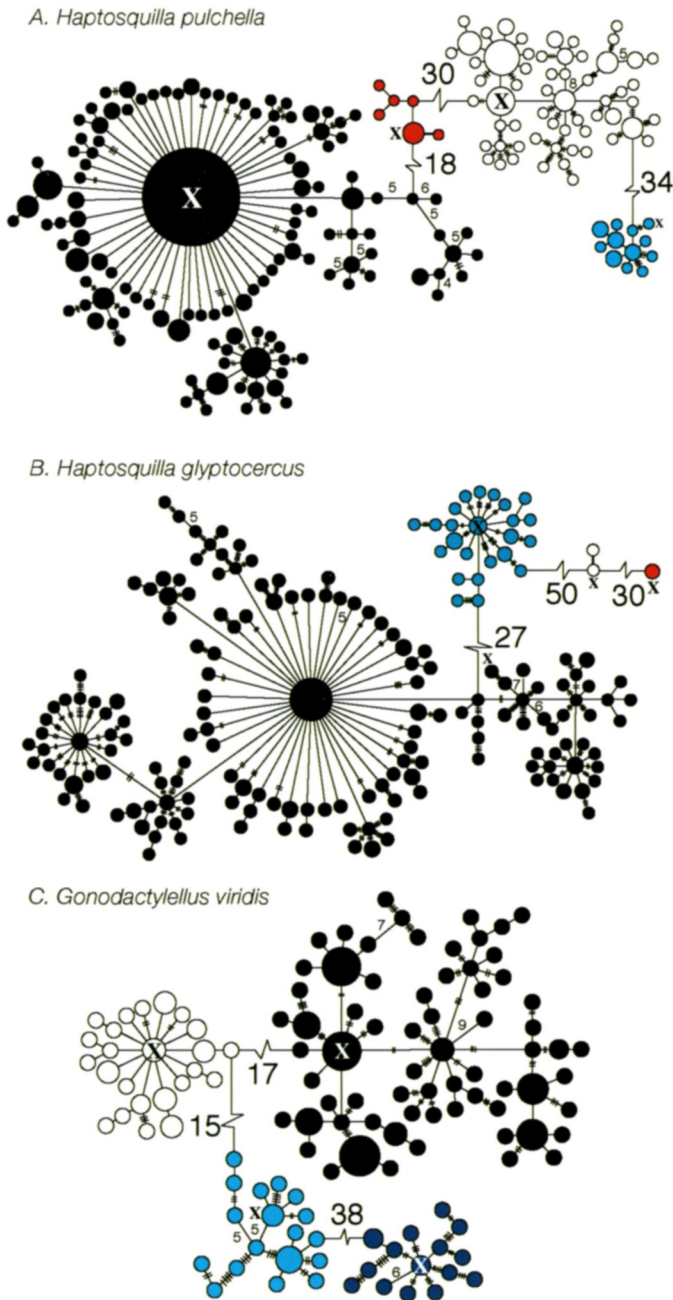


FIG. 3. Minimum spanning trees of mitochondrial cytochrome oxidase C, subunit-1 haplotypes for (A) *Haptosquilla pulchella*, (B) *H. glyptocercus*, and (C) *Gonodactylellus viridis* as produced in Arlequin (Schneider et al. 2000). Clades in excess of 10 bp different are color coded and correspond to pie diagrams in Figure 4. Exemplar haplotypes used in the phylogenetic analysis (Fig. 2) are denoted with an X.

A total of 47.9% of the variation was among regions, 4.8% among populations within regions, and 47.3% was within populations. Finally, excluding both the *G. c.f. erdmanni* haplotypes and the divergent dark blue clade, *G. viridis* populations were also highly structured with $\Phi_{ST} = 0.674$ ($P < 0.00001$). A total of 43.5% of the variation was among regions, 23.9% among populations within regions, and 32.7% within populations. Again, even when only black clade hap-

