



Mosaics in the mangroves: allopatric diversification of tree-climbing mudwhelks (Gastropoda: Potamididae: *Cerithidea*) in the Indo-West Pacific

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The Indo-Australian Archipelago (IAA) is the richest area of biodiversity in the marine realm, yet the processes that generate and maintain this diversity are poorly understood and have hardly been studied in the mangrove biotope. *Cerithidea* is a genus of marine and brackish-water snails restricted to mangrove habitats in the Indo-West Pacific, and its species are believed to have a short pelagic larval life. Using molecular and morphological techniques, we demonstrate the existence of 15 species, reconstruct their phylogeny and plot their geographical ranges. Sister species show a pattern of narrowly allopatric ranges across the IAA, with overlap only between clades that show evidence of ecological differentiation. These allopatric mosaic distributions suggest that speciation may have been driven by isolation during low sea-level stands, during episodes preceding the Plio-Pleistocene glaciations. The Makassar Strait forms a biogeographical barrier hindering eastward dispersal, corresponding to part of Wallace's Line in the terrestrial realm. Areas of maximum diversity of mangrove plants and their associated molluscs do not coincide closely. © 2013 The Natural History Museum. *Biological Journal of the Linnean Society* © 2013 The Linnean Society of London, 2013, 110, 564–580.

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INTRODUCTION

The archipelago at the centre of the greatest marine biogeographical province, the Indo-West Pacific (IWP), is known by various names, including the Indo-Australian Archipelago (IAA), the Indo-Malayan region and the Coral Triangle, and is renowned as the site of the highest biodiversity in the marine realm (Carpenter & Springer, 2005; Hoeksema, 2007). The major component of this diversity is the biota of coral reefs, characterized in large part by species with very wide distributional ranges on the scale of ocean

basins, whereas narrow-range endemics are found mainly on the most remote, peripheral archipelagos (Hughes, Bellwood & Connolly, 2002; Paulay & Meyer, 2002). For the well-studied corals and reef fish, these wide ranges have been described as a 'stack of pancakes' that overlap to generate a 'single massive global marine hotspot' within the IAA (Bellwood, Renema & Rosen, 2012: 216, 221). The location of the hotspot is correlated most strongly with reef area, yet a mid-domain effect (the central overlap of a random distribution of ranges within the bounded domain of the two ocean basins) is also significant (Bellwood *et al.*, 2005). It has also been discovered that the location of the hotspot has shifted eastwards across the globe, from the western Tethys

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(i.e. western Europe) in the Eocene to its present position, according to the shifting arrangement of continents and their shallow seas (Renema *et al.*, 2008).

Marine species have not simply migrated from historic hotspots to populate the IAA, because many appear to have arisen since the IAA hotspot was established in the Miocene (Renema *et al.*, 2008; Williams & Duda, 2008). To understand the generation of the IAA hotspot, it is therefore necessary to infer the historical processes of origination, accumulation and extinction of species that have operated within the IWP. Diverse evolutionary hypotheses have been proposed, broadly summarized as: centre of origin (speciation within the IAA and dispersal to the periphery of the IWP); centre of overlap (vicariant speciation between Indian and Pacific Ocean basins and subsequent overlap across the boundary); centre of accumulation (peripheral origination of species and dispersal to the IAA); and centre of survival (the IAA acts as a refuge) (see reviews by Hoeksema, 2007; Bellwood *et al.*, 2012; Gaither & Rocha, 2013). These hypotheses are not mutually exclusive in either operation or definition, but each makes different predictions about the location and age of speciation events and of endemics (and whether these represent young species or old relicts; Bellwood & Meyer, 2009). In addition, their relative importance may have shifted over time (Cowman & Bellwood, 2013).

These hypotheses mostly make the implicit assumption that large, broadly overlapping ranges are the norm and (as speciation almost always involves geographical isolation) all require post-speciation dispersal to achieve this overlap. Some genetic studies are consistent with this assumption of large distributions maintained by long-distance dispersal and high gene flow (Paulay & Meyer, 2002; Lessios, Kane & Robertson, 2003; Crandall *et al.*, 2008; Horne *et al.*, 2008). Nevertheless, as molecular investigations reveal more and more cases of cryptic species (Knowlton, 2000), it is clear that the 'stack of pancakes' model is not appropriate for all groups. At least among gastropod molluscs, there is a rough correlation between reproductive mode (i.e. length of pelagic larval life and inferred dispersal potential) and range size, which determines the geographical scale of speciation (Paulay & Meyer, 2002, 2006; Kohn, 2012). Species with long-lived larvae, wide dispersal and high gene flow speciate at the scale of ocean basins, displaying endemics on the most isolated archipelagos at the periphery of their wide ranges (Frey, 2010). If dispersal is limited by a shorter pelagic period, speciation occurs on a finer scale within basins (Williams & Reid, 2004; Meyer, Geller & Paulay, 2005), or even between islands of an archipelago in the extreme case of nonplanktotrophic

development (Cunha *et al.*, 2008). There are many exceptions, sometimes explicable by poor taxonomy, habitat specificity or remote endemics (Paulay & Meyer, 2006; Claremont *et al.*, 2011). Nevertheless, among gastropods with low or moderate potential for larval dispersal, a frequent pattern is of a mosaic of narrowly allopatric distributions of sister species and closely related taxa.

Mosaic distributions are of special importance for inferences about the location and mechanism of speciation. Unlike the ambiguous cases of isolated endemics, narrowly allopatric ranges imply speciation rather than reliction, especially if located at recognized biogeographical boundaries. They also suggest that the geography of the original speciation event has been maintained, without being obscured by subsequent dispersal (unless change has been reciprocal; Malay & Paulay, 2010). These distributions may be maintained by a strong physical or ecological barrier, by competitive exclusion (Quenouille *et al.*, 2011) or (if reproductive isolation is not complete) by interbreeding and the loss of introgressed genes (Meyer *et al.*, 2005), and can persist for millions of years (e.g. 10–30 Myr; Williams & Reid, 2004; Meyer *et al.*, 2005). These mosaics do not contribute to alpha diversity, and have therefore been considered of little relevance in the generation of the IAA hotspot (Bellwood *et al.*, 2012). They do, however, increase gamma (regional) diversity (many descriptions of the general diversity pattern have not distinguished between the two; Hoeksema, 2007) and provide evidence to test general hypotheses of the geography of speciation.

Coral reefs have been a worthy focus for research in this field. Mangrove forests are another iconic tropical marine biotope, dominating about one-quarter of tropical coastlines (Spalding, Blasco & Field, 1997), but are now under global threat from deforestation (Valiela, Bowen & York, 2001). In contrast with reefs, however, mangroves are of low diversity. The mangrove plants consist of only about 70 species worldwide, belonging to 21 families of trees, shrubs and ferns (Ellison, Farnsworth & Merkt, 1999; Ricklefs, Schwarzbach & Renner, 2006). Many have large distributions, spanning the continental shores of Asia, Australia and high islands of the western Pacific (Spalding *et al.*, 1997). These distributions overlap to produce the highest species diversity within the IAA, in an area encompassing Malaysia, Borneo, Indonesia, New Guinea and northern Australia (Groombridge & Jenkins, 2002). As in marine animals, ecological and historical explanations have been advanced for this pattern (Duke *et al.*, 1998; Ellison *et al.*, 1999; Plaziat *et al.*, 2001; Ellison, 2002; Ricklefs *et al.*, 2006). However, studies of individual mangrove genera have not revealed clear geographical signals of speciation events within the IWP,

probably because of their wide dispersal by floating propagules (Duke *et al.*, 1998; Duke, Lo & Sun, 2002). In addition, mangrove forests have suffered extreme disruption during the glacial cycles of the Plio-Pleistocene, when sea levels fluctuated by up to 120 m (Voris, 2000; Miller *et al.*, 2005; Fig. 2E). In Sundaland, for example, mangrove forests were severely reduced and limited to the edge of the continental shelf during low sea-level stands (Woodroffe & Grindrod, 1991), only to expand and relocate to the inner margins of the South China Sea in a few thousand years as sea levels rose (Cannon, 2012; Morley, 2012).

