Zoologica Scripta

KUNGL. VETENSKAPS-AKADEMIEN
THE ROYAL SWEDISH ACADEMY OF SCIENCES

Towards a phylogenetic classification of reef corals: the Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae)

Danwei Huang, Francesca Benzoni, Roberto Arrigoni, Andrew H. Baird, Michael L. Berumen, Jessica Bouwmeester, Loke Ming Chou, Hironobu Fukami, Wilfredo Y. Licuanan, Edward R. Lovell, Rudolf Meier, Peter A. Todd & Ann F. Budd

Submitted: 10 February 2014
Accepted: 28 April 2014
doi:10.1111/zsc.12061

Huang D., Benzoni F., Arrigoni R., Baird A.H., Berumen M.L., Bouwmeester J., Chou L.M., Fukami H., Licuanan W.Y., Lovell E.R., Meier R., Todd P.A., Budd A.F. (2014). Towards a phylogenetic classification of reef corals: the Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae). — *Zoologica Scripta*, *43*, 531–548.

Recent advances in scleractinian systematics and taxonomy have been achieved through the integration of molecular and morphological data, as well as rigorous analysis using phylogenetic methods. In this study, we continue in our pursuit of a phylogenetic classification by examining the evolutionary relationships between the closely related reef coral genera *Merulina*, *Goniastrea*, *Paraclavarina* and *Scapophyllia* (Merulinidae). In particular, we address the extreme polyphyly of *Favites* and *Goniastrea* that was discovered a decade ago. We sampled 145 specimens belonging to 16 species from a wide geographic range in the Indo-Pacific, focusing especially on type localities, including the Red Sea, western Indian Ocean and central Pacific. Tree reconstructions based on both nuclear and mitochondrial markers reveal a novel lineage composed of three species previously placed in *Favites* and *Goniastrea*. Morphological analyses indicate that this clade, *Paragoniastrea* Huang, Benzoni & Budd, gen. n., has a unique combination of corallite and subcorallite features observable with scanning electron microscopy and thin sections. Molecular and morphological evidence furthermore indicates that the monotypic genus *Paraclavarina* is nested within *Merulina*, and the former is therefore synonymised.

Corresponding author: *Danwei Huang, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA 52242, USA. E-mail: huangdanwei@nus.edu.sg*

Danwei Huang, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA, 52242, USA and Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA and Department of Biological Sciences, National University of Singapore, Singapore 117543, Singapore. E-mail: huangdanwei@nus.edu.sg

Francesca Benzoni and Roberto Arrigoni, Department of Biotechnology and Biosciences, University of Milano-Bicocca, Piazza della Scienza 2, 20126, Milan, Italy. E-mails: francesca.benzoni@unimib.it, roberto.arrigoni@unimib.it

Andrew H. Baird, ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, 4811, Australia. E-mail: andrew.baird@jcu.edu.au

Michael L. Berumen and Jessica Bouwmeester, Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Jeddah, 23955, Kingdom of Saudi Arabia. E-mails: michael.berumen@kaust.edu.sa, jessica.bouwmeester@kaust.edu.sa

Loke Ming Chou, Department of Biological Sciences, National University of Singapore, Singapore 117543, Singapore. E-mail: dbsclm@nus.edu.sg

Hironobu Fukami, Department of Marine Biology and Environmental Science, University of Miyazaki, Miyazaki, 889-2192, Japan. E-mail: hirofukami@cc.miyazaki-u.ac.jp

Wilfredo Y. Licuanan, Br. Alfred Shields FSC Ocean Research Center and Biology Department, De La Salle University, Manila, 1004, The Philippines. E-mail: wilfredo.licuanan@dlsu.edu.ph

Edward R. Lovell, School of Marine Studies, University of the South Pacific, Laucala Campus, Suva, Fiji. E-mail: lovell.fiji@gmail.com

Rudolf Meier and Peter A. Todd, Department of Biological Sciences, National University of Singapore, Singapore 117543, Singapore. E-mails: dbsmr@nus.edu.sg, dbspat@nus.edu.sg
Ann F. Budd, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, IA 52242, USA. E-mail: ann-budd@uiowa.edu

Introduction

Merulinidae Verrill, 1865 is a reef coral family that comprises 139 species in 24 genera (Huang *et al.* 2014a; see also Veron 2000). It is widely distributed throughout the Indo-Pacific and Caribbean, but absent in the eastern Pacific. Many merulinid species are among the most ecologically dominant reef corals in various regions of the world (Goreau 1959; Veron *et al.* 1977; Chen 1999; Bellwood & Hughes 2001; Huang *et al.* 2014b).

Initially included within Fungacea by Verrill (1865), Merulinidae (type genus *Merulina*; see Table 1 for classification and authorities of genera mentioned in this study) was not recognised as a valid family by subsequent authors (Quenstedt 1881; Quelch 1886; Vaughan 1918; Hoffmeister 1925; Faustino 1927; Matthai 1928; Yabe *et al.* 1936), until Vaughan & Wells (1943) revived it to include *Merulina*, *Boninastrea*, *Clavarina* and *Scapophyllia* (see also Wells 1956). This arrangement became convention through the use of this classification in Veron & Pichon (1980) and Veron (1985, 1986, 2000). Minor modifications were proposed by Veron (1985) who added *Hydnophora* and *Paraclavarina* to the family and synonymised *Clavarina* with *Merulina* (Table 1; see also Umbgrove 1940; Chevalier 1975).

Table 1 List of genera mentioned in the text (see also Huang *et al.* 2014a)

Genus	Authority
Family Merulinidae	
Merulina	Ehrenberg, 1834: 328
Astrea	Lamarck, 1801: 371
Barabattoia (junior synonym of *Dipsastraea*)	Yabe & Sugiyama, 1941: 72
Boninastrea	Yabe & Sugiyama, 1935: 402
Clavarina (junior synonym of *Merulina*)	Verrill, 1864: 56
Coelastrea	Verrill, 1866: 32
Dipsastraea	de Blainville, 1830: 338
Favites	Link, 1807: 162
Goniastrea	Milne Edwards & Haime, 1848: 495
Hydnophora	Fischer von Waldheim, 1807: 295
Orbicella	Dana, 1846: 205
Paraclavarina	Veron, 1985: 179
Paramontastraea	Huang & Budd in Huang *et al.* 2014a
Phymastrea (junior synonym of *Favites*)	Milne Edwards & Haime, 1848: 494
Scapophyllia	Milne Edwards & Haime, 1848: 492
Trachyphyllia	Milne Edwards & Haime, 1848: 492
Family Montastraeidae	
Montastraea	de Blainville, 1830: 339
Family Mussidae	
Favia	Milne Edwards & Haime, 1857: 426

In the last decade, phylogenetic analyses employing molecular (Fukami *et al.* 2004b, 2008; Huang *et al.* 2009, 2011; Benzoni *et al.* 2011; Arrigoni *et al.* 2012) and morphological (Huang *et al.* 2009; Budd & Stolarski 2011; Budd *et al.* 2012) data have revealed that this conventional grouping masks the evolutionary relationships of its constituent genera. Indeed, the taxon is polyphyletic and nested within a clade popularly known as 'Bigmessidae' (Budd 2009), which also includes species from Faviidae, Pectiniidae and Trachyphylliidae (Huang *et al.* 2011). Based on molecular phylogenies by Fukami *et al.* (2008) and Huang *et al.* (2011), as well as morphology at the corallite and subcorallite scales (Budd & Stolarski 2011), Merulinidae was expanded to include all members of 'Bigmessidae' – Faviidae was demoted to subfamily Faviinae as a group limited to the Atlantic, and the remaining two families were synonymised (Budd *et al.* 2012).

At the genus level, the polyphyly of *Favia*, *Favites*, *Goniastrea* and *Montastraea* as traditionally delineated has been a considerable hurdle for taxonomic revisions (Huang *et al.* 2011). Fortunately, a phylogenetic classification started to emerge with the resurrection of *Dipsastraea* (Pacific '*Favia*'), *Phymastrea* (Pacific '*Montastraea*') and *Orbicella* ('*Montastraea*' *annularis* complex; Budd *et al.* 2012). To eliminate most of the polyphyly in the above genera, Huang *et al.* (2014a) enacted further changes, that is, synonymising *Barabattoia* and *Phymastrea* as *Dipsastraea* and *Favites*, respectively, resurrecting *Astrea* and *Coelastrea* and establishing a new genus, *Paramontastraea* (Table 1).

Challenges remain in *Favites* and *Goniastrea*, however, as *F. russelli* and *G. australensis* render their respective genera paraphyletic, but these have yet to be revised due to uncertain phylogenetic placements and insufficient sampling (Huang *et al.* 2011). *Merulina*, *Goniastrea* and *Scapophyllia* also remain entangled and unresolved within a major merulinid subclade (A *sensu* Budd & Stolarski 2011; Huang *et al.* 2011, 2014a). Furthermore, specimens used in recent phylogenetic reconstructions of Merulinidae were mostly

© 2014 Royal Swedish Academy of Sciences, **43**, 5, September 2014, pp 531–548

samples collected outside of species' type localities. Given that Fukami *et al.* (2008) and Huang *et al.* (2009, 2011) recovered different interspecific relationships, it is also possible that some samples were misidentified by one or the other team. Both teams have joined efforts here to resolve these inconsistencies.

In this study, we present a phylogenetic analysis of the merulinid genera in subclade A, *Merulina*, *Goniastrea*, *Paraclavarina* and *Scapophyllia*, based on nuclear and mitochondrial DNA sequences. To avoid misidentifications, we include samples collected from type localities and compare the present collection with type material. We also examine corallite and subcorallite skeletal morphology in search of diagnostic characters for clades (see Cuif *et al.* 2003; Forsman *et al.* 2009, 2010; Kitahara *et al.* 2012, 2013; Luck *et al.* 2013; Marti-Puig *et al.* 2014; Schmidt-Roach *et al.* 2014). Our results show that *Goniastrea australensis*, *G. deformis* and *Favites russelli* constitute a novel clade with unique morphological features, resulting in the establishment of a new genus *Paragoniastrea* Huang, Benzoni & Budd. The separation of *Paraclavarina* from *Merulina* is also deemed unnecessary, and the former is thus synonymised.

Material and methods

Molecular

Corals were sampled from a large proportion of Merulinidae's geographic range in the Indo-Pacific, extending from Saudi Arabia in the Red Sea to Fiji in the central Pacific (Table S1). Species identifications followed original descriptions, aided by Veron *et al.* (1977), Veron & Pichon (1980, 1982) and Veron (1986, 2000, 2002), and species delimitations were based on the phylogenetic (diagnosable) species concept (Nelson & Platnick 1981; Cracraft 1983; Nixon & Wheeler 1990; see also de Queiroz 2005a,b,c, 2007). In total, 145 specimens spanning 16 species were collected for this study (Table S1). These belong to *Coelastrea*, *Favites*, *Goniastrea*, *Merulina*, *Paraclavarina* and *Scapophyllia*, which are primarily associated with subclades A and B according to Budd & Stolarski (2011) and Huang *et al.* (2011).

We photographed each colony in the field and collected between 10 and 100 cm^2 of coral from each colony using a hammer and chisel, with ~2 cm^2 of tissue preserved in 100% ethanol or CHAOS solution (Sargent *et al.* 1986; Fukami *et al.* 2004a; Huang *et al.* 2008; Nunes *et al.* 2008, 2009). The rest of the colony sample was cleaned with a powerful water jet prior to being bleached in dilute sodium hypochlorite. The skeletons were rinsed in fresh water, dried and deposited at the Lee Kong Chian Natural History Museum (LKCNHM, Singapore; specimens with HD code), University of the Philippines Marine Science Institute (UP, the Philippines; TB code), Museum of Tropical Queensland (MTQ, Australia; GB, LH and SL codes), King Abdullah University of Science and Technology (KAUST, Saudi Arabia; SA code), Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO, USA; FJ and SC codes), University of Miyazaki Division of Fisheries Science (MUFS, Japan; JP code), Kyoto University Seto Marine Biological Laboratory (SMBL, Japan; JP code) and University of Milano-Bicocca (UNIMIB, Italy; DJ, MY, NC and PFB codes).