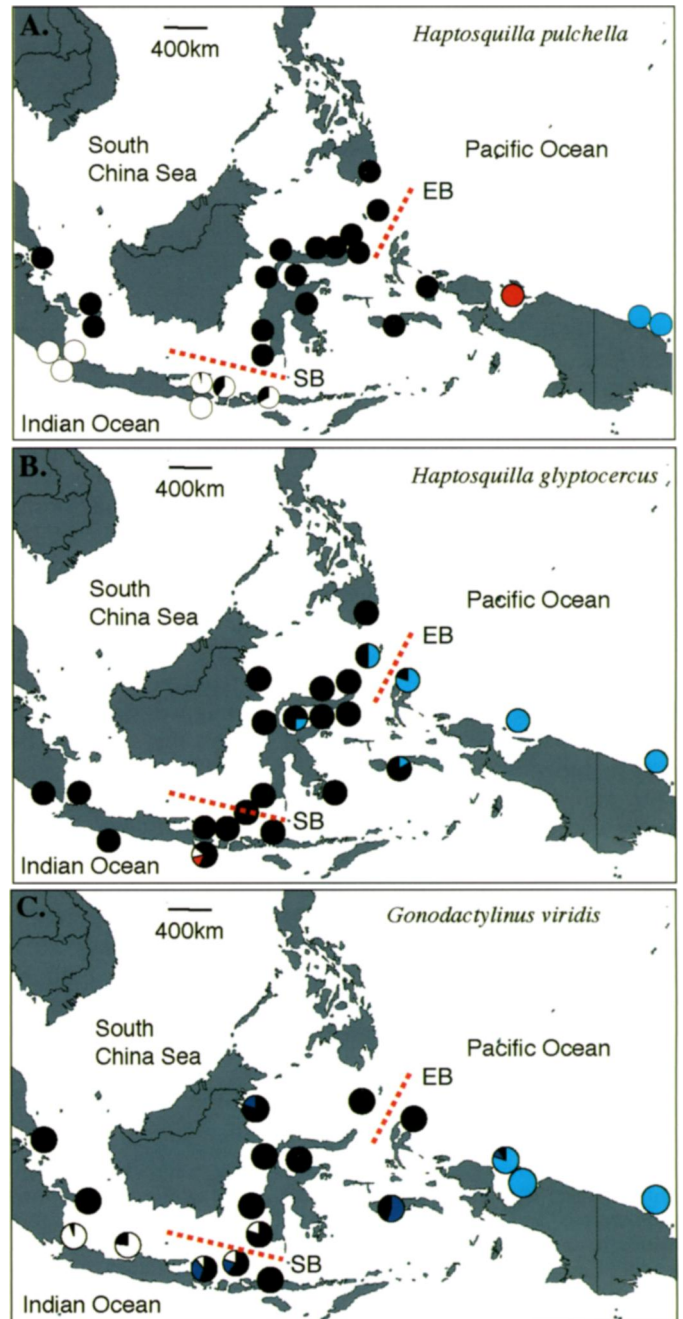


FIG. 4. Pie diagrams showing the relative frequency of highly divergent clades of mitochondrial cytochrome *c* oxidase, subunit-1 as depicted in Figure 3 for (A) *Haptosquilla pulchella*, (B) *H. glyptocercus*, and (C) *Gonodactylellus viridis*. Dashed red lines highlight the location of the hypothesized Eastern Barrier (EB) and Southern Barrier (SB) across the Maluku and Flores Seas, respectively.

lotypes are considered, significant structure is seen in *G. viridis* ($\Phi_{ST} = 0.055$, $P < 0.0009$). Equivalent results for all analyses were obtained with Kimura two-parameter distances (results not shown). Results from all species are summarized in Table 3.

Analysis of gene flow among regions (Table 4) revealed patterns of limited to rare genetic exchange between Papua

TABLE 3. AMOVA results showing degrees of freedom (df), variance components (Var.), percent variation (% Var.) and Φ -statistics for *Haptosquilla pulchella*, *H. glyptocercus*, and *Gonodactylus viridis*. Runs included all populations as described in the text. Asterisk indicates significance at the $P < 0.00001$ level.

	Among regions				Among populations within regions				Within populations			
	df	Var.	% Var.	Φ_{CT}	df	Var.	% Var.	Φ_{SC}	df	Var.	% Var.	Φ_{ST}
<i>H. pulchella</i>	2	4.8	77.2	0.772*	14	0.18	2.9	0.125*	259	1.24	19.9	0.800*
<i>H. glyptocercus</i>	2	4.3	47.9	0.479*	17	0.44	4.8	0.092*	187	4.33	47.3	0.527*
<i>G. viridis</i>	2	4.30	43.5	0.434*	13	2.36	23.9	0.423*	142	3.23	32.7	0.674*