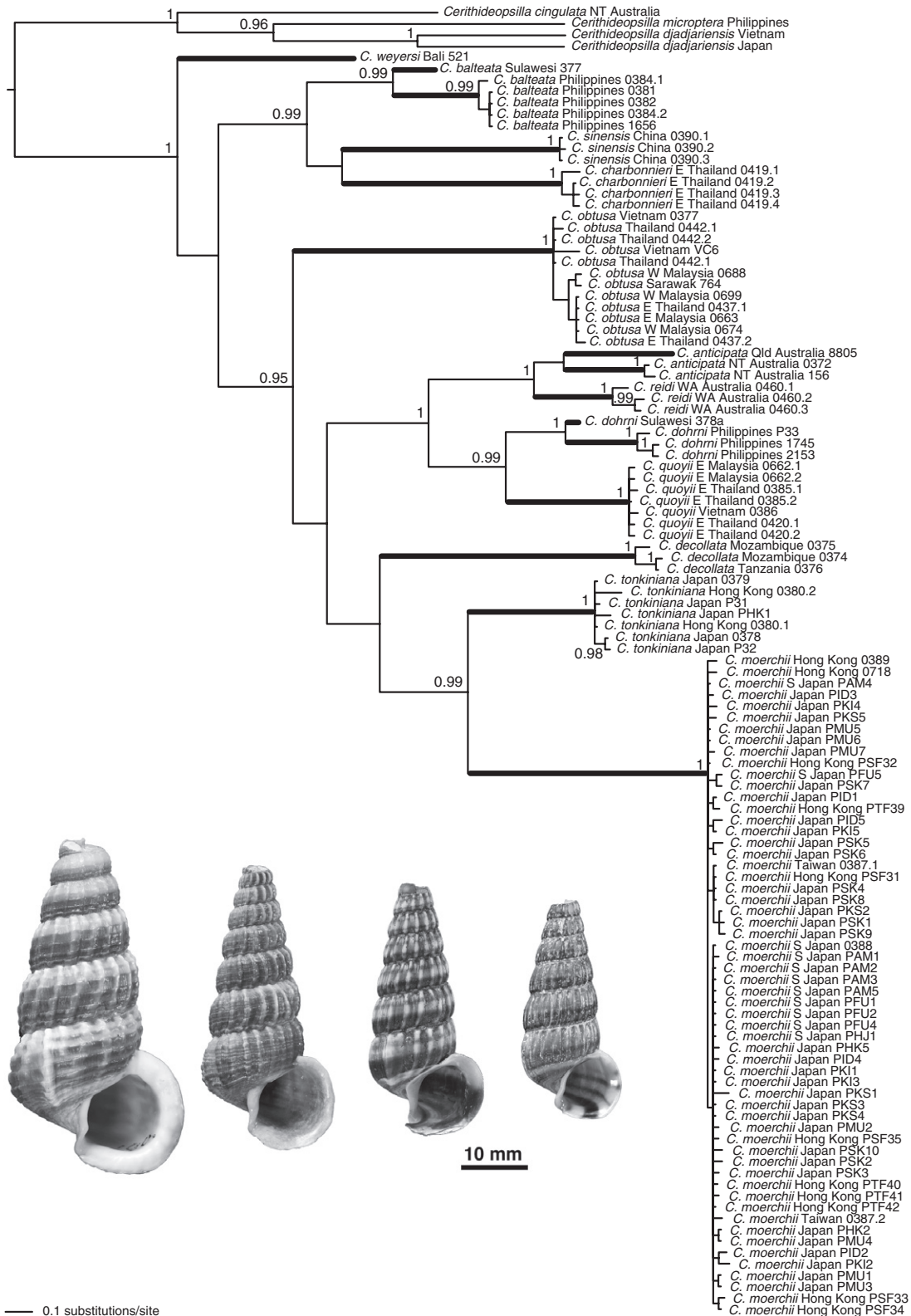
The fauna of mangrove forests is also of relatively low diversity, their distinctive assemblages of macroinvertebrates being dominated by three families of gastropods (Littorinidae, Potamididae and Ellobiidae) and several of crabs (Jones, 1984; Plaziat, 1984; Glaubrecht, 1997). In broad terms, the diversity of the mangrove fauna follows the familiar pattern and is highest in South-East Asia and at the centre of the IWP (Vermeij, 1973; Ellison *et al.*, 1999), but there has been very little of the detailed phylogenetic, biogeographical and evolutionary research needed to increase the poor understanding of diversification in this biotope. So far, the necessary combination of accurate taxonomy, distributional data, near-complete sampling and molecular phylogeny is available only for *Littoraria* (Littorinidae), of which the 39 living species mostly live solely on mangrove trees (Reid, 1986, 2001; Reid, Dyal & Williams, 2010). Many of the *Littoraria* species of IWP mangroves show wide distributions, some extending from East Africa to the western Pacific, consistent with their inferred pelagic larval life of up to 10 weeks. There is only limited geographical signal in the form of allopatric, parapatric or narrowly overlapping sister species, which suggests speciation in peripheral areas of mangrove distribution, such as the Bay of Bengal, Australia and the north-western Pacific. Within South-East Asia there are no such examples. Instead, the distributions overlap broadly in the 'stack of pancakes' manner to produce a peak of diversity in the South China Sea and Malay Peninsula (Reid, 1986). This poor geographical signal has been explained by probable high dispersal (not only as larvae, but also through possible rafting on plant debris) and by the

disruption of mangrove distributions during Plio-Pleistocene glacial cycles (Reid *et al.*, 2010).

To search for speciation patterns on a smaller geographical scale within the mangroves of South-East Asia and the IAA, it is necessary to choose a strictly mangrove-associated, monophyletic group that can be comprehensively sampled and which, crucially, has restricted dispersal. The potamidid genus *Cerithidea* fulfils these criteria. Of the three major families of mangrove gastropods, the Potamididae are the most intimately connected with the habitat. The majority of potamidids depend on trees for substrate, shelter or food, and the fossil record shows that the family first radiated in the Tethys Sea during the middle Eocene, shortly after the appearance of the modern mangrove biotope in the same region (Glaubrecht, 1996, 1997; Ellison *et al.*, 1999; Kowalke, 2003; Reid *et al.*, 2008). A recent review of the family estimated a worldwide total of 29 living morphospecies, classified into six monophyletic genera (Reid *et al.*, 2008). Of these, *Cerithidea* is restricted to the tropical and subtropical IWP. These snails live attached to the roots and trunks of mangrove trees, or occasionally among other halophytes, and at low tide migrate down to the substrate to feed on algae or detritus (Ohtaki, Maki & Tomiyama, 2002; Vannini *et al.*, 2006). This tree-climbing behaviour is believed to be connected with both escape from predatory fish and crabs, and avoidance of physiological stress (McGuinness, 1994; Vannini *et al.*, 2006). The larval development of *Cerithidea* species has not been clearly described, but the pelagic phase is believed to be moderately short (12–20 days; Kojima *et al.*, 2006) or even absent (Houbrick, 1984). About ten species have been distinguished by their shells (e.g. Brandt, 1974; Houbrick, 1986; Brown, 1994; Hasegawa, 2000; Ma, 2004; Fig. 1), but previous morphological identifications are unreliable (Reid *et al.*, 2008), their distributions are largely unknown and taxonomic revision is required. The phylogeography of three species has been studied, two in Japan (Kojima *et al.*, 2006; Kamimura *et al.*, 2010; these studies included other potamidids now assigned to different genera) and one in East Africa (Madeira *et al.*, 2012).

Here, our aims are: (1) to determine the number of valid species of *Cerithidea* by sampling as widely as possible across the IWP and using a combination of

Figure 1. Molecular phylogeny of *Cerithidea* species produced by MrBayes analysis of cytochrome oxidase I (COI) sequences, using *Cerithideopsisilla* species as outgroup. Localities are abbreviated and followed by the last four digits of the registration or reference number (for full details, see Table S1). Support values are MrBayes posterior probabilities; only values > 0.95 (strong support) are shown. Significant clusters determined by the GMYC function in the SPLITS package (Ezard *et al.*, 2009) are indicated by thickened stems. Representative shells (from left): *Cerithidea obtusa*, *C. antcipata*, *C. balteata* and *C. weyersi*.



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Figure 2. A–D, Distribution maps and phylogenetic relationships of *Cerithidea* species. Filled circles indicate sequenced samples (Table S1); thick open circles are verified museum records; thin open circles are reliable literature records (Quoy & Gaimard, 1834; Morlet, 1889; Brandt, 1974; Houbriek, 1986; Subba Rao, 2003; Lee & Chao, 2004; Ma, 2004; Thach, 2005, 2007; Hong *et al.*, 2010). Phylogenetic relationships supported by molecular analyses (Figs 1, S1, S2) are shown as full lines; relationships inferred from the subjective assessment of shell resemblance are shown as broken lines. The distribution of *C. decollata* in East Africa (Kenya to South Africa and Madagascar) is not shown. Approximate ages of divergence are indicated (see text); 95% highest posterior density intervals are: *C. tonkiniana/maerchii* 2.5–10.0 Ma; *C. quoyii/dohrni* 1.9–8.5 Ma; *C. reidi/anticipata* 1.4–7.0 Ma (D. G. Reid & M. Claremont, unpubl. data). E, Palaeo-coastline (120 m below present sea level; Voris, 2000) and main present-day sea surface currents (Wyrtki, 1961; Gordon & Fine, 1996; Loder, Boicourt & Simpson, 1998; Shetye & Gouveia, 1998). Seasonally reversing currents are shown as broken lines. EAC, East Australian Current; ECC, Equatorial Counter Current; IT, Indonesian Throughflow; KC, Kuroshio Current; LC, Leeuwin Current; MC, Mindanao Current; NEC, North Equatorial Current; NECC, North Equatorial Counter Current; NGCC, New Guinea Coastal Current; SEC, South Equatorial Current. F, Distribution of mangrove forests (after Giri *et al.*, 2011); this small-scale map greatly exaggerates the actual area of mangrove forests, but shows the major gaps in coastal mangroves and their latitudinal limits. Wallace's Line is shown as a full red line and its modification by Huxley as a broken red line (Hall, 2012).

phylogenetic, statistical and morphological evidence; (2) to use one nuclear and two mitochondrial genes to reconstruct their phylogenetic relationships; and (3) to plot their geographical distributions. The combination of phylogeny with distributions will be used to assess whether the diversity pattern of *Cerithidea* corresponds to the 'stack of pancakes' model (i.e. wide, overlapping ranges, as suggested by the glacial disruption of their mangrove habitat and potential for dispersal by rafting) or the mosaic model (i.e. narrowly allopatric ranges of sister species, as suggested by their short planktonic larval duration). The results will add to the limited knowledge of the diversification processes of the mangrove fauna and to the growing understanding of the accumulation of species within the IAA hotspot.

MATERIAL AND METHODS

TAXONOMY, DISTRIBUTIONS AND SAMPLING OF TAXA

The definition of the genus *Cerithidea* follows Reid *et al.* (2008; cf. broader concept of Houbriek, 1984). No comprehensive taxonomic study of *Cerithidea* species has been performed for more than a century, and so identifications were based on original research in a concurrent taxonomic and morphological study (D. G. Reid, unpubl. data). Illustrations of some species can be found in works by Brandt (1974), Houbriek (1986), Brown (1994), Hasegawa (2000), Ma (2004) and Lozouet & Plaziat (2008), but some of the names used are incorrect or invalid (in parentheses): *C. balteata* and *C. tonkiniana* (both as *C. 'ornata'*); *C. quoyii* and *C. dohrni* (both as *C. 'quadrata'*); *C. maerchii* (*C. 'rhizophorarum'*) (see Supporting Information Table S1 for taxonomic authorities).

