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Allopatry and overlap in a clade of snails from mangroves and mud flats in the Indo-West Pacific and Mediterranean (Gastropoda: Potamididae: *Cerithideopsilla*)

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Cerithideopsilla is a genus of potamidid snails found in high abundance on sedimentary intertidal flats and beneath mangrove trees on continental shores in the tropical and subtropical Indo-West Pacific region and Mediterranean Sea. Taxonomic revisions have recognized four species, but recent molecular studies have hinted at a higher diversity. Here, we analyse 377 individuals sampled from across the known range and use a combination of molecular phylogenetic (mitochondrial COI and 16S rRNA, and nuclear 28S rRNA genes), statistical (generalized mixed Yule-coalescent GMYC method) and morphological (shell form) criteria to delimit 16 species. These form four species groups, corresponding with the traditionally recognized species *C. alata*, *C. 'djadjariensis'* (for which the valid name is *C. incisa*), *C. cingulata* and *C. conica*. Distribution maps were compiled using museum specimens identified by diagnostic shell characters. In combination with the molecular phylogenetic trees, these suggest an allopatric speciation mode, with diversification centred on the East Asian coastline and northern Australia, and a pronounced gap in the 'eastern Indonesian corridor', an area of low oceanic productivity. There is, however, frequently geographical overlap between sister species and we suggest from several sources of evidence (e.g. presence of *C. conica* in isolated saline lakes 900 km from the sea) that post-speciation transport by migratory birds has occurred. Nine of the 16 species occur between the Gulf of Tonkin and Hong Kong, so southern China is significant for both the evolution and conservation of *Cerithideopsilla* species. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 212–228.

ADDITIONAL KEYWORDS: allopatric speciation – GMYC – marine biogeography – southern China.

INTRODUCTION

Biodiversity in the shallow marine tropics shows a global maximum in the central Indo-West Pacific (IWP) (Hoeksema, 2007). Documentation of this pattern, and studies of the processes that have produced and maintain it, have concentrated above all on the exceptionally species-rich biotope of the coral reef (see recent reviews by Bellwood, Renema & Rosen, 2012; Bowen *et al*., 2013; Briggs & Bowen, 2013; Cowman & Bellwood, 2013). In contrast, the evolution and biogeography of the biota of another characteristic but far less diverse tropical biotope, the mangrove forest, have been relatively neglected (Ellison, Farnsworth & Merkt, 1999; Plaziat *et al*., 2001; Ellison, 2002; Ricklefs, Schwarzbach & Renner, 2006). The mangrove plants, of which there are only about 70 species worldwide, typically have wide distributions that overlap to generate the highest diversity within the Indo-Australian Archipelago (IAA) at the

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centre of the IWP (Spalding, Blasco & Field, 1997; Groombridge & Jenkins, 2002; Daru *et al*., 2013). The observed global diversity gradient of mangrove-associated animals is believed to be broadly similar, with a peak in the central IWP, but information on their distributions remains limited (Ellison *et al*., 1999; Ellison, 2002). Some members of the mangrove fauna have been included in molecular phylogenetic analyses, either within wider systematic studies (e.g. Schubart *et al*., 2006) or in taxonomic groups that range across adjacent habitats such as intertidal rocky (Frey & Vermeij, 2008; Frey, 2010) and sedimentary shores (Shih & Suzuki, 2008; Ozawa *et al*., 2009; Shih *et al*., 2009; Yin *et al*., 2009; Golding, 2012; Chen *et al*., 2014; Polgar *et al*., 2014). However, studies of strictly mangrove-associated clades, from which to draw inferences about phylogeography and diversification within the mangrove biotope itself, are rare. The few studied examples include decapod crabs (Fratini *et al*., 2005; Ragionieri *et al*., 2009) and molluscs (Reid *et al*., 2008, 2013; Miura, Torchin & Bermingham, 2010; Reid, Dyal & Williams, 2010; Miura *et al*., 2012; Reid & Claremont, 2014).

Gastropods are a major component of the macrofauna of mangrove habitats, although the number of species is relatively low; for example only about 44 and 65 species of mangrove-associated molluscs (of which most are gastropods) have been recorded in the diversity focus of the central IWP, in Borneo (Ashton, Macintosh & Hogarth, 2003) and the Philippines (Lozouet & Plaziat, 2008) respectively. Only one family-level taxon shows a close association with mangroves and warm-temperate salt marshes – the Potamididae (review by Reid *et al*., 2008). This group includes the large, ground-dwelling mudwhelks *Terebralia* and *Telescopium*, which shelter beneath mangrove trees and consume detritus, algae and (in *Terebralia palustris* alone) fallen leaves. It also includes the genus *Cerithidea* of smaller, thin-shelled species that climb on mangrove vegetation to avoid intense crushing predation and, perhaps, for temperature control. Until recently, the worldwide diversity of the family was estimated at 29 species, based on taxonomic assessment of shell morphology. A molecular phylogenetic framework is now available (Reid *et al*., 2008), defining six monophyletic genera: *Terebralia*, *Telescopium* and *Cerithidea* in the IWP only; *Tympanotonos* in West Africa; *Cerithideopsis* in the Americas and IWP; and *Cerithideopsilla* in the IWP and Mediterranean. Both the fossil record and the phylogenetic reconstruction of ancestral habitats suggest that the living potamidids are an adaptive radiation that has been associated with mangroves since its origin in the Middle Eocene (Reid *et al*., 2008). Detailed molecular and morphological analysis of *Cerithidea* has increased its known diversity from ten to 15 species (Reid *et al*., 2013; Reid, 2014), and of IWP *Cerithideopsis* from one to three species (Reid & Claremont, 2014), although study of *Cerithideopsis* in Central America has suggested a reduction in its diversity (Miura *et al*., 2010, 2012).

After *Cerithidea* and *Cerithideopsis*, the third largest potamidid genus is *Cerithideopsilla*. A classical study of shell morphology recognized just four species in the central IWP (Van Regteren Altena, 1940), but molecular study has added another from the western Indian Ocean and Mediterranean (Reid *et al*., 2008). Furthermore, the diversity of mitochondrial lineages within several of the nominal species strongly suggests that diversity has been underestimated (Kojima *et al*., 2006; Reid *et al*., 2008; Kamimura *et al*., 2010). A systematic revision based on thorough sampling throughout the range is clearly required. The association with the mangrove environment is less strict than in some other potamidid genera. All of the nominal species of *Cerithideopsilla* occur on intertidal mud and sandy mud substrates, and several are most frequently found in the shade and shelter of mangrove trees (Wells, 1985; Maki, Ohtaki & Tomiyama, 2002; Lozouet & Plaziat, 2008). However, the distributions of some *Cerithideopsilla* species extend beyond the northern limit of mangroves in Japan and Korea (Hasegawa, 2000; Maki *et al*., 2002; Hong, Choi & Tsutsumi, 2010) and, in the Mediterranean (where no mangroves are found), *C. conica* occupies intertidal flats, shallow lagoons and even isolated saline lakes (Lozouet, 1986; Plaziat, 1993; Kowalke, 2001). In the IWP, *C. cingulata* occurs abundantly on open mud and sand flats (at densities of up to 4800 m^{-2}), often adjacent to mangroves, but not necessarily sheltered by them (Vohra, 1970; Balaparameswara Rao & Sukumar, 1982; Wells, 1985; Maki *et al*., 2002; Ando & Tomiyama, 2005; Willan, 2013). Densities in fish ponds may be even higher (up to 7000 m^{-2}; Lantin-Olaguer & Bagarinao, 2001). Information on mode of larval development is fragmentary. Both *C. cingulata* and *C. djadjariensis* are reported to be planktotrophic with a length of larval life of about 11–20 days (Habe, 1955; Lantin-Olaguer & Bagarinao, 2001; Kimura *et al*., 2002; Kojima *et al*., 2006), but *C. conica* has non-planktotrophic development with no planktonic stage (Kowalke, 2001).

