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Systematics of merulinidae (Scleractinia) and conservation phylogenetics of reef corals

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UNIVERSITY OF CALIFORNIA, SAN DIEGO

Systematics of Merulinidae (Scleractinia) and Conservation Phylogenetics of Reef Corals

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Danwei Huang

Committee in charge:

Professor Gregory Rouse, Chair
Professor Philip Hastings
Professor Nicholas Holland
Professor Nancy Knowlton
Professor Kaustuv Roy

2012

The Dissertation of Danwei Huang is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2012

DEDICATION

To the coral reefs of the world

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Chapter 3, in full, is a reproduction of the material as it appears in BMC Evolutionary Biology 2011. Huang, Danwei; Licuanan, Wilfredo Y; Baird, Andrew H; Fukami, Hironobu, BioMed Central, 2011. The dissertation author was the primary investigator and author of this paper.

Chapter 4 contains several proposals of modifications to biological nomenclature. It should be noted that presentation of taxonomic changes in this dissertation does not constitute formal publication.

Chapter 5, in full, is a reproduction of the material as it appears in PLoS ONE 2012. Huang, Danwei, PLoS, 2012. The dissertation author was the primary investigator and author of this paper.

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ABSTRACT OF THE DISSERTATION

Systematics of Merulinidae (Scleractinia) and Conservation Phylogenetics of Reef Corals

by

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Doctor of Philosophy in Marine Biology

University of California, San Diego, 2012

Professor Gregory Rouse, Chair

Coral systematics have been plagued by a host of problems. Traditional identification methods based on gross anatomy often fail to recognise natural taxa because of morphological convergence, environment-induced phenotypic variability, and recent speciation. I first summarised levels of paraphyly for taxa within Scleractinia and showed that paraphyly was also a significant problem in Faviidae, the second-most speciose reef-building family. Phylogenetic reconstruction based on two mitochondrial markers amplified for 41 species representing 13 genera illustrated that at least five genera and Faviidae were paraphyletic. Morphological characters currently used to identify these corals similarly failed to recover many genera.

The analysis was then expanded to the clade 'Bigmessidae' that comprised Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. To reconstruct a robust and resolved molecular phylogeny, three nuclear and two mitochondrial loci were sequenced from 76 of the 132 'Bigmessidae' species collected from five reef regions in the central Indo-Pacific and Atlantic. Results indicated numerous examples of cryptic taxa due to unexpected phylogenetic placements of several species, but the recovery of most 'Bigmessidae' genera with only minor degrees of paraphyly offered hope for impending taxonomic amendments.

Congruence between molecular data and morphology was then determined by mapping 47 corallite and subcorallite characters onto the 'Bigmessidae' (= Merulinidae) molecular phylogeny. Subcorallite traits diagnostic of natural groups included characters associated with wall microstructure and septal tooth micromorphology. Based on these results and a larger collection of corals, I conducted a taxonomic revision of *Merulina*, type genus of Merulinidae, and its sister group, *Goniastrea*.

Finally, I used the supertree approach to reconstruct a comprehensive tree of life for Scleractinia that included all 837 living reef species, one-third of which are threatened with extinction. A composite measure of phylogenetic distinctiveness and extinction risk was used to identify the most endangered lineages, some of which would not be given top conservation priority on the basis of risk alone. Tests for phylogeny-associated patterns showed that corals susceptible, resistant or resilient to impacts such as bleaching and

disease tended to be close relatives. Intensification of these threats or extirpation of the endangered lineages could therefore result in disproportionate pruning of the coral tree of life.

CHAPTER 1

General introduction

Scleractinia Bourne, 1900, is a major clade within Hexacorallia, Anthozoa, Cnidaria, that comprises Recent stony coral species as well as fossils that are nearly all from post-Paleozoic (Wells, 1956). Since the foundation of biological nomenclature of animals as set forth in the tenth edition of Carl Linnaeus's (1758) *Systema Naturae*, more than 1,500 living species of corals have been described (Cairns, 1999; Wallace, 1999; Veron, 2000; Cairns, 2009).

The taxonomic arrangement of species in Scleractinia has undergone numerous changes at every level. Works in the 18th century, including Linnaeus's, focused on the naming of about 100 stony coral species that were all placed within the genus *Madrepora* Linnaeus, 1758. It was Jean-Baptiste Pierre Lamarck (1816) who initiated the distribution of coral species into several genera. These were then placed into family-level groups in various combinations by Oken (1815), Ehrenberg (1834), Dana (1846), Milne-Edwards and Haime (1848a,b) and several others. Building upon the family classification by Milne-Edwards and Haime (1857a,b; 1860), Vaughan and Wells (1943) followed by Wells (1956) divided the extant Scleractinia into five suborders that persist today—Astrocoeniina, Fungiina, Faviina, Caryophylliina and Dendrophylliina.

The number of known extant species increased from about 100 at the end of the 18th century to 1314 in 1999 (Cairns, 1999). Subsequently, over 100 species were each described by Veron (2000) and Cairns (compiled in Cairns, 2009), for zooxanthellate and azooxanthellate corals respectively, thereby expanding the species count for Scleractinia to about 1550. The entire taxonomic record had thus far been based solely on qualitative morphological traits.

By the end of the 20th century, however, the field of coral systematic biology had already entered a new era with the usage of DNA sequence data and robust phylogenetic methods. Seminal work at broad taxonomic scales based on mitochondrial and nuclear genes carried out by Romano and Palumbi (1996; 1997) and Veron et al. (1996), respectively, were beginning to uncover deep-seated complexities surrounding the systematics of corals. Both teams noted that at least one of the traditional suborders was not monophyletic. Furthermore, the mitochondrial data revealed that almost all suborders were not monophyletic, and that Scleractinia was divided into two major clades, the robust and complex groups (Romano and Palumbi, 1996; 1997; see also Romano and Cairns, 2000).

Until 2004, these phylogenetic results had little impact on the way species were described. Despite warnings that qualitative colony and corallite traits frequently overlapped among species and may not reflect evolutionary relationships (Veron et al., 1977; Lang, 1984), coral taxonomy continued to rely solely on these characters (Wallace, 1997; Wallace and Wolstenholme, 1998; Wallace, 1999; Veron, 2000; 2002; Ditlev, 2003; Vermeij et al., 2003). Two influential studies were published in 2004, one finding that several zooxanthellate genera and families present in both Atlantic and Pacific realms were not monophyletic, with the Atlantic taxa forming a divergent lineage that had never been recognised due to morphological convergence (Fukami et al., 2004a); and the second suggesting that the classification of azooxanthellate corals such as Caryophyllidae and Oculinidae was also not consistent with evolutionary history (Le Goff-Vitry et al., 2004). Subsequent analyses with greater species and geographic coverage, based on more molecular markers, have essentially supported Scleractinia as monophyletic, but not most of its lower taxonomic groups (Fukami et al., 2008; Kitahara et al., 2010).

Following these studies, the change in focus reflected in recent work has been evident. Most authors now use corallite and subcorallite morphological characteristics in combination with molecular data to support new species descriptions (e.g. Pichon et al., 2012) and revisions (e.g. Benzoni et al., 2007; 2010; Stefani et al., 2008a,b; Kongjandtre et al., 2012). Focusing on the clade Merulinidae (comprising Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae spp. prior to recent revision by Budd et al., in press), the present study illustrated the process that involved the recognition of unnatural groups (Chapter 2), accumulation of support from both molecular and morphological characters (Chapter 3), and finally the formal revision of taxa (Chapter 4). The new age of integrated coral taxonomy has begun.

Apart from their traditional use to delineate taxa, coral phylogenies had not been applied to broad-scale evolutionary and conservation questions (but see Pandolfi, 1992), despite many innovative uses of phylogenetic trees for other organisms. For instance, on the topic of macroevolution, a seminar paper by Nee et al. (1992) estimated cladogenetic rates using a tree derived from DNA-DNA hybridisation studies of birds. It was also argued that conservation prioritisation of species should take into account evolutionary distinctiveness on the basis of phylogenetic relationships (Vane-Wright et al., 1991). These analyses generally relied on complete species-level phylogenetic hypotheses (Nee et al., 1992; Purvis et al., 2000) that unfortunately had not been available for relationships within Scleractinia.

Supertrees, in which available phylogenetic information are combined to produce more comprehensive phylogenies, represented the best solution to this problem thus far (Bininda-Emonds, 2004; Bininda-Emonds et al., 2002). While complete species supertrees were available for many vertebrate clades such as primates (Purvis, 1995), carnivores (Bininda-Emonds et al., 1999), bats (Jones et al., 2002), insectivores (Grenyer and Purvis, 2003), lagomorphs (Stoner et al., 2003) and marsupials (Cardillo et al., 2004), no such reconstructions existed for any invertebrate group. For corals, Kerr (2005) generated a supertree of 1016 species, representing about 66% of the known species diversity of Scleractinia. This tree sampled a higher proportion of reef-building corals (possessing coral-zooxanthellae symbiosis) relative to non-reef (azooxanthellate) species, but even then, it was not close to complete for the former. Furthermore, subsequent molecular evidence, particular from Fukami et al. (2008) and Kitahara et al. (2010), had falsified some of the relationships proposed in Kerr's (2005) supertree. These issues hindered the investigation of coral macroevolutionary patterns.