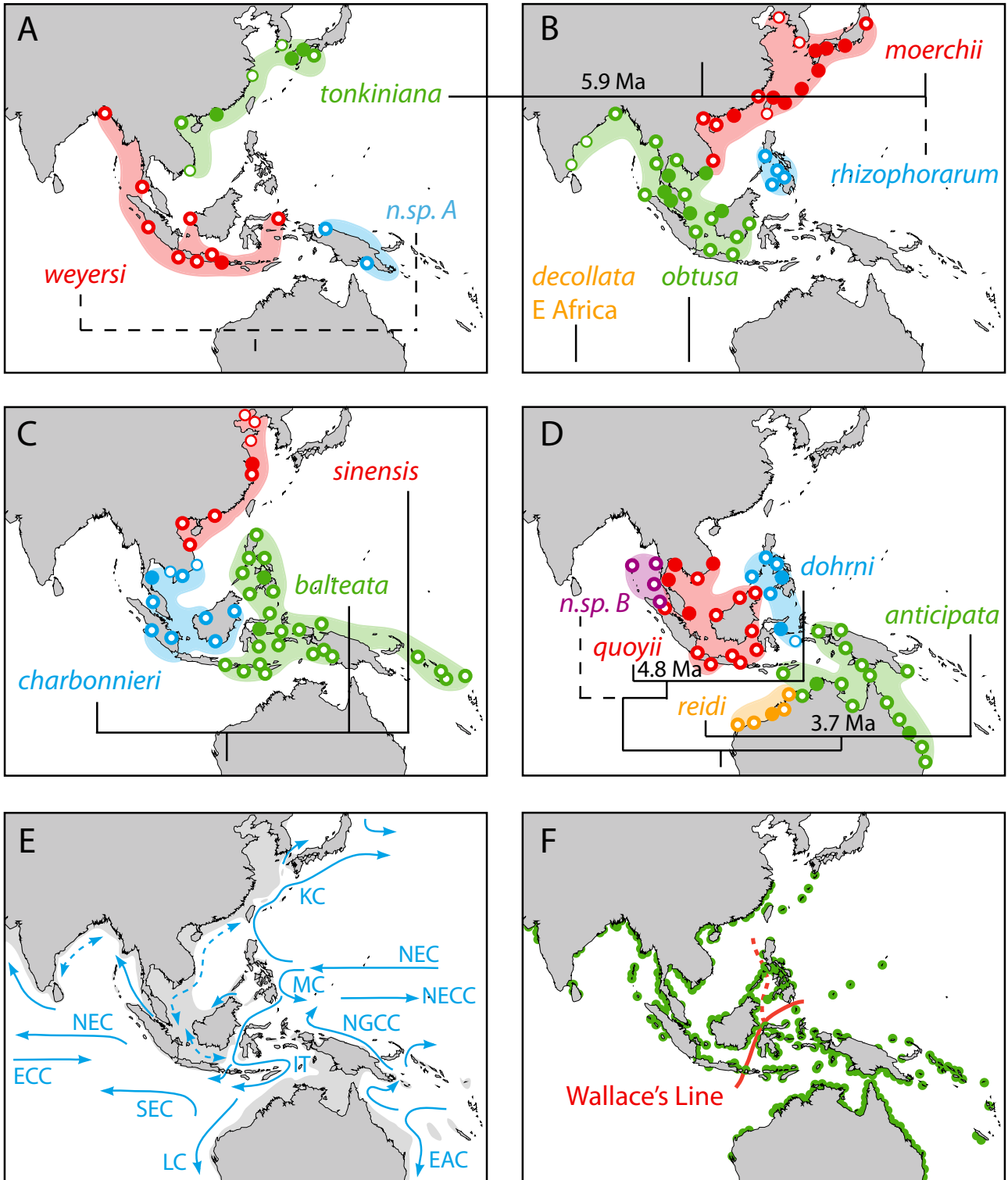
During the taxonomic study, 13 named and two undescribed species were distinguished. The ingroup

for the molecular phylogenetic analysis comprised 12 of these species, a total of 111 individuals (Table S1). Most species were represented by 3–12 individuals, with the exception of *C. weyersi* (one individual) and *C. maerchii* (58 individuals). The four outgroup taxa were three species of *Cerithideopsis*, identified as the sister genus of the monophyletic *Cerithidea* in a molecular phylogeny of the Potamididae (Reid *et al.*, 2008). Voucher material has been deposited in museum collections (Table S1).

Distribution maps were compiled from material in major museum collections (Natural History Museum, London; Australian Museum, Sydney; Muséum National d'Histoire Naturelle, Paris; Netherlands Centre for Biodiversity Naturalis, Leiden; Museum für Naturkunde, Berlin; National Museum of Natural History, Smithsonian Institution, Washington DC) and reliable literature records (see legend of Fig. 2).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

DNA was extracted from mantle or foot tissue of ethanol-preserved material using a cetyltrimethylammonium bromide (CTAB) extraction method (Reid, Dyal & Williams, 2012), because polymerase chain reaction (PCR) inhibitors co-purify with DNA using the Qiagen QIAmp kits suitable for other molluscan groups. Portions of three genes were amplified and sequenced: the nuclear 28S rRNA and the mitochondrial cytochrome oxidase I (COI) and 16S rRNA genes. COI was sequenced for all samples, and 16S and 28S for a reduced subset (21 and 42 samples, respectively, including all outgroup taxa). PCRs were used to amplify approximately 1474 bp of 28S rRNA and 658 bp of COI (protocol of Reid *et al.*, 2008) and



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515 bp of 16S rRNA (protocol of Williams & Ozawa, 2006). All sequences have been deposited in GenBank (accession numbers listed in Table S1). Of the 179 sequences available for analysis, 38 have already been published (Reid *et al.*, 2008).

SEQUENCE ANALYSIS AND PHYLOGENY RECONSTRUCTION

Sequences for ribosomal genes (28S and 16S) were aligned using the G-INS-i method of MAFFT (Multiple Alignment using Fast Fourier Transform, v6.847b; Katoh & Toh, 2008), because sequences were not expected to be highly divergent. Long gaps in the alignment were also not expected, and so the offset value was set to 0.1. The resulting alignments were adjusted by eye in MacClade (v4.06 OSX; Maddison & Maddison, 2003). Gblocks (v0.91beta; Castresana, 2000) was then used to remove poorly aligned sites (minimum number of sequences for a conserved position, 70%; minimum number of sequences for a flanking position, 90%; maximum number of contiguous nonconserved positions, 3; minimum length of a block, 5; all gap positions allowed). COI sequences were aligned by eye in MacClade. For each gene partition, 24 different models of nucleotide substitution were tested with MrModelTest (v2.2; Nylander, 2004). Two concatenated alignments were constructed, consisting of two genes (28S and COI) and three genes (28S, 16S and COI), each including only those specimens for which all the respective genes were available. Before combining gene partitions, posterior probabilities (PPs) of all clades were compared among individual-gene Bayesian trees. Conflict among strongly supported clades (PP > 95%) is evidence of genetic incongruence that suggests divergent phylogenetic histories of loci, whereas conflict among weakly supported clades (PP < 95%) may be caused by stochastic error (Wiens, 1998; Williams & Reid, 2004). Lack of resolution does not indicate conflict.

All alignments were analysed using Bayesian inference and the Markov chain Monte Carlo (MCMC) method (MrBayes v3.1; Huelsenbeck & Ronquist, 2001). Model parameters for each gene were set according to the model selected by MrModelTest and were free to vary among gene partitions. The MCMC analysis was run twice for each alignment; convergence between runs was tested by examining traces in Tracer (v1.5; Drummond & Rambaut, 2007) and the potential scale reduction factor (PSRF). The number of generations per analysis varied on the basis of the preliminary convergence results: 5 million generations for 16S, 10 million for 28S, 10 million for COI + 28S and 15 million for COI + 28S + 16S. Based on the traces in Tracer, a 10% 'burnin' was used for all

analyses, except COI (20%). Branches in consensus trees with PP < 50% were collapsed.

MOLECULAR SPECIES DELIMITATION

A statistical method was used to define species-level clusters in the molecular tree. BEAST (v1.6.1; Drummond & Rambaut, 2007) was used to generate an ultrametric tree from the COI sequences, for use in a species-delimitation analysis. Site models were again set on the basis of the models chosen by MrModelTest. In this analysis, only relative clade ages were of interest, and so a relaxed-clock model (uncorrelated log-normal; Drummond *et al.*, 2006) was used, without time calibration. The starting tree was random and the coalescent tree prior was set to a constant population size. Priors were adjusted on the basis of preliminary analyses in order to improve the effective sample size (ESS) values. Two analyses of 50 million generations were sampled every 5000 generations to generate 10 000 trees each. The length of the 'burnin' (10%) was determined by the examination of traces in Tracer. Tree files were combined with LogCombiner (v1.6.1, part of the BEAST package; Drummond & Rambaut, 2007). The final tree was calculated with maximum clade credibility and median node heights using TreeAnnotator (v1.6.1, part of the BEAST package). In order to find significant clusters within the BEAST tree, the GMYC function from the SPLITS package (Ezard, Fujisawa & Barraclough, 2009) in R (R Development Core Team, 2009) was applied. This function optimizes the likelihood of genetic clusters, where branching rates between species follow a Yule model, but branching rates within species follow a neutral coalescent model (Pons *et al.*, 2006; Fontaneto *et al.*, 2007). This method has been shown to help identify phylogenetic species and cryptic taxa in other gastropods (Claremont *et al.*, 2011). As further evidence for species delimitation, the uncorrected pairwise distances over all pairs of COI sequences were estimated among and within clusters using MEGA5 (Tamura *et al.*, 2007) and the nuclear 28S gene was examined for fixed differences.