DNA extraction and polymerase chain reaction (PCR) protocols followed Huang *et al.* (2011). Three molecular markers were amplified and directly sequenced from the samples, namely the nuclear histone H3 (Colgan *et al.* 1998), nuclear internal transcribed spacers 1 and 2 (ITS; including 5.8S rDNA, with only one chromatogram peak detected per sample; Takabayashi *et al.* 1998a,b; see also Chen *et al.* 2004; Forsman *et al.* 2005) and mitochondrial non-coding intergenic region (IGR; between cytochrome oxidase subunit I and the formylmethionine transfer RNA gene; Fukami *et al.* 2004a). Sequences were organised into three separate data matrices using Mesquite 2.75 (Maddison & Maddison 2011). The histone H3 data set was supplemented with all sequences from Huang *et al.* (2011), while 13 other species across the Merulinidae clade were included as out-groups for the ITS and IGR data sets (Table S1). Alignments were carried out using the E-INS-i option in MAFFT 7.110 (Katoh *et al.* 2002, 2009; Katoh & Toh 2008; Katoh & Standley 2013) under default parameters. Phylogenetic reconstructions were performed separately for each marker and also on the concatenated data set partitioned by gene.

Three phylogenetic tree optimality criteria were employed. First, maximum likelihood trees were inferred using RAxML 7.7.9 (Stamatakis 2006; Stamatakis *et al.* 2008) with the GTRGAMMA model and 50 random starting trees. Multiparametric bootstrap analyses were carried out using 1000 bootstrap replicates. Second, for Bayesian analyses, we determined the most suitable model of molecular evolution for each gene partition using jModelTest 2.1.4 (Guindon & Gascuel 2003; Posada 2008; Darriba *et al.* 2012), testing for a total of 24 models based on the Akaike Information Criterion (AIC). Bayesian inferences were carried out in MrBayes 3.2.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist *et al.* 2012). Four Markov chains of 6 million generations were implemented in two runs, logging one tree per 100 generations. MCMC convergence among runs was monitored using Tracer 1.5 (Rambaut & Drummond 2009), which determined that the first 10001 trees from each analysis were to be discarded as burn-in. Third, under the maximum parsimony framework, heuristic searches in

PAUP* 4.0b10 (Swofford 2003) were carried out with 10000 random additions. Nodal supports were assessed using 1000 bootstrap replicates (100 random additions per replicate).

Morphology

Coral skeletal structure was examined using methods described by Budd & Stolarski (2009, 2011). Morphological features from three scales – macromorphology, micromorphology and microstructure – were the basis of taxonomic classifications proposed by Budd *et al.* (2012) and Huang *et al.* (2014a).

Briefly, observations of macromorphology were made using a stereomicroscope to study the structure and development of the colony, calice, septa, columella, theca and coenosteum (Vaughan & Wells 1943; Wells 1956; Beauvais *et al.* 1993; Johnson 1998; Wallace 1999; Budd & Smith 2005; Huang *et al.* 2009). Micromorphology was visualised via scanning electron microscopy (SEM) at magnifications <200× of calices mounted on stubs (Budd & Stolarski 2009, 2011), revealing the shapes of teeth along the wall, septa, columella and septal face granulations (Hoeksema 1989; Beauvais *et al.* 1993; Cuif & Perrin 1999; Cuif *et al.* 2003; Budd & Smith 2005). For microstructure, each calice was cut transversely, impregnated with epoxy and sectioned to a thickness of ~30 μm prior to visualisation under a stereo or light microscope at magnifications <100× (Budd & Stolarski 2009, 2011). The resulting thin sections enabled the examination of rapid accretion deposits and thickening deposits or fibres within the wall, septa and columella (Alloiteau 1952; Chevalier & Beauvais 1987; Beauvais *et al.* 1993; Stolarski & Roniewicz 2001; Cuif *et al.* 2003; Stolarski 2003; Nothdurft & Webb 2007; Brahmi *et al.* 2010; Cuif 2010).

Morphological data for 12 of the 16 species examined here were derived from the 44-character matrix in Huang *et al.* (2014a). The remaining four species were characterised for macromorphology; micromorphology was examined for *G. minuta* Veron, 2000, *Merulina scheeri* Head, 1983 and *Paraclavarina triangularis* (Veron & Pichon, 1980), with the latter further characterised for microstructure. In addition to vouchers deposited in the institutions mentioned earlier, specimens and type material from the following museums were studied: Hunterian Museum and Art Gallery, University of Glasgow (GLAHM, UK); Muséum national d'Histoire naturelle de Paris (MNHN, France); MTQ; Natural History Museum, London (NHMUK, UK); Naturalis Biodiversity Center (RMNH, the Netherlands); Paleontology Repository, University of Iowa (SUI, USA); Tôhoku Imperial University (TIU, Japan); Florida Museum of National History, University of Florida (UF, USA); National Museum of Natural History, Smithsonian Institution (USNM, USA); Yale Peabody Museum of Natural History (YPM, USA); and Museum für Naturkunde, Berlin (ZMB, Germany). All specimens illustrated here for micromorphology and microstructure are figured for the first time and designated as hypotypes. The morphological matrix, here with 16 in-group and 12 out-group species (similar to the ITS and IGR data), was analysed via maximum parsimony as described earlier to infer apomorphies for the novel clade.

Results

Three aligned DNA data sets were assembled and analysed (Data S1). The histone H3 data consist of 375 base pairs (bp; 77 parsimony-informative characters, or PICs) represented by 247 tips. The ITS data contain 970 bp (282 PICs) from 150 taxa, and the IGR data comprise 1226 bp (484 PICs) from 144 taxa. The best nucleotide substitution models are K80 + G for histone H3, GTR + I + G for ITS and GTR + G for IGR. Due to conflict in topology between the IGR and nuclear gene trees, we focus on the results of each gene rather than the concatenated analysis (Fig. S1).

The broad-based histone H3 tree recovered the same groups as before (Huang *et al.* 2011), including the clades Diploastraeidae + Montastraeidae, Merulinidae and Lobophylliidae, although only the latter is considered well supported (Fig. 1). All of the Merulinidae subclades defined by Budd & Stolarski (2011) and Huang *et al.* (2011), except D/E, are supported by all optimality criteria – maximum likelihood, Bayesian and parsimony. *Merulina ampliata* (Ellis & Solander, 1786), the name-bearing type of the family, is nested within the well-supported subclade A, which comprises most of the taxa collected for this study – *Merulina*, *Paraclavarina*, *Scapophyllia* and most of *Goniastrea*. Species falling out of subclade A include *Coelastrea aspera* and *C. palauensis*, which were extracted from *Goniastrea* by Huang *et al.* (2014a) for their positions in subclade B, as well as *G. australensis* and *G. deformis* that form a clade with *F. russelli* and an unidentified *Favites* species.

The nDNA ITS tree contains the same Merulinidae subclades above, but with better resolution (Fig. 2). *Goniastrea* within subclade A is an unsupported monophyletic group, while *Merulina* is polyphyletic and split into three clades. Only *M. scheeri* forms a well-supported group, sister to several *M. scabricula* sequences with *P. triangularis* nested within. The remaining *M. scabricula* terminals are indistinguishable from *M. ampliata* in the deepest-branching clade of subclade A.

Analyses based on the mtDNA IGR marker recovered nearly all of the ITS clades within subclade A, but with considerable topological differences (Fig. 2). Subclade A is split into two deeply divergent clades, with *G. retiformis*, *G. minuta* and *G. stelligera* within one (A1 + A2), and all

© 2014 Royal Swedish Academy of Sciences, **43**, 5, September 2014, pp 531–548

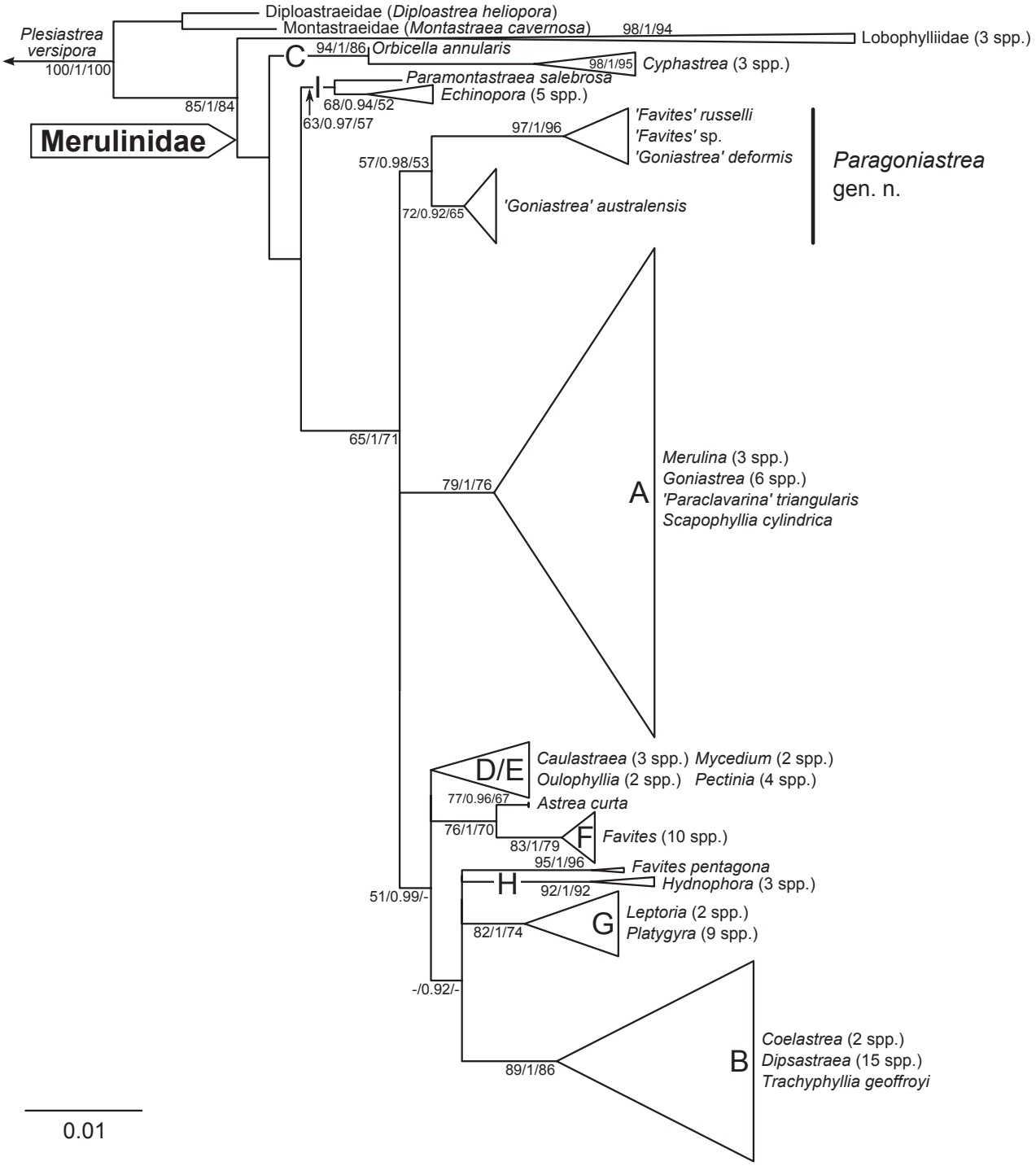

Fig. 1 Maximum likelihood phylogeny of the reef coral families Diploastraeidae, Montastraeidae, Merulinidae and Lobophylliidae (clades XV–XX *sensu* Fukami *et al.* 2008) based on the nuclear histone H3 gene. Subclades within Merulinidae are labelled A to I according to Budd & Stolarski (2011) and Huang *et al.* (2011), with vertical extent of clades proportional to sample size. Numbers adjacent to branches represent support values (maximum likelihood bootstrap ≥50/Bayesian posterior probability ≥0.8/maximum parsimony bootstrap ≥50; lower values of support not shown).