Chapter 5 of this dissertation reconstructed the complete reef coral supertree using both molecular and available morphological phylogenetic hypotheses from both reef and non-reef corals. The latter group was critical for this exercise as many azooxanthellate corals were nested within zooxanthellate clades (Le Goff-Vitry et al., 2004; Kitahara et al., 2010; Stolarski et al., 2011). The resultant 1293-species tree was then used to determine conservation priorities of corals by integrating results of the recent IUCN Red List of Threatened Species assessment (Carpenter et al., 2008). Such a perspective in conservation was proposed by Vane-Wright et al. (1991) and practised initially on Crustacea by Crandall (1998) and Pérez-Losada et al. (2002), who were one of the first to use the titled term 'conservation phylogenetics' in published literature (see also Krajewski, 1991, cited by Weitzman, 1992; Krajewski, 1994).

It is hoped that this work provides a generalised framework for the resolution of taxonomic complexities concerning scleractinian corals, and motivates formal revisions in the clade and conservation prioritisation of corals based on evolutionary history.

CHAPTER 2

Evidence for pervasive paraphyly in scleractinian corals: systematic study of Southeast Asian Faviidae based on molecular and morphological data

INTRODUCTION

As coral reefs experience unprecedented losses around the world (Knowlton, 2001; Hughes et al., 2003; Pandolfi et al., 2003; 2005; Bellwood et al., 2004; Wilkinson, 2004; Bruno and Selig, 2007), studies of the phylogeographic and phylogenetic history of reef-builders offer a glimpse of how these ecosystems varied in the past and how they may change in the future (van Oppen and Gates, 2006). A thorough understanding of speciation and biogeographic events that shaped the distribution of scleractinian corals may also help predict responses of reefs to oceanographic modifications resulting from climate change (Pandolfi, 1992; Palumbi, 1997; Barber et al., 2006). However, without appropriate species, genus and family delineation, errors in estimates of diversity are inevitable (Knowlton and Jackson, 1994; Agapow et al., 2004; Isaac et al., 2004). Unfortunately, recent molecular research on scleractinian corals suggests that published information on the biology and distribution of corals is currently based on taxon concepts that are unlikely to reflect natural units (e.g. Romano and Palumbi, 1996; 1997; Fukami et al., 2004a).

An important model group for studying the problems with coral taxonomy is Faviidae Gregory, 1900 (Cnidaria: Anthozoa: Scleractinia), the most genus-rich zooxanthellate scleractinian family and whose species diversity is second only to Acroporidae (Veron et al., 1977; Cairns, 1999). Here, we reconstruct the first species-level phylogeny of faviid corals based on molecular and morphological data to test whether currently recognised taxa are monophyletic and if the different types of data support similar conclusions.

Despite a long history of taxonomic work on the Scleractinia (e.g. Linnaeus, 1758; Forsskål, 1775; Lamarck, 1816), the taxonomy and phylogenetic relationships of this group remain largely unresolved (Daly et al., 2007). Until the 1990s, the classification of scleractinian corals relied heavily on qualitative morphological traits that frequently overlap among species and are thus unlikely to reflect evolutionary relationships (Veron et al., 1977; Lang, 1984). With the recent usage of DNA sequence data, biologists have begun to realise further complexities surrounding the taxonomy and systematics of corals. Seminal research at broad taxonomic scales based on mitochondrial and nuclear genes has been published by Romano and Palumbi (1996; 1997) and Veron et al. (1996) respectively. Both teams suggested that some taxa at the subordinal level are paraphyletic. Since then, almost all DNA sequence studies that have examined familial relationships among corals have found at least one family to be paraphyletic (Table 2.1). In fact, 11 of 16 scleractinian families surveyed most recently by Fukami et al. (2008) are not monophyletic. At the species and genus level, paraphyly was found in the majority of studies. Unfortunately, with the exception of Acroporidae only limited knowledge on the phylogenetic relationships at the genus- and species-level is available. An example of a taxon lacking in such information is Faviidae, where more than a decade was spent resolving the taxonomy of the *Montastraea annularis* complex in the Caribbean (e.g. Knowlton et al., 1992; Lopez et al., 1999; Medina et al., 1999; Fukami et al., 2004b). Much less data have been published on the remaining Faviidae (but see Lam and Morton,

Table 2.1: Level of paraphyly in studies of coral phylogeny that use DNA sequence data. Shown are the number of paraphyletic taxa out of the total number of taxa tested (≥ 2 OTUs) at the species, genus and family levels. (ITS = internal transcribed spacer regions, including 5.8S; β-tub = β-tubulin; h2ab = partial histone 2A and 2B; MCI 2 = mini-collagen intron 2; PCI = Pax-C intron; MPC = mt putative control region; IGR = mt intergenic region).

Marker(s) used	Species	Genus	Family	Reference
Scleractinia				
16S	–	0/5 (0%)	1/10 (10%)	Romano and Palumbi, 1996
28S	–	0/1 (0%)	0/4 (0%)	Veron et al., 1996
28S	–	0/2 (0%)	1/7 (14%)	Chen et al., 2000
16S; 28S	–	2/13 (15%)	4/16 (25%)	Romano and Cairns, 2000
12S	–	1/1 (100%)	2/5 (40%)	Chen et al., 2002
28S	–	4/5 (80%)	5/8 (63%)	Cuif et al., 2003
ITS2	–	1/1 (100%)	2/3 (67%)	Chen et al., 2004
cytB; COI; β-tub	4/68 (6%)	12/21 (57%)	4/5 (80%)	Fukami et al., 2004a
16S	1/1 (100%)	7/11 (64%)	5/14 (36%)	Le Goff-Vitry et al., 2004
ITS	6/11 (55%)	0/2 (0%)	0/3 (0%)	Forsman et al., 2006
mt genome	–	–	1/2 (50%)	Medina et al., 2006
5.8S; ITS2	6/17 (35%)	2/2 (100%)	2/2 (100%)	Benzoni et al., 2007
β-tub; IGR	2/12 (17%)	3/3 (100%)	2/2 (100%)	Nunes et al., 2008
Acroporidae				
ITS	2/5 (40%)	–	–	Odorico and Miller, 1997
MCI 2	5/5 (100%)	–	–	Hatta et al., 1999
cytB; ATPase 6	–	1/4 (25%)	–	Fukami et al., 2000
PCI; ITS	3/3 (100%)	–	–	van Oppen et al., 2000
PCI; MPC	13/16 (81%)	–	–	van Oppen et al., 2001
ITS	5/5 (100%)	–	–	van Oppen et al., 2002
PCI; MPC	2/2 (100%)	–	–	Márquez et al., 2002
5.8S	7/7 (100%)	–	–	Márquez et al., 2003
28S	4/4 (100%)	–	–	Wolstenholme et al., 2003
PCI; MPC	9/13 (69%)	–	–	van Oppen et al., 2004
ITS	3/3 (100%)	–	–	Vollmer and Palumbi, 2004
MPC	3/5 (60%)	–	–	Wolstenholme, 2004
cytB; h2ab	3/7 (43%)	1/4 (25%)	–	Wallace et al., 2007
Faviidae				
ITS	3/3 (100%)	–	–	Medina et al., 1999
ITS	0/2 (0%)	–	–	Lam and Morton, 2003
ITS; IGR	3/3 (100%)	–	–	Fukami et al., 2004b
COI; IGR	9/23 (39%)	5/8 (63%)	2/3 (67%)	This study
Pocilloporidae				
mt genome	0/2 (0%)	–	–	Chen et al., 2008
ITS2	3/5 (60%)	–	–	Flot and Tillier, 2006
Siderastreidae				
ITS	3/5 (60%)	–	–	Forsman et al., 2005
β-tub	2/3 (67%)	–	–	Stefani et al., 2008a
5.8S; ITS2; 28S	3/4 (75%)	–	–	Stefani et al., 2008b

Table 2.1: Level of paraphyly in studies of coral phylogeny, continued.

Marker(s) used	Species	Genus	Family	Reference
Madracis				
ITS	3/5 (60%)	–	–	Diekmann et al., 2001
Porites				
ITS	0/2 (0%)	–	–	Hunter et al., 1997

2003; Fukami et al., 2004a; Nunes et al., 2008), making the most genus-rich family in the Scleractinia one of the least well understood.

Faviidae is known to be a taxonomically difficult group of corals in need of thorough revision (Powers and Rohlf, 1972; Wijsman-Best, 1974b; Veron et al., 1977). Its members possess a high diversity of growth forms and several taxa exhibit considerable phenotypic plasticity in response to the environment (Dustan, 1975; Miller, 1992; Todd et al., 2001; Todd et al., 2004a,b). For instance, corallite expansion and exsertion increased in *Favia speciosa* and *Diploastrea heliopora* specimens transplanted to shallow depths, possibly enhancing light capture or self-shading as a response to increased irradiance (Todd et al., 2004b). Not surprisingly, inconsistencies in Faviidae taxonomy and systematics have emerged. For instance, *Leptastrea* is more closely related to members of the suborder Fungiina than to the remaining genera in the family (Romano and Palumbi, 1996; 1997; Romano and Cairns, 2000), and the rift between Atlantic and Indo-Pacific species cannot be reconciled under current generic concepts (Fukami et al., 2004a; Fukami et al., 2008; Nunes et al., 2008). Yet, it is striking that this problem has largely been ignored although the first report of paraphyly in the family appeared 40 years ago in a coral study employing numerical taxonomy (Powers and Rohlf, 1972).