and Northern Indonesian populations across the Eastern Barrier. Estimates of N_m from Φ_{ST} and MDiv were highly consistent with the exception of N_m values of *H. glyptocercus*. For *H. pulchella*, the presence of multiple phylogroups in Papua prevented a true Papua–Northern Indonesia comparison of gene flow. Instead, two separate comparisons were made. First, populations from Northern Indonesia and Sorong (western Papua) were compared to Yapen, the next sampled population of conspecifics to the East in Papua. The resulting Φ_{ST} between Northern Indonesia and Yapen was 0.89 ($P < 0.00001$), yielding an N_m estimate of 0.064 similar to the $N_m = 0.12$ obtained from Mdiv. To examine gene flow specifically across the Maluku Sea, a comparison between populations from Northern Indonesia and Sorong was done, yielding $\Phi_{ST} = 0.16$ ($P < 0.002$), even though this comparison only included populations containing black clade haplotypes. This comparison yielded an N_m estimate of 2.61, similar to $N_m = 3.8$ obtained from Mdiv. Populations of *H. glyptocercus* had a $\Phi_{ST} = 0.66$ ($P < 0.00001$) resulting in $N_m = 0.26$, but $N_m = 1.58$ was obtained from Mdiv. For *G. viridis*, $\Phi_{ST} = 0.73$ ($P < 0.00001$) resulting in $N_m = 0.20$, roughly similar to the $N_m = 0.68$ obtained from Mdiv. Although individual clades of haplotypes spanned the Maluku Sea in both *H. glyptocercus* and *G. viridis*, sample sizes were too limited to permit analysis of gene flow within individual clades as with *H. pulchella*.

Gene flow between Northern and Southern Indonesia

TABLE 4. Summary of gene flow (N_m) estimates across the Eastern and Southern Barriers in populations of *Haptosquilla pulchella*, *H. glyptocercus* and *Gonodactylus viridis* as calculated from Φ_{ST} values from Arlequin (ARL) and directly from Mdiv. Because *H. pulchella* had multiple phylogeographic regions in Papua, comparisons were not made between Northern Indonesia and Papua populations. Instead, two separate comparisons were made: (1) Northern Indonesia populations (including Sorong, see text) were compared to Yapen, and (2) Northern Indonesia populations were compared to Sorong. Results include estimates that include divergent clades as well as estimates derived using only haplotypes from a single (black) clade, noted by double asterisks.

	<i>H. pulchella</i>	<i>H. glyptocercus</i>	<i>G. viridis</i>
Papua vs. North, ARL	n.a.	0.26	0.20
Papua vs. North, Mdiv	n.a.	1.58	.28
North vs. Yapen, ARL	.064	n.a.	n.a.
North vs. Yapen, Mdiv	0.12	n.a.	n.a.
North vs. Sorong, ARL**	2.61	n.a.	n.a.
North vs. Sorong, Mdiv**	3.80	n.a.	n.a.
North vs. South, ARL	0.095	n.a.	0.94
North vs. South, Mdiv	0.042	n.a.	2.06
North vs. South, ARL**	4.26	3.94	7.83
North vs. South, Mdiv**	4.02	4.02	5.14

across the Flores and Java Seas across the Southern Barrier was similar in all three species (Table 4). Including only black clade haplotypes, populations of *H. pulchella* had $\Phi_{ST} = 0.105$ ($P < 0.00001$) across this span, yielding $N_m = 4.26$, comparable to the $N_m = 4.02$ obtained from Mdiv. However, these values would drop to $N_m = 0.095$ and 0.042, respectively, were the black and white clades found to be conspecific. Nearly identical results were obtained from *H. glyptocercus* with $\Phi_{ST} = 0.113$ ($P < 0.00001$) across the Flores Sea, resulting in $N_m = 3.9$, similar to $N_m = 4.02$ obtained from Mdiv. Excluding only the dark blue clade, genetic structure in *G. viridis* was $\Phi_{ST} = 0.35$ ($P < 0.00001$), yielding $N_m = 0.94$, or $N_m = 2.06$ from Mdiv. Including only the black clade haplotypes, genetic structure was still significant, with $\Phi_{ST} = 0.06$ ($P < 0.0009$), yielding $N_m = 7.83$, or $N_m = 5.14$ as obtained from Mdiv.