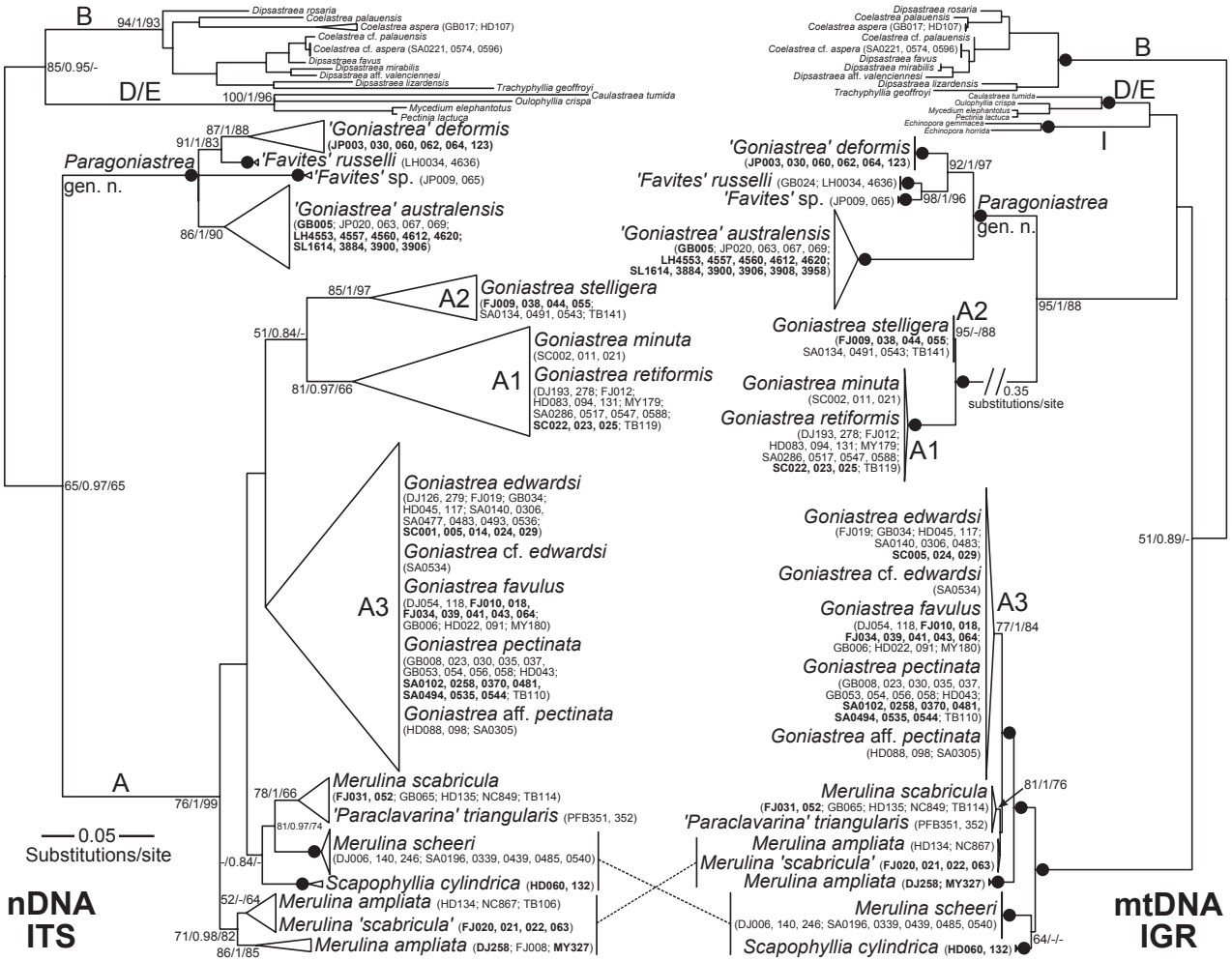

Fig. 2 Maximum likelihood phylogeny of *Merulina*, *Goniastrea* and *Scapophyllia* (subclade A *sensu* Budd & Stolarski 2011; Huang *et al.* 2011) based on the nuclear internal transcribed spacers (ITS; left) and the mitochondrial intergenic region (IGR; right). Clades are arranged in the same top-to-bottom order on both trees, except where indicated. Trees are rooted by *Paramontastraea salebrosa* (subclade I), with subclades B and D/E constituting other out-groups. Numbers adjacent to branches represent support values (maximum likelihood bootstrap ≥50/Bayesian posterior probability ≥0.8/maximum parsimony bootstrap ≥50; lower values of support not shown; major clades and in-group only). Filled circles indicate well-supported clades (bootstrap ≥98 and posterior probability of 1). Bold specimen numbers denote topotypic material.

other species in the second (including *Goniastrea* clade A3). The first clade, sister to *G. australensis* + *G. deformis* + *F. russelli* + *F.* sp., is subtended by an extremely long branch resulting partly from a 175-bp region in the middle of the IGR data set that was difficult to align for members of the clade (see Data S1). Removal of this region weakens the support for the grouping, which we regard as unreliable and thus defer to the nDNA trees for the placement of A1 + A2. Further differences between the ITS and IGR trees are evident in the relationships between *Merulina*, *Paraclavarina* and *Scapophyllia*.

The molecular grouping of *P. triangularis* with *M. scabricula* is supported by every morphological feature examined. The monotypic genus shares all character states with *Merulina*, including the <3 cycles of septa (<24 septa) per centre, thus uniting *Merulina* and *Paraclavarina* to the exclusion of *Scapophyllia* (see also Huang *et al.* 2014a).

None of the *Goniastrea* species within clades A1 and A3 can be distinguished via sequence similarity based on any of the three markers. Uncorrected intra- and interspecific pairwise distances (Srivathsan & Meier 2012) completely overlap for the nDNA ITS and mtDNA IGR sequences (Fig. 3). Not surprisingly, distances between the three *Goniastrea* clades (A1–A3) are generally larger. For IGR in particular, even the smallest interclade distances do not overlap with intra- or interspecific distances.

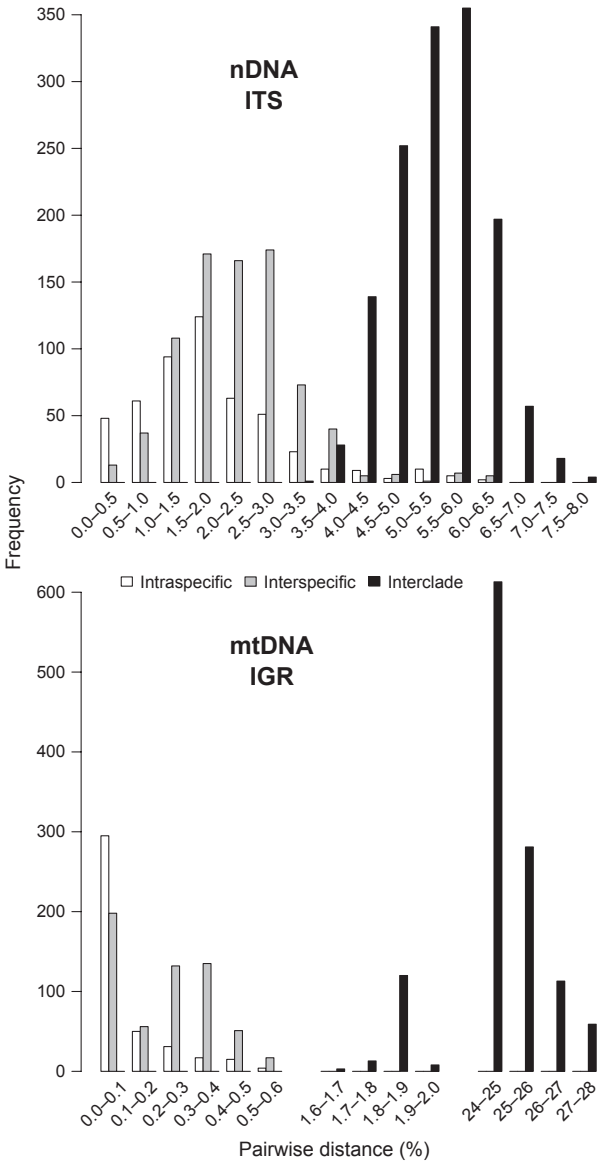

Fig. 3 Bar plots showing frequencies of uncorrected pairwise comparisons at each range of *Goniastrea* (excluding *G. australensis* and *G. deformis*) sequence divergence. Data for the nuclear internal transcribed spacers (ITS; top) and mitochondrial intergenic region (IGR; bottom) are portioned into distances within species (intraspecific), between species (interspecific) and among clades A1, A2 and A3 (interclade) as defined in Fig. 2. See text for the smallest interspecific distances (Meier *et al.* 2006, 2008).

As shown with the histone H3 tree, ITS and IGR place *Coelastrea* firmly within subclade B, most closely related to *Dipsastraea* and *Trachyphyllia*. Unexpectedly, sequences from Saudi Arabian specimens putatively identified as *C. aspera* and *C. palauensis* are distinct from those derived from the central Indo-Pacific.

The well-supported clade formed by *G. australensis*, *G. deformis* and *F. russelli* is present in all three reconstructions (Figs 1 and 2). The *Favites* species from Japan (JP009, JP065) is closely related to *F. russelli* and *G. deformis*, but morphologically, its septa and walls are not as irregular. They also exhibit no signs of separate walls and extremely thickened first-order costosepta (as in *F. russelli*), or 'groove and tubercle' formation (as in *G. deformis*). Overall, this novel clade is distinct from both *Goniastrea* and *Favites*, except in the case of the IGR tree, which recovers the long branch of three *Goniastrea* spp. as its sister group. However, morphological evidence at each of the three examined scales is unequivocal in uniting the new group to the exclusion of the rest of *Goniastrea* in having higher calice relief (3–6 mm), spongy columellae (>3 threads), internal lobes that are only uniaxial (paliform), greater septal tooth height (0.3–0.6 mm) and spacing (0.3–1 mm), walls formed by dominant paratheca without abortive septa and wider spacing between costal centre clusters (0.3–0.6 mm; Figs 4 and 5; see also Fig. S2).

Discussion

Molecular phylogeny

This study presents the most comprehensive phylogeny to date of Merulinidae subclade A (*sensu* Budd & Stolarski 2011), which comprises the family's type genus *Merulina*, as well as *Goniastrea*, *Paraclavarina* and *Scapophyllia*. Complete species sampling has been achieved for these genera except *Goniastrea*. The phylogenetic positions of *G. columella* Crossland, 1948; *G. ramosa* Veron, 2000; and *G. thecata* Veron, DeVantier & Turak, 2000 are still unknown, although they are probably related to either *Goniastrea* or the new clade recovered in this study (see Huang 2012; Huang & Roy 2013). Unfortunately, only skeleton material is known for *Boninastrea* (Best & Suharsono 1991), and no tissue samples are available.