To date, only Fukami et al. (2004a) in their study involving a broad taxonomic sample across the Scleractinia have attempted to reconstruct the phylogeny of Faviidae (see also Fukami et al., 2008). Generic and specific relationships were not resolved, however, and only molecular data were employed. In the present study, we sequenced two mitochondrial markers for 81 terminals representing 41 faviid species and 13 genera from tropical reefs in Singapore. This taxon sample comprises a substantial fraction of the 103 described extant species that are currently classified in 24 genera (Cairns, 1999). The molecular markers used were cytochrome oxidase subunit I and a noncoding region of the mitochondrial genome, which have been effective in resolving scleractinian relationships at the family and subgenus levels respectively (Fukami et al., 2004a,b; Fukami et al., 2008; Nunes et al., 2008). We also collected morphological data for monocentric species (single-polyp corallites). Both data types were examined separately as well as combined for a total evidence analysis.

MATERIALS AND METHODS

Specimen collection and preparation

Specimens were collected from coral reefs surrounding the offshore islands of southern Singapore between September 2006 and May 2007. Faviid corals were sampled based on features that can be recognised in the field; identification was later confirmed in the laboratory after examining skeletal traits. In total, 81 colonies from 41 species were collected (Table 2.2). Two non-faviid species—*Acanthastrea echinata* (Mussidae) and *Scapophyllia cylindrica* (Merulinidae)—were also obtained as outgroup taxa. Each colony was photographed to record its general appearance and living tissue characteristics. Colony form, size and colour were also noted. Samples between 10 and 100 cm^2 were collected from each colony for morphological and molecular analyses.

DNA extraction, PCR amplification and sequencing

For each colony, DNA was extracted from ~2 cm^2 of tissue digested in twice their volume of CHAOS solution (4M guanidine thiocyanate, 0.1% N-lauroyl sarcosin sodium,

Table 2.2: Data partitions and GenBank accession numbers for the 83 specimens from 43 species sampled in this study (asterisk denotes taxon designated as outgroup).

No.	Taxon	Specimen No.	COI	Intron	IGR	Morphology
1	*Acanthastrea echinata**	ZRC.CNI.0130	EU371658	–	FJ345526	X
2	*Barabattoia amicorum* 1	ZRC.CNI.0174	FJ345412	–	FJ345480	X
3	*Barabattoia amicorum* 2	ZRC.CNI.0196	FJ345413	–	FJ345481	X
4	*Caulastraea echinulata*	ZRC.CNI.0171	FJ345414	FJ345445	FJ345496	
5	*Cyphastrea chalcidicum*	ZRC.CNI.0188	FJ345415	–	FJ345453	X
6	*Cyphastrea microphthalma*	ZRC.CNI.0181	FJ345416	–	FJ345454	X
7	*Cyphastrea serailia* 1	ZRC.CNI.0123	EU371659	–	FJ345455	X
8	*Cyphastrea serailia* 2	ZRC.CNI.0177	FJ345417	–	FJ345456	X
9	*Diploastrea heliopora* 1	ZRC.CNI.0167	EU371660	FJ345446	FJ345462	X
10	*Diploastrea heliopora* 2	ZRC.CNI.0168	EU371661	FJ345447	FJ345463	X
11	*Echinopora gemmacea*	ZRC.CNI.0203	FJ345418	FJ345448	FJ345457	X
12	*Echinopora lamellosa*	ZRC.CNI.0193	FJ345419	FJ345449	FJ345458	X
13	*Echinopora pacificus*	ZRC.CNI.0194	FJ345420	–	FJ345459	X
14	*Favia* aff. *favus* 1	ZRC.CNI.0183	FJ345421	–	FJ345503	X
15	*Favia* aff. *favus* 2	ZRC.CNI.0184	FJ345422	–	FJ345504	X
16	*Favia danae* 1	ZRC.CNI.0159	EU371663	–	FJ345476	X
17	*Favia danae* 2	ZRC.CNI.0190	FJ345423	–	FJ345477	X
18	*Favia favus* 1	ZRC.CNI.0124	EU371664	–	FJ345465	X
19	*Favia favus* 2	ZRC.CNI.0136	EU371665	–	FJ345466	X
20	*Favia favus* 3	ZRC.CNI.0178	FJ345424	–	FJ345470	X
21	*Favia favus* 4	ZRC.CNI.0179	FJ345425	–	FJ345467	X
22	*Favia helianthoides* 1	ZRC.CNI.0139	EU371666	–	FJ345468	X
23	*Favia helianthoides* 2	ZRC.CNI.0140	EU371667	–	FJ345469	X
24	*Favia lizardensis*	ZRC.CNI.0148	EU371668	–	FJ345484	X
25	*Favia matthaii* 1	ZRC.CNI.0107	EU371669	–	FJ345471	X
26	*Favia matthaii* 2	ZRC.CNI.0114	EU371670	–	FJ345472	X
27	*Favia matthaii* 3	ZRC.CNI.0128	EU371671	–	FJ345473	X
28	*Favia matthaii* 4	ZRC.CNI.0137	EU371672	–	FJ345474	X
29	*Favia matthaii* 5	ZRC.CNI.0166	EU371673	–	FJ345475	X
30	*Favia maxima* 1	ZRC.CNI.0142	EU371674	–	FJ345478	X
31	*Favia maxima* 2	ZRC.CNI.0182	FJ345426	–	FJ345479	X
32	*Favia pallida* 1	ZRC.CNI.0133	EU371675	–	FJ345482	X
33	*Favia pallida* 2	ZRC.CNI.0144	EU371676	–	FJ345483	X
34	*Favia rotumana* 1	ZRC.CNI.0180	FJ345427	–	FJ345485	X
35	*Favia rotumana* 2	ZRC.CNI.0197	FJ345428	–	FJ345486	X
36	*Favia speciosa* 1	ZRC.CNI.0103	EU371677	–	FJ345505	X
37	*Favia speciosa* 2	ZRC.CNI.0125	EU371680	–	FJ345506	X
38	*Favia speciosa* 3	ZRC.CNI.0126	EU371681	–	FJ345507	X
39	*Favia speciosa* 4	ZRC.CNI.0132	EU371683	–	FJ345519	X
40	*Favia speciosa* 5	ZRC.CNI.0158	EU371685	–	FJ345520	X
41	*Favites complanata* 1	ZRC.CNI.0109	EU371689	–	FJ345524	X
42	*Favites complanata* 2	ZRC.CNI.0149	EU371691	–	FJ345523	X
43	*Favites complanata* 3	ZRC.CNI.0161	EU371692	–	FJ345525	X
44	*Favites flexuosa*	ZRC.CNI.0131	EU371693	–	FJ345522	X
45	*Favites paraflexuosa*	ZRC.CNI.0165	EU371694	–	FJ345521	X
46	*Favites pentagona* 1	ZRC.CNI.0157	EU371695	–	FJ345460	X
47	*Favites pentagona* 2	ZRC.CNI.0195	FJ345429	–	FJ345461	X
48	*Goniastrea aspera*	ZRC.CNI.0191	FJ345430	–	FJ345487	X
49	*Goniastrea australensis* 1	ZRC.CNI.0186	FJ345431	–	FJ345490	

Table 2.2: Data partitions and GenBank accession numbers, continued.

No.	Taxon	Specimen No.	COI	Intron	IGR	Morphology
50	*Goniastrea australensis* 2	ZRC.CNI.0164	EU371696	–	FJ345491	
51	*Goniastrea edwardsi* 1	ZRC.CNI.0138	EU371697	–	FJ345492	X
52	*Goniastrea edwardsi* 2	ZRC.CNI.0200	FJ345432	–	FJ345493	X
53	*Goniastrea favulus* 1	ZRC.CNI.0122	EU371698	–	FJ345494	
54	*Goniastrea favulus* 2	ZRC.CNI.0187	FJ345433	–	FJ345495	
55	*Goniastrea palauensis*	ZRC.CNI.0121	EU371699	–	FJ345488	X
56	*Goniastrea pectinata*	ZRC.CNI.0173	FJ345434	–	FJ345489	
57	*Goniastrea retiformis* 1	ZRC.CNI.0155	EU371700	–	FJ345527	X
58	*Goniastrea retiformis* 2	ZRC.CNI.0160	EU371701	–	FJ345528	X
59	*Leptoria phrygia*	ZRC.CNI.0153	EU371705	–	FJ345529	
60	*Montastraea curta* 1	ZRC.CNI.0115	EU371707	–	FJ345508	X
61	*Montastraea curta* 2	ZRC.CNI.0116	EU371708	–	FJ345509	X
62	*Montastraea curta* 3	ZRC.CNI.0119	EU371709	–	FJ345510	X
63	*Montastraea magnistellata* 1	ZRC.CNI.0105	EU371710	–	FJ345511	X
64	*Montastraea magnistellata* 2	ZRC.CNI.0150	EU371711	–	FJ345512	X
65	*Montastraea magnistellata* 3	ZRC.CNI.0151	EU371712	–	FJ345513	X
66	*Montastraea valenciennesi* 1	ZRC.CNI.0108	EU371713	–	FJ345514	X
67	*Montastraea valenciennesi* 2	ZRC.CNI.0110	EU371714	–	FJ345515	X
68	*Montastraea valenciennesi* 3	ZRC.CNI.0113	EU371716	–	FJ345516	X
69	*Montastraea valenciennesi* 4	ZRC.CNI.0120	EU371718	–	FJ345517	X
70	*Montastraea valenciennesi* 5	ZRC.CNI.0135	EU371719	–	FJ345518	X
71	*Oulastrea crispata*	ZRC.CNI.0192	FJ345435	–	FJ345464	X
72	*Oulophyllia bennettae* 1	ZRC.CNI.0169	FJ345436	FJ345450	FJ345497	X
73	*Oulophyllia bennettae* 2	ZRC.CNI.0172	FJ345437	FJ345451	FJ345498	X
74	*Oulophyllia bennettae* 3	ZRC.CNI.0175	FJ345438	FJ345452	FJ345499	X
75	*Oulophyllia crispa* 1	ZRC.CNI.0145	EU371721	–	FJ345500	
76	*Oulophyllia crispa* 2	ZRC.CNI.0202	FJ345439	–	FJ345501	
77	*Platygyra daedalea*	ZRC.CNI.0199	FJ345440	–	FJ345530	
78	*Platygyra lamellina*	ZRC.CNI.0198	FJ345441	–	FJ345531	
79	*Platygyra pini* 1	ZRC.CNI.0134	EU371722	–	FJ345532	
80	*Platygyra pini* 2	ZRC.CNI.0152	EU371723	–	FJ345533	
81	*Platygyra sinensis*	ZRC.CNI.0201	FJ345442	–	FJ345534	
82	*Platygyra verweyi*	ZRC.CNI.0170	FJ345443	–	FJ345535	
83	*Scapophyllia cylindrica**	ZRC.CNI.0176	FJ345444	–	FJ345502	