The modern diversity of potamidid genera and species is highest in the central IWP. This, combined with their strict dependence on mangroves, makes them a key group for the study of diversification in this biotope. The classic explanations for the diversity focus in the IAA have been based on various models of allopatric speciation (Bellwood *et al*., 2012) and, although there is a growing recognition of the role of parapatric ecological speciation (Bowen *et al*., 2013),

it is acknowledged that a degree of spatial separation is usually required during speciation in marine animals. The combination of complete species-level phylogenies with geographical distributions is therefore a powerful tool for the study of the historical, geographical and ecological correlates of speciation. In the few studies of this kind in mangrove-associated organisms, two contrasting patterns can be seen. The 21 mangrove littorinids (*Littoraria* spp.) in the IWP mostly show large ranges, often on the scale of ocean basins, that overlap to accumulate high diversity in the central IWP (Reid, 1986, 2001; Reid, Dyal & Williams, 2012), as in the classic 'stack of pancakes' model prevalent in coral-reef taxa (Bellwood *et al*., 2012). Narrow-range endemic species are present only in peripheral locations, suggesting peripheral speciation. A similar pattern has been claimed for some potamidids, studied by classical morphology (Houbrick, 1991). However, molecular studies have repeatedly questioned the generality of this model. The members of two genera of IWP potamidids (15 *Cerithidea* spp. and three *Cerithideopsis* spp.) show strikingly allopatric, closely adjoining distributions on the scale of seas, termed the 'mosaic' model (Reid *et al*., 2013; Reid, 2014; Reid & Claremont, 2014). Overlap between sister species is non-existent and high regional diversity is built up through a mosaic of smaller distributions and by overlap only between clades with contrasting ecology. This pattern has been interpreted as driven by isolation during low sea-level stands of the late Miocene and early Pliocene, and possibly maintained by competitive exclusion, and appears to have persisted during the major sea-level changes of the later Plio-Pleistocene glaciations. Studies of smaller clades of mangrove-associated crabs (Shih & Suzuki, 2008; Shih *et al*., 2009; Yin *et al*., 2009) and mudskippers (Chen *et al*., 2014; Polgar *et al*., 2014) likewise point to mainly narrow distributions and limited geographical overlap.

At least in gastropods, the contrast between the extreme 'stack of pancakes' and 'mosaic' patterns has been linked to high dispersal via long-lived planktonic eggs and larvae (up to 10 weeks) in *Littoraria* species and shorter larval duration (less than 3 weeks) in potamidids (Reid *et al*., 2013). An additional means of long-distance dispersal may be available for some invertebrates on intertidal sedimentary shores. In the tropical eastern Pacific and western Atlantic, six species of *Cerithideopsis* occur in mangrove, salt-marsh and mud-flat habitats on either side of the Central American Isthmus. Here, mismatches between geographical distribution across the isthmus, morphology and mitochondrial haplotypes suggest two episodes of dispersal (and introgression) across the isthmus, which post-date the latest marine connection between the Pacific and Atlantic oceans at 1.9 Ma. It has been suggested that this is the result of transport of snails or their eggs between the two oceans by migratory birds (Miura *et al*., 2010, 2012).

The objectives of this study are: (1) to define the species of *Cerithideopsilla* by sampling widely across the IWP and Mediterranean range and using a combination of molecular phylogenetics, statistical delimitation and shell morphology; (2) to reconstruct their phylogenetic relationships using one nuclear and two mitochondrial genes; and (3) to plot their geographical distributions using material identified by molecular and morphological means. We aim to establish whether distributions conform to the strictly allopatric 'mosaic' pattern of *Cerithidea*, or whether there is evidence for post-speciation dispersal and possible introgression as in *Cerithideopsis*. Comparison with other mangrove and mud-flat fauna will reveal if there are common patterns of divergence and endemicity.

MATERIAL AND METHODS

Taxonomy, distributions and sampling

Cerithideopsilla was formerly classified as a subgenus of *Cerithidea*, but was raised to generic rank as a result of the molecular phylogenetic study of potamidid genera by Reid *et al*. (2008). Following a taxonomic revision by Van Regteren Altena (1940), four nominal species of *Cerithideopsilla* have been recognized in the central IWP region (e.g. Oyama, 1959; Brandt, 1974; Lozouet, 2008). These are: *C. alata* (Philippi, 1849), *C. cingulata* (Gmelin, 1791), *C. djadjariensis* (Martin, 1899) and *C. microptera* (Kiener, 1841). To these, Reid *et al*. (2008) added *C. conica* (Blainville, 1829) (formerly *Pirenella conica* or *Potamides conicus*; Lozouet, 1986) from the Mediterranean and Indian Ocean. In a concurrent taxonomic and morphological study (D. G. Reid, unpublished) all original descriptions have been examined, revealing that *C. djadjariensis* is a fossil member of the *C. alata* group, and that the valid name of the species referred to in recent literature as *C. djadjariensis* is *C. incisa* (Hombron & Jacquinot, 1848). For simplicity, because most are undescribed and some available names are unfamiliar (Table 1), the 16 species distinguished here will be referred to by letters within four monophyletic species groups: *C. alata* A–D, *C. incisa* A–C, *C. cingulata* A–H and *C. conica*. Only '*Cerithideopsilla*' is abbreviated as '*C.*' in the following text.

Following the present molecular study, it was found that the 16 species can mostly be distinguished by details of shell sculpture, so distribution maps were compiled from shell material in major museum collections (including Natural History Museum, London;

Table 1. Summary of support for species status of evolutionarily significant units (ESUs) of *Cerithideopsilla*. Uncorrected pairwise (p) distances were calculated from 579 positions of COI sequence. 28S fixed differences are the number of positions (in an alignment of 1332 bp) at which the ESU has a unique base (or gap) when compared with other ESUs in the same group (i.e. *C. alata* group, *C. cingulata* group, *C. incisa* group; see Table S3). Abbreviations: BI, MrBayes analysis; N, paraphyly supported (DNA) or no diagnostic morphology (shell); na, only one sequence available; Y, significant support (for DNA, PP > 0.95) or diagnostic morphology (subjective assessment of shells); y, characteristic shell morphology, but not entirely diagnostic; query, no significant support (but not contradicted); dash, no data