Our results are based on nuclear markers histone H3 and ITS, as well as the mitochondrial IGR (Figs 1 and 2). The nuclear gene trees are congruent with each other, although higher resolution is achieved using the ITS (see Flot & Tillier 2006; Flot *et al.* 2008b). Between IGR and the nuclear markers, however, there are a number of conflicts, most notably in the placement of *Goniastrea* clade A1 + A2 and the position of *Echinopora* among the out-groups. Minor variations are also evident in the relationships between *Merulina* and *Scapophyllia* species. The extremely long branches produced by the mitochondrial data (e.g. the branch leading to A1 + A2) suggest an underlying problem with using certain mtDNA sequences as phylogenetic markers (Aranda *et al.* 2012; see also Flot *et al.* 2008a). Reconstruction using the concatenated data set gave mixed results – some parts of the combined

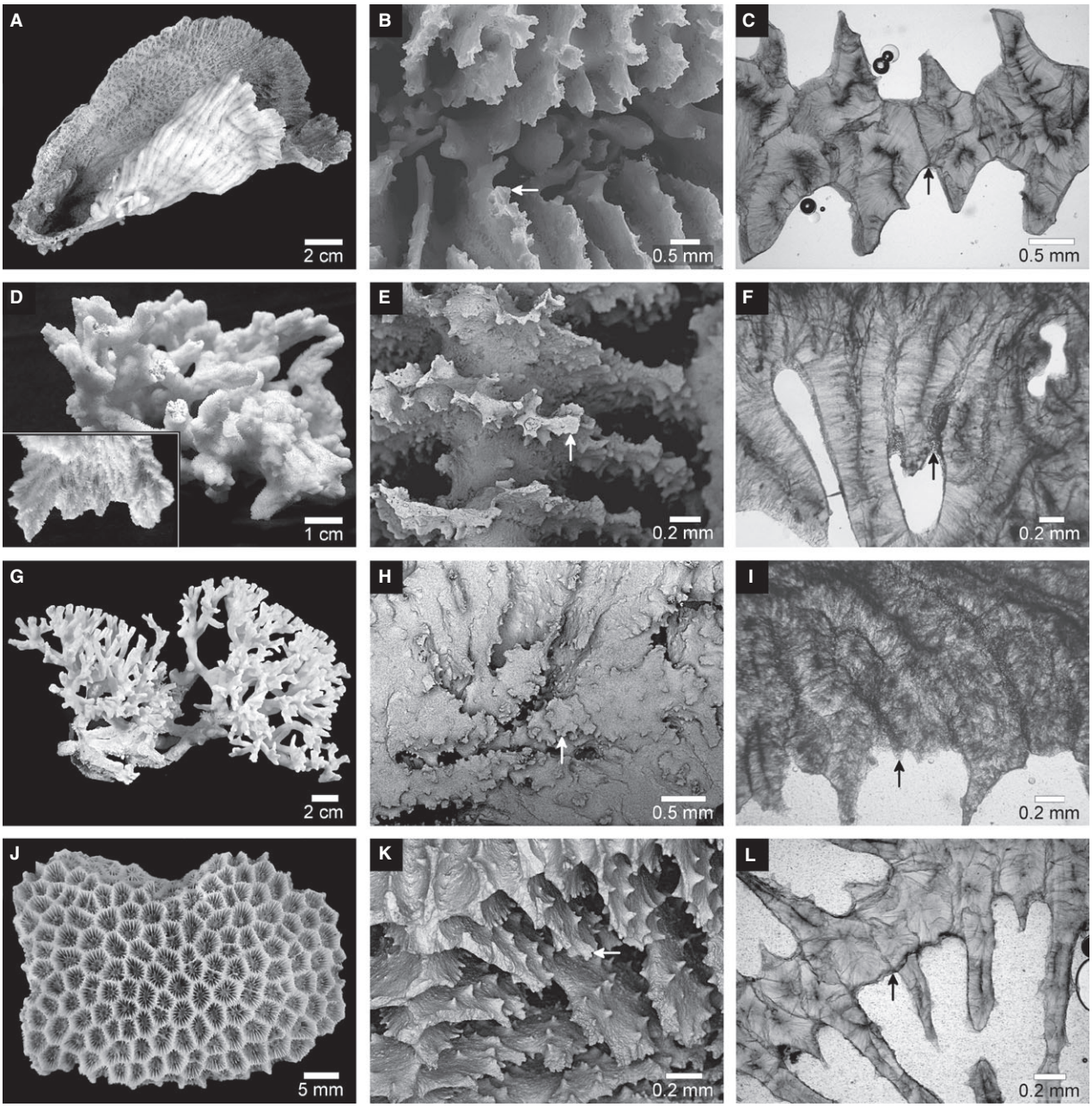

Fig. 4 Species in subclade A have small to medium calices (≤15 mm) that are of low relief (<3 mm), compact columellae and well-developed paliform lobes. Septal teeth (white arrows) are low (<0.3 mm) and narrowly spaced (<0.3 mm). Walls formed by strong abortive septa (black arrows). A–C. *Merulina ampliata* (Ellis & Solander, 1786) —A. Macromorphology, holotype GLAHM 104015, unknown locality (photograph by Kenneth Johnson) —B. Micromorphology (scanning electron microscopy), hypotype USNM 100519, Madagascar —C. Microstructure (transverse thin section), hypotype USNM 100519. D–F. *Merulina scabricula* Dana, 1846 —D. Macromorphology, syntypes YPM 1927A and 1927B (inset), Fiji —E. Micromorphology, hypotype USNM 93775, Madang, Papua New Guinea —F. Microstructure, hypotype USNM 93775. G–I. *Merulina triangularis* (Veron & Pichon, 1980) —G. Macromorphology, holotype NHMUK 1983.9.27.2, Bushy Island-Redbill Reef, Australia —H. Micromorphology, hypotype UNIMIB PFB351, Madang, Papua New Guinea —I. Microstructure, hypotype UNIMIB PFB351. J–L. *Goniastrea retiformis* (Lamarck, 1816) —J. Macromorphology, holotype MNHN IK-2010-693, unknown locality —K. Micromorphology, hypotype UP P1L02149, Batangas, the Philippines —L. Microstructure, hypotype UP P1L02149.

© 2014 Royal Swedish Academy of Sciences, **43**, 5, September 2014, pp 531–548

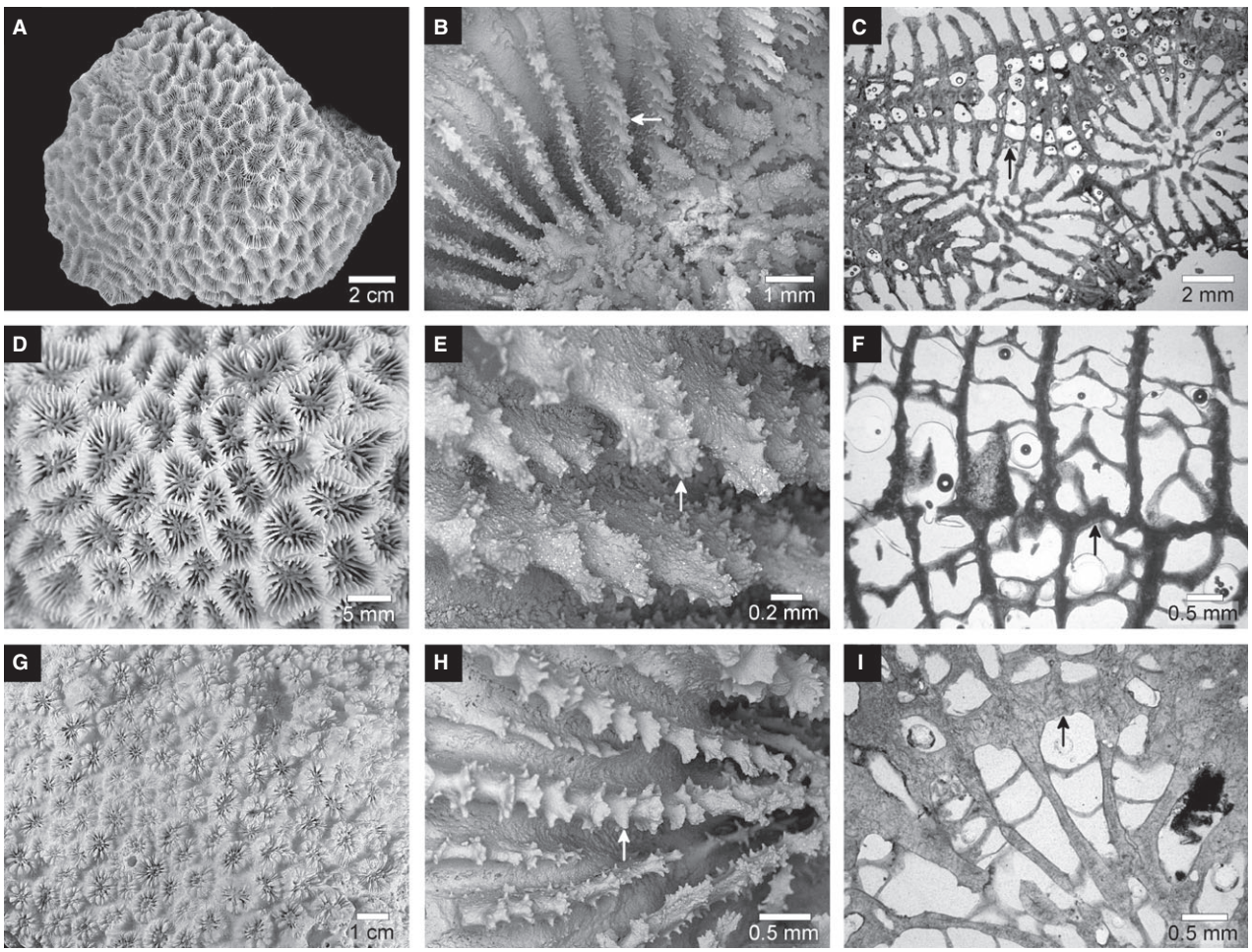

Fig. 5 *Paragoniastrea* Huang, Benzoni & Budd, this study, has medium-size (4–15 mm) and medium-relief (3–6 mm) calices, spongy columellae and well-developed paliform lobes. Septal teeth (white arrows) with medium height (0.3–0.6 mm) and spacing (0.3–1 mm). Walls formed by dominant paratheca (black arrows). A–C, E, F. *Paragoniastrea australensis* (Milne Edwards & Haime, 1857) —A. Macromorphology, holotype MNHN IK-2010-409, Australia —B, E. Micromorphology, hypotype MTQ G61876, Pelorus Island, Australia —C. Microstructure, hypotype MTQ G61876 —F. Microstructure, hypotype RMNH 14150, New Caledonia. D. *Paragoniastrea deformis* (Veron, 1990), macromorphology, holotype MTQ G32487, Kushimoto, Japan. G–I. *Paragoniastrea russelli* (Wells, 1954) —G. Macromorphology, holotype USNM 45004, Bikini Atoll, Marshall Islands —H. Micromorphology, hypotype MTQ G61895, Orpheus Island, Australia —I. Microstructure, hypotype MTQ G61895.

phylogeny are congruent with the ITS tree (e.g. *Echinopora*), and others agree with the IGR tree (e.g. exclusion of A1 + A2 from subclade A; Fig. S1). Nevertheless, we draw support for taxonomic changes only from well-supported relationships that are common among all markers.

Merulina, '*Paraclavarina*' and *Scapophyllia*

One of the most significant issues addressed by our study is the species boundaries of *M. ampliata*, in part because it is the type species of *Merulina*, but also because some specimens identified as *M. scabricula* are nested among its representatives. Note that these putative *M. scabricula* specimens were collected from the type locality of Fiji. On the one hand, this identification follows the original description of the syntype of *M. scabricula*, a branching colony with 'obtuse truncate extremities of the branches, as broad as below, and with the lamellae as close and even' (Dana 1846: 275; Fig. 4D). On the other hand, the primarily branching specimens close to this description (FJ020, FJ021, FJ022 and FJ063) form a clade with *M. ampliata* that is moderately supported on the ITS tree (Fig. 2) and thus should be considered as *M. ampliata* instead.

It is worth noting that taxonomists have had much difficulty differentiating these two species, for example 'les différences entre *M. scabricula* et *M. ampliata* n'ont pas été définies avec précision' (Chevalier 1975: 225).

Contemporary interpretations of *M. scabricula* tend to emphasis the 'lamellae' part of the description (Fig. 4D, inset), rather than the ramose form. None of the photographs and descriptions depicting this species in Veron's (1986, 2000) monographs display the latter morphology. Instead, the author sets the thin laminar colony of *M. scabricula* in contrast to the thicker and coarser skeleton of *M. ampliata* (Veron 2000). Our results support this view as the *M. scabricula* clade members comprising laminar colonies (FJ031, FJ052, GB065, HD135, NC849 and TB114) have thin and delicate theca and septa. We surmise that Dana's (1846) separation between the two species is accurate, but greater emphasis should be given to the thin laminar morphology rather than the branching patterns. *M. ampliata* is almost as likely as *M. scabricula* to have a ramose colony form despite the holotype exhibiting no branching at all (Fig. 4A).