10mM Tris pH 8, 0.1M 2-mercaptoethanol) for at least three days at room temperature before DNA extraction using a phenol-chloroform based method with a phenol extraction buffer (100 mM TrisCl pH8, 10 mM EDTA, 0.1% SDS) (Sargent et al., 1986; Fukami et al., 2004b; Huang et al., 2008). The rest of the colony was sprayed with a powerful water jet to remove as much tissue as possible before being bleached in 5% sodium hypochlorite solution. The skeletons were rinsed in fresh water, dried and deposited in the Raffles Museum of Biodiversity Research (National University of Singapore).

The cytochrome oxidase subunit I (COI) gene was amplified using Scleractinia-specific primers MCOIF(5'–TCT ACA AAT CAT AAA GAC ATA GG–3') and MCOIR (5'–GAG AAA TTA TAC CAA AAC CAG G–3') (Fukami et al., 2004a) with the protocol of 95°C for 2 min, 35 cycles of 94°C for 45 s, 55°C for 45 s and 72°C for 1.5 min, ending with 72°C for 5 min (Huang et al., 2008). For specimens where an intron was detected by gel electrophoresis (amplified sequence length 1.75–1.80 kb), the following internal primers were used to obtain entire gene sequences (protocol as above): cox1_intF (5'–ACA ACG ATT TTC AAC ATG CGA GCC C–3') and cox1_intR (5'–TAA CCA TCT GCA TCT AAA AAC CC–3') (Fukami et al., 2007).

To determine DNA sequences for the noncoding intergenic region situated between COI and the formylmethionine transfer RNA gene (IGR in short), Faviidae-specific primers MNC1f (5'–GAG CTG GGC TTC TTT AGA GTG–3') and MNC1r (5'–GTG AGA CTC GAA CTC ACT TTT C–3') were used for PCR (Fukami et al., 2004b; Nunes et al., 2008). The protocol employed was the same reaction as COI amplification, but some genera had long T repeats (*Oulophyllia* and *Goniastrea*; ~20 bp) or had sequences in excess of 1.3 kb (*Cyphastrea*). Additional primers were then designed in order to obtain the full sequence (MNC2f: 5'–GGT TTT CAA CCA TAT TAC TTT GCT A–3', and MNC2r: 5'–TTA TAA TCA AAA TGA GCC ATT AAT T–3' for *Cyphastrea*; MNC3f 5'–AAG TAA GTC CTG CTC ATT CTG GGG T–3', and MNC3r 5'–ACC TTT GTC TGC TCT TAA ATA CTG G–3' for *Goniastrea*; MNC4f 5'–AGG AGG TGA CTC CTT GTC TAT ATT T–3', and MNC4r 5'–AAG TAA AGC CAC TCA AAT TCC CCT T–3' for *Oulophyllia*). PCR products were purified with SureClean (BIOLINE) and sequenced using the BigDye Terminator kit (Perkin Elmer) and ABI 3100 capillary genetic analyser. Sequences were deposited in GenBank (accession numbers FJ345412–FJ345535). Fifty COI sequences were recently published in Huang et al. (2008) and have been archived in the same database (Table 2.2).

Morphological data

Twenty-one descriptive traits and morphometric parameters (Table 2.3) were used to construct a morphological data matrix for the monocentric species (67 taxa). Characters 1–15 are based on features traditionally and commonly used to identify species in the Faviidae (Vaughan and Wells, 1943; Wells, 1956; Wijsman-Best, 1974a; 1976; 1977b; 1980; Moll and Best, 1984; Veron et al., 1977; Best et al., 1984; Budd, 1993; Veron, 2000; Budd and Smith, 2005). 'Colony form', 'fleshiness', and 'polyp colour' were recorded *in situ* while the remainder was determined in the laboratory after tissue-removal, bleaching and drying. Characters 16–21 are morphometric variables obtained from multiple measurements of the coral skeletons (modified from Todd et al. 2004a,b,c; Budd and Smith, 2005). Four corallites were randomly selected for all characters except for 'corallite separation', where four distances among adjacent corallites were chosen

Table 2.3: List and synopses of morphological characters, including descriptive and morphometric parameters, used to analyse the monocentric species. Character states and corresponding codes are indicated.

No.	Character	Description	State	Code
1	Colony form	Growth form of colony	massive	0
			encrusting	1
			columnar	2
			laminar	3
2	Corallite form	Growth form of individual corallites, determined by wall structure	plocoid	0
			subplocoid	1
			cerioid	2
			tubular	3
3	Corallite shape	Shape of individual corallites, determined by degree of compactness	circular	0
			angular	1
4	Septal dentation	Size of teeth-like structures on septa	fine	0
			short	1
			exsert	2
5	Septal order		irregular	0
			two	1
			three	2
			four	3
6	Paliform lobes	Projections from inner edges of septa	absent	0
			present	1
			crown	2
7	Paliform crown		absent	0
			present	1
8	Columella form	Development of spongy mass at corallite axis	loose	0
			compact	1
9	Costae pattern	Formation of primary and secondary costae	equal	1
			unequal	2
10	Costae dentation	Size of teeth-like structures on costae	fine	0
			short	1
			exsert	2
11	Costae alignment	Merging of costae between adjoining corallites	absent	0
			present	1
12	Coenosteum	Form of exothecal surface	absent	0
			smooth	1
			blistered	2
13	Groove and tubercle		absent	0
			present	1
14	Fleshiness	Daytime mantle expansion	absent	0
			present	1
15	Polyp colour	Colour pattern between wall and center of polyp	uniform dull	0
			center bright	1
			wall bright	2
			uniform bright	3
16	Calice width	Average of maximum and minimum calice diameter (mm)	≤ 3.0	0
			3.5–6.0	1
			6.5–9.5	2
			10.0–13.0	3
			≥ 14.0	4

Table 2.3: List and synopses of morphological characters, continued.

No.	Character	Description	State	Code
17	Corallite separation	Distance between two adjacent corallites (mm), relative to mean calice width	0.00	0
			0.10–0.20	1
			0.25–0.50	2
			≥ 0.55	3
18	Calice depth	Vertical distance from columella to septal apex, relative to calice width	≤ 0.25	0
			0.30–0.45	1
			≥ 0.50	2
19	Septal slope	Average of maximum and minimum angle between septa and horizontal (º)	≤ 40	0
			50–65	1
			≥ 70	2
20	Septal number	Fraction of total number of septa that fuse with columella	≤ 0.45	0
			≥ 0.50	1
21	Columella width	Average of maximum and minimum columella diameter, relative to calice width	≤ 0.20	0
			0.21–0.24	1
			0.25–0.35	2
			≥ 0.40	3

randomly. Linear measurements (characters 16, 17, 18 and 21) were made using digital Vernier calipers and scaled according to calice width. 'Septal slope' was obtained by positioning a needle along and parallel with the septal slope and determining its angle relative to the colony surface with a protractor. Continuous variables obtained for each morphometric parameter were coded into character states so that each state was clearly delimited from another (see Lang, 1984). In determining features and parameters for analysis, some commonly used traits such as modes of asexual reproduction (i.e. intra- and extra-tentacular budding) and exact colour patterns, were excluded because they are variable even within an individual colony due to habitat-induced phenotypic changes (Vaughan and Wells, 1943; Wijsman-Best, 1977a,b; see also Todd et al., 2001; Todd et al., 2002a,b; Todd et al., 2004a,b).

Phylogenetic analyses

To determine an individual-level phylogeny of the terminals based on the maternally-inherited mitochondrial COI and IGR, we concatenated DNA sequence data for the two molecular markers from 93 taxa in the Scleractinia, comprising 85 terminals from Faviidae and eight putative outgroup taxa, i.e. *Acropora tenuis*, *Anacropora matthai* and *Montipora cactus* (Acroporidae), *S. cylindrica* (Merulinidae), *A. echinata* and *Mussa angulosa* (Mussidae), *Porites porites* (Poritidae) and *Siderastrea radians* (Siderastreidae). Except for *A. echinata* and *S. cylindrica*, the outgroup sequences and sequences for four Caribbean faviid species (*Colpophyllia natans* and three spp. of the *Montastraea annularis* complex: *M. annularis*, *M. franksi, M. faveolata*) were taken from GenBank (accession numbers in the above-mentioned order: AF338425, AY903295,

AY903296, DQ643834, DQ643837, DQ643838, DQ643833, AP008973, AP008976, AP008977). *Porites porites* was used to root the analyses unless otherwise stated.