ESU	Taxonomic species (if named)	GMYC analysis	COI monophyly (BI)	16S monophyly (BI)	28S monophyly (BI)	p dist. from sister lineage	p dist. within ESU	28S fixed diffs	Shell morphology
C. alata A	*C. alata* (Philippi, 1849)	Y	Y	?	?	0.085	0.017	1	Y
C. alata B	*C. microptera* (Kiener, 1841)	2 entities	Y	Y	?	0.085	0.039	1	Y
C. alata C		Y	Y	?	Y	0.113	0.001	2	Y
C. alata D		Y	Y	?	?	0.113	0.011	2	Y
C. cingulata A	*C. cingulata* (Gmelin, 1791)	Y	N	?	?	0.033	0.012	0	N
C. cingulata B	*C. retifera* (G. B. Sowerby II, 1855)	Y	Y	?	na	0.095	0.013	1	y
C. cingulata C		Y	Y	Y	?	0.095	0.010	1	Y
C. cingulata D		Y	Y	?	?	0.112	0.010	0	Y
C. cingulata E		Y	Y	?	na	0.090	0.005	2	Y
C. cingulata F		Y	Y	na	na	0.099	0.015	2	Y
C. cingulata G		Y	Y	na	?	0.085	0.007	2	N
C. cingulata H		Y	Y	na	na	0.033	0.009	3	y
C. conica	*C. conica* (Blainville, 1829)	Y	Y	Y	Y	0.145	0.016	–	Y
C. incisa A	*C. incisa* (Hombron & Jacquinot, 1848)	5 entities	N	?	?	0.082	0.026	2	Y
C. incisa B		2 entities	Y	?	?	0.113	0.011	9	Y
C. incisa C	*C. caiyingyai* (Qian, Fang & He, 2013)	Y	Y	Y	?	0.082	0.002	1	Y

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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, D.C.; D. G. Reid, unpublished).

A total of 377 individuals, including all the five recognized morphospecies, was sampled from 51 localities across the known range of *Cerithideopsilla* and four species of the sister genus *Cerithidea* (Reid *et al*., 2008) were used as outgroup (Table S1).

DNA extraction, amplification and sequencing

DNA was extracted from mantle or foot tissue of ethanol-preserved specimens using a CTAB extraction method (Reid *et al*., 2012). Portions of three genes were amplified and sequenced: the nuclear 28S rRNA and the mitochondrial COI and 16S rRNA genes. COI was sequenced for almost all samples, and 16S and 28S for reduced subsets (of 98 and 117 samples respectively, including all outgroup taxa). Polymerase chain reactions were used to amplify approximately 1474 bp of 28S rRNA and 658 bp of COI (protocol of Reid *et al*., 2008) and 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 589 sequences available for analysis, 46 have already been published (Reid *et al*., 2008, 2013).

Sequence analysis and phylogeny reconstruction

Sequence alignment and analysis followed the methods described by Reid *et al*. (2013). As well as the individual-gene alignments, a single concatenated alignment of all three genes was constructed, consisting of those 86 specimens for which sequences of all the genes were available. Before combining the three-gene partitions, posterior probabilities (PP) of all clades were compared among individual-gene Bayesian trees, to seek cases of incongruence among strongly supported clades (PP > 95%), which could indicate divergent phylogenetic histories of loci. 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 ran twice for each alignment; convergence between runs was tested by examining both traces in Tracer (v1.5; Drummond & Rambaut, 2007) and the potential scale reduction factor (PSRF). The number of generations per analysis varied based on preliminary convergence results: 5 million generations for 16S, 5 million for 28S and 10 million for the three-gene alignment. Based on the traces in Tracer, a 10% burnin was used for all analyses. Branches in consensus trees with PP < 50% were collapsed.

Molecular species delimitation

The 'generalized mixed Yule-coalescent' (GMYC) method (Pons *et al*., 2006; Fontaneto *et al*., 2007) was used to define potential species-level clusters in the COI tree, as also used and described in more detail by Reid *et al*. (2013). Briefly, BEAST (v1.6.1, Drummond & Rambaut, 2007) was used to generate an ultrametric tree from the COI sequences. Three analyses of 50 million generations were sampled every 5000 generations to generate 10 000 trees each. 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.

As further evidence for species delimitation, the uncorrected pairwise (p) distances (i.e. number of base differences per site, excluding positions with gaps or missing data) over all pairs of COI sequences were estimated among and within clusters using MEGA5 (Tamura *et al*., 2011) and the nuclear 28S gene was examined for fixed differences. In addition, shells were examined for diagnostic morphological traits.

Timing of diversification

The timing of diversification was not estimated in this study, because reliable fossils of *Cerithideopsilla* are scarce. However, the molecular data have been incorporated in a larger BEAST analysis of the entire Potamididae (D. G. Reid & M. Claremont, unpublished), calibrated using the ages of a range of potamidid fossils. Three fossil *Cerithideopsilla* from Japan and Java were included: *C. minoensis* from the Early Miocene (Itoigawa *et al*., 1982; *C. alata* + *incisa* clade; 18–23 Ma); *C. yatsuoensis* from the Middle Miocene (Kaneko & Goto, 1997; *C. incisa* clade; 16–23 Ma); *C. prenagerensis* from the late Middle Miocene (Shuto, 1978; Batenburg *et al*., 2011; *C. cingulata* clade; 10–23 Ma). These were judged to be the oldest members of their clades, so the calibration dates were placed at the base of the stem of the respective clades. Preliminary results are used in the discussion below.

RESULTS

Gene sequences

The COI dataset consisted of 377, the 16S dataset of 98 and the 28S dataset of 117 sequences (Table S1). After the removal of primer sequences and ambiguous regions, the 28S alignment (initially 1474 bp) was 1332 bp (90%) and the 16S alignment (initially 515 bp) was 461 bp (90%). The COI alignment was 658 bp. In the alignments, 91 bp of 28S, 86 bp of 16S and 245 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 (Figs 1, S1, S2).

Phylogeny

The PSRF values for the MrBayes analyses were less than 1.06 and effective sample size (ESS) values were greater than 200, indicating that all trees had reached stationarity, as confirmed by examination of traces in Tracer (v1.5; Drummond & Rambaut, 2007). The ingroup of *Cerithideopsilla* species was monophyletic in all MrBayes analyses (Figs 1, 2, S1, S2). In all analyses (except 28S, in which resolution was poor; Fig. S2), three clades were distinguished: the *C. alata* group, the *C. incisa* group and the *C. cingulata+conica* group (PP > 0.99 in each case). In the COI tree the first two of these were sister groups (PP = 0.99), but the relationships among the three were not resolved in the other analyses. The *C. alata* group corresponds with the two traditional morphospecies *C. alata* and *C. microptera*, and the *C. incisa* group with *C. incisa* (formerly *C.* '*djadjariensis*'). In the COI and all-gene trees the *C. cingulata+conica* group contained two sister clades (PP > 0.97), corresponding with the morphospecies *C. conica* and *C. cingulata* respectively.

Species delimitation and distribution

The ESS values in the BEAST analysis were all greater than 350. The GMYC analysis of COI recovered 22 significant entities (Fig. 1; ML clusters = 21, 95% confidence interval 14–27; ML entities = 22, 95% confidence interval 14–29; likelihood of null model = 3571.075; likelihood of GMYC model = 3581.267; $P < 0.00014$).