The fully branching *P. triangularis* (Veron & Pichon, 1980), originally described in the context of currently synonymised genus *Clavarina*, has affinities to *M. scabricula*, which is the type species of *Clavarina* in the first place (Verrill 1864; Veron & Pichon 1980). However, Veron (1985) deemed *P. triangularis* to be distinct from *Merulina*. Our results show that this generic distinction is unnecessary because its close relationship with *M. scabricula* is well supported by both nuclear and mitochondrial markers (Fig. 2). Furthermore, there are no diagnosable morphological differences between *Merulina* and *Paraclavarina* (Fig. 4). The amount of ramosity and cross-sectional shape of tip branches have conventionally been used to separate *P. triangularis* from *Merulina* species (Veron 1986, 2000). Based on the original descriptions, branching intensities of colonies increase in the order of *M. scheeri*, *M. ampliata*, *M. scabricula* and *P. triangularis*. The latter is fully branching, but the type series of *M. scabricula* (Fig. 4D) and many *M. ampliata* specimens we analysed (e.g. FJ020, FJ021, FJ022 and FJ063) are almost entirely branched save for a reduced laminar base. Therefore, the extent of colony branching can neither be unambiguously traced on the phylogeny, nor reliably used to separate all species. *P. triangularis* is perhaps unique as a species in being completely branched, but this character confers limited utility to distinguish it at the genus level. Similarly, the 'three-pointed star-shaped' (Veron & Pichon 1980: 225) tip branches are used to describe *P. triangularis* (Veron 1986, 2000), yet *M. ampliata* (e.g. FJ020, FJ021, FJ022 and FJ063) and *M. scabricula* (e.g. syntypes USNM 165, YPM 1927A; Fig. 4D) also have triangular tip branches, albeit not nearly as sharply defined because of their thicker skeletons.

Integrating both molecular and morphological lines of evidence, we propose to move *Clavarina triangularis* Veron & Pichon, 1980 into *Merulina*. This follows Best & Suharsono (1991), who cogently expressed that, 'this bushy *Merulina* species is a distinct species, but to place it in a separate genus *Clavarina* Veron & Pichon, 1979 [*sic*] or *Paraclavarina* Veron, 1986 [*sic*], is not realistic if only based on the triangular form of the branches. *M. triangularis* branches show a triangular form at the periphery, but so do the branches in *M. scabricula*' (Best & Suharsono 1991: 339). We note that an alternate classification is to revive *Clavarina* for *C. scabricula* + *C. triangularis*, but this renders the taxon *Merulina* all the more indefensible because *M. ampliata* and *M. scheeri* are comparatively more distant to each other on both ITS and IGR trees.

The paraphyly of *Merulina* and *Scapophyllia* on all molecular trees remains a problem. However, the branch supports and lengths defining this grade are low on the ITS tree, and some clades are in conflict with the IGR topology (e.g. *M. ampliata* in the former and *M. scheeri* + *S. cylindrica* Milne Edwards & Haime 1849a in the latter). Therefore, we refrain from oversplitting these genera until nDNA-based trees with better resolution are available to test their interrelationships.

The Goniastrea clades

Goniastrea retiformis (Lamarck, 1816), the type species of *Goniastrea* Milne Edwards & Haime, 1848, is most closely related to *G. minuta* (clade A1; Fig. 2). Its sequences, including those collected from the type locality of Seychelles, are closely allied with those of *G. stelligera* (clade A2) including samples from the type locality, Fiji. This lends support to the new combination *G. stelligera* (Dana, 1846) first proposed by Huang *et al.* (2014a).

Goniastrea retiformis and *G. minuta* are indistinguishable from each other on the phylogeny. The main morphological character used by Veron (2000, 2002) to separate the two species is corallite size, but this trait showed extensive overlap. Deeper corals were observed to have smaller calices, within the range of 2–3 mm in diameter for *G. minuta*, but they also possessed larger ones. It is noteworthy that Milne Edwards & Haime (1849b) described Lamarck's (1816) holotype of *Astrea retiformis* as 'grande diagonale des calices, 3 millimètres environ' (Milne Edwards & Haime 1849b: 161). Their and our observations indicate that *G. retiformis* may possess small corallites comparable to *G. minuta* that Veron (2000, 2002) described. As it is likely that the type of *A. retiformis* Lamarck, 1816 was collected from the shore of Seychelles at a non-diving depth, we included a specimen from the Mahé intertidal (SC025) in the analysis. Expectedly, its sequences fell within clade A1 comprising both *G. retiformis* and *G. minuta* (Fig. 2). Nevertheless, we preserve the status of *G. minuta* because we were unable to examine samples from its type locality in Papua New Guinea.

© 2014 Royal Swedish Academy of Sciences, **43**, 5, September 2014, pp 531–548

Our analyses incorporated samples from the type localities for *G. edwardsi* (Seychelles; Chevalier 1971), *G. favulus* (Fiji; Dana 1846) and *G. pectinata* (Red Sea; Ehrenberg 1834). Two specimens in the same clade (HD088 and HD098) were previously identified as *G. australensis* (Huang *et al.* 2011), but evidently this name should apply to specimens in the novel clade (GB, LH and SL codes), which were collected mostly from the type locality of Australia. Specimens HD088 and HD098 from Singapore have consequently been reidentified as *Goniastrea* aff. *pectinata* (Fig. 2). All inferred trees further demonstrate the paraphyly of every species in this clade (A3; Fig. S3), but we preserve these species groups as they do form distinct morphotypes in the present collections (Fig. S4).

For *Goniastrea* clades A1 and A3, we caution against identifying species based on any of the markers used in this study. Even for the more variable ITS and IGR, intra- and interspecific distances within and among these species, respectively, overlap (Fig. 3). The lack of a 'barcoding gap' (*sensu* Meyer & Paulay 2005) for each of these markers is evident, and especially so because the smallest interspecific distance for every species is 0% for both markers, except for *G. edwardsi*'s most similar allospecific ITS sequence (0.98% vs. *G. favulus*). In other words, a *Goniastrea* specimen from clade A1 or A3 cannot be reliably identified to species based on either ITS or IGR because its sequence will match the wrong species virtually all the time (Meier *et al.* 2006, 2008). Until more variable markers become available for species in these clades, corallite macromorphology (Veron *et al.* 1977; Veron 1986, 2000, 2002) remains the only means to identify them.

The novel clade

The recovery of the clade comprising *G. australensis*, *G. deformis* and *F. russelli* is a fascinating result, first and foremost because it is well supported in all three gene trees. None of the previous reconstructions have recovered this grouping – the five-gene phylogeny of Huang *et al.* (2011) showed *G. australensis* and *F. russelli* as a paraphyly with *A. curta* nested within them, while Arrigoni *et al.* (2012) supported the sister relationship between *F. russelli* and *A. curta*. The histone H3 tree built here indicates that *A. curta* is most closely related to *Favites* and phylogenetically distant from this novel clade (Fig. 1). The IGR data could not be reliably aligned with *A. curta* and was thus omitted from the combined analysis of Huang *et al.* (2011). It is possible that the missing data could have played a role in the association of *A. curta* with *F. russelli*.

Indeed, the phylogenetic placement of *A. curta* remains uncertain, with different gene trees showing distinct sister group relationships – to *Cyphastrea* based on cytochrome oxidase I (Fukami *et al.* 2008; Benzoni *et al.* 2011; Huang *et al.* 2011), *Favites* based on histone H3 (Huang *et al.* 2011; this study) and *Platygyra* based on ITS (Benzoni *et al.* 2011). Morphologically, it is nested within *Astrea*, its current genus (Huang *et al.* 2014a). *Astrea curta* has never been associated with the novel clade recovered here based on any single marker, so its previous affiliation with *F. russelli* is possibly an artefact of missing data.

Another interesting feature of this clade is that its members are morphologically more similar to one another than any of them are to *Goniastrea* or *Favites*, particularly at the subcorallite scale (Fig. S2). They can be distinguished easily from *Goniastrea* by their dominant paratheca, and from *Favites* with their weaker costal centre clusters and lack of transverse septal crosses (Figs 4 and 5; see fig. 13C, F, I, L in Huang *et al.* 2014a).

The out-groups

The placement of *C. aspera* and *C. palauensis* sequences in subclade B, grouping with *Dipsastraea* and *Trachyphyllia* spp., is well supported for all three markers. Once again, their previous association with *Goniastrea* is shown to be superficial; microstructurally, they possess parathecal walls with no abortive septa, strong costa and septum medial lines, as well as transverse septal crosses, features not present in *Goniastrea* (Huang *et al.* 2014a). We note that the genetic diversity of *Coelastrea* spp. is much higher than previously thought (*cf.* Huang *et al.* 2011), now that samples outside of the central Indo-Pacific have been analysed. Our trees show that both species of *Coelastrea* exhibit deep intraspecific divergences between the central Indo-Pacific and Indian Ocean (Red Sea) populations, a pattern first observed by Arrigoni *et al.* (2012) among *Dipsastraea* and *Favites* species. Further instances of this phenomenon may be anticipated, but none of the other species we have examined here show such divergences. Better geographic sampling of *Coelastrea* spp., particular in the central Indian Ocean, is needed to unravel their intraspecific diversity.

A final word

Overall, we have demonstrated that robust phylogenetic analyses of critical species derived from their type localities, integrated with an evolutionary perspective of coral morphology, can help resolve the extreme polyphyly of traditionally defined genera such as *Goniastrea*. The type material of centuries-old species, devoid of any soft tissue, does not allow for molecular investigation. Nevertheless, examination of new material comparable to these specimens in terms of morphology and locality can certainly be illuminating.

Systematics

Merulina Ehrenberg, 1834: 328.

Synonyms. *Clavarina* Verrill, 1864: 56 (type species: *M. scabricula* Dana, 1846: 275; pl. 16: figs 2, 2a, b; original designation, Verrill 1864: 56); *Paraclavarina* Veron, 1985: 179 (type species: *C. triangularis* Veron & Pichon, 1980: 223; figs 375–384; original designation, Veron 1985: 179).

Merulina triangularis (Veron & Pichon, 1980: 223; figs 375–384; Best & Suharsono 1991; Fig. 4G–I).

Material examined. *Merulina triangularis*: holotype from Bushy Island-Redbill Reef, 5 m depth, dry specimen (NHMUK 1983.9.27.2); 2 specimens from Madang, Papua New Guinea, dry specimens (UNIMIB PFB351, PFB352; Fig. S4).

Remarks. *Clavarina triangularis* Veron & Pichon, 1980: 223 is the only species to have been placed in *Paraclavarina*. Our analyses show that there are no diagnosable morphological differences between *Merulina* and *Paraclavarina* (Fig. S2), and genetically, *C. triangularis* is more closely related to *M. scabricula* than are the other species of *Merulina* (Fig. 2). Therefore, we validate Best & Suharsono's (1991) combination of *M. triangularis*, effectively synonymising *Paraclavarina* with *Merulina*.

Paragoniastrea Huang, Benzoni & Budd, gen. n.

Type species. *Prionastræa australensis* Milne Edwards & Haime, 1857: 520; by original designation (Figs 5 and 6).

Etymology. The name alludes to its superficial similarities with *Goniastrea*, particularly its well-developed paliform lobes, but is distinguished from the latter based on molecular and subcorallite characteristics.

Diagnosis. Colonial (Fig. 6); mostly intracalicular budding, with some degree of extracalicular budding in monocentric species. Corallites monomorphic; discrete (1–3 centres) or uniserial; monticules absent. Walls generally fused, but may also occur as double walls. Coenosteum, if present, limited and costate. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta may be confluent. Septa in 3 cycles (24–36 septa). Free septa present but irregular. Septa spaced 6–11 septa per 5 mm. Costosepta generally unequal in relative thickness. Columellae trabecular and spongy (>3 threads), <1/4 of calice width, and continuous among adjacent corallites. Paliform (uniaxial) lobes well developed. Epitheca well developed. Endotheca low-moderate (tabular) (Fig. 5A, D, G).

Tooth base at mid-calice circular. Tooth tip at mid-calice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with >6 teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 5B, E, H).

Walls formed by dominant paratheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costal centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; generally 0.3–0.5 mm between clusters, but may be closer in some septa; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 5C, F, I).

Species included. *Paragoniastrea australensis* (Milne Edwards & Haime, 1857: 520); holotype from Australia, dry specimen (MNHN IK-2010-409; Fig. 5A). *Paragoniastrea deformis* (Veron, 1990: 142; figs 48–50, 83); holotype from Kushimoto, Japan, 4 m depth, dry specimen (MTQ G32487; Fig. 5D). *Paragoniastrea russelli* (Wells, 1954: 460; pl. 174: figs 7, 8); holotype from seaward slope of Bikini Atoll, Marshall Islands, 53–77 m depth, dry specimen (USNM 45004; Fig. 5G).