Relative divergence times in Mdiv were scaled assuming a rate of CO1 sequence divergence of 1.4%/million years (MY; Knowlton and Weigt 1998) and a minimum generation time of two years. For *H. pulchella*, populations from Northern Indonesia and Yapen are estimated to have diverged 2.64 million years ago (MYA), whereas divergence within the black clade between Northern Indonesia and Sorong has been more recent at 0.47 MYA (Table 5). For *H. glyptocercus* and *G. viridis*, divergence between Northern Indonesia and Papua New Guinea populations were estimated at 3.34 MYA and 2.42 MYA, respectively. Divergence times between Northern and Southern Indonesia populations were 0.37 MYA for *H. pulchella*, 0.96 MYA for *H. glyptocercus*, and 0.81 MYA for

TABLE 5. Theta and divergence time estimates between populations of *Haptosquilla pulchella*, *H. glyptocercus*, and *Gonodactylus viridis* from Northern Indonesia (North) and Papua and Northern and Southern Indonesia (South) as computed with Mdiv. Due to multiple clades of *H. pulchella* in Papua, multiple comparisons were required as described in the text. Results include estimates that include divergent clades as well as estimates derived using only haplotypes from a single (black) clade, noted by double asterisks.

	θ	Years
North-Papua		
<i>H. pulchella</i> (North-Yapen)	54.9	2.64
<i>H. pulchella</i> (North-Sorong)**	41.3	0.47
<i>H. glyptocercus</i>	54.1	3.34
<i>G. viridis</i>	24.4	2.41
North-South		
<i>H. pulchella</i>	48.0	4.8
<i>H. pulchella</i> **	39.9	0.37
<i>H. glyptocercus</i> **	59.7	0.96
<i>G. viridis</i>	18.7	0.81
<i>G. viridis</i> **	16.6	0.53

G. viridis. Even when only black clade haplotypes were examined, divergence of *G. viridis* populations across this span was similar at 0.53 MYA. θ values were similar for *H. pulchella* (39.9–54.9) and *H. glyptocercus* (54.1–59.7), but these were two to three times as large as θ values for *G. viridis* (18.6–24.4).

DISCUSSION

Regional Patterns of Isolation

Three ecologically similar mantis shrimp species show broad similarity of deep genetic structure throughout the Indonesian Archipelago. All three species include genetically distinct southern populations on the Indian Ocean side of the archipelago, distinct eastern populations along the coast of Papua and distinct central populations in between. Although Indonesia has long been described as an area of strong genetic breaks between the Pacific and Indian Oceans (Lacson and Clark 1995; Lavery et al. 1996; Duke et al. 1998; Williams and Benzie 1998; Benzie 1999; Duda and Palumbi 1999; Williams et al. 2002), our results show that these breaks are not the simple genetic clines seen across genetic breaks in other oceans (Avice 1996). Instead, the population patterns described here show a complex genetic mosaic within the complex oceanography and insular geography of the Indonesian Archipelago. Although the broad patterns among species are similar, the detailed edges of the internal genetic mosaics and the timing of population differentiation among mosaic patches vary slightly among species.

The commonalities of phylogeographic pattern and gene flow at the largest spatial scale observed in all three taxa suggests that the action of common regional scale physical process(es) have acted in their creation (Avice 2000). However, for patterns to be maximally concordant, they must also exhibit temporal concordance (Cunningham and Collins 1994). Yet each of the three species is unique in its response to the physical processes acting in this region with individualistic patterns, depths, and timing of regional genetic divergence. This result indicates that processes promoting regional genetic differentiation are strong, but that these processes may be occasionally swamped by gene flow during periods of altered dispersal. A nonexclusive alternative is that chance events or short-term environmental forcing affects some aspects of regional population-level differentiation within the Indonesian Archipelago. Such variable environmental impacts may be common in complex habitats such as Indonesia and during complex climate periods such as the Pleistocene.

Divergence across the Eastern Barrier

All three taxa show evidence of isolation in the region of the Eastern Barrier between populations on the island of Papua and the Indonesian islands west of the Maluku Sea (Fig. 3). In each case, major clades divergent by 15–38 nucleotide substitutions separate haplotypes on either side of this break, and for two of three species these divergent haplotypes form sister clades in the phylogenetic reconstruction (Fig. 2). The low estimates of gene flow and population divergence dating to the Pliocene suggests that this structure has evolved from

limited genetic exchange over an extended period of time. However, the recovery of pronounced genetic structure even within the black clade of *H. pulchella* indicates that this region continues to be a barrier to gene flow. Similar genetic discontinuities across this region are also seen in nautilus (Wray et al. 1995) as well as in human populations (Capelli et al. 2001), supporting the notion that this region is a biogeographic barrier.