The protein-coding COI was aligned using AlignmentHelper 1.2, which translates the nucleotide sequences into amino acid sequences, aligns them with ClustalW (Thompson et al., 1994), and translates the results back to DNA data. The IGR sequences were aligned using MUSCLE (Edgar, 2004a,b), first with default parameters, and subsequently with the 'refine' function. Mesquite 2.0 (Maddison and Maddison, 2011) was then used to adjust the IGR alignment manually (alignment available on TreeBASE). Uncorrected intra- and interspecific pairwise distances were calculated in TaxonDNA (Meier et al., 2006). The character matrix (93 terminals; COI 1832 total and 246 parsimony informative characters (PIC); IGR 1955 total and 1405 PIC) was analysed using maximum parsimony, Bayesian likelihood, and maximum likelihood methods.

Maximum parsimony (MP) analysis was performed using the new search technologies (Goloboff, 1999; Nixon, 1999) as implemented in the programme TNT 1.1 (Goloboff et al., 2008). The tree searches in TNT consisted of 10,000 random addition sequence replicates each employing the default sectorial, ratchet, drift and tree fusing parameters, treating gaps as missing data. A strict consensus tree was generated based on the most parsimonious trees (MPTs). Clade stability was determined through bootstrapping (250 replicates of 100 random addition sequences).

The phylogenetic relationships were also inferred using Bayesian likelihood (BL) with the models selected using MrModeltest 2.2. According to the hLRT, the GTR + G model is preferred for both partitions (COI and IGR) while AIC favoured the same model for IGR but GTR + I + G for COI. Two separate analyses in MrBayes v3.1 (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al., 2001; Ronquist and Huelsenbeck, 2003) were thus performed following both criteria using the default priors and with partitions unlinked for separate parameter estimations: 'unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all)'. Four Markov chains of 2,000,000 generations were implemented, saving a tree every 100th generation. Upon inspecting the log likelihood plots for MCMC convergence, the first 2,501 trees were discarded as burn-in. For the maximum likelihood (ML) inference utilising PhyML, suitable models were determined with Modeltest 3.7 (Posada and Crandall, 1998): AIC chose TVM + I + G while hLRT selected GTR + I + G. Data were analysed separately with both criteria using PhyML v2.4.4 (Guindon and Gascuel, 2003; Guindon et al., 2005) on default settings, and generating 250 bootstrap replicates. But, as TVM + I + G could not be implemented in the program, GTR + I + G was employed.

The 67-taxon morphological dataset (21 total characters, all PIC) was analysed in TNT under the MP criterion. The tree was rooted to *Oulastrea crispata* that was identified as the sister group to the remaining terminals based on the molecular data (see also Fukami et al., 2004a). Both data types were afterwards combined to yield a combined matrix with 93 terminals and 3808 characters. This matrix was analysed under MP (TNT) and BL (MrBayes) using the same parameters described above. The MK + G model was implemented for the morphology partition. In all cases, AIC and hLRT did not give significantly different results, hence only those inferred from the latter criterion are reported. To assess the relative contribution of the molecular and morphology data, partitioned Bremer support values were calculated based on the MP strict consensus tree using TreeRot.v2.

We tested the monophyly of Faviidae, and of genera with multiple species, using the Templeton nonparametric Wilcoxon Signed Ranked test (Templeton, 1983; 1987). In PAUP* 4.0b10 (Swofford, 2003), the monophyly was constrained for each of the taxa tested and the parsimonious trees under this constraint were compared to the unconstrained MPTs. Note, that this test makes the potentially problematic assumption of character independence; results should thus be interpreted with care.

RESULTS

Gene and intron amplification

Amplification of cytochrome oxidase subunit I (COI) was successful for all 83 specimens collected (Table 2.2). The COI intron was detected in only eight specimens from five species: *Caulastraea echinulata* (1,116 bp), *Diploastrea heliopora* (1,094 bp), *Echinopora gemmacea* (1,065 bp), *E. lamellosa* (1,096 bp) and *Oulophyllia bennettae* (1,126 bp). The introns are recognised as group 1 introns in the COI gene and represent two of the four types of noncoding sequence with the characteristic LAGLI-DADG motif that was first reported in the sea anemone *Metridium senile* (Beagley et al., 1996; Fukami et al., 2007). *Caulastraea echinulata* and *O. bennettae* have the Type 4 intron, while Type 1 is found in *D. heliopora*, *E. gemmacea* and *E. lamellosa*. *Oulophyllia crispa* possesses a regular-length COI (~650 bp) even though a Type 4 intron is expected (Fukami et al., 2007). The internal primer pair (cox1_intF and cox1_intR) did not successfully amplify any sequence, even after repeating the PCR multiple times under several reaction conditions.

Uncorrected genetic distances

As expected for Anthozoa, pairwise intra- and interspecific COI distances are small (Shearer et al., 2002; Huang et al., 2008). Intraspecific distances do not exceed 1.5% (mean 0.096% ± S.E. 0.029%), while closest congeneric interspecific variation ranges from 0.0% to 1.8% (mean 0.191% ± S.E. 0.039%). The majority of intraspecific sequences (66.7%) are invariant while 22.4% of species pairs share the same sequences. Conversely, IGR is more variable. Mean divergences are 1.04% (± S.E. 0.53%) within species and 5.47% (± S.E. 1.13%) among closest congeneric species. Only 3.4% of species pairs share sequences, and fewer intraspecific pairs are invariant (52.4%). Distances were calculated with the exclusion of *Favia* aff. *favus* sequences due to uncertain identification.

Molecular phylogenetic analyses

Maximum parsimony (MP) analysis of the full molecular dataset produced eight most parsimonious trees (MPTs) that are largely congruent with the maximum likelihood (ML) and Bayesian likelihood (BL) reconstructions (Figure 2.1). Two major clades, each comprising several species, are present in trees obtained from all three analyses (see Clades I and II in Figure 1). The non-faviids *Acanthastrea echinata* (Clade II), *Mussa angulosa* ('basal') and *Scapophyllia cylindrica* (Clade I) are nested within the ingroups. They constitute the clade representing a paraphyletic Faviidae that is sister to Acroporidae. The paraphyly of the family is also supported by the Templeton test that indicates that trees with a monophyletic Faviidae have a significantly worse fit to the data (Table 2.4).