Taxonomic remarks. *Paragoniastrea* gen. n. is hereby established based on a combination of molecular and morphological evidence from Huang *et al.* (2011, 2014a) and the present analysis. Of its three constituent species, *P. deformis* is the first to be examined phylogenetically. Based on mitochondrial cytochrome oxidase I and cytochrome b genes, Fukami *et al.* (2008) recovered it as the deepest-branching lineage within subclade A (*sensu* Budd & Stolarski 2011), the clade containing *Merulina*, *Goniastrea* and *Scapophyllia*. It is clearly distinct from two of the three clades of *Goniastrea* as defined here (A2 and A3; Fig. 2). Later, a suite of five genes, including the three used in this study, showed that *P. australensis* and *P. russelli* are outside subclade A (Huang *et al.* 2011).

The present study is the first to place all three species of *Paragoniastrea* in the same context, with data pointing to a well-supported monophyly that defines this new genus. Based on the histone H3 marker, *Paragoniastrea* is sister to the least inclusive clade comprising *Merulina* and *Dipsastraea*, but this relationship is not supported (Fig. 1). Together, they form a relatively well-supported clade that excludes *Echinopora* and *Paramontastraea*. With the latter as out-groups, the nuclear ITS recovers *Paragoniastrea* as sister to subclade A with moderate support, while mitochondrial IGR groups the new genus with the clade containing *G. retiformis*, *G. minuta* and *G. stelligera* (A1 + A2; Fig. 2). However, we note above that the extremely long branch produced by the IGR data suggests that this grouping may not be reliable. Taken together, *Paragoniastrea* is distinct from all other merulinid genera but is likely to be the sister group to subclade A as suggested by the ITS tree. *Paragoniastrea* and subclade A could also be a paraphyly with

© 2014 Royal Swedish Academy of Sciences, **43**, 5, September 2014, pp 531–548

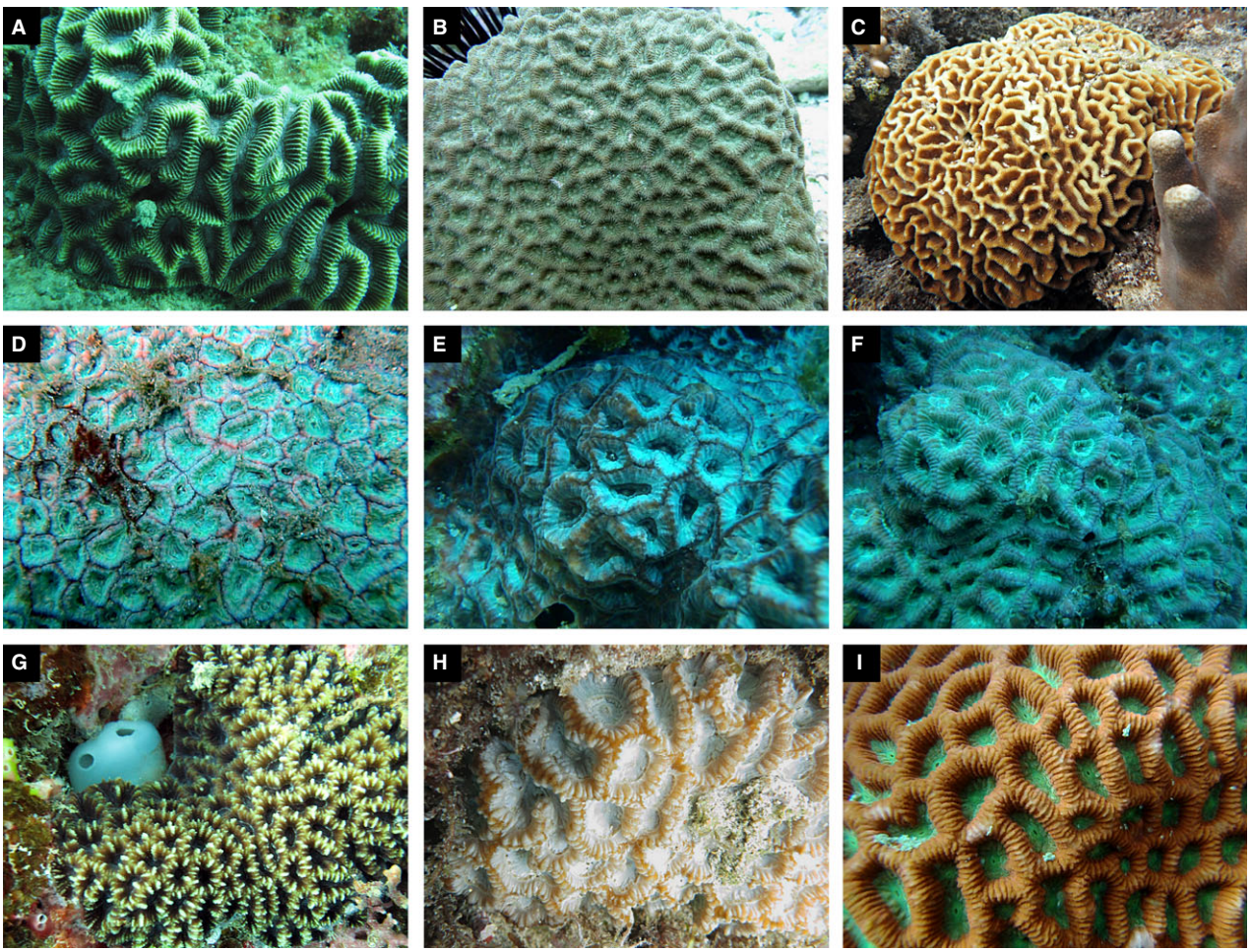

Fig. 6 *Paragoniastrea* Huang, Benzoni & Budd, this study; *in situ* photographs of corals analysed. A–C. *Paragoniastrea australensis* (Milne Edwards & Haime, 1857) —A. GB005, MTQ G61876, Pelorus Island, Australia —B. SL3958, MTQ, Solitary Islands, Australia —C. LH4553, MTQ, Lord Howe Island, Australia. D–F. *Paragoniastrea deformis* (Veron, 1990) —D. JP060, MUFS C74, Kushimoto, Wakayama —E. JP062, MUFS C75, Kushimoto, Wakayama —F. JP064, MUFS C77, Kushimoto, Wakayama. G, H. *Paragoniastrea russelli* (Wells, 1954) —G. FJ035, SIO Co2761, Moturiki, Fiji —H. LH4636, MTQ, Lord Howe Island, Australia. I. *Paragoniastrea* sp., JP065, MUFS C78, Kushimoto, Wakayama.

respect to the least inclusive clade comprising *Caulastraea* and *Dipsastraea*, although this has received much less support from histone H3.

Paragoniastrea is widely distributed on reefs of the Indo-Pacific, recorded as far east as the Pitcairn Islands in the southern hemisphere (Glynn *et al.* 2007) and Marshall Islands in the northern hemisphere (Wells 1954; Veron *et al.* 2009, 2011).

Morphologic remarks. *Paragoniastrea* is morphologically similar to *Goniastrea* and *Favites*, with members being classed in these genera prior to the present revision. Due in part to several symplesiomorphies shared between *Paragoniastrea* and members of subclade A on the morphological phylogeny (e.g. well-developed paliform lobes and absence of transverse crosses), no unambiguous synapomorphies could be inferred (Fig. S2). A transition from moderate (<corallite diameter) to limited coenosteum amount occurred on the *Paragoniastrea* branch, but the walls became fused in *P. australensis* and *P. deformis*. Wall fusion also independently evolved within subclade A (in *Merulina*, *Scapophyllia* and most *Goniastrea* spp.), *C. aspera* and *Oulophyllia crispa*.

Paragoniastrea can be distinguished macromorphologically from *Goniastrea* in having higher calice relief (3–6 mm), spongy columellae (>3 threads) and internal lobes that are only uniaxial (paliform). For subcorallite features, *Paragoniastrea* has greater septal tooth height (0.3–0.6 mm) and

spacing (0.3–1 mm), walls formed by dominant paratheca without abortive septa, and wider spacing between costal and septum centre clusters (0.3–0.6 mm).

Paragoniastrea has fewer morphological characters separating it from *Favites* – smaller number of septal cycles (24–36 septa), less abundant endotheca, weaker costal centre clusters and no transverse septal crosses (see fig. 13 in Huang *et al.* 2014a).

The three species in *Paragoniastrea* can be distinguished based on their macromorphology (Fig. 6). *Paragoniastrea australensis* is the only species with uniserial corallites and walls that are always fused between adjacent valleys (Fig. 5A; Milne Edwards & Haime 1857), while *P. deformis* possesses more irregular skeletal elements and the 'groove' and tubercle' formation, as in the holotype (Fig. 5D; Veron 1990). *Paragoniastrea russelli* exhibits varying degrees of wall fusion and coenosteum development, and unlike its congenerics, it usually has considerable size differentiation between costoseptal cycles, the first being greatly thickened and exsert (Fig. 5G; Wells 1954). The unidentified *Paragoniastrea* sp. from Japan has affinities to both *P. deformis* and *P. russelli* but has more regular corallite features (Fig. 6I). It may be a new species, but its boundaries are in need of clarification with more extensive sampling.

Acknowledgements

Special acknowledgement is due to Gregory Rouse for continuing advice and support. We thank Bert Hoeksema, Nicholas Holland, Nancy Knowlton and Michel Pichon for comments on taxonomy, and two anonymous reviewers for suggestions that helped improve the manuscript. We received invaluable assistance in the field and laboratory from Carmen Ablan-Lagman, Norievill Espana, Katrina Luzon, Eznairah-Jeung Narida, Monica Orquieza and Glenn Oyong (De La Salle University), Zeehan Jaafar, Lionel Ng, Ywee Chieh Tay, Kok Ben Toh and Karenne Tun (National University of Singapore), Joape Ginigini and staff of the Institute of Applied Sciences (University of the South Pacific), Mia Hoogenboom (James Cook University), Keiichi Nomura (Kushimoto Marine Park Center), Ronley Fanchette (Seychelles Ministry of Environment and Energy), Denis Matatiken (Seychelles National Parks Authority), Elvis Nicette (Seychelles Bureau of Standards), David Oliver (Aquarium Fish Fiji), Chris Turnier (Walt Smith International), as well as staff of Viti Water Sports (Fiji) and Underwater Centre (Seychelles). Sampling in Djibouti and Mayotte was possible thanks to the Tara Oceans scientific expedition, the OCEANS Consortium, and the collaboration of A. O. Dini (l'Aménagement du Territoire et de l'Environnement de Djibouti), M. Jalludin and M. Nabil (CERD), J.-F. Breton (IFAR Djibouti), A. Gigou and D. Laybourne (DAF Mayotte). Sampling in New Caledonia was made possible by the support of the Institut de Recherche pour le Développement, C. Payri, J. Butscher, A. Arnaud and E. Folcher. The Niugini Biodiversity Expedition and Philippe Bouchet (MNHN) are acknowledged for allowing specimen collection in Papua New Guinea. Collections were made in Australia under Great Barrier Reef Marine Park Authority permit G09/29715.1, in the Philippines under Department of Agriculture gratuitous permit FBP-0027-09, in Fiji under the approval of its Ministry of Education, and in Seychelles under research approval A0347 and CITES permit A611 issued by the Seychelles Bureau of Standards and the Ministry of Environment and Energy, respectively. We appreciate the following for museum support: Harim Cha (SIO), Tiffany Adrain (SUI), Stephen Cairns, Tim Coffer and Chad Walter (USNM), Aude Andouche and Pierre Lozouet (MNHN), Carden Wallace, Paul Muir and Barbara Done (MTQ), Jill Darrell, Kenneth Johnson and Nadia Santodomingo (NHMUK), Siong Kiat Tan and Keng Soon Chua (LKCNHM), Bert Hoeksema and Koos van Egmond (RMNH), Gustav Paulay (UF), Eric Lazo-Wasem (YPM) and Carsten Lüter (ZMB). Matthew Wortel (Petrographic Facilities, University of Iowa) prepared thin sections. Scanning electron microscopy was performed at the University of Iowa Central Microscopy Research Facility. Funds were provided by the US National Science Foundation Grant DEB-1145043-1145408 to AFB, Wildlife Reserves Singapore Ah Meng Memorial Conservation Fund R-154-000-507-720 to DH and LMC, KAUST baseline research funding and award CRG-1-BER-002 to MLB and JSPS KAKENHI Grant 22370033 to HF. Data reported here are available as Supporting Information and in the public databases Corallosphere and GenBank (accession numbers KJ666168-KJ666531).