For recognition of the GMYC entities as evolutionarily significant units (ESUs), we required independent corroboration from either the nuclear 28S gene, or a diagnostic morphological character. Data from 28S were of limited value, because for 6 of the entities considered as ESUs only 1 or 2 sequences were available (Table S3). The 28S tree was poorly resolved (Fig. S2); only *C. alata* C was monophyletic with strong support (PP = 1), but there were no cases of significant conflict with the ESUs defined by COI analysis and morphology. Examination of the shells of the sequenced specimens revealed diagnostic shell characters for 9 of the individual GMYC entities (*C. alata* A, C, D; *C. cingulata* C, D, E, F; *C. conica*, *C. incisa* C), 8 of which also showed at least one fixed difference in 28S within its species group (Table 1, S3). The ninth, *C. cingulata* D, showed three fixed differences in 28S from the two others in its immediate clade (*C. cingulata* B and C; Table S3). These nine were therefore accepted as ESUs. Among them, the p distances within ESUs were < 0.017 and p distances between ESUs > 0.104 (between *C. cingulata* E and F; Table S2), indicating a 'barcode gap' (Puillandre *et al.*, 2012).

The delimitation of the remaining ESUs is less clear and further investigation is required. Meanwhile, we adopted a conservative approach. GMYC entities were combined into single ESUs if they shared diagnostic morphology and if the resulting ESUs were monophyletic in the MrBayes analysis of COI (the clades with strong support were identical in MrBayes and BEAST analyses). This defined *C. alata* B and *C. incisa* B as single ESUs, although each had been resolved as 2 GMYC entities and the former had a high within-ESU p distances of 0.039 (Fig. 1; Table 1). Five GMYC entities were included in *C. incisa* A and its monophyly was not significantly supported (or contradicted) in the COI analyses; it was, nevertheless, accepted as an ESU, because *C. incisa* A and C were reciprocally monophyletic in the all-gene analysis (Fig. 2), with a p distance of 0.082 and 3 fixed differences between them in 28S (Table 1, S2, S3). In the *C. cingulata* group, all the GMYC entities were accepted as ESUs on the basis of additional evidence. The entity *C. cingulata* G formed a clade in the COI analysis with its two closest entities, the well defined ESUs E and F, and all three were morphologically distinct (although G was not distinct from *C. cingulata* A; Fig. 1; Table 1). Also in the *C. cingulata* group, entity B was sister to ESU C with a p distance of 0.095 and the two were morphologically distinct (although shells of B and A were not always distinct). The separation of entities *C. cingulata* A and H was the least certain, but justified by distinctive (although not diagnostic) shells and three fixed differences in the single 28S sequence of the latter, although the monophyly of the former was not significantly supported in the COI analysis and the p distance between them was only 0.033.

In total, we recognized 16 ESUs, which was within the lower bound of the 95% confidence intervals for entities and clusters in the GMYC analysis. The evidence is summarized in Table 1.

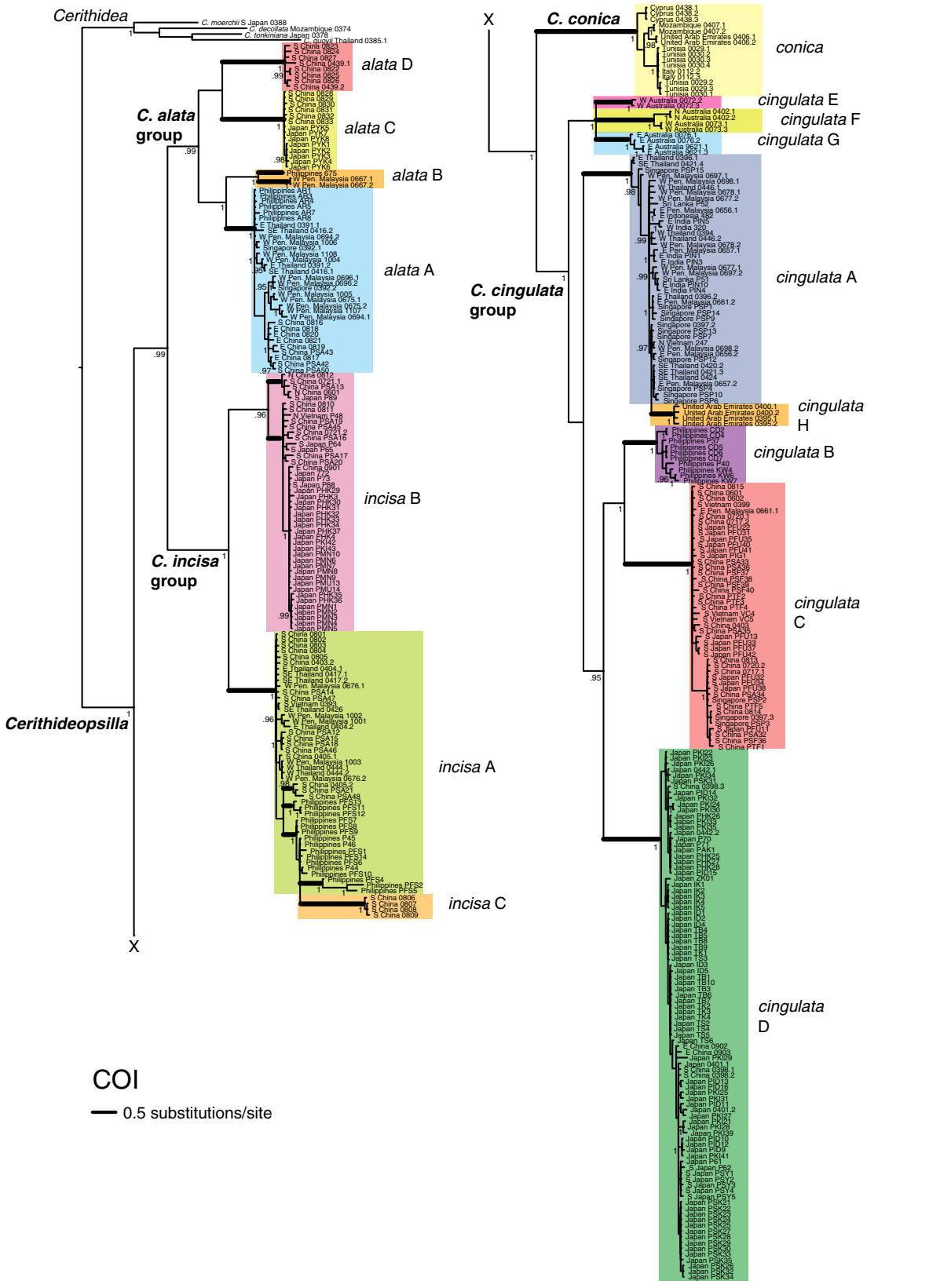
Cerithidea
C. moerchii S Japan 0388
C. decollata Mozambique 0374
C. tonkiniana Japan 0379
C. quoyii Thailand 0385.1
C. alata group
alata D
alata C
alata B
alata A
C. incisa group
incisa B
incisa A
incisa C
Cerithideopsilla
X
C. conica
conica
cingulata E
cingulata F
cingulata G
C. cingulata group
cingulata A
cingulata H
cingulata B
cingulata C
cingulata D
COI
0.5 substitutions/site

Figure 1. Molecular phylogeny of *Cerithideopsilla* species produced by MrBayes analysis of COI sequences, using *Cerithidea* 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 GMYC function in SPLITS package (Ezard *et al*., 2009) are indicated by thickened stems. Coloured boxes indicate proposed taxonomic species.