TIMING OF DIVERSIFICATION

The timing of diversification was not estimated in this study, because reliable fossils of *Cerithidea* are extremely scarce. However, the molecular data have been incorporated into a larger BEAST analysis of the entire Potamididae (D. G. Reid & M. Claremont, unpubl. data), calibrated using the ages of a range of potamidid fossils. One fossil *Cerithidea* was included: the oldest certain member of the genus *C. tokunariensis* from the early middle Miocene

(Masuda, 1956) with an age range of 14–23 million years ago (Ma). On the basis of shell morphology, this species was placed in the clade of *C. quoyii*, *C. dohrni*, *C. anticipata* and *C. reidi* (D. G. Reid, unpubl. data). Preliminary results are used in the discussion below.

RESULTS

GENE SEQUENCES

The COI dataset consisted of 115, the 16S dataset of 22 and the 28S dataset of 43 sequences (Table S1). *Cerithidea weyersi* was represented by a single COI sequence; *C. charbonnieri*, *C. balteata* and *C. sinensis* were represented by COI and 28S sequences; other species were represented by samples sequenced for all three genes. After the removal of primer sequences and ambiguous regions, the 28S alignment (initially 1474 bp) was 1445 bp (98%) and the 16S alignment (initially 515 bp) was 502 bp (97%). The COI alignment was 658 bp. In the alignments, 84 bp of 28S, 75 bp of 16S and 233 bp of COI were informative; the remaining bases were either constant or parsimony uninformative. The model chosen by MrModelTest was GTR + I + G for each gene. Inspection of the individual gene trees did not reveal any well-supported clades in conflict (Fig. 1, Supporting Information Figs S1, S2).

PHYLOGENY

PSRF values for the MrBayes analyses were less than 1.01 and ESS values were greater than 350, indicating that all trees had reached stationarity. The ingroup of *Cerithidea* species was monophyletic in all MrBayes analyses (Figs 1, S1, S2). Within *Cerithidea*, four clades were recognized. (1) The ‘*C. quoyii* group’ (*C. quoyii*, *C. dohrni*, *C. anticipata* and *C. reidi*) was supported in the COI, 16S, COI + 28S and all-gene analyses. On the basis of shell resemblance (D. G. Reid, unpubl. data), an unsampled fifth species (*C. n. sp. B*) was added as the likely sister of *C. quoyii* and *C. dohrni*. (2) The ‘*C. balteata* group’ (*C. balteata*, *C. charbonnieri* and *C. sinensis*) was supported in the COI, 28S and COI + 28S analyses. (3) The ‘*C. rhizophorarum* group’ (*C. moerchii* and *C. tonkiniana*) was supported in the COI, 28S, COI + 28S and all-gene analyses. On the basis of shell resemblance (D. G. Reid, unpubl. data), the unsampled *C. rhizophorarum* was added as the likely sister of *C. moerchii*. (4) The ‘*C. weyersi* group’ was represented by a single COI sequence from *C. weyersi* and its relationship with other clades was unresolved. An additional species, *C. n. sp. A*, was recognized as its probable sister on the basis of shell resemblance (D. G. Reid, unpubl. data). The relationships of *C. decollata* and *C. obtusa* were unresolved.

SPECIES DELIMITATION AND DISTRIBUTION

Almost all the named species (recognized from shell morphology) for which sequences were available were monophyletic, with significant support, in the MrBayes COI analysis (Fig. 1). The only exception was *C. anticipata*, the two lineages of which formed a clade with *C. reidi*. The ESS values of the BEAST analysis were all greater than 1000. The GMYC analysis recovered a further three significant entities, 15 in total [Fig. 1; maximum likelihood (ML) clusters = 11; ML entities = 15; likelihood of null model = 851.0301; likelihood of GMYC model = 865.3725; $P < 0.0001$]. Variation in 28S sequences was limited and sample sizes were small, so that few fixed differences were detected. Within the *C. quoyii* group, there were no fixed differences, but there were 25 differences between *C. charbonnieri* and *C. sinensis*. For the named taxa, uncorrected pairwise distances between species were all greater than 0.076 (the distance between *C. anticipata* and *C. reidi*), whereas distances within species were less than 0.012, except for the three species *C. balteata* (0.018), *C. dohrni* (0.025) and *C. anticipata* (0.072). The GMYC analysis recovered two entities within each of these three named species. The support for the species status of the evolutionarily significant units (ESUs *sensu* Moritz, 1994) of *Cerithidea* is summarized in Table 1. The distributions of the recognized species are plotted in Figure 2 (except for *C. decollata*, from South Africa to Kenya and Madagascar).

DISCUSSION

DELIMITATION AND TAXONOMY OF *CERITHIDEA* SPECIES

Although many recent textbooks and regional taxonomic guides have illustrated shells of *Cerithidea* species (see Material and Methods above), the only monographic accounts date from the 19th century (Sowerby, 1866; Tryon, 1887; Kobelt, 1888–1898). Since then, only a single critical taxonomic study has appeared, describing one new Australian species (Houbrick, 1986). These taxonomic accounts have so far been based only on shell characters, but these, if uncritically applied, can be a poor guide to identification. Thus, a recent phylogeographical study of *C. moerchii* showed that two morphologically distinct geographical ‘subspecies’ were conspecific (Kojima *et al.*, 2006, as ‘*C. rhizophorarum*’), whereas a phylogenetic analysis of the Potamididae showed that the morphospecies ‘*C. ornata*’ was composed of two phylogenetic species (Reid *et al.*, 2008). Taxonomic revision is clearly required.

Noninterbreeding biological species can be inferred if sister clades remain morphologically and

Table 1. Summary of support for species status of evolutionarily significant units (ESUs) of *Cerithidea*. Each named species is supported by diagnostic characters of shell morphology (D. G. Reid, unpubl. data) and all named species (for which sequences are available) are monophyletic in the cytochrome oxidase I (COI) MrBayes analysis (except for *C. anticipata*). Species ordered as in Figure 1. N, no diagnostic morphology; na, only one sequence available; Y, significant support (DNA) or diagnostic morphology (shell); query, no significant support (but not contradicted); dash, no data

ESU	GMYC analysis	COI monophyly	16S monophyly	28S monophyly	Shell morphology
<i>C. weyersi</i>	Y	na	–	–	Y
<i>C. n. sp. A</i>	–	–	–	–	Y
<i>C. balteata</i>	Y	na	–	–	N
Sulawesi 377					
<i>C. balteata</i> other	Y	Y	–	Y	N
<i>C. sinensis</i>	Y	Y	–	Y	Y
<i>C. charbonnieri</i>	Y	Y	–	?	Y
<i>C. obtusa</i>	Y	Y	Y	?	Y
<i>C. anticipata</i>	Y	na	na	na	N
Qld Australia 8805					
<i>C. anticipata</i> other	Y	?	na	?	N
<i>C. reidi</i>	Y	Y	na	?	Y
<i>C. dohrni</i>	Y	na	na	?	–
Sulawesi 378a					
<i>C. dohrni</i> other	Y	Y	na	?	N
<i>C. quoyii</i>	Y	Y	?	?	Y
<i>C. n. sp. B</i>	–	–	–	–	Y
<i>C. decollata</i>	Y	Y	Y	?	Y
<i>C. tonkiniana</i>	Y	Y	Y	?	Y
<i>C. moerchii</i>	Y	Y	?	?	Y
<i>C. rhizophorarum</i>	–	–	–	–	Y

genetically distinct where their ranges overlap, but this criterion cannot be applied in *Cerithidea*, where all potential sister species are allopatric (note that *C. tonkiniana* and *C. moerchii*, although partially sympatric sisters in Figure 1, would probably not be so if sampling of species was complete, because the unsampled *C. rhizophorarum* is the predicted sister of *C. moerchii*; Fig. 2B). Therefore, our operational criteria for the recognition of species (Table 1) include reciprocal monophyly of at least two independent loci (e.g. nuclear as well as mitochondrial genes), statistical analysis of lineage branching (BEAST/GMYC analysis), genetic distance (greater than the minimum between other recognized sister-species pairs) and diagnostic morphological characters (Knowlton, 2000; Avise, 2004; Coyne & Orr, 2004; Fujita *et al.*, 2012; Puillandre *et al.*, 2012). This integrative approach has been successfully applied in similar studies of other gastropods (Claremont *et al.*, 2011). The 28S nuclear gene in fact has low resolving power at the level of sister species, supporting the monophyly of only two morphospecies (Fig. S1), with few fixed differences. However, we assume that diagnostic morphological (shell) characters have a genetic basis. These will

be reported elsewhere (D. G. Reid, unpubl. data), showing that each named species is morphologically distinct. Sampling and resolution were highest for the COI mitochondrial gene (Fig. 1), which supported the monophyly of all named species except *C. anticipata*, which was unresolved. In addition, pairwise genetic distances were greater between than within all named species, although distances were high within *C. anticipata*, *C. dohrni* and *C. balteata*. The BEAST/GMYC analysis supported most of these named species as significant entities, but recognized two entities within each of *C. anticipata*, *C. dohrni* and *C. balteata* (Fig. 1). Sampling is inadequate to resolve the status of these controversial cases and further study is necessary. For the present, we refer to them as species with strong genetic structure. In freshwater members of the same superfamily, Cerithioidea, many studies have detected complex patterns of nonmonophyly and taxonomic incongruence in phylogenies constructed from mitochondrial genes, with various explanations, including introgressive hybridization, incomplete lineage sorting and complex patterns of vicariance and dispersal between river drainage systems (Miura *et al.*, 2013,

and references cited therein). Such patterns were not detected in the present study, possibly as a result of limited intraspecific sampling.