References

Alloiteau, J. (1952). Embranchement des coelentérés. In J. Piveteau (Ed.) *Traité de paléontologie. Tome premier* (pp. 376–684). Paris: Masson.

Aranda, M., DeSalvo, M. K., Bayer, T., Medina, M. & Voolstra, C. R. (2012). Evolutionary insights into scleractinian corals using comparative genomic hybridizations. *BMC Genomics*, *13*, 501.

Arrigoni, R., Stefani, F., Pichon, M., Galli, P. & Benzoni, F. (2012). Molecular phylogeny of the Robust clade (Faviidae, Mussidae, Merulinidae, and Pectiniidae): an Indian Ocean perspective. *Molecular Phylogenetics and Evolution*, *65*, 183–193.

Beauvais, L., Chaix, C., Lathuilière, B. & Löser, H. (1993). Termes morphologiques utilisés pour décrire les Scléractiniaires: liste préliminaire [Morphological terms for describing Scleractinia: a preliminary list]. *Fossil Cnidaria and Porifera Newsletter*, *22*, 50–72.

Bellwood, D. R. & Hughes, T. P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, *292*, 1532–1534.

Benzoni, F., Arrigoni, R., Stefani, F. & Pichon, M. (2011). Phylogeny of the coral genus *Plesiastrea* (Cnidaria, Scleractinia). *Contributions to Zoology*, *80*, 231–249.

Best, M. B. & Suharsono. (1991). New observations on Scleractinian corals from Indonesia: 3. Species belonging to the Merulinidae with new records of *Merulina* and *Boninastrea*. *Zoologische Mededelingen Leiden*, *65*, 333–342.

de Blainville, H.-M. D. (1830). Zooph-Zyt. *Dictionnaire des Sciences Naturelles*, *60*, 1–631.

Brahmi, C., Meibom, A., Smith, D. C., Stolarski, J., Auzoux-Bordenave, S., Nouet, J., Doumenc, D., Djediat, C. & Domart-Coulon, I. (2010). Skeletal growth, ultrastructure and composition of the azooxanthellate scleractinian coral *Balanophyllia regia*. *Coral Reefs*, *29*, 175–189.

Budd, A. F. (2009). *Encyclopedia of Life Synthesis Meeting Report: Systematics and Evolution of Scleractinian Corals*. Washington, DC: National Museum of Natural History, Smithsonian Institution.

Budd, A. F. & Smith, N. D. (2005). Diversification of a new Atlantic clade of scleractinian reef corals: insights from phylogenetic analysis of morphologic and molecular data. *Paleontological Society Papers*, *11*, 103–128.

Budd, A. F. & Stolarski, J. (2009). Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. *Acta Zoologica*, *90*, 142–165.

Budd, A. F. & Stolarski, J. (2011). Corallite wall and septal microstructure in scleractinian reef corals: comparison of molecular clades within the family Faviidae. *Journal of Morphology*, *272*, 66–88.

Budd, A. F., Fukami, H., Smith, N. D. & Knowlton, N. (2012). Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, *166*, 465–529.

Chen, C. A. (1999). Analysis of scleractinian distribution in Taiwan indicating a pattern congruent with sea surface temperatures and currents: examples from *Acropora* and Faviidae corals. *Zoological Studies*, *38*, 119–129.

Chen, C. A., Chang, C. C., Wei, N. V., Chen, C.-H., Lein, Y. T., Lin, H. E., Dai, C.-F. & Wallace, C. C. (2004). Secondary structure and phylogenetic utility of the ribosomal internal transcribed spacer 2 (ITS2) in scleractinian corals. *Zoological Studies*, *43*, 759–771.

Chevalier, J.-P. (1971). Les scléractiniaires de la Mélanésie française (Nouvelle Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Première partie. *Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie*, *5*, 1–307.

Chevalier, J.-P. (1975). Les scléractiniaires de la Mélanésie française (Nouvelle Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Deuxième partie. *Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie*, 7, 1–407.

Chevalier, J.-P. & Beauvais, L. (1987). Ordre des scléractiniaires: XI. Systématique. In P.-P. Grassé & D. Doumenc (Eds) *Traité de zoologie. Tome III. Cnidaires: Anthozoaires* (pp. 679–764). Paris: Masson.

Colgan, D. J., McLauchlan, A., Wilson, G. D. F., Livingston, S. P., Edgecombe, G. D., Macaranas, J., Cassis, G. & Gray, M. R. (1998). Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology*, *46*, 419–437.

Cracraft, J. (1983). Species concepts and speciation analysis. *Current Ornithology*, *1*, 159–187.

Crossland, C. (1948). Reef corals of the South African coast. *Annals of the Natal Museum*, *11*, 169–205.

Cuif, J.-P. (2010). The converging results of microstructural analysis and molecular phylogeny: consequence for the overall evolutionary scheme of post-Paleozoic corals and the concept of Scleractinia. *Palaeoworld*, *19*, 357–367.

Cuif, J.-P. & Perrin, C. (1999). Micromorphology and microstructure as expressions of scleractinian skeletogenesis in *Favia fragum* (Esper, 1795) (Faviidae, Scleractinia). *Zoosystema*, *21*, 137–156.

Cuif, J.-P., Lecointre, G., Perrin, C., Tillier, A. & Tillier, S. (2003). Patterns of septal biomineralization in Scleractinia compared with their 28S rRNA phylogeny: a dual approach for a new taxonomic framework. *Zoologica Scripta*, *32*, 459–473.

Dana, J. D. (1846). *U.S. Exploring Expedition (1838-1842). Zoophytes*. Philadelphia: C. Sherman.

Darriba, D., Taboada, G. L., Doallo, R. & Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, *9*, 772.

Ehrenberg, C. G. (1834). Die Corallenthiere des rothen Meeres physiologisch untersucht und systematisch verzeichnet. Beiträge zur physiologischen Kenntniss der Corallenthiere im allegemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, *1832*, 225–380.

Ellis, J. & Solander, D. C. (1786). *The Natural History of Many Curious and Uncommon Zoophytes Collected from Various Parts of the Globe*. London: Benjamin White and Son; and Peter Elmsly.

Faustino, L. A. (1927). *Recent Madreporaria of the Philippine Islands*. Manila: Bureau of Printing.

Fischer von Waldheim, G. (1807). Mis en ordre systématique et décrit. *Museum Demidoff*, *3*, 1–330.

Flot, J.-F. & Tillier, S. (2006). Molecular phylogeny and systematics of the scleractinian coral genus *Pocillopora* in Hawaii. *Proceedings of the 10th International Coral Reef Symposium*, 24–29.

Flot, J.-F., Licuanan, W. Y., Nakano, Y., Payri, C., Cruaud, C. & Tillier, S. (2008a). Mitochondrial sequences of *Seriatopora* corals show little agreement with morphology and reveal the duplication of a tRNA gene near the control region. *Coral Reefs*, *27*, 789–794.

Flot, J.-F., Magalon, H., Cruaud, C., Couloux, A. & Tillier, S. (2008b). Patterns of genetic structure among Hawaiian corals of the genus *Pocillopora* yield clusters of individuals that are compatible with morphology. *Comptes Rendus Biologies*, *331*, 239–247.

Forsman, Z. H., Guzman, H. M., Chen, C. A., Fox, G. E. & Wellington, G. M. (2005). An ITS region phylogeny of *Siderastrea* (Cnidaria: Anthozoa): is *S. glynni* endangered or introduced? *Coral Reefs*, *24*, 343–347.

Forsman, Z. H., Barshis, D. J., Hunter, C. L. & Toonen, R. J. (2009). Shape-shifting corals: molecular markers show morphology is evolutionarily plastic in *Porites*. *BMC Evolutionary Biology*, *9*, 45.

Forsman, Z. H., Concepcion, G. T., Haverkort, R. D., Shaw, R. W., Maragos, J. E. & Toonen, R. J. (2010). Ecomorph or endangered coral? DNA and microstructure reveal Hawaiian species complexes: *Montipora dilatata/flabellata/turgescens* & *M. patula/verrilli*. *PLoS ONE*, *5*, e15021.

Fukami, H., Budd, A. F., Levitan, D. R., Jara, J., Kersanach, R. & Knowlton, N. (2004a). Geographic differences in species boundaries among members of the *Montastraea annularis* complex based on molecular and morphological markers. *Evolution*, *58*, 324–337.

Fukami, H., Budd, A. F., Paulay, G., Solé-Cava, A. M., Chen, C. A., Iwao, K. & Knowlton, N. (2004b). Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature*, *427*, 832–835.

Fukami, H., Chen, C. A., Budd, A. F., Collins, A. G., Wallace, C. C., Chuang, Y.-Y., Dai, C.-F., Iwao, K., Sheppard, C. R. C. & Knowlton, N. (2008). Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PLoS ONE*, *3*, e3222.

Glynn, P. W., Wellington, G. M., Riegl, B. M., Olson, D. B., Borneman, E. & Wieters, E. A. (2007). Diversity and biogeography of the scleractinian coral fauna of Easter Island (Rapa Nui). *Pacific Science*, *61*, 67–90.

Goreau, T. J. (1959). The ecology of Jamaican coral reefs I. Species composition and zonation. *Ecology*, *40*, 67–90.

Guindon, S. & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, *52*, 696–704.

Head, S. M. (1983). An undescribed species of *Merulina* and a new genus and species of siderastreid coral from the Red Sea. *Journal of Natural History*, *17*, 419–435.

Hoeksema, B. W. (1989). Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen Leiden*, *254*, 1–295.

Hoffmeister, J. E. (1925). Some corals from American Samoa and the Fiji Islands. Papers from the Department of Marine Biology of the Carnegie Institution of Washington, *22*, 1–90.

Huang, D. (2012). Threatened reef corals of the world. *PLoS ONE*, 7, e34459.

Huang, D. & Roy, K. (2013). Anthropogenic extinction threats and future loss of evolutionary history in reef corals. *Ecology and Evolution*, *3*, 1184–1193.

Huang, D., Meier, R., Todd, P. A. & Chou, L. M. (2008). Slow mitochondrial COI sequence evolution at the base of the metazoan tree and its implications for DNA barcoding. *Journal of Molecular Evolution*, *66*, 167–174.

Huang, D., Meier, R., Todd, P. A. & Chou, L. M. (2009). More evidence for pervasive paraphyly in scleractinian corals: systematic study of Southeast Asian Faviidae (Cnidaria; Scleractinia) based on molecular and morphological data. *Molecular Phylogenetics and Evolution*, *50*, 102–116.

Huang, D., Licuanan, W. Y., Baird, A. H. & Fukami, H. (2011). Cleaning up the 'Bigmessidae': molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evolutionary Biology*, *11*, 37.

Huang, D., Benzoni, F., Fukami, H., Knowlton, N., Smith, N. D. & Budd, A. F. (2014a). Taxonomic classification of the reef coral families Merulinidae, Montastraeidae and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, *171*, 277–355.

Huang, D., Licuanan, W. Y., Hoeksema, B. W., Chen, C. A., Ang, P. O., Huang, H., Lane, D. J. W., Vo, S. T., Waheed, Z., Affendi, Y. A., Yeemin, T. & Chou, L. M. (2014b). Extraordinary diversity of reef corals in the South China Sea. *Marine Biodiversity* (in press). doi: 10.1007/s12526-014-0236-1.

Huelsenbeck, J. P. & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*, 754–755.

Johnson, K. G. (1998). A phylogenetic test of accelerated turnover in Neogene Caribbean brain corals (Scleractinia: Faviidae). *Palaeontology*, *41*, 1247–1268.

Katoh, K. & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780.

Katoh, K. & Toh, H. (2008). Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, *9*, 286–298.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*, 3059–3066.