Using diagnostic and characteristic shell traits it was possible to identify shells belonging to 13 ESUs in museum collections (and, sometimes, type specimens or figures, in order to assign available names) and to plot distribution maps, presented in simplified form in Figure 3 (locality records and detailed maps will be given elsewhere; D. G. Reid, unpublished). Where useful shell characters could not be found, the distributions remain incomplete or hypothetical. For the *C. alata* and *C. incisa* groups all ESUs could be distinguished morphologically, so distributions are reliable (Fig. 3A, B). In the *C. cingulata* group, shells of ESUs A, B, G and H could not be reliably distinguished from each other, so the plotted distributions reflect apparent gaps in the available records and known biogeographic affinities (e.g. shells from New Guinea are more likely to belong to a species from Australia than to one from the Philippines; Reid *et al*., 2013) and are therefore hypothetical (Fig. 3C).

There were several cases of occurrence of sister ESUs (with identification confirmed by COI sequences) at the same locality: *C. alata* A, C and D (Fangchenggang, Beibu Gulf, China); *C. incisa* A and C (Fangchenggang, Beibu Gulf, China); *C. cingulata* E and F (Broome, Western Australia). Based on museum records, the distributions of all members of the *C. alata* group overlapped (Fig. 3A), as did those of the *C. incisa* group (Fig. 3B), and those of the Australian clade of the *C. cingulata* group (E, F, G; Fig. 3C).

DISCUSSION

Delimitation and taxonomy of *Cerithideopsilla* species

The only critical revision of this group (Van Regteren Altena, 1940; treated as a subgenus of *Cerithidea*) was based on assessment of shell variation and concluded that there were four valid species in the IWP: *C. alata*, *C. microptera*, *C. djadjariensis* (here renamed *incisa*) and *C. cingulata*. This arrangement has been followed by almost all subsequent authors (e.g. Oyama, 1959; Brandt, 1974; Lozouet, 2008). These four morphospecies correspond with three clades in the present study (Figs 1, 2): the *C. alata* group (which includes *C. microptera* = *C. alata* B), the *C. incisa* group and the *C. cingulata* group. A fourth clade corresponds with the morphospecies *C. conica* (see Lozouet, 1986), which was added to the present genus by Reid *et al*. (2008). Several molecular studies have, however, suggested that the species diversity of *Cerithideopsilla* is much higher (Kojima *et al*., 2006; Reid *et al*., 2008; Kamimura *et al*., 2010).

Our GMYC analysis of COI distinguished 22 significant entities. However, this method is known to overestimate species lineages if sampling of intraspecific variation is incomplete (Lohse, 2009; Papadopoulou *et al*., 2009; Williams *et al*., 2011). Therefore, to recognize ESUs, we adopted an integrative approach (e.g. Fujita *et al*., 2012; Puillandre *et al*., 2012), based on corroboration from shell morphology (assumed to have a nuclear genetic basis), limited support from the nuclear 28S gene (monophyly and fixed differences), reciprocal monophyly of COI and average thresholds of genetic distance for COI (p within ESUs < 0.039, between ESUs > 0.033) (Table 1). Using these methods, we recognized 16 ESUs.

If sister ESUs remain genetically and morphologically distinct in sympatry, this is evidence that they do not interbreed and are therefore separate biological species (Knowlton, 2000; Avise, 2004; Coyne & Orr, 2004). This evidence is strong for the four members of the *C. alata* group, which all overlap broadly in southern China (Figs 1, 3A); we therefore take these to be species (although we note that *C. alata* B includes two divergent mitochondrial lineages widely separated in the Philippines and western peninsular Malaysia, which require more study). Similarly, the three members of the *C. incisa* group are likely to be species, showing broad sympatry in northern Vietnam and southern China, where the three ESUs are morphologically distinct from each other (Figs 1, 3B, S2). Another case is the Australian clade of *C. cingulata*; sampling was limited to ten specimens, but these fall into three reciprocally monophyletic clades that remain morphologically distinct from each other across their broadly sympatric distributions (Figs 1, 3C). Elsewhere in the *C. cingulata* group there is no known sympatry of sister ESUs. Since levels of genetic divergence and morphological difference are similar among the 16 ESUs, our hypothesis is that all represent separate

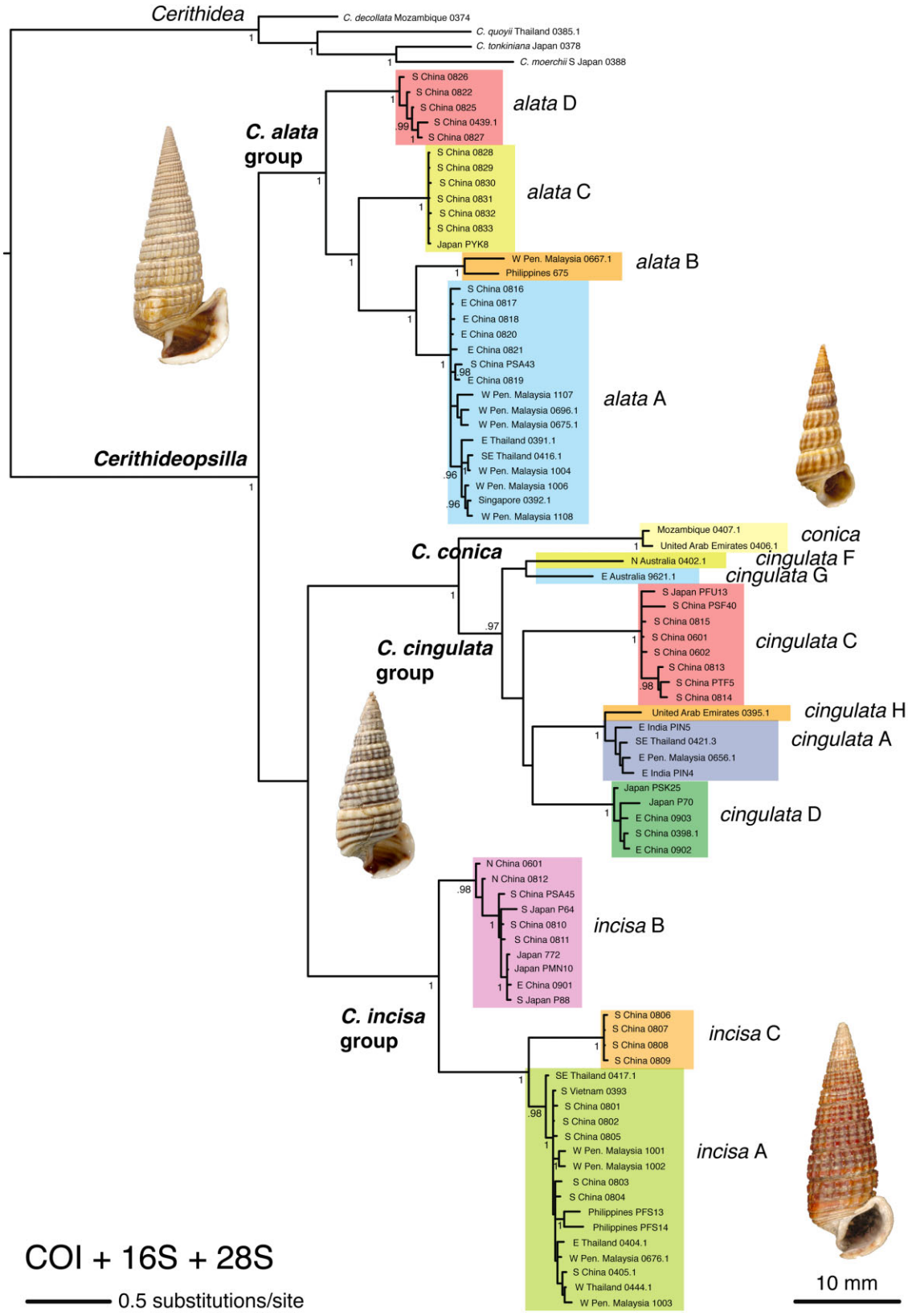
Cerithidea
C. decollata Mozambique 0374
C. quoyii Thailand 0385.1
C. tonkiniana Japan 0378
C. moerchii S Japan 0388
C. alata group
S China 0826
S China 0822
S China 0825
S China 0439.1
S China 0827
alata D
S China 0828
S China 0829
S China 0830
S China 0831
S China 0832
S China 0833
Japan PYK8
alata C
W Pen. Malaysia 0667.1
Philippines 675
alata B
S China 0816
E China 0817
E China 0818
E China 0820
E China 0821
S China PSA43
E China 0819
W Pen. Malaysia 1107
W Pen. Malaysia 0696.1
W Pen. Malaysia 0675.1
E Thailand 0391.1
SE Thailand 0416.1
W Pen. Malaysia 1004
W Pen. Malaysia 1006
Singapore 0392.1
W Pen. Malaysia 1108
alata A
Cerithideopsilla
Mozambique 0407.1
United Arab Emirates 0406.1
conica
C. conica
N Australia 0402.1
cingulata F
E Australia 9621.1
cingulata G
S Japan PFU13
S China PSF40
S China 0815
S China 0601
S China 0602
S China 0813
S China PTF5
S China 0814
cingulata C
C. cingulata group
United Arab Emirates 0395.1
cingulata H
E India PIN5
SE Thailand 0421.3
E Pen. Malaysia 0656.1
E India PIN4
cingulata A
Japan PSK25
Japan P70
E China 0903
S China 0398.1
E China 0902
cingulata D
N China 0601
N China 0812
S China PSA45
S Japan P64
S China 0810
S China 0811
Japan 772
Japan PMN10
E China 0901
S Japan P88
incisa B
C. incisa group
S China 0806
S China 0807
S China 0808
S China 0809
incisa C
SE Thailand 0417.1
S Vietnam 0393
S China 0801
S China 0802
S China 0805
W Pen. Malaysia 1001
W Pen. Malaysia 1002
S China 0803
S China 0804
Philippines PFS13
Philippines PFS14
E Thailand 0404.1
W Pen. Malaysia 0676.1
S China 0405.1
W Thailand 0444.1
W Pen. Malaysia 1003
incisa A
COI + 16S + 28S
0.5 substitutions/site
10 mm