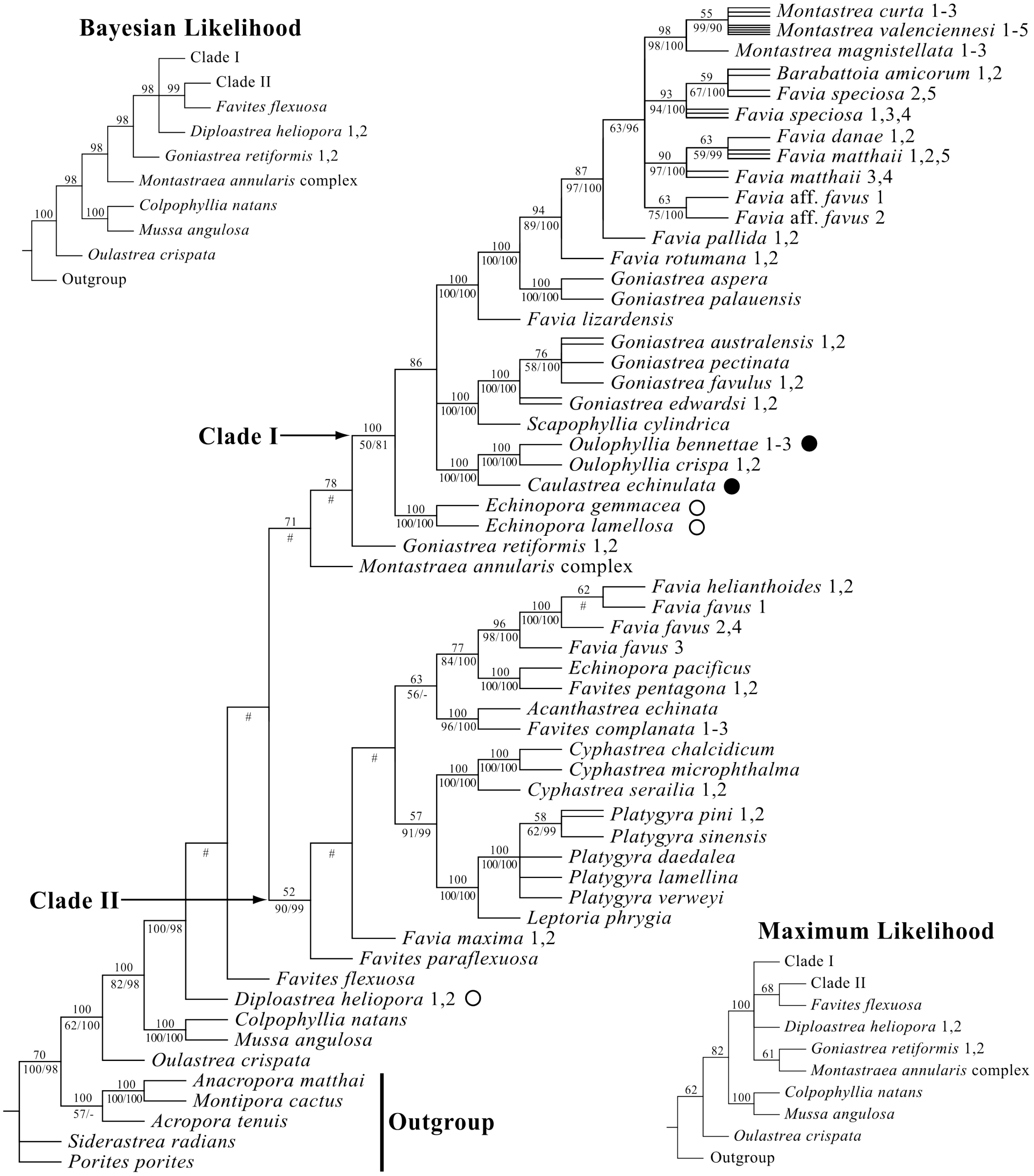

Figure 2.1: Strict consensus cladogram from eight maximum parsimony (MP) trees based on COI and IGR sequence data (93 taxa). The symbol '#' indicates conflict with the maximum likelihood (ML) or Bayesian likelihood (BL) majority-rule consensus trees (shown as insets). Numbers above branches of the strict consensus tree are MP bootstrap values (only ≥ 50 shown); those below are ML bootstrap supports (only ≥ 50 shown), followed by BL posterior probabilities (only ≥ 80 shown). Monospecific clades supported by bootstraps ≥ 50 and posterior probabilities ≥ 80 are grouped into single terminals. Taxa denoted by open circles contain Type 1 group 1 intron in COI while filled circles denote taxa with Type 4 intron.

Table 2.4: Results of the Templeton nonparametric tests (N: number of maximum parsimony trees in constrained searches; P: significance value for testing monophyly).

Taxon	**Molecular data**		**Morphological data**		**Combined data**	
	N	**P**	**N**	**P**	**N**	**P**
Faviidae	810	< 0.0001	–	–	10485	< 0.0001
Cyphastrea	1399	1.0000	471	≥ 0.7055	11153	1.0000
Echinopora	2802	< 0.0001	145	1.0000	8793	< 0.0001
Favia	5731	< 0.0001	1788	≥ 0.4000	10766	< 0.0001
Favites	9708	< 0.0001	17599	≥ 0.0833	11559	< 0.0001
Goniastrea	117	< 0.0001	7292	≥ 0.0833	2808	< 0.0001
Montastraea	4937	< 0.0001	41	≥ 0.5637	7800	< 0.0001
Oulophyllia	1402	1.0000	–	–	11103	1.0000
Platygyra	1394	1.0000	–	–	6829	1.0000

Most sequences from species represented by more than one specimen form clades with at least moderate support (bootstrap values ≥ 50; posterior probabilities ≥ 80): *Cyphastrea serailia* (n = 2), *Diploastrea heliopora* (n = 2), *Favia danae* (n = 2), *F. helianthoides* (n = 2), *F. maxima* (n = 2), *F. pallida* (n = 2), *F. rotumana* (n = 2), *Favites complanata* (n = 3), *F. pentagona* (n = 2), *Goniastrea favulus* (n = 2), *G. retiformis* (n = 2), *Oulophyllia bennettae* (n = 3), *O. crispa* (n = 2), *Montastraea magnistellata* (n = 3). Two sequences from putative *Favia favus* (in Clade I) also form a clade with moderate support values, but the sequences are only distantly related to the remaining ones for the same species (*F. favus* in Clade II). The sequences for some species are forming grades with other species nested within. These include *Favia favus*, *F. matthaii* and *F. speciosa* and this lack of separation is likely due to small interspecific distances, e.g. *F. danae* vs. *F. matthaii* (mean IGR interspecific distance 0.11% ± S.E. 0.01%) and *Barabattoia amicorum* vs. *F. speciosa* (mean 0.01% ± S.E. 0.007%). The relationships between sequences from *Goniastrea australiensis*, *G. edwardsi*, *Montastraea curta*, *M. valenciennesi* and *Platygyra pini* are also unresolved. Interspecific genetic distances in these groups are small, e.g. *Platygyra* spp. (mean closest IGR distance 0.008% ± S.E. 0.008%).

With the exception of *Cyphastrea*, *Oulophyllia* and *Platygyra*, none of the genera with multiple species are monophyletic, a conclusion consistent with tests rejecting the null hypothesis of monophyly for *Echinopora*, *Favia*, *Favites*, *Goniastrea* and *Montastraea* (Table 2.4). For instance, *Goniastrea* is split into *Goniastrea retiformis* and two distinct monophyletic groups in Clade I, while *Favites* spp. are in both Clade II and *Favites flexuosa*. *Echinopora pacificus* clusters with *Favites pentagona* with high clade support rather than grouping with its congenerics (*E. gemmacea* + *E. lamellosa*). *Favia* is polyphyletic, being distributed widely across Clades I and II. The Indo-Pacific *Montastraea* forms a well-supported taxon within Clade I (IGR mean closest interspecific distance 0.055% ± S.E. 0.021%), distinct from the Caribbean *Montastraea* spp. complex that has been excluded from the same major clade. Mean IGR closest interspecific distance within the complex is 0.083% (± S.E. 0.033%), not statistically different from that among Indo-Pacific congeners (t-test, d.f. = 12, T = 0.627, P = 0.271).

Morphological analysis

Parsimony analysis of the 67 taxa, 21 character matrix resulted in 15 MPTs, yielding a strict consensus tree that is generally not congruent with the reconstruction based on molecular characters (Figure 2.2). The topological conflict is striking. No grouping above the species level is congruent between the morphological and molecular tree.

Most species are recovered as distinct clades, except for *Cyphastrea serailia*, *Favia favus* and *F. helianthoides*, which are largely unresolved. In contrast, most genera do not form monophyletic groups. However, the tests did not reject the null hypothesis of monophyly for all genera (Table 2.4). The only genus with multiple species recovered as a clade is *Echinopora*.

Total evidence analyses

MP analysis of the combined dataset yielded 267 MPTs. The strict consensus of these trees is topologically similar to the BL majority-rule consensus cladogram (Figure

2.3). Clades I and II are again recovered by both MP and BL methods. The nodes are well-supported except for Clade II on the MP tree. Within Clade I, the relationships among species are more resolved here than in the molecular trees. *Barabattoia amicorum* specimens are grouped together as a clade rather than dispersed among *Favia speciosa* terminals. The distinction between *Montastraea curta* and *M. valenciennesi* is also clear, but relationships are unresolved among the three species. As in the molecular analyses, Faviidae and all genera with more than one species are paraphyletic, except for *Cyphastrea*, *Oulophyllia and Platygyra* (Templeton tests of monophyly; Table 2.4).

The total partitioned Bremer support for IGR is 20.78 (± S.E. 4.18), much higher than the support for COI (1.45 ± S.E. 1.16) and the morphology partition (0.65 ± S.E. 0.23). However, when normalised by dividing through the number of PIC, the values are more similar (COI: 0.0172, IGR: 0.0161, Morphology: 0.0308).

DISCUSSION

Phylogenetic analyses based on molecular, morphological and combined data indicate that paraphyly is pervasive in Faviidae; even the family itself was not recovered as a clade. Of eight genera tested using molecular and total evidence, only three are monophyletic, i.e. *Cyphastrea*, *Oulophyllia* and *Platygyra*. For instance, *Favia* is polyphyletic and distributed among the major Clades I and II. Two members of *Echinopora* are at the base of Clade I, while the third is in Clade II. *Montastraea* falls into two well-supported clades. The Indo-Pacific species, *M. curta*, *M. magnistellata* and *M. valenciennesi* are distantly related to the Atlantic *M. annularis* complex. This confirms Fukami et al.'s (2004) conclusion that certain congeneric species among the two oceanic

Figure 2.2: Strict consensus of 15 equally most parsimonious trees derived from analysis of the 67-taxon morphological dataset comprising 21 characters. Monospecific clades supported by bootstraps ≥ 50 are grouped into single terminals. All other nodes with bootstrap values < 50. Stars represent clades also recovered in the molecular and total evidence analyses, while those only in the latter are marked with squares.