The region is also host to two historically named biogeographic breaks, Weber's Line (through the Maluku Sea, see Van den Bergh et al. 2001) and Lydekker's Line (through the Halmahera Sea, see Van Oosterzee 1997). The former was defined as the middle of a zone of faunal mixing of Oriental and Australian fresh water fauna, whereas the latter marks the edge of the Sahul Continental shelf and the very far eastern reaches of Wallace's zoogeographic province. Both lines denote a strong west-east decline in terrestrial species of Oriental origin across this region, with different species showing slightly different biogeographic patterns. Likewise, although our three mantis shrimp species show genetic breaks from Papua New Guinea to the Indonesian Archipelago, the precise location of this break varies. For *H. glyptocercus*, the break occurs across the 400-km-wide Maluku Sea, whereas for *H. pulchella* and *G. viridis*, the break occurs farther to the east between Halmahera and Papua. Further evidence for isolation across the Maluku Sea comes from analysis of intraclade genetic structure in *H. pulchella*. In this species, black clade haplotypes extend across the Maluku Sea from Northern Indonesia to western Papua. However, genetic structure within the black clade between Northern Indonesia and western Papua was still pronounced ($\Phi_{ST} = 0.161$, $P < 0.005$) further indicating limited genetic exchange between these regions.

Based on Mdiv results, divergences between major clades in Northern Indonesia and Papua date to 3.34 MYA and 2.42 MYA, respectively, for *H. glyptocercus* and *G. viridis* and to 2.64 MYA for *H. pulchella*. These dates broadly mark the end of the Pliocene and a period of marked sea-level fluctuations that began 2.6 MYA (Pillans et al. 1998), a process that has long been hypothesized to have sparked marine speciation (Potts 1985). Increased upwelling during low sea-level stands (Fleminger 1986) may have acted to isolate both Indian and Pacific populations as well as populations in Indonesia and Papua that span the Eastern Barrier.

An alternative but not mutually exclusive explanation is that regional dispersal is limited by low water transport from Papua to Indonesia across the Maluku Sea even at high sea levels. The retroflexion of South Pacific waters by the Halmahera Eddy results in limited water exchange between Papua and the remainder of Indonesia. Although these are present-day surface currents, they result from processes that are highly stable. First, the proximity of Asia and Australia continents and their respective shallow continental shelves (see Fig. 1) constricts the waterways between the Pacific and Indian Oceans, a constriction that has been pronounced for at least the past 12 million years (Hall 1998). Because of this constriction, trade winds caused by convective heating in the tropics combined with the eastward rotation of the earth creates a sea surface height and pressure differential between the Pacific and Indian Ocean, driving the Indonesian

Throughflow (Wyrski 1987) and shaping the associated Western Boundary Currents (e.g., Mindanao and Halmahera Eddies). Although there is variability in the intensity of the Indonesian Throughflow (Bray et al. 1996), particularly with respect to climate events such as the El Niño/Southern Oscillation (ENSO; Meyers 1996), many of the features that drive the physical oceanography of this region have been in place and operating for millions of years. The intensity of the Throughflow and associated currents may have diminished at times, but a wholesale reversal with Indian to Pacific transport is unlikely (R. Lukas, pers. comm.). Thus, while variation is expected, the currents associated with the Indonesian Throughflow have likely been a persistent feature of this oceanographic region since the middle Miocene. Limited water and larval transport between distinct geographic regions for large parts of the past several million years may promote lineage diversification *de novo*, and/or may act to reinforce Pleistocene vicariance, and may explain the genetic structure across this region even within the black clade of *H. pulchella*.

Divergence in Southern Indonesia

Regional genetic differentiation among populations spanning the Flores Sea was also seen in all three taxa. The strongest phylogeographic pattern was observed in *H. pulchella* (see also Barber et al. 2000, 2002a), in which very limited mixing was seen between populations dominated by divergent haplotypes on the southern versus northern shores of the Flores and Java Seas. Across the same area, *G. viridis* showed a less pronounced genetic break across the Flores Sea: instead, differentiation occurred along the southern shores of the Java Sea, particularly along the islands of Java and Belitung off the coast of Sumatra (Fig. 4). Just as in *H. pulchella*, a dramatic genetic shift occurs along a 200-km stretch of coast between these two islands. These deep phylogeographic breaks vary greatly in age, with divergence across the Flores Sea dating to 4.8 MYA in *H. pulchella* and only 0.81 MYA in *G. viridis*. Thus, they either originated from different processes separated by millions of years, or, perhaps more likely, by a physical process that has been present for an extended period of time.