Figure 2. Molecular phylogeny of *Cerithideopsilla* species produced by MrBayes analysis of concatenated COI, 16S and 28S sequences, using *Cerithidea* 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. Coloured boxes indicate proposed taxonomic species (colour coding as in Figure 1). Representative shells of the four groups (*C. alata* group, *C. conica*, *C. cingulata* group, *C. incisa* group) are shown (to same scale).

biological species, although further sampling is needed to test this assertion.

Of all the nominal species of *Cerithideopsilla*, the one with the most striking morphological variation in its shell is *C. conica* (Plaziat, 1993). This is also the only species known to have nonplanktotrophic larval development (Lozouet, 1986; Kowalke, 2001). The consequent restriction of gene flow has been connected with an increased rate of speciation in some nonplanktotrophic lineages (e.g. *Littorina*; Reid, 1996). Nevertheless, our sampling of five localities across the wide geographical range yielded no evidence of cryptic species in *C. conica*.

Our study has therefore increased the likely global diversity of *Cerithideopsilla* from five to 16 species, matching increases demonstrated in similar studies of other potamidid genera (ten to 15 spp. of *Cerithidea*, Reid *et al*., 2013; one to three spp. of *Cerithideopsis*, Reid & Claremont, 2014). Of these, seven appear to have been named (Table 1) while the others will be described elsewhere.

Geographical distribution of *Cerithideopsilla* species

The genus is distributed largely within tropical latitudes, although *C. conica* extends through much of the Mediterranean and *C. cingulata* D is entirely extratropical in the East China Sea and southern Japan. Everywhere, it is restricted to continental margins with high nutrient levels and to large high islands on or near to (e.g. Ryukyu Islands) the continental shelf. The absence of *Cerithideopsilla* species from the 'eastern Indonesian corridor' (the oceanic area of low primary productivity between Sulawesi and New Guinea, including the Banda Sea; Reid *et al*., 2006) is striking. Distributions in this area are not very well known, but nevertheless this absence is apparently not a sampling artefact, because other mangrove-associated molluscs from the area are well represented in museum collections (Reid, 1986, 2014). A similar avoidance of this region of low productivity has been reported in littorinids with distributions of a 'continental' type (e.g. *Littoraria articulata*, Reid, 1986; *Echinolittorina malaccana*, Reid *et al*., 2006; Reid, 2007).

The distributions of individual *Cerithideopsilla* species are at the scale of seas within ocean basins. Although the determinants of range size in the sea are complex and debated (e.g. Lester *et al*., 2007), this is consistent with the rough correlation between range and length of larval life in gastropods (Paulay & Meyer, 2002, 2006). Other gastropods with a comparable larval life of around 3 weeks or less show patterns of similar scale (e.g. Williams & Reid, 2004; Williams *et al*., 2011; Reid *et al*., 2013), in contrast with the much wider trans-oceanic scale of those with longer pelagic life (e.g. Reid *et al*., 2010; Claremont *et al*., 2011). There is, however, one obvious exception: *C. conica* is the only member of the genus with nonplanktonic development, yet has a distribution far larger than any congener. This suggests that another means of dispersal could be at work.

Allopatry, overlap and possible dispersal by birds

The distributions of *Cerithideopsilla* species show a geographical signal that implies allopatric or parapatric speciation, as in other studies of diversification in mud-flat and mangrove-associated animals (Shih & Suzuki, 2008; Shih *et al*., 2009; Yin *et al*., 2009; Reid *et al*., 2010, 2013; Golding, 2012; Chen *et al*., 2014; Polgar *et al*., 2014; Reid & Claremont, 2014) and in the marine realm in general (Bellwood *et al*., 2012; Bowen *et al*., 2013). Nevertheless, four of the six sister-species pairs (including one trichotomy) show extensive overlap (100% of the range of the more narrowly distributed member of each pair). This contrasts with the situation in the tree-climbing sister genus *Cerithidea*, in which there is no overlap between sisters, but only between clades with differences in microhabitat, suggesting possible maintenance of the mosaic pattern by competitive interactions (Reid *et al*., 2013). There is little ecological information about the sediment-dwelling *Cerithideopsilla* species but, where members of the different species groups (*C. alata*, *C. incisa*, *C. cingulata*, *C. conica*) are sympatric, they tend to occupy different microhabitats in terms of sediment grain size, shading by trees, tidal level and salinity (Wells, 1985; Maki *et al*., 2002; Plaziat & Younis, 2005). Nevertheless, they appear to be opportunistic and fast-growing snails that occasionally occur at extremely high densities in natural habitats (up to 4800 m^{-2}; Vohra, 1970; Balaparameswara Rao &