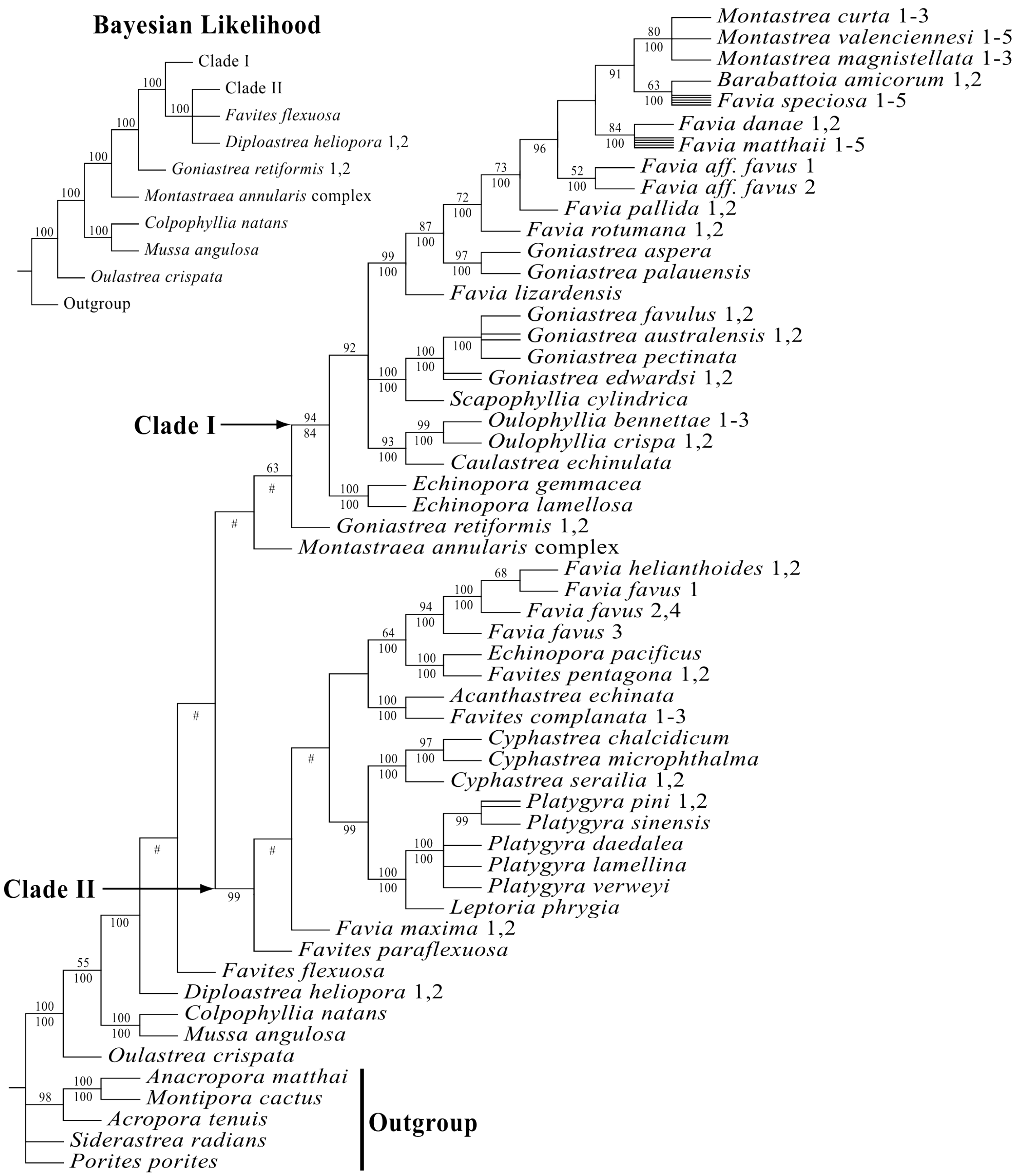

Figure 2.3: Results of analyses on combined data (COI, IGR and morphology), showing strict consensus of 267 maximum parsimony (MP) trees. The symbol '#' represents conflict with the Bayesian likelihood tree (shown as inset). Numbers above branches are bootstrap values from the MP test (only ≥ 50 shown), and those below are Bayesian posterior probabilities (only ≥ 80 shown).

provinces are less closely related to one another than to taxa from other genera or even other families. Indeed, *Scapophyllia cylindrica* (Family Merulinidae) is deeply nested within Clade I, while *Acanthastrea echinata* (Family Mussidae) is in Clade II, and *Mussa angulosa* forms a well-supported clade with faviids that excludes *Oulastrea crispata*. The paraphyly of Faviidae is also supported by the Templeton test.

One of the causes of paraphyly in conventional (i.e. phenotypic) taxonomic units is convergent evolution (Fukami et al., 2004a). For instance, three morphotypes of *Favia favus* are sampled here. Four specimens are readily identifiable according to Veron et al. (1977) and Veron (2000), but two others, *F.* aff. *favus* 1 and 2, fit the morphological description for all but one character each. For instance, all six *F. favus* specimens have circular plocoid corallites, short septal dentation, irregular septal order and smooth coenosteum. They also possess similar corallite widths and separation distances. Yet *F.* aff. *favus* 1 possesses paliform lobes while *F.* aff. *favus* 2 has well-developed, compact columellae, traits not typically present in this species. Molecular and combined analyses placed the two putative morphospecies together with Clade I *Favia* spp., which excludes the conventional *Favia favus*. Based on their positions on the molecular trees and the mapping of characters, we conclude that all the above-listed characters evolved independently in the lineages leading to *Favia* aff. *favus* and *Favia favus*. Thus, it is likely that the three morphs have undergone morphological convergence since Clades I and II diverged, and *F.* aff. *favus* 1 and 2 may represent new species yet to be described.

Some clades recovered in this study are also present in Fukami et al.'s (2004) analysis based on COI and cytB. These include the meandroid taxon *Leptoria phrygia* + *Platygyra*, *Oulophyllia* and *Cyphastrea*. *Goniastrea pectinata* and *Merulina* (Family

Merulinidae) were sister groups in Fukami et al. (2004). Hence, the placement of *Scapophyllia cylindrica*, another merulinid, deep in Clade I with four *Goniastrea* spp. (including *G. pectinata*) provides further support to Fukami et al.'s (2004) significant finding. There are, however, conflicting results between the two studies. For instance, *Echinopora gemmacea* and *E. pacificus* previously formed a well-supported clade. In our study they are separated with *Echinopora gemmacea* being sister to *E. lamellosa* in Clade I, while *E. pacificus* is clustered with *Favites pentagona* in Clade II.

Fukami et al. (2007) found the group 1 intron in *Oulophyllia crispa*, but we did not, even after multiple repetitions of the PCR. The exclusion of *Caulastraea echinulata* from the *Oulophyllia* clade indicates that the indel of Type 4 intron would have been acquired in the common ancestor of *C. echinulata* and *Oulophyllia* but lost in *O. crispa*. Our results also point to two independent origins of the Type 1 intron, in *Diploastrea heliopora* and *Echinopora gemmacea* + *E. lamellosa*. Observed differences from Fukami et al. (2007) in the emergence of the Type 4 intron may have been due to population-level variation. The samples that Fukami et al. (2004) examined were from subtropical and temperate colonies. Those used in the present study, however, were collected from Singapore, a tropical location. Intron sampling of *Caulastraea*, *Echinopora*, *Oulophyllia*, *Mycedium* and *Pectinia* at more sites between the regions could clarify the evolution of the indels.

Most faviid species examined here are considered well-defined since their sequences have been found to cluster with high node supports, corroborated by combined data. The exceptions include *Favia favus*, *F. matthaii* and *F. speciosa* that each includes one other species within their clades. Sequences from some other species form polytomies (e.g. *Goniastrea* spp., *Montastraea* spp. and *Platygyra* spp.). It is likely that these species underwent speciation only recently, and nucleotide variations in the two markers tested have yet to accumulate significantly between them to be informative in our reconstructions. The similarity in *Montastraea* IGR interspecific distances among biogeographic regions also reflects inconsistencies in coral systematics. While separate species are conventionally recognised among the Indo-Pacific *Montastraea* spp., the validity of *M. annularis*, *M. franksi* and *M. faveolata* is disputed, even though morphological, molecular and ecological data show clear species boundaries (Knowlton et al., 1992; van Veghel and Bak, 1993; 1994; van Veghel and Kahmann, 1994; Weil and Knowlton, 1994; van Veghel et al., 1996; Lopez and Knowlton, 1997; Lopez et al., 1999; Manica and Carter, 2000; Knowlton and Budd, 2001; Fukami et al., 2004b; Levitan et al., 2004; but see van Veghel, 1994; Szmant et al., 1997; Medina et al., 1999).

In some cases, poor species delimitation in Faviidae can be attributed to the lack of genetic variation among morphospecies. Limited variation in gene sequences among *Platygyra* spp. has been found in this study, and also between *P. daedalea* in Kenya and *P. sinensis* in Hong Kong (Mangubhai et al., 2007). These results confirm the lack of genetic distinction in this group, as first described through allozymes by Miller and Benzie (1997), and support the hypothesis that the members of this genus may have only recently diverged. Indeed, in the Great Barrier Reef, there are few barriers to fertilisation among morphospecies of *Platygyra*. Spawning times among species have been shown to overlap, while interspecific hybridisation occurs at rates comparable to within-species fertilisations and give rise to larvae that exhibit similar rates of settlement and growth (Miller and Babcock, 1997; Willis et al., 1997). Morphologically, four of the five species that we examined, i.e. *P. daedalea*, *P. lamellina*, *P. pini* and *P. sinensis*, do not differ by a large degree; only two characters, each with two non-discrete states, have traditionally been used to segregate them: valley length and wall thickness (Wijsman-Best, 1976; Veron et al., 1977; Veron, 2000). Nevertheless, the presence of four common and distinct morphotypes suggests that reproductive barriers may exist. To clarify the species status of members in *Platygyra*, more data and experiments are needed.