The least genetic structure was observed in *H. glyptocercus*, in which a shift between major haplotypes did not occur. However, genetic structuring among closely related haplotypes between Northern and Southern Indonesian populations was observed ($\Phi_{ST} = 0.112$, $P < 0.00001$) with levels of gene flow much less than would be expected of a taxon with a four- to six-week pelagic larval dispersal phase in an environment where strong currents should facilitate dispersal. Similar conclusions are drawn from *H. pulchella* and *G. viridis*, in which comparable levels of genetic structure were seen across the Flores Sea, even when clades of deeply divergent haplotypes were excluded from the analysis. In all three species, divergence within individual clades spanning the Flores Sea dates to the mid- to late Pleistocene (0.37–0.96 MYA, Table 5). Given at least 10,000 years of modern oceanographic conditions since the end of the last glacial maxima, strong gene flow across the Flores Sea would be expected to erase any incomplete genetic boundaries sepa-

rating populations north and south of the Flores Sea, yet significant levels of genetic structure remain. The combination of deeply divergent phylogeographic lineages of highly varied temporal origins with continued evidence of limited genetic exchange across the Flores Sea suggests that isolation most likely results from a process with a prolonged effect. However, unlike divergence across the Maluku Sea, there is no obvious physical process to explain divergence across this span.

Strong genetic differentiation across the Flores Sea shows that individual ecological requirements of these three species do not strictly control dispersal. The tendency of *H. pulchella* to settle only on reefs in proximity to freshwater influx could prevent the use of small oceanic islands in the Flores Sea as stepping-stones, whereas the other two species are free of this constraint. However, the small degree of leakage of *H. pulchella* black clade haplotypes across the Maluku Sea combined with gene flow estimates that are similar in all three species across this span indicates that dispersal can occur in the absence of stepping-stones. This result suggests that stepping-stone islands do not strongly influence migration across the Flores Sea in these stomatopods.

Genetic Endemism and the Metapopulations of Indonesia

The islands of the IAA have complex geologic origins with a mixture of continental shelf and deepwater ocean origins. Habitat differences among islands could conceivably account for some of the phylogenetic breaks observed here. For example, Springer (1982) noted a distinct shift in shallow-water fish fauna on islands of adjacent tectonic plates. For cowries, an association between larval dispersal duration and ocean habitat type experienced by the larvae contributes to patterns of diversification (Meyer 2003). Genetic differences across the Halmahera Sea correspond geographically to the edge of the Sahul Shelf. However, habitat-based explanations are unlikely because we see similar genetic breaks in species with specialist and generalist habitat requirements. *Haptosquilla pulchella* is stenotopic in its habitat requirements, preferring only shallow reef flats in close proximity to freshwater sources. In over 13 years of collecting these animals throughout the Indo-Pacific, we have found *H. pulchella* only in these areas. In contrast, *G. viridis* is extremely tolerant of habitat quality. Even within a single observed phylogeographic region (e.g., black clade), this taxon can be found in oceanic reefs and coastal/continental reefs, as well as in pristine reefs and highly eutrophied reefs that are nearly dead (Erdmann 1997; P. H. Barber and M. V. Erdmann, pers. obs.). *Haptosquilla glyptocercus* is found across similarly divergent habitat types, although it is less tolerant of eutrophication than *G. viridis*. Thus, because habitat variation within phylogeographic regions exceeds that among regions, habitat variation is an unlikely explanation for the generation of phylogeographic structure.

In addition, the phylogeographic structure does not correspond in a simple way to the geologic origin of the islands they inhabit. For example, genetic homogeneity is observed along the shores of Sulawesi (Barber et al. 2002a), an island with multiple geologic origins (Hall 1998). In contrast, the islands of Sumatra and Java have similar geologic origins,

yet there are major genetic breaks at their juncture in two of three species. Explanations for sharp genetic breaks in taxa with high potential dispersal remain obscure (Barber et al. 2000; Taylor and Hellberg 2003). However, the interaction of extrinsic habitat variation and intrinsic forces such as swimming (Katz et al. 1994; Yoshimura et al. 1999), vertical migrations (Cronin and Forward 1986; Tankersley and Forward 1994; Forward et al. 1997), or resident adults interfering with larval recruitment (Woodin 1976; Morgan 1995) cannot be completely discounted.