Katoh, K., Asimenos, G. & Toh, H. (2009). Multiple alignment of DNA sequences with MAFFT. In D. Posada (Ed.) *Bioinformatics for DNA Sequence Analysis* (pp. 39–63). New York: Humana Press.

Kitahara, M. V., Stolarski, J., Cairns, S. D., Benzoni, F., Stake, J. L. & Miller, D. J. (2012). The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis. *Invertebrate Systematics*, *26*, 303–315.

Kitahara, M. V., Cairns, S. D., Stolarski, J. & Miller, D. J. (2013). Deltocyathiidae, an early-diverging family of Robust corals (Anthozoa, Scleractinia). *Zoologica Scripta*, *42*, 201–212.

Lamarck, J.-B. P. (1801). *Système des animaux sans vertèbres*. Paris: Lamarck et Deterville.

Lamarck, J.-B. P. (1816). *Histoire naturelle des animaux sans vertèbres. Tome Second*. Paris: Verdière.

Link, H. F. (1807). *Beschreibung der Naturalien-Sammlung der Universität zu Rostock*. Rostock: Adlers Erben.

Luck, D. G., Forsman, Z. H., Toonen, R. J., Leicht, S. J. & Kahng, S. E. (2013). Polyphyly and hidden species among Hawai'i's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae). *PeerJ*, *1*, e132.

Maddison, W. P. & Maddison, D. R. (2011). *Mesquite: A Modular System for Evolutionary Analysis*. Version 2.75. Available via http://mesquiteproject.org

Marti-Puig, P., Forsman, Z. H., Haverkort-Yeh, R. D., Knapp, I. S. S., Maragos, J. E. & Toonen, R. J. (2014). Extreme phenotypic polymorphism in the coral genus *Pocillopora*; micromorphology corresponds to mitochondrial groups, while colony morphology does not. *Bulletin of Marine Science*, *90*, 211–231.

Matthai, G. (1928). A monograph of the Recent meandroid Astræidæ. *Catalogue of the Madreporarian Corals in the British Museum (Natural History)*, 7, 1–288.

Meier, R., Kwong, S., Vaidya, G. & Ng, P. K. L. (2006). DNA barcoding and taxonomy in Diptera: a tale of high intraspecific variability and low identification success. *Systematic Biology*, *55*, 715–728.

Meier, R., Zhang, G. & Ali, F. (2008). The use of mean instead of smallest interspecific distances exaggerates the size of the "barcoding gap" and leads to misidentification. *Systematic Biology*, *57*, 809–813.

Meyer, C. P. & Paulay, G. (2005). DNA barcoding: error rates based on comprehensive sampling. *PLoS Biology*, *3*, e422.

Milne Edwards, H. & Haime, J. (1848). Note sur la classification de la deuxième tribu de la famille des Astréides. *Comptes Rendus des Séances de l'Académie des Sciences*, *27*, 490–497.

Milne Edwards, H. & Haime, J. (1849a). Recherches sur les polypiers. Quatrième mémoire. Monographie des Astréides (I). Tribu II. Astréens (Astreinae). *Annales des Sciences Naturelles*, *3e série*, *11*, 233–312.

Milne Edwards, H. & Haime, J. (1849b). Recherches sur les polypiers. Quatrième mémoire. Monographie des Astréides (I). (Suite.) Quatrième section. Astréens agglomérés. Astreinae aggregatae. *Annales des Sciences Naturelles*, *3e série*, *12*, 95–197.

Milne Edwards, H. & Haime, J. (1857). *Histoire naturelle des coralliaires, ou polypes proprement dits. Tome second. Zoanthaires sclérodermés (Zoantharia Sclerodermata) ou madréporaires*. Paris: Roret.

Nelson, G. & Platnick, N. I. (1981). *Systematics and Biogeography*. New York: Columbia University Press.

Nixon, K. C. & Wheeler, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, *6*, 211–223.

Nothdurft, L. D. & Webb, G. E. (2007). Microstructure of common reef-building coral genera *Acropora*, *Pocillopora*, *Goniastrea* and *Porites*: constraints on spatial resolution in geochemical sampling. *Facies*, *53*, 1–26.

Nunes, F. L. D., Fukami, H., Vollmer, S. V., Norris, R. D. & Knowlton, N. (2008). Re-evaluation of the systematics of the endemic corals of Brazil by molecular data. *Coral Reefs*, *27*, 423–432.

Nunes, F. L. D., Norris, R. D. & Knowlton, N. (2009). Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. *Molecular Ecology*, *18*, 4283–4297.

Posada, D. (2008). jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, *25*, 1253–1256.

de Queiroz, K. (2005a). A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences*, *56*, 196–215.

de Queiroz, K. (2005b). Different species problems and their resolution. *BioEssays*, *27*, 1263–1269.

de Queiroz, K. (2005c). Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 6600–6607.

de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, *56*, 879–886.

Quelch, J. J. (1886). Report of the reef-corals collected by the H.M.S. Challenger during the years 1873–1976. *Report on the Scientific Results of the Voyage of H.M.S. Challenger (1873-76), Zoology*, *16*, 1–203.

Quenstedt, F. A. (1881). *Petrefactenkunde Deutschlands (Sechster Band) Röhren- und Sternkorallen*. Leipzig: Fues's Verlag.

Rambaut, A. & Drummond, A. J. (2009). *Tracer: MCMC Trace Analysis Tool*. Version 1.5. Available via http://beast.bio.ed.ac.uk

Ronquist, F. & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542.

Sargent, T. D., Jamrich, M. & Dawid, I. B. (1986). Cell interactions and the control of gene activity during early development of *Xenopus laevis*. *Developmental Biology*, *114*, 238–246.

Schmidt-Roach, S., Miller, K. J., Lundgren, P. & Andreakis, N. (2014). With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zoological Journal of the Linnean Society*, *170*, 1–33.

Srivathsan, A. & Meier, R. (2012). On the inappropriate use of Kimura-2-parameter (K2P) divergences in the DNA-barcoding literature. *Cladistics*, *28*, 190–194.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2690.

Stamatakis, A., Hoover, P. & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology*, *57*, 758–771.

Stolarski, J. (2003). Three-dimensional micro- and nanostructural characteristics of the scleractinian coral skeleton: a biocalcification proxy. *Acta Palaeontologica Polonica*, *48*, 497–530.

Stolarski, J. & Roniewicz, E. (2001). Towards a new synthesis of evolutionary relationships and classification of Scleractinia. *Journal of Paleontology*, *75*, 1090–1108.

Swofford, D. L. (2003). *PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4*. Available via http://paup.csit.fsu.edu

Takabayashi, M., Carter, D. A., Loh, W. K. W. & Hoegh-Guldberg, O. (1998a). A coral-specific primer for PCR amplification of the internal transcribed spacer region in ribosomal DNA. *Molecular Ecology*, *7*, 928–930.

Takabayashi, M., Carter, D. A., Ward, S. & Hoegh-Guldberg, O. (1998b). Inter- and intra-specific variability in ribosomal DNA sequence in the internal transcribed spacer region of corals. *Proceedings of the Australian Coral Reef Society 75th Anniversary Conference, Heron Island, October 1997* (pp. 241–248). Brisbane: School of Marine Science, University of Queensland.

Umbgrove, J. H. F. (1940). Madreporaria from the Togian reefs (Gulf of Tomini, North-Celebes). *Zoologische Mededelingen Leiden*, *22*, 265–310.

Vaughan, T. W. (1918). Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. *Papers from the Department of Marine Biology of the Carnegie Institution of Washington*, *9*, 49–234.

Vaughan, T. W. & Wells, J. W. (1943). Revision of the suborders, families, and genera of the Scleractinia. *Geological Society of America Special Papers*, *44*, 1–345.

Veron, J. E. N. (1985). New Scleractinia from Australian coral reefs. *Records of the Western Australian Museum*, *12*, 147–183.

Veron, J. E. N. (1986). *Corals of Australia and the Indo-Pacific*. Sydney: Angus & Robertson.

Veron, J. E. N. (1990). New Scleractinia from Japan and other Indo-West Pacific countries. *Galaxea*, *9*, 95–173.

Veron, J. E. N. (2000). *Corals of the World*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N. (2002). *New Species Described in Corals of the World*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N. & Pichon, M. (1980). *Scleractinia of eastern Australia. Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae,*

Merulinidae, *Mussidae*, *Pectiniidae*, *Caryophylliidae*, *Dendrophylliidae*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N. & Pichon, M. (1982). *Scleractinia of Eastern Australia. Part IV. Family Poritidae*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N., Pichon, M. & Wijsman-Best, M. (1977). *Scleractinia of eastern Australia. Part II. Families Faviidae*, *Trachyphylliidae*. Townsville: Australian Institute of Marine Science.

Veron, J. E. N., DeVantier, L. M., Turak, E., Green, A. L., Kininmonth, S., Stafford-Smith, M. G. & Peterson, N. (2009). Delineating the Coral Triangle. *Galaxea*, *11*, 91–100.

Veron, J. E. N., DeVantier, L. M., Turak, E., Green, A. L., Kininmonth, S., Stafford-Smith, M. G. & Peterson, N. (2011). The Coral Triangle. In Z. Dubinsky & N. Stambler (Eds) *Coral Reefs: An Ecosystem in Transition* (pp. 47–55). Dordrecht: Springer.

Verrill, A. E. (1864). List of the polyps and corals sent by the Museum of Comparative Zoölogy to other institutions in exchange, with annotations. *Bulletin of the Museum of Comparative Zoölogy*, *1*, 29–60.

Verrill, A. E. (1865). Classification of polyps: (extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). *Proceedings of the Essex Institute*, *4*, 145–152.

Verrill, A. E. (1866). Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Captain John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, naturalist to the expedition. With descriptions of some additional species from the west coast of North America. *Proceedings of the Essex Institute*, *5*, 17–50.

Wallace, C. C. (1999). *Staghorn Corals of the World: A Revision of the Coral Genus Acropora*. Collingwood: CSIRO Publishing.

Wells, J. W. (1954). Recent corals of the Marshall Islands. *United States Geological Survey Professional Paper*, 260–I, 385–486.

Wells, J. W. (1956). Scleractinia. In R. C. Moore (Ed.) *Treatise on Invertebrate Paleontology. Part F: Coelenterata* (pp. F328–F444). Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Yabe, H. & Sugiyama, T. (1935). Revised lists of the reef corals from the Japanese seas and of the fossil reef corals of the raised reefs and the Ryûkyû limestone of Japan. *Journal of the Geological Society of Japan*, *42*, 379–403.

Yabe, H. & Sugiyama, T. (1941). Recent reef-building corals from Japan and the South Sea Islands under the Japanese mandate. II. *Science Reports of the Tôhoku Imperial University*, *Second Series (Geology)*, *Special Volume*, *2*, 67–91.

Yabe, H., Sugiyama, T. & Eguchi, M. (1936). Recent reef-building corals from Japan and the South Sea Islands under the Japanese mandate. I. *Science Reports of the Tôhoku Imperial University*, *Second Series (Geology)*, *Special Volume*, *1*, 1–66.

Supporting Information

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

Fig. S1. Maximum likelihood phylogeny of *Merulina*, *Goniastrea* and *Scapophyllia* (subclade A *sensu* Budd & Stolarski 2011; Huang *et al.* 2011) resulting from a partitioned analysis of the concatenated molecular dataset.

Fig. S2. Strict consensus of 20 equally most-parsimonious trees based on morphological data.

Fig. S3. Maximum likelihood phylogenetic relationships among species in *Goniastrea* clade A3 (derived from Fig. 2).

Fig. S4. *Merulina* Ehrenberg, 1834; *Goniastrea* Milne Edwards & Haime, 1848; and *Scapophyllia* Milne Edwards & Haime, 1848; *in situ* photographs of corals analysed.

Table S1. List of specimens analysed in this study, detailing sampling localities, voucher information (see text for institution abbreviations), and GenBank accession numbers (bold = new sequences) for nuclear histone H3, internal transcribed spacers 1 and 2 (ITS), and mitochondrial non-coding intergenic region (IGR).

Data S1. Nexus data file containing the molecular (aligned) and morphological data matrices used in this study, as well as maximum likelihood, Bayesian and parsimony trees obtained from the phylogenetic analyses.