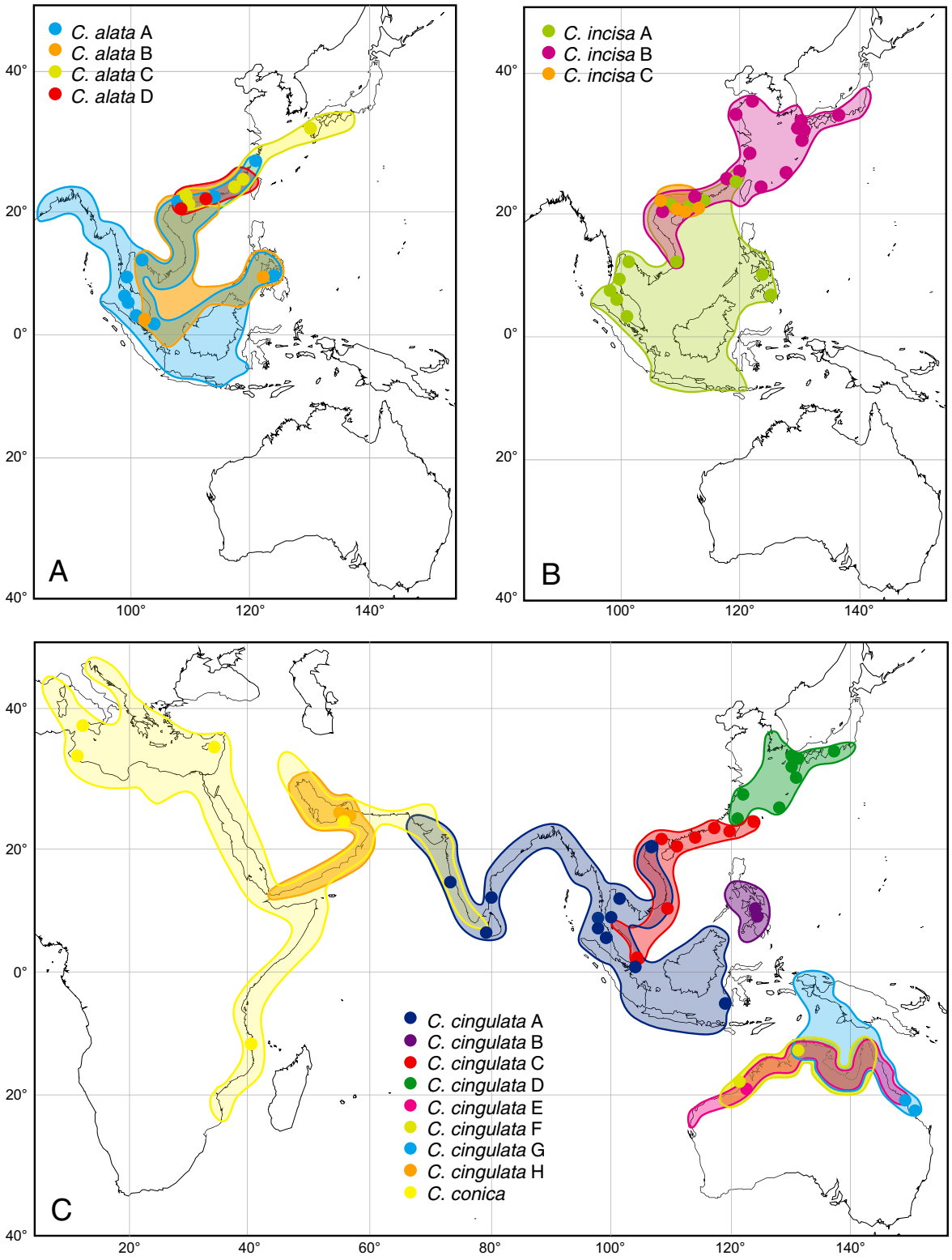

Figure 3. Distribution maps of *Cerithideopsilla* species (for phylogenetic relationships see Figure 1; colour coding of species is the same in both figures). Coloured spots indicate localities of sequenced specimens (see Table S1 for details). Coloured areas indicate extent of geographical distribution of each species along coastlines, as determined from live-collected shells in museum collections. Note that *C. conica* also occurs in inland saline lakes in northern Egypt, central Iraq and southern Pakistan.

Sukumar, 1982; Wells, 1985; Maki *et al*., 2002; Ando & Tomiyama, 2005), which could imply that resources are seldom limiting, and thus that competition between sister species is low.

The contrast between *Cerithideopsilla* (found in high densities on open sediment) and *Cerithidea* (found mainly on and beneath mangrove vegetation, in low densities) has another important consequence. Migratory wading birds forage on intertidal flats and have been implicated in the long-distance transport of potamidid snails. In an indirect, but persuasive, example, Miura *et al*. (2012) showed that haplotypes of *Cerithideopsis* have crossed the Central American Isthmus at least twice between 13 000 and 1 100 000 years ago. Since this age postdates the latest marine connection (1.9 Ma) and predates human activity, birds are the only likely vector. Successful establishment across the isthmus may be highly unlikely, but becomes probable over such a long time scale. In the Middle East and North Africa, the euryhaline *C. conica* can be found in saline lakes that have never had a direct connection with the open sea. During the Holocene, predating possible human transport, it lived in lakes of the Sahara up to 900 km from the sea; again, transport by birds has been suggested (Lozouet, 1986; Plaziat, 1993). From the sister relationship of *C. conica* with the *C. cingulata* group, and from the fossil record of the genus in the Mediterranean, it has been deduced that the planktotrophic ancestor of *C. conica* reached the Mediterranean from the Indian Ocean during the Early or Middle Miocene (when marine connections across the Isthmus of Suez still existed). It has also been suggested that *C. conica* spread from the Mediterranean to the Indian Ocean during the Pleistocene, when it could have been transported across the uplifted isthmus by birds. This hypothesis was proposed by Reid *et al*. (2008) and is supported by our new evidence that *C. conica* is a single species across its range in the Mediterranean and Indian Ocean. In this case the nonplanktonic development of *C. conica* presumably facilitates passive dispersal and establishment, as in the nonplanktonic marine snail *Littorina saxatilis*, which readily establishes on distant oceanic islands (Johannesson, 1988). This could explain the counter-intuitive observation that *C. conica* has the widest geographical range of all *Cerithideopsilla*, despite being the only species known to have lost the pelagic larval stage. The means of transport by birds is a matter for speculation, but juvenile potamidids can survive ingestion by birds (Sousa, 1993) and there are many records of attachment of molluscs to feet and plumage (Rees, 1965).

It is possible, therefore, that the habitat and ecology of *Cerithideopsilla*, and consequent likelihood of dispersal by birds combined with low competition in a productive environment, can account for the often broad overlap between sister species. Wading birds often migrate over long distances, within defined corridors running north–south, termed 'flyways'. The distribution of *C. conica* in the Indian Ocean lies almost entirely within the 'West Asian–East Africa flyway' (Boere & Stroud, 2006). In eastern Asia, overlap between species within each of the three species groups of *Cerithideopsilla* is restricted largely to the north–south direction on the Pacific coast of the Asian mainland, within the route of the 'East Asian–Australasian flyway' (Boere & Stroud, 2006). The contiguous coastline of the eastern Asian mainland presumably also enhances dispersal through marine larvae. Our relatively coarse sampling does not reveal any obvious cases of long-distance or overland dispersal that can be explained solely by bird transport, and we have not found any evidence of genetic introgression in areas of overlap between sister species, as shown by Miura *et al*. (2010, 2012) in *Cerithideopsis*.