The mosaic nature of genetic structure in Indonesian stomatopods is also seen in the geographic distribution of genetic endemics. Distinct mtDNA haplotypes or clades often occur in just one or two collection localities. Sometimes these haplotypes are just a few base pairs different from haplotypes elsewhere, for example in the Togian Islands (location 26, Fig. 1) in Sulawesi (see Barber et al. 2002b). Similarly, a distinct group of haplotypes in *H. pulchella* was found only at Yapen in West Papua (location 34, Fig. 1; red haplotypes in Figs. 3 and 4). In contrast, a highly divergent clade of *G. viridis* haplotypes was found in only a few disjunct locations but over a wide geographic area. Individuals with blue clade haplotypes were found near Bali and over 1000 km away on Banda and Kalimantan (locations 3, 13, 18, and 30, Fig. 1; dark blue haplotype in Figs. 3 and 4), yet no representatives of this clade were found in the numerous intervening populations.

Private haplotypes are common in populations that disperse poorly. In marine species, however, such haplotypes tend to be young ones because, in general, older haplotypes have had the opportunity for long-distance dispersal and tend to be widespread (Palumbi 1997). The occurrence of old private haplotypes in Indonesian stomatopods suggests a long history of restricted gene flow, or a metapopulation structure in which occasional long-distance gene flow and habitat colonization is followed by local population retention and periodic extinction.

In some cases, metapopulation models can also help explain the high F_{ST} values seen here and in other high dispersal marine species (for review see Hellberg et al. 2002). When colonization of a new habitat occurs from a small subsample of adjacent habitats, then extinction and recolonization events increase F_{ST} dramatically (the propagule-pool model of Slatkin 1977). In contrast, if recolonization derives from immigrants from the whole metapopulation (the migrant-pool model), extinction and recolonization decreases F_{ST} (Slatkin 1977; Wakeley 2000). For stomatopods, genetic data from recolonization of the reefs of Krakatau show that adjacent populations may have contributed more heavily to the colonists (Barber et al. 2002a), supporting the propagule-pool model for these species.

The impact of metapopulation dynamics on marine genetic diversity is only likely to be seen in cases where extinction rate per population per generation is greater than the migration rate per population per generation (for discussion see Pannell 2003). Shallow-water reef populations, especially near rivers, may have a high rate of local extinction from typhoons and extended periods of either low salinity due to torrential rains or extreme temperatures from ENSO events. If so, we might predict lower F_{ST} values among ecologically

similar deepwater stomatopods with lower exposure to local extinction.

Ideally, we would be able to estimate extinction and migration parameters from the kinds of population genetic data presented here. However, simulations show that single-locus genealogical data have low power to detect the dynamics of metapopulation processes (Pannell 2003), and such calculations require more extensive multilocus genealogical data.

Taxonomy and Speciation

Levels of genetic diversity were extremely high in all three taxa, with genetic divergences among clades similar to those seen in species of alpheid shrimp (Knowlton and Weigt 1998). Although phylogenetic analysis indicated that some of these lineages were clearly polyphyletic (e.g., *G. viridis* clades allied with *G. erdmanni*), other divergent clades within monophyletic taxa might be cryptic species based on depth of genetic divergence. The taxonomic status of these groups, however, can only be substantiated with thorough, detailed morphological study and/or genetic analysis of nuclear genes. Whether these clades are eventually determined to be morphologically distinct species or simply highly divergent conspecific lineages, the results of this study indicate that present levels of biodiversity in the IAA—the center of all marine biodiversity (Myers et al. 2000; Hughes et al. 2002; Roberts et al. 2002)—may be significantly underestimated (Knowlton 1993). Similar conclusions are drawn from Paulay and Meyer (2002), Meyer (2003), Williams and Reid (2004), Kirkendale and Meyer (2004), and Meyer et al. (2005), each of which show deep regional divergences within individual taxa of a variety of marine invertebrates throughout the Indo-Pacific, and from Barber and Boyce (2006) who discovered multiple new stomatopod taxa through DNA bar coding of stomatopod larvae.

More importantly, rather than merely indicating multiple cryptic lineages within these three taxa, the results suggest a mechanism for the creation of biodiversity in the IAA. All three taxa demonstrate varied degrees of genetic isolation across the Eastern and Southern Barriers. In both regions this isolation ranges from statistically detectable limits to gene flow within individual clades to nearly reciprocal monophyletic phylogeographic regions to putative cryptic species. Thus, these patterns suggest a progression of regional genetic diversification, indicating that these barriers to gene flow may both contribute to the creation of distinct phylogeographic lineages as well as ultimately drive cladogenesis and the creation of species diversity, providing a mechanism to support the center of origin hypothesis.