Intraspecific sampling was thorough only in *C. moerchii*, and supports the finding of Kojima *et al.* (2006; as '*C. rhizophorarum*') that the distinctive shell form found in the Ryukyu Islands is conspecific with populations from the mainland of Japan. (Confusingly, all previous authors have used the name *C. rhizophorarum* for the mainland form, whereas this is correctly applied to a species, not sampled here, that is endemic to the Philippines; D. G. Reid, unpubl. data). The geographical range of available molecular samples was limited in most species, and so distributions are based on the morphological identification of museum material. The validity of this approach is supported by the degree of congruence between the genetic and morphological delimitation of species, but remains to be thoroughly tested by more intensive sampling. In particular, the range of *C. balteata* is especially wide and, from available samples, disjunct; the few shells that have been seen from the eastern part (Solomon Islands) are at the extreme of the morphological range and may prove to be a distinct species. During the concurrent taxonomic study (D. G. Reid, unpubl. data), three additional morphospecies were discovered (*C. n. sp. A*, *C. n. sp. B*, *C. rhizophorarum*), for which no genetic samples were available; these are included in Figure 2 for the sake of completeness, with an indication of their predicted phylogenetic relationships based on shell resemblance.

DISTRIBUTION AND DISPERSAL OF *CERITHIDEA* SPECIES

The distributions of *Cerithidea* species lie strictly within the range of mangroves in most cases, extending beyond these limits only in the north-western Pacific (Fig. 2), where three species can also be found in salt marshes, reed beds and even on firm mud (Ohtaki *et al.*, 2002; Wada & Nishikawa, 2005; Hong, Choi & Tsutsumi, 2010). Their recorded habitats are summarized in Supporting Information Table S2. Details are not known for all species, but there appears to be a division between those that are typical of fully marine habitats (*C. decollata*, *C. obtusa* and members of the *C. quoyii* group) and the rest, which inhabit estuarine sites and only the landward fringes of mangrove forests. At least two species (*C. weyersi* and *C. n. sp. A*) are recorded from almost freshwater habitats alone. There is therefore a phylogenetic pattern, for the members of each of the four main clades share a similar range of habitats.

The mode of larval development and the possibility of pelagic dispersal are not well known in

Cerithidea species. Habe (1955) reported that eggs of *C. moerchii* (as '*C. rhizophorarum*') were 0.35 mm in diameter. In a member of another potamidid genus, *Cerithideopsis scalariformis*, eggs of 0.28 mm in diameter hatch into larvae that metamorphose almost immediately, with no planktonic stage, and therefore Houbriek (1984) predicted a similar development for *C. moerchii*. *Cerithideopsis pliculosa* hatches with a larval shell of 0.3 mm in diameter and its swimming-crawling, planktotrophic larvae metamorphose after 6–13 days (Miura, Frankel & Torchin, 2011). Kimura *et al.* (2002) reported planktonic larvae in *C. moerchii* (as '*C. rhizophorarum*') and Kojima *et al.* (2006) claimed 12–20 days for a range of potamidids (including *C. moerchii*, but with no details) in Japan. It is a reasonable inference that planktonic life in *Cerithidea* species is short to moderate. Consistent with the rough correspondence between larval life and range size in gastropods (Paulay & Meyer, 2002, 2006), ranges of *Cerithidea* species are at a similar scale to those of other groups with short to moderate lengths of pelagic development (e.g. a few days in *Astrarium*, Meyer *et al.*, 2005; 24 days in *Echinolittorina*, Williams & Reid, 2004; 4 days in *Lunella*, Williams *et al.*, 2011). In contrast with *Littoraria*, another genus of mangrove-associated snails, but with a pelagic life of up to 10 weeks (Reid *et al.*, 2010), there are no species that range widely across the entire IAA. Other means of dispersal could include migratory birds in marshes and mudflats (Miura *et al.*, 2012) and perhaps rafting on mangrove vegetation.

Three *Cerithidea* species (*C. obtusa*, *C. quoyii* and *C. charbonnieri*) are distributed all around the present coastlines of the Sunda Shelf (Fig. 2). This, in itself, indicates powers of dispersal in these three species from marine and estuarine mangroves, for the shelf was exposed as dry land during the low sea-level intervals of the Plio-Pleistocene glaciations, most recently 17 000 years ago (Voris, 2000). The distribution of *C. weyersi* is in marked contrast, found mainly on coastlines at the western and southern margins of the Sunda Shelf (only two records from the Sunda Shelf: Madura Island and south-east Borneo) and Halmahera in the Molucca Sea. With the exception of a record from Bangladesh, these are coasts of steep topography, where little migration would have been necessary with changes in sea level. This contrast has been pointed out in relation to the mangrove and rainforest trees of Sundaland, in which areas of stability can act as refugia for species with limited dispersal ability (Cannon, 2012). It is unknown whether *C. weyersi* is similarly restricted, for example by short (or absent) pelagic larval development. Its near-freshwater habitat could also limit its potential for dispersal.

One other distribution deserves comment: *C. balteata* (if indeed it is a single species, see above) stands out as the only member of the genus with a wide range on numerous high islands from the Philippines, across eastern Indonesia to western New Guinea and the Solomon Islands (Fig. 2C). Most other species show a pronounced restriction to presently (or historically) contiguous coastlines, with only a few cases of distributions that require dispersal across significant open-water gaps (see *C. weyersi*, *C. dohrni*, *C. quoyii* and *C. n. sp. B* for the few exceptions; Fig. 2). This range of *C. balteata* could perhaps indicate a longer pelagic phase for dispersal but, if so, its absence from southern New Guinea and Australia is unexpected. Being largely restricted to high-island archipelagos, *C. balteata* recalls some *Echinolittorina* species, which appear to be restricted to ‘oceanic’ coastlines of relatively low primary productivity (Reid *et al.*, 2006).

SPECIATION AND ALLOPATRY IN THE CENTRAL IWP

All the sister-species pairs of *Cerithidea*, and the one unresolved trichotomy of species, show allopatric distributions (Fig. 2). [This statement requires some qualification: it assumes that the unsampled *C. rhizophorarum* is correctly placed as sister to *C. moerchii*; Houbrick (1986) reported that the ranges of *C. reidi* and *C. anticipata* overlap slightly in north-western Australia, but examination of the specimens cited by him has not confirmed this; *C. quoyii* and *C. n. sp. B* are present in a single sample from north-eastern Sumatra, but shell morphology suggests that these two are not sister species; D. G. Reid, unpubl. data.] This strong geographical signal is consistent with the orthodox view that the prevailing mode of speciation is allopatric (Coyne & Orr, 2004), even in the sea (Quenouille *et al.*, 2011; but see Bowen *et al.*, 2013), as has repeatedly been shown in other genera of tropical marine gastropods (Williams & Reid, 2004; Meyer *et al.*, 2005; Frey, 2010; Claremont *et al.*, 2011; Williams *et al.*, 2011; but see Krug, 2011). More significant is the finding that sister species show narrowly allopatric ranges, implying that the geography of the speciation events has been preserved (or that any change in distribution of sisters has been reciprocal) (Malay & Paulay, 2010) and that concerns about post-speciation dispersal acting to obscure the geographical signal are not justified in this case (Losos & Glor, 2003; Quenouille *et al.*, 2011). In *Cerithidea*, the available estimates of the ages of sister species are 3.7 Ma (1.4–7.0 Ma) and 4.8 Ma (1.9–8.5 Ma) (for *C. anticipata/reidi* and *C. quoyii/dohrni*, respectively, with 95% highest posterior density intervals; D. G. Reid & M. Claremont, unpubl. data), yet dispersal can be rapid, for three species

have recolonized the new coastline of Sundaland in the past 17 000 years. It seems unlikely that geographical barriers to dispersal are sufficiently strong to maintain allopatry over millions of years, and so competitive exclusion may be operating (Quenouille *et al.*, 2011). The *Cerithidea* species that do occur sympatrically show differences in zonation within the mangrove forest (in relation to tidal level and salinity range) and contrasting shell thickness (correlated with tree-climbing behaviour and predation risk in mangrove snails, Reid, 1992; Table S2), which could indicate competitive effects. Alternatively, if reproductive isolation between incipient species is not complete, limited interbreeding and loss of introgressed genes could reinforce the allopatric pattern (Meyer *et al.*, 2005).

Despite the labile distributions of some species across the periodically emergent continental shelves, it can be assumed that the allopatry of sister species of *Cerithidea* broadly reflects the geography of speciation events. If so, speciation in this genus has evidently occurred at various locations across the IWP, but most frequently within the IAA, consistent with ‘centre of origin’ models (Bellwood *et al.*, 2012). There are no cases of narrow-range peripheral endemics, as frequently seen in taxa with larger ranges and long-lived pelagic larvae (Paulay & Meyer, 2002, 2006). The IAA has been considered to be a ‘species pump’ driven by sea-level changes of up to 120 m during the Plio-Pleistocene, but many species are now known to be considerably older than this (Williams & Duda, 2008; Bellwood *et al.*, 2012), and the signature of Plio-Pleistocene events is apparent mainly in the genetic structure within species (Carpenter *et al.*, 2011). Nevertheless, sea-level changes of 30–60 m have occurred since the Oligocene, with increasing frequency in the late Miocene (Miller *et al.*, 2005; Morley, 2012), so that patterns of speciation predicted by this eustatic model may predate the major glaciations of the past 2.5 Myr. One predicted outcome of repeated isolation during glacial intervals is speciation centred in isolated refugia in the Andaman Sea, the South China Sea and the Sulu Sea (Fig. 2E), with recolonization of the Sunda Shelf proceeding each time from the north-east and the south-east as sea levels rose (see maps of Voris, 2000). This is close to the observed pattern in *C. n. sp. B*, *C. quoyii* and *C. dohrni*, respectively (Fig. 2D), where the estimated age of the first pair is 4.8 Ma (1.9–8.5 Ma). Similarly, the differentiation of marine species on the east and west coasts of tropical Australia has been linked with the periodic emergence of the Sahul Shelf, although (as in the case of *C. anticipata* and *C. reidi*) the modern boundary or overlap between eastern and western sister taxa is commonly much further to the west than the shal-

lowest part of the shelf at the Torres Strait. This discrepancy has been explained in terms of prevailing westward dispersal through the Arafura Sea (Reid *et al.*, 2006, 2010).