Endemicity and the geography of speciation

Areas of endemicity have been a focus of biogeographic study, not only because of their importance for provincial classification and conservation, but also for inferences about speciation. Narrow ranges of recently diverged species can indicate areas of origin (or of reliction of old species), and narrowly allopatric (or parapatric) ranges can indicate speciation across recognized geographical boundaries (Bellwood & Meyer, 2009; Reid *et al*., 2013). In *Cerithideopsilla* the geographical pattern is partly obscured by overlap of ranges. Nevertheless, there is some evidence of speciation within the classical high-diversity focus of the IAA, with one endemic in the Philippines and three forming a monophyletic radiation in northern Australia (*C. cingulata* B, E, F and G respectively). There is a phylogenetic division between the Australian endemics and the rest of the *C. cingulata* group, dated as 9.5 (6.2–13) Ma (D. G. Reid & M. Claremont, unpublished), for which there is a geographical and chronological parallel in *Cerithidea* (Reid *et al*., 2013) and another in *Cerithideopsis* (Reid & Claremont, 2014). In contrast to *Cerithidea*, all three species of *Cerithideopsilla* that occur in southern Borneo cross Wallace's Line to reach southern Sulawesi. This, and the absence of *Cerithideopsilla* from the Banda Sea mentioned above, suggests that the isolation of the Australian from Asian species is connected with unsuitable ecological conditions in the intervening region, rather than the isolating effect of the Indonesian Throughflow (Reid *et al*., 2013). The distributions and ages of *Cerithidea* species in the central IWP correspond in part with marine basins isolated during low sea level stands preceding the Plio-Pleistocene glaciations (Reid *et al*., 2013) but, with the exception

of *C. cingulata* B in the Philippines, this is not the case in *Cerithideopsilla*, although estimated ages of sister-species pairs are similar (range 2.5–6 Ma; D. G. Reid & M. Claremont, unpublished). Instead, the focal area of diversification in the latter is the East Asian coastline between Japan and the Malay Peninsula. Whether this indicates a fundamental difference in the drivers of diversification, or simply a stronger ecological preference for continental margins in *Cerithideopsilla*, is unknown.

It is recognized that patterns of speciation along linear continental margins may differ from those across two-dimensional island groups, in particular because contiguous coastlines facilitate range extension, so that opportunities for allopatric isolation are likely to be less frequent and of shorter duration (Hellberg, 1998; Williams & Reid, 2004; Williams *et al*., 2011). On coastlines running north–south, range endpoints tend to cluster at recognized biogeographic boundaries, which often correspond with thermal and physical discontinuities. In *Cerithideopsilla* species, for example, a cluster of three endpoints occurs in the northern Taiwan Strait, 6 between the Gulf of Tonkin and Hong Kong, and one in south-central Vietnam. The first of these is a major boundary between the temperate Northern Pacific and tropical Central Indo-Pacific biogeographic realms, the second corresponds approximately with a boundary between ecoregions and the third is a significant junction between the South China Sea and Sunda Shelf biogeographic provinces (Spalding *et al*., 2007). Of these, the third matches known endpoints in the sister genus *Cerithidea* (Reid *et al*., 2013; Reid, 2014) and the second an endpoint in *Cerithideopsis* (Reid & Claremont, 2014). These boundaries, and the ranges they circumscribe, also find parallels in the distributions of crab species from mangrove and mudflat habitats in the northwestern Pacific (Shih & Suzuki, 2008; Shih *et al*., 2009; Yin *et al*., 2009), and even in gastropods from intertidal rocky shores (Williams & Reid, 2004; Frey, 2010; Williams *et al*., 2011). It remains unclear to what extent modern biogeographic boundaries also correspond with historical barriers that have driven speciation (Marko, 1998). Speciation along the East Asian coast has been explained in terms of vicariance caused by changes in global sea level and temperature (e.g. Yin *et al*., 2009; Tang *et al*., 2010; Shen *et al*., 2011; Chen *et al*., 2014). For example, during episodes of low sea level (during the Plio-Pleistocene and earlier) the East China Sea was largely exposed and Taiwan was connected with the mainland (Yin *et al*., 2009; Shen *et al*., 2011). In *Cerithideopsilla*, there are at least two cases of sister relationships between species (or clades) centred in the East China Sea and South China Sea (i.e. *C. incisa* A + C versus B; *C. cingulata* C + B versus D), suggesting that their divergence may have been driven by isolation in northern and southern refugia at times of low sea level. The Taiwan Strait between these seas remains a major biogeographic boundary. The search for general historical patterns, however, must await a more rigorous analysis of correspondence between times of species divergence, environmental change and the fossil record. (So far, within *Cerithideopsilla*, only the origin and dispersal of *C. conica* have been considered from a combined phylogenetic and palaeontological perspective; Reid *et al*., 2008.) Meanwhile, it is clear that East Asia has been a centre of speciation in coastal habitats from the Late Miocene to the Plio-Pleistocene, producing numerous narrow-range endemics.

In *Cerithideopsilla*, this diversification in East Asia, combined with apparent post-speciation dispersal – possibly by birds as well as by planktonic larvae – has resulted in an extraordinary accumulation of nine species (56% of the 16 known) in a narrow area between the Gulf of Tonkin and Hong Kong. Southern China is therefore of special significance in the evolution and conservation of these snails.

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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 *Cerithideopsilla* species produced by MrBayes analysis of 16S rRNA sequences, using *Cerithidea* 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. Coloured boxes indicate proposed taxonomic species (colour coding as in Figs 1, 2 and Fig. S2).

Figure S2. Molecular phylogeny of *Cerithideopsilla* species produced by MrBayes analysis of 28S rRNA sequences, using *Cerithidea* 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. Coloured boxes indicate proposed taxonomic species (colour coding as in Figs 1, 2 and Fig. S1).

Table S1. Specimens of *Cerithideopsilla* (abbreviated *C.*) used in this study, with location of vouchers and 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); Fudan Zoological Museum, Fudan University, Shanghai (FDZM); Berlin Museum of Natural History (ZMB); Muséum Nationale d'Histoire Naturelle, Paris (MNHN). Vouchers from the collection of T. Ozawa are deposited in NHMUK. GenBank accession numbers beginning with AM were published by Reid *et al*. (2008) and 16S sequences of the four *Cerithidea* species (used here as outgroup taxa) by Reid *et al*. (2013). Species identification is based on the clades indicated by the analyses of COI sequences (Fig. 1); the seven individuals lacking COI data are assigned on the basis of 16S or 28S sequences, as indicated.

Table S2. Uncorrected pairwise distances between and within ESUs of *Cerithideopsilla* (based on 579 positions of COI). Values on the diagonal are distances within ESUs.

Table S3. Sequence variation in alignment of 1332 bp of 28S rRNA within each of three groups of *Cerithideopsilla* (*C. alata* group, *C. cingulata* group. *C. incisa* group). ESUs within groups are indicated by letters (see Table S1).