Particularly instructive is the case of *H. pulchella*, in which there is evidence of limited gene flow on multiple levels. Within populations with black clade haplotypes, there is moderately strong isolation ($\Phi_{ST} = 0.161$, $P < 0.005$) between Northern Indonesia and Sorong across the Eastern Barrier. Then there is increased isolation between Northern Indonesia/Sorong (black clade haplotypes) and Yapen (red clade haplotypes), the next sampled population about 400 km to the east. Although there may be an as yet unidentified process creating this phylogeographic break along the shores of Western Papua, a likely explanation is that this break arose because

of isolation across the Eastern Barrier and that there has been a subsequent breach of this barrier by populations containing black clade haplotypes leading to the present unity of Western Papua and Northern Indonesia. This may have occurred from rare dispersal across the Eastern Barrier or via stepping-stones across the islands south of the Maluku Sea, as suggested by black clade haplotypes on the island of Obi (Fig. 4A; population 30 in Table 2). On a deeper time scale, such a process may have also given rise to the blue clade of *H. pulchella* in eastern Papua, resulting in a type of founder speciation seen in peripheral habitats of the Indo-West Pacific (Meyer et al. 2005).

Similar patterns are seen in populations of all three taxa that span the Flores Sea. In each species, limited gene flow within individual clades parallels deeper phylogeographic breaks that may represent cryptic lineages. Particularly interesting is the contrast between *H. pulchella* and *G. viridis*. Including the deeply divergent black and white clades, results for *H. pulchella* indicate that these lineages have been diverging for nearly five million years. When the white clade is excluded, the history of limited genetic exchange is much more recent (0.37 MYA), a result that closely mirrors divergence of *H. pulchella* populations that span the Maluku Sea. In contrast, populations of *G. viridis* have a history of divergence across the Flores Sea that dates to 0.81 MYA when both black and white clades are included and 0.53 MYA when the divergent white clade is removed. These results highlight the temporal variability in lineage divergence as well as show that lineage divergence across the same geographic area can occur in relatively rapid succession. Similarly, they argue against discrete individual events as their cause.

Combined, these results suggest a gradual diversification due to limited gene flow in two regions of Indonesia, and support the notion of lineage diversification within Indonesia as predicted by the center of origin hypothesis (Briggs 2000). Although a center of origin is likely not the only explanation for high marine biodiversity in the IAA (Barber and Bellwood 2005; Meyer et al. 2005), the patterns seen in stomatopods appear to support lineage diversification within the Coral Triangle. By understanding the processes that create biodiversity, we can then improve our ability to conserve this biodiversity through appropriately directed conservation efforts (Moritz 1999; Moritz 2002).

Consequences for Conservation

The connectivity of marine populations is a critical gap in present scientific knowledge needed for large-scale marine conservation planning (Palumbi 2004; Sale et al. 2005). Many tropical marine conservation efforts are presently focused on the development of networks of marine protected areas (MPAs) that are connected through demographic exchange of adults or larvae (e.g., Roberts et al. 2003), implying that a thorough understanding of patterns of genetic and demographic connectivity among distant populations is a priority.

However, equally important to understanding connectivity is identifying regions where connectivity is lacking, as well as understanding the processes that limit that connectivity. The data in this study suggest that limited gene flow across

the Maluku and Flores/Java Seas leads to the creation of pronounced phylogeographic structure, and possibly cryptic speciation. This limited gene flow likely results from limited dispersal and connectivity among these geographic regions through interactions of individual larvae with their physical environment. Thus, our results suggest the importance of regional filters to dispersal and gene flow within the IAA, data that has been used to support current seascape-level initiatives by defining boundaries of regionally distinct biogeographic regions in which to create regional networks of genetically and ecologically connected MPAs that will both conserve the rich marine biodiversity of the Indo-West Pacific (e.g., Green and Mous 2004; MPA News 2004). Furthermore, the long-term maintenance of biodiversity requires the conservation of processes that create this biodiversity (Briggs 2005). Allopatric divergence across the Maluku and Flores Seas may be one important process generating biodiversity in the Coral Triangle.

It is not yet clear whether the Eastern and Southern Barriers in the regions of the Maluku and Flores Seas represent dispersal barriers only to stomatopods, or whether these are broadly acting barriers that may be shaping patterns of intraspecific genetic diversity across a wide range of taxa. Determination of the overall importance and general applicability of these barriers will require comparisons across a wide range of codistributed invertebrate and vertebrate taxa, and should be considered a top priority in the developing marine conservation strategies for the region.

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