Another striking feature of the distributions of *Cerithidea* species is a boundary at, or close to, the Makassar Strait. This separates *C. charbonnieri* and *C. balteata* (two members of an unresolved trichotomy; Fig. 2C), *C. dohrni* and *C. quoyii* (possible sister species, but note the single record of *C. quoyii* from the eastern side of the strait; Fig. 2D) and forms the eastern boundary of the range of *C. obtusa* (Fig. 2B). This is part of the famous Wallace's Line at the eastern edge of the Sunda Shelf (Fig. 2F), a marine passage that has been in place since the Eocene, providing a partial barrier to the dispersal of terrestrial organisms between South-East Asia and Australasia (Hall, 2012). Quite why the Makassar Strait represents a strong barrier to a marine group, even one with apparently limited larval dispersal such as *Cerithidea*, is unclear. The Indonesian Throughflow (Fig. 2E) may contribute to this effect and the current is stronger during low sea levels when the strait is narrowed (Hall, 2012). Nevertheless, the presence of *C. balteata*, *C. anticipata* and *C. reidi* in Australasia indicates that this barrier has been breached at least twice in the past, following the collision between the Eurasian and Indian–Australian lithospheric plates at the beginning of the Miocene, when the deep-water channel was closed between the Bird's Head of western new Guinea and Sulawesi (Hall, 2012). There is little evidence that the Makassar Strait acts as a barrier in other marine taxa (although the term 'marine Wallace's Line' has been used in a different context, to describe a phylogeographical break across the Java Sea; Barber *et al.*, 2000). In another mangrove-associated gastropod genus, *Littoraria*, six species span the Makassar Strait, whereas five do not, being restricted to areas of Sundaland to the west of the strait (Reid, 1986, 2001; Reid *et al.*, 2010). The strait has been claimed as the location of a phylogeographical break in one coastal marine fish (Lourie & Vincent, 2004; Lourie, Green & Vincent, 2005) and even in a pelagic one (Rohfritsch & Borsa, 2005), but in neither case have populations been compared on each shore in order to equate the break with the strait itself. In rock-dwelling, intertidal *Echinolittorina* species, there is also a potent barrier (separating sister species and delimiting ranges of species) in eastern Indonesia, but this lies in the Banda Sea to the east of Sulawesi and has been explained in terms of the 'oceanic' habitat of the Banda Sea and 'continental' Sunda and Sahul Shelves (Reid *et al.*, 2006). Extinction may also have shaped the ranges of molluscs in shallow waters of high productivity in South-East Asia during the late

Miocene and early Pliocene (Ozawa *et al.*, 2009). Clearly, these historical and ecological barriers crossing eastern Indonesia within the IAA require more detailed study.

There are two other repeated patterns of distribution in this genus. Three *Cerithidea* species are endemic to the north-western Pacific, from Vietnam to China, sometimes including Japan and the Ryukyu Islands (Fig. 2A–C). This is repeated in some other gastropods, although without precise correspondence of their southern range boundaries (Reid, 1986, 2007; Williams *et al.*, 2011). Restriction by latitude and temperature regime is a common feature of marine distributions outside the tropics (Williams, 2007; Frey & Vermeij, 2008; Malay & Paulay, 2010), and may have been promoted by episodes of isolation in warm refugia during periods of climatic cooling. Two *Cerithidea* species are endemic to the Philippines, in one case extending south to the Molucca Sea (Fig. 2B,D). Diversification within the Philippine archipelago has been linked to isolation of its marine basins during low sea-level stands (Carpenter & Springer, 2005), but phylogeographical patterns within these islands have yet to be studied in detail.

CONCLUSION: DIVERSITY PATTERNS WITHIN THE CENTRAL IWP

Sister species within the genus *Cerithidea* show narrowly allopatric ranges, producing a mosaic across the central IWP. Secondary sympatry appears to be achieved slowly and only between clades with ecological differences. As a result, five species are found sympatrically in southern Vietnam, three in the South China Sea, Andaman Sea, Philippines and southern China, two in New Guinea and one in Australia and East Africa. This is a small sample of only 15 species, but it is nonetheless notable that the highest species richness is not found in eastern Indonesia at the heart of the 'Coral Triangle' or IAA (Hoeksema, 2007), instead lying further to the west, as also observed in mangrove-associated littorinids (Reid, 1986, 2001). This could indicate a correlation between the diversity of mangrove molluscs and habitat area (as in reef fish and corals; Bellwood *et al.*, 2005), as mangrove habitats reach their greatest areal extent in South-East Asia (Spalding *et al.*, 1997) and most *Cerithidea* species are restricted to continental coasts and high islands. Nevertheless, in contrast with *Cerithidea*, the focus of species diversity of mangrove plants includes not only South-East Asia, but also eastern Indonesia, New Guinea and northern Australia (Groombridge & Jenkins, 2002).

Molecular study of supposedly widespread species of IWP gastropods has revealed other cases of mosaic-

type differentiation of cryptic species across the region, at a scale that is smallest in those that, like *Cerithidea*, are believed to have limited potential for larval dispersal (Paulay & Meyer, 2002). The location of individual species ranges depends not only on historical factors, but also on ecology; for example, species of reefs and limestone shores differentiate on oceanic archipelagos (Kirkendale & Meyer, 2004; Meyer *et al.*, 2005), those of continental coasts (such as *Cerithidea*) differentiate on continents and high islands (Williams *et al.*, 2011) and those of rocky shores differentiate across the entire IWP (Williams & Reid, 2004; Frey & Vermeij, 2008). These mosaic distributions contrast with the prevailing wide and overlapping distributions of corals and fish, which contribute largely to the IAA hotspot (Bellwood *et al.*, 2012). Mosaic distributions do not contribute directly to alpha diversity, but provide crucial insight into the causes of allopatric speciation in the marine tropics.

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REFERENCES

- Awise JC. 2004.** *Molecular markers, natural history, and evolution, 2nd edn.* Sunderland, MA: Sinauer Associates.
- Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2000.** A marine Wallace's line? *Nature* **406**: 692–693.
- Bellwood DR, Hughes TP, Connolly SR, Tanner J. 2005.** Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters* **8**: 643–651.
- Bellwood DR, Meyer CP. 2009.** Searching for heat in a marine biodiversity hotspot. *Journal of Biogeography* **36**: 569–576.
- Bellwood DR, Renema W, Rosen BR. 2012.** Biodiversity hotspots, evolution and coral reef biogeography: a review. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia, Systematics Association Special Volume 82.* Cambridge: Cambridge University Press, 216–245.
- Bowen BW, Rocha LA, Toonen RJ, Karl SA, Members of Toba Laboratory. 2013.** The origins of tropical marine biodiversity. *Trends in Ecology & Evolution* **28**: 359–366.
- Brandt RAM. 1974.** The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde* **105**: 1–423.
- Brown DS. 1994.** *Freshwater snails of Africa and their medical importance, 2nd edn.* London: Taylor & Francis.
- Cannon CH. 2012.** Quaternary dynamics of Sundaland forests. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia, Systematics Association Special Volume 82.* Cambridge: Cambridge University Press, 115–137.
- Carpenter KE, Barber PH, Crandall ED, Ablan-Lagman MCA, Ambariyanto, Mahardika GN, Manjaji-Matsumoto BM, Juinio-Meñez MA, Santos MD, Starger CJ, Toha AHA. 2011.** Comparative phylogeography of the Coral Triangle and implications for marine management. *Journal of Marine Biology* **2011**: 396982.
- Carpenter KE, Springer VG. 2005.** The center of marine shore fish biodiversity: the Philippine Islands. *Environmental Biology of Fishes* **72**: 467–480.
- Castresana J. 2000.** Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.
- Claremont M, Williams ST, Barraclough TG, Reid DG. 2011.** The geographic scale of speciation in a marine snail with high dispersal potential. *Journal of Biogeography* **38**: 1016–1032.
- Cowman PF, Bellwood DR. 2013.** The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *Journal of Biogeography* **40**: 209–224.
- Coyne JA, Orr HA. 2004.** *Speciation.* Sunderland, MA: Sinauer Associates.
- Crandall ED, Frey MA, Grosberg RK, Barber PH. 2008.** Contrasting demographic history and phylogeographical patterns in two Indo-Pacific gastropods. *Molecular Ecology* **17**: 611–626.
- Cunha RL, Tenorio MJ, Afonso C, Castilho R, Zardoya R. 2008.** Replaying the tape: recurring biogeographical patterns in Cape Verde *Conus* after 12 million years. *Molecular Ecology* **17**: 885–901.
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006.** Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: e88.
- Drummond AJ, Rambaut A. 2007.** BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7**: 214.
- Duke NC, Benzie JAH, Goodall JA, Ballment ER. 1998.** Genetic structure and evolution of species in the mangrove genus *Avicennia* (Avicenniaceae) in the Indo-West Pacific. *Evolution* **52**: 1612–1626.
- Duke NC, Lo EYY, Sun M. 2002.** Global distribution and genetic discontinuities of mangroves – emerging patterns in the evolution of *Rhizophora*. *Trees* **16**: 65–79.

- Ellison AM. 2002.** Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees* **16**: 181–194.
- Ellison AM, Farnsworth EJ, Merkt RE. 1999.** Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography* **8**: 95–115.
- Ezard T, Fujisawa T, Barraclough TG. 2009.** SPLITS: species' limits by threshold statistics. R package version 1.0-11/r29. Available at: <http://R-Forge.R-project.org/projects/splits/>
- Fontaneto D, Herniou EA, Boschetti C, Caprioli M, Melone G, Ricci C, Barraclough TG. 2007.** Independently evolving species in asexual bdelloid rotifers. *PLoS Biology* **5**: 914–921.
- Frey MA. 2010.** The relative importance of geography and ecology in species diversification: evidence from a tropical marine intertidal snail (*Nerita*). *Journal of Biogeography* **37**: 1515–1528.
- Frey MA, Vermeij GJ. 2008.** Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (genus: *Nerita*): implications for regional diversity patterns in the marine tropics. *Molecular Phylogenetics and Evolution* **48**: 1067–1086.
- Fujita MK, Leaché AD, Burbrink FT, McGuire JA, Moritz C. 2012.** Coalescent-based species delimitation in an integrative taxonomy. *Trends in Ecology and Evolution* **27**: 480–488.
- Gaither MR, Rocha LA. 2013.** Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: evidence for the centre of overlap hypothesis. *Journal of Biogeography* **40**: 1638–1648.
- Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T, Masek J, Duke N. 2011.** Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography* **20**: 154–159.
- Glaubrecht M. 1996.** *Evolutionsökologie und Systematik am Beispiel von Süß- und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): ontogenese-Strategien, paläontologische Befunde und historische Zoogeographie*. Leiden: Backhuys.
- Glaubrecht M. 1997.** Ökologie von Mangroven und Mangroveschnecken. *Natur und Museum* **127**: 285–305.
- Gordon AL, Fine RA. 1996.** Pathways of water between the Pacific and Indian Oceans in the Indonesian seas. *Nature* **379**: 146–149.
- Groombridge B, Jenkins MD. 2002.** *World atlas of biodiversity*. Berkeley, CA: University of California Press.
- Habe T. 1955.** Spawning of *Cerithidea djadjariensis* and *C. rhizophorarum*. *Venus* **18**: 204–205.
- Hall R. 2012.** Sundaland and Wallacea: geology, plate tectonics and palaeogeography. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia, Systematics Association Special Volume 82*. Cambridge: Cambridge University Press, 32–78.
- Hasegawa K. 2000.** Family Potamididae. In: Okutani T, ed. *Marine mollusks in Japan*. Tokyo: Tokai University Press, 133–134.
- Hoeksema BW. 2007.** Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema W, ed. *Biogeography, time and place: distributions, barriers and islands*. Dordrecht: Springer, 117–178.
- Hong J-S, Choi J-W, Tsutsumi H. 2010.** Concluding remarks on the joint survey of macrobenthic fauna on Suncheon Tidal Flats by the participants of 'Korea and Japan Joint Symposium on Biology of Tidal Flats 2009'. *Plankton & Benthos Research* **5** (Suppl.): 255–263.
- Horne JB, van Herwerden L, Choat JH, Robertson DR. 2008.** High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. *Molecular Phylogenetics and Evolution* **49**: 629–638.
- Houbrick RS. 1984.** Revision of higher taxa in genus *Cerithidea* (Mesogastropoda: Potamididae) based on comparative morphology and biological data. *American Malacological Bulletin* **2**: 1–20.
- Houbrick RS. 1986.** *Cerithidea reidi*, spec. nov., from Western Australia. *Veliger* **28**: 280–286.
- Huelsenbeck JP, Ronquist F. 2001.** MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.
- Hughes TP, Bellwood DR, Connolly SR. 2002.** Biodiversity hotspots, centres of endemism and the conservation of coral reefs. *Ecology Letters* **5**: 775–784.
- Jones DA. 1984.** Crabs of the mangal ecosystem. In: Por I, ed. *Hydrobiology of the mangal: the ecosystem of the mangrove forests. Developments in Hydrobiology 20*. The Hague: W. Junk, 89–110.
- Kamimura S, Itoh H, Ozeki S, Kojima S. 2010.** Molecular diversity of *Cerithidea* gastropods inhabiting Suncheon Bay, and the Japanese and Ryukyu Islands. *Plankton & Benthos Research* **5** (Suppl.): 250–254.
- Katoh K, Toh H. 2008.** Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* **9**: 286–298.
- Kimura T, Fujioka E, Kimura S, Aoki S. 2002.** A comparative morphology of eggs and larvae of nine gastropods in tidal flat and marsh of the reed. *Venus* **61**: 114–115 (In Japanese).
- Kirkendale LA, Meyer CP. 2004.** Phylogeography of the *Patelloida profunda* group (Gastropoda: Lottiidae): diversification in a dispersal-driven marine system. *Molecular Ecology* **13**: 2749–2762.
- Knowlton N. 2000.** Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* **420**: 73–90.
- Kobelt W. 1888–1898.** Die Gattung *Cerithium* Lam. In: Küster HC, Kobelt W, eds. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Nürnberg: Bauer & Raspe, parts 359, 374, 377, 396, 398, 418, 434, 439; 1–297 + 47 pls.
- Kohn AJ. 2012.** Egg size, life history, and tropical marine gastropod biogeography. *American Malacological Bulletin* **30**: 163–174.
- Kojima S, Kamimura S, Iijima A, Kimura T, Kurozumi T, Furota T. 2006.** Molecular phylogeny and population structure of tideland snails in the genus *Cerithidea* around Japan. *Marine Biology* **149**: 525–535.

- Kowalke T.** 2003. Verbreitung der Potamididae H. & A. Adams, 1854 (Caenogastropoda: Cerithiimorpha: Cerithioidea) im europäischen Känozoikum. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **227**: 301–320.
- Krug PJ.** 2011. Patterns of speciation in marine gastropods: a review of the phylogenetic evidence for localized radiations in the sea. *American Malacological Bulletin* **29**: 169–186.
- Lee S-C, Chao S-M.** 2004. Shallow-water marine shells from Kenting National Park, Taiwan. *Collections and Research* **17**: 33–57.
- Lessios HA, Kane J, Robertson DR.** 2003. Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution* **57**: 2026–2036.
- Loder JW, Boicourt WC, Simpson JH.** 1998. Western ocean boundary shelves. In: Robinson AR, Brink KH, eds. *The global coastal ocean*. New York: John Wiley, 3–28.
- Losos JB, Glor RE.** 2003. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution* **18**: 220–227.
- Lourie SA, Green DM, Vincent ACJ.** 2005. Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: *Hippocampus*). *Molecular Ecology* **14**: 1073–1094.
- Lourie SA, Vincent ACJ.** 2004. A marine fish follows Wallace's Line: the phylogeography of the three-spot seahorse (*Hippocampus trimaculatus*, Syngnathidae, Teleostei) in Southeast Asia. *Journal of Biogeography* **31**: 1975–1985.
- Lozouet P, Plaziat J-C.** 2008. *Mangrove environments and molluscs. Abatan River, Bohol and Panglao Islands, central Philippines*. Hackenheim: ConchBooks.
- Ma X.** 2004. Order Mesogastropoda. In: Qi Z, ed. *Seashells of China*. Beijing: China Ocean Press, 31–81.
- Maddison D, Maddison W.** 2003. MacClade. Version 4.06 OSX. Sunderland, MA: Sinauer Associates.
- Madeira C, Alves MJ, Mesquita N, Silva SE, Paula J.** 2012. Tracing geographical patterns of population differentiation in a widespread mangrove gastropod: genetic and geometric morphometrics surveys along the eastern African coast. *Biological Journal of the Linnean Society* **107**: 647–663.
- Malay MCD, Paulay G.** 2010. Peripatric speciation drives diversification and distributional pattern of reef hermit crabs (Decapoda: Diogenidae: *Calcinus*). *Evolution* **64**: 634–662.
- Masuda K.** 1956. Miocene Mollusca from Noto Peninsula, Japan. Part 1, (II). *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* **21**: 161–167.
- McGuinness KA.** 1994. The climbing behaviour of *Cerithidea anticipata* (Mollusca: Gastropoda): the roles of physical and biological factors. *Australian Journal of Ecology* **19**: 283–289.
- Meyer CP, Geller JB, Paulay G.** 2005. Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. *Evolution* **59**: 113–125.
- Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF.** 2005. The Phanerozoic record of global sea-level change. *Science* **310**: 1293–1298.
- Miura O, Frankel V, Torchin ME.** 2011. Different developmental strategies in geminate snails, *Cerithideopsis californica* and *C. pliculosa*, across the Isthmus of Panama. *Journal of Molluscan Studies* **77**: 255–258.
- Miura O, Köhler F, Lee T, Li J, Ó Foighil D.** 2013. Rare, divergent Korean *Semisulcospira* spp. mitochondrial haplotypes have Japanese sister lineages. *Journal of Molluscan Studies* **79**: 86–89.
- Miura O, Torchin ME, Bermingham E, Jacobs DK, Hechinger RF.** 2012. Flying shells: historical dispersal of marine snails across Central America. *Proceedings of the Royal Society B* **279**: 1061–1067.
- Moritz C.** 1994. Defining 'evolutionarily significant units' for conservation. *Trends in Ecology and Evolution* **9**: 373–375.
- Morlet L.** 1889. Catalogue des coquilles recueillies, par M. Pavie, dans le Cambodge et le Royaume de Siam, et description d'espèces nouvelles. *Journal de Conchyliologie* **37**: 121–199.
- Morley RJ.** 2012. A review of the Cenozoic palaeoclimate history of Southeast Asia. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST, eds. *Biotic evolution and environmental change in Southeast Asia, Systematics Association Special Volume 82*. Cambridge: Cambridge University Press, 79–114.
- Nylander J.** 2004. *MrModeltest*. Version 2. Program distributed by the author. Uppsala: Evolutionary Biology Centre, Uppsala University.
- Ohtaki H, Maki E, Tomiyama K.** 2002. Tree climbing behaviour of the snail *Cerithidea rhizophorarum* (Gastropoda: Potamididae). *Venus* **61**: 215–223.
- Ozawa T, Köhler F, Reid DG, Glaubrecht M.** 2009. Tethyan relicts on continental coastlines of the northwestern Pacific Ocean and Australasia: molecular phylogeny and fossil record of batillariid gastropods (Caenogastropoda, Cerithioidea). *Zoologica Scripta* **38**: 503–525.
- Paulay G, Meyer C.** 2002. Diversification in the tropical Pacific: comparison between marine and terrestrial systems and the importance of founder speciation. *Integrative and Comparative Biology* **42**: 922–934.
- Paulay G, Meyer C.** 2006. Dispersal and divergence across the greatest ocean region: do larvae matter? *Integrative and Comparative Biology* **46**: 269–281.
- Plaziat J-C.** 1984. Mollusk distribution in the mangal. In: Por FD, Dor I, eds. *Hydrobiology of the mangal: the ecosystem of the mangrove forests. Developments in hydrobiology 20*. The Hague: W. Junk, 111–143.
- Plaziat J-C, Cavagnetto C, Koeniguer J-C, Baltzer F.** 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. *Wetlands Ecology and Management* **9**: 161–179.
- Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP.** 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* **55**: 595–609.

- Puillandre N, Modica MV, Zhang Y, Sirovich L, Boisselier M-C, Cruaud C, Holford M, Samadi S. 2012.** Large-scale species delimitation method for hyperdiverse groups. *Molecular Ecology* **21**: 2671–2691.
- Quenouille B, Hubert N, Bermingham E, Planes S. 2011.** Speciation in tropical seas: allopatry followed by range change. *Molecular Phylogenetics and Evolution* **58**: 546–552.
- Quoy JRC, Gaimard JP. 1834.** *Voyage de découvertes de l'Astrolabe zoologie, Vol. 3*. Paris: J. Tastu.
- R Development Core Team. 2009.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.R-project.org>
- Reid DG. 1986.** *The littorinid molluscs of mangrove forests in the Indo-Pacific region: the genus Littoraria*. London: British Museum (Natural History).
- Reid DG. 1992.** Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. In: Grahame J, Mill PJ, Reid DG, eds. *Proceedings of the Third International Symposium on Littorinid Biology*. London: Malacological Society of London, 141–151.
- Reid DG. 2001.** New data on the taxonomy and distribution of the genus *Littoraria* Griffith and Pidgeon, 1834 (Gastropoda: Littorinidae) in Indo-West Pacific mangrove forests. *Nautilus* **115**: 115–139.
- Reid DG. 2007.** The genus *Echinolittorina* Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. *Zootaxa* **1420**: 1–161.
- Reid DG, Dyal P, Lozouet P, Glaubrecht M, Williams ST. 2008.** Mudwhelks and mangroves: the evolutionary history of an ecological association (Gastropoda: Potamididae). *Molecular Phylogenetics and Evolution* **47**: 680–699.
- Reid DG, Dyal P, Williams ST. 2010.** Global diversification of mangrove fauna: a molecular phylogeny of *Littoraria* (Gastropoda: Littorinidae). *Molecular Phylogenetics and Evolution* **55**: 185–201.
- Reid DG, Dyal P, Williams ST. 2012.** A global molecular phylogeny of 147 periwinkle species (Gastropoda, Littorininae). *Zoologica Scripta* **41**: 125–136.
- Reid DG, Lal K, Mackenzie-Dodds J, Kaligis F, Littlewood DTJ, Williams ST. 2006.** Comparative phylogeography and species boundaries in *Echinolittorina* snails in the central Indo-West Pacific. *Journal of Biogeography* **33**: 990–1006.
- Renema W, Bellwood DR, Braga JC, Bromfield K, Hall H, Johnson KG, Lunt P, Meyer CP, McMonagle LB, Morley RJ, O'Dea A, Todd JA, Wesselingh FP, Wilson MEJ, Pandolfi JM. 2008.** Hopping hotspots: global shifts in marine biodiversity. *Science* **321**: 654–657.
- Ricklefs RE, Schwarzbach AE, Renner SS. 2006.** Rate of lineage origin explains the diversity anomaly in the world's mangrove vegetation. *American Naturalist* **168**: 805–810.
- Rohfritsch A, Borsa P. 2005.** Genetic structure of Indian scad mackerel *Decapterus russelli*: Pleistocene vicariance and secondary contact in the central Indo-West Pacific seas. *Heredity* **95**: 315–322.
- Shetye SR, Gouveia AD. 1998.** Coastal circulation in the north Indian Ocean. In: Robinson AR, Brink KH, eds. *The global coastal ocean*. New York: John Wiley, 523–556.
- Sowerby GB. 1866.** Monograph of the genus *Cerithidea*. In: Reeve LA, ed. *Conchologia iconica*. London: LA Reeve, 1–4.
- Spalding MD, Blasco F, Field CD. 1997.** *World mangrove atlas*. Okinawa: International Society for Mangrove Ecosystems.
- Subba Rao NV. 2003.** Indian seashells. Part 1. Polyplacophora and Gastropoda. *Records of the Zoological Survey of India. Occasional Paper* **192**: 1–416.
- Tamura K, Dudley J, Nei M, Kumar S. 2007.** MEGA4: Molecular Evolutionary Genetic Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* **24**: 1596–1599.
- Thach NN. 2005.** *Shells of Vietnam*. Hackenheim: Conchbooks.
- Thach NN. 2007.** *Recently collected shells of Vietnam*. Ancona: L'Informatore Piceno.
- Tryon GW. 1887.** *Manual of conchology, Vol. 9*. Philadelphia, PA: Tryon.
- Valiela I, Bowen JL, York JK. 2001.** Mangrove forests: one of the world's threatened major tropical environments. *BioScience* **51**: 807–815.
- Vannini M, Rorandelli R, Lähteenoja O, Mrabu E, Fratini S. 2006.** Tree-climbing behaviour of *Cerithidea decollata*, a western Indian Ocean mangrove gastropod (Mollusca: Potamididae). *Journal of the Marine Biological Association of the United Kingdom* **86**: 1429–1436.
- Vermeij GJ. 1973.** Molluscs in mangrove swamps: physiognomy, diversity, and regional differences. *Systematic Zoology* **22**: 609–624.
- Voris HK. 2000.** Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**: 1153–1167.
- Wada K, Nishikawa C. 2005.** Habitat use by the potamidid gastropod *Cerithidea rhizophorarum* living in an estuarine salt marsh. *Japanese Journal of Benthology* **60**: 23–29 (In Japanese).
- Wiens JJ. 1998.** Combining data sets with different phylogenetic histories. *Systematic Biology* **47**: 568–581.
- Williams ST. 2007.** Origins and diversification of Indo-West Pacific marine fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). *Biological Journal of the Linnean Society* **92**: 573–592.
- Williams ST, Apte D, Ozawa T, Kaligis F, Nakano T. 2011.** Speciation and dispersal along continental coastlines and island arcs in the Indo-West Pacific turbinid gastropod genus *Lunella*. *Evolution* **65**: 1752–1771.
- Williams ST, Duda TF. 2008.** Did tectonic activity stimulate Oligo-Miocene speciation in the Indo-West Pacific? *Evolution* **62**: 1618–1634.
- Williams ST, Ozawa T. 2006.** Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution* **39**: 33–51.

- Williams ST, Reid DG. 2004.** Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* **58**: 2227–2251.
- Woodroffe CD, Grindrod J. 1991.** Mangrove biogeography: role of Quaternary sea-level change. *Journal of Biogeography* **18**: 479–492.
- Wyrтки K. 1961.** Physical oceanography of the Southeast Asian waters. *Naga Report* **2**: 1–195.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Molecular phylogeny of *Cerithidea* species produced by MrBayes analysis of 16S rRNA (A) and 28S rRNA (B) sequences, using *Cerithideopsisilla* species as outgroup. Localities are abbreviated and followed by the last four digits of the registration or reference number (for full details, see Table S1). Support values are MrBayes posterior probabilities; only values > 0.95 (strong support) are shown.

Figure S2. Molecular phylogeny of *Cerithidea* species produced by MrBayes analysis of concatenated COI + 28S rRNA (A) and COI + 16S rRNA + 28S rRNA (B) sequences, using *Cerithideopsisilla* species as outgroup. Localities are abbreviated and followed by the last four digits of the registration or reference number (for full details, see Table S1). Support values are MrBayes posterior probabilities; only values > 0.95 (strong support) are shown.

Table S1. Specimens of *Cerithidea* (abbreviated *C.*) used in this study, with GenBank accession numbers for 28S, 16S and COI sequences. Not all genes were sequenced for each specimen; unavailable sequences are indicated with a dash. Voucher locations: Natural History Museum, London (NHMUK); Berlin Museum of Natural History (ZMB); Muséum Nationale d'Histoire Naturelle, Paris (MNHN). GenBank accession numbers beginning with AM were published by Reid *et al.* (2008). Outgroup taxa are the four species of *Cerithideopsisilla*. Some of the *Cerithidea* species listed have appeared in recent literature under incorrect or invalid names: *C. balteata* [= *C. ornata* (G. B. Sowerby II, 1855)]; *C. tonkiniana* (= *C. ornata* of authors, not G. B. Sowerby II, 1855); *C. quoyii* and *C. dohrni* (together = *C. quadrata* G. B. Sowerby II, 1866); *C. moerchii* (= *C. rhizophorum* of authors, not A. Adams, 1855).

Table S2. Recorded habitat range of *Cerithidea* species. Shell thickness may indicate degree of exposure to crushing predation by crabs and other predators, as in *Littoraria* species, in which thickness is greatest in species that spend most time at lower tidal levels on trees (Reid, 1992). Symbols: ++, typical habitat; +, recorded habitat.