From a taxonomic perspective, some taxa recovered by the molecular analyses could also be ill-defined due to the oversplitting of species (Funk and Omland, 2003). Intraspecific variation may have been mistaken for species and even genus-level differences. In the *Favia speciosa* + *Barabattoia amicorum* clade, for example, unusually low interspecific genetic distances segregate the two species. The separation is doubtful at the species level, and even more so for genus *Barabattoia*. Superficially, three morphological characters define *B. amicorum* as distinct from *F. speciosa* in this study: corallite form, coenosteum and polyp colour (Wijsman-Best, 1974a; Veron et al., 1977; Veron, 2000). Similar traits have been employed to recognise *B. amicorum* in traditional taxonomy, but the boundaries are not always clear and species may overlap in one or more of the above characters (see also Todd et al., 2004a,b). Our results show that variants of a single species may have been incorrectly described as different species. Arguably, given the morphological and genetic similarities, *Barabattoia* has been erroneously separated from *Favia*.

The high bootstrap support for the Indo-Pacific *Montastraea* spp. with little internal resolution in the molecular analyses is remarkable on two counts. Firstly, it is known that the genus is poorly defined, and is distinguished from *Favia* based only on its extra-tentacular mode of budding (Veron et al., 1977; Wijsman-Best, 1977a). In fact, colonies seem to demonstrate both intra- and extra-tentacular budding (pers. obs.; see images in Veron et al., 1977). Since the Indo-Pacific members of this genus are well-delimited genetically, it may be possible to describe more definitive synapomorphies associated with this group. Secondly, the lack of resolution within the clade is not consistent with the morphological analysis. The latter produced three taxa each with one *Montastraea* species, scattered across the maximum parsimony trees. Clearly, morphospecies within the genus are well-defined, but molecular data suggest otherwise—only *Montastraea magnistellata* has been recovered—likely owing to recent speciation events. The above issues highlight the fact that taxa delineated based on genetic markers may not be morphologically separable, and vice versa.

Our analyses reveal widespread incongruence between molecular and morphology trees. None of the major clades and genera with multiple exemplars have been recovered by either type of data. This could be due to misleading taxonomic characters, unreliable molecular data, or a combination of both. Introgression is one of the factors that may have resulted in such disparity, where the gene tree does not resemble the species tree, and neither is well-correlated with morphological evolution (Doyle, 1992; Bromham et al., 2002). Over geological timescales, rates of interbreeding among species vary due to changes in surface circulation patterns, thus driving speciation and hybridisation (Veron, 1995). As a result of a reticulate evolutionary process, phylogenies based on a single data type that are obtained at the present time may not reflect the natural history of species. A multi-character phylogeny, integrating several data types, may therefore be more effective in demarcating species boundaries in Scleractinia. Incorporating characters derived from other techniques, such as reproductive trials and ecological surveys, is likely to increase the overall rigour of coral phylogeny and taxonomy.

CONCLUSIONS

Our broad-based survey of Faviidae's species-level relationships has revealed pressing problems in coral taxonomy and systematics. Taxonomic conventions in the family have been challenged and phylogenetic reconstructions based on mitochondrial sequence data and morphological characters are incongruent. These results are similar to what has been found in other scleractinian corals. But how can these problems be overcome? We propose more detailed studies of specific genera based on morphology and DNA sequences of particularly problematic groups (e.g. *Favia*, *Goniastrea*, *Montastraea* spp., *Platygyra* spp., and inter-oceanic taxa). These studies should ideally utilise morphological, mitochondrial, and nuclear genetic markers, since slow COI evolution among anthozoans has limited its effectiveness in delineating species (Shearer et al., 2002; Huang et al., 2008). We believe that IGR would be a good choice because in our study fewer species pairs share 'barcodes' for IGR than for COI. Additional markers that should be considered are 16S rDNA, nuclear internal transcribed spacers and SRP54 (e.g. Reimer et al., 2007a,b; 2008; Concepcion et al., 2008; Fukami et al., 2008). However, one particular problem with research on scleractinian corals is the difficulty with exchanging specimens due to CITES regulations (Green and Hendry, 1999; Green and Shirley, 1999; see also Roberts and Solow, 2008). Yet, species will have to be sampled across their ranges that do not follow national borders. We believe that the best way forward is research in different countries using the same markers. This will allow for combining of data but requires agreement among coral systematists which markers should be used.

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CHAPTER 3

Cleaning up the 'Bigmessidae': molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae

INTRODUCTION

For the last two decades, coral systematists have been untangling the complex evolutionary relationships among scleractinian species using DNA sequence data. Seminal molecular phylogenetic work by Romano and Palumbi (1996; 1997) divided the Scleractinia into two major clades, the robust and complex groups, and indicated many problems with traditional taxonomy based on morphology (see also Chen et al., 2002). For instance, *Leptastrea* was recovered within a Fungiina clade rather than the suborder Faviina, where morphological studies had placed it (e.g. Wells, 1956; Veron et al., 1977). Gradually, using more genetic loci, further evidence was uncovered to show that non-monophyly of coral taxa is widespread in Scleractinia (e.g. Romano and Cairns, 2000; van Oppen et al., 2001; Fukami et al., 2004a; Le Goff-Vitry et al., 2004; Kerr, 2005; Benzoni et al., 2007). This culminated in a comprehensive survey of the entire taxon by Fukami et al. (2008), which showed that while Scleractinia is monophyletic, most taxonomic groups within it are not. In fact, a staggering 11 of 16 conventional families are polyphyletic.

Undoubtedly, one of the most challenging clades that have been recovered by recent analyses is a group of robust corals in clade XVII (Fukami et al., 2008). The disarray within the clade is epitomised by its informal name 'Bigmessidae' (Budd, 2009). This clade contains species from four traditional coral families, Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae, interspersed among one another in the tree based on mitochondrial cytochrome oxidase I (COI) and cytochrome b gene sequences (Fukami et al., 2008). With the exception of the *Montastraea annularis* complex, all members of this clade are from the Indo-Pacific. Families with all species included within clade XVII are Trachyphylliidae (monospecific) and Merulinidae, the latter being polyphyletic, while Faviidae and Pectiniidae have representatives present within and outside clade XVII. Although the clade has not been examined in detail, Huang et al. (2009) showed that representatives from other families (Merulinidae and Mussidae) are also nested within it, and several genera are not monophyletic (i.e. *Echinopora*, *Favia*, *Favites, Goniastrea and Montastraea*). In addition, Fukami et al. (2008) found para- or polyphyly in *Leptoria*, *Oulophyllia* and *Platygyra* for at least one marker.

Clearly, there exists an urgent need for taxonomic revisions in this clade, amidst the ongoing disarray in the Scleractinia. But in order to begin any form of revision for clade XVII, it is first necessary to determine which subclades are problematic, using as complete a morphological and genetic coverage as possible. Up to this point, the largest number of markers used for analysis of this group has been derived from Fukami et al. (2008), who used the aforementioned mitochondrial genes, as well as the nuclear β-tubulin and 28S rDNA separately. However, only 33 species represented by 38 terminals were analysed for clade XVII, and several subclades were not resolved due to their short branches. Resolution was improved in Huang et al. (2009), which included 85 terminals from 43 species, but that study used only COI and a noncoding intergenic mitochondrial region (IGR).

In this study, we present data for five molecular markers—two mitochondrial and three nuclear loci—from 76 of the 132 currently recognised species in clade XVII (Fukami et al., 2008). We also included seven species from other robust corals as outgroups. Corals were sequenced from five reef regions—the central and northern Great Barrier Reef in Australia, Wakayama in Japan, Batangas in the Philippines, Singapore and the Caribbean. We reconstruct the evolutionary history of clade XVII and identify subclade placement of species that have not been studied in a molecular phylogenetic context. As some species were sampled from multiple locations, we also test if these corals were as widespread as previously recorded.

MATERIALS AND METHODS

Specimen collection and DNA extraction

Specimens were collected from coral reefs in five regions—Singapore, Wakayama (Japan), Queensland (Australia), Batangas (The Philippines), and the Caribbean. To ensure consistency in identifications among localities, each coral was sampled by at least two authors, based on morphological features that can be recognised in the field. The identity was later confirmed in the laboratory after examining skeletal traits (Veron et al., 1977; Veron and Pichon, 1980; Veron, 1985; 1986; 2000; 2002). In total, 124 specimens from 83 species in clades XIV–XXI have been included in the present analysis (Table 3.1). 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 ~2cm^2 of tissue preserved in 100% ethanol.

For each colony from Singapore, Japan and the Caribbean, DNA was extracted from ~2 cm^2 of tissue digested in twice their volume of CHAOS solution (not an

Table 3.1: Species and DNA sequences examined in this study. Unless indicated by roman numerals and/or family names in parentheses, all species belong to clade XVII and Faviidae, respectively. Species placed in a molecular phylogenetic context for the first time are in bold. Specimens with voucher numbers starting with 'G' are from Great Barrier Reef (Australia), 'S' from Singapore, 'J' from Japan, 'P' from the Philippines, and 'A' from the Atlantic. GenBank accession numbers are displayed for each molecular marker.

No.	Species	Voucher	28S rDNA	histone H3	ITS rDNA	mt COI	mt IGR
1	*Acanthastrea echinata* (XX; Mussidae)	S031	HQ203399	HQ203520	HQ203308	EU371658	
2	*Barabattoia amicorum*	S047	HQ203400	HQ203521	HQ203309	FJ345412	FJ345480
3	*Caulastraea echinulata*	S041	HQ203401	HQ203522		FJ345414	FJ345496
4	*Caulastraea furcata*	P108	HQ203402	HQ203523		HQ203248	HQ203639
5	***Caulastraea tumida***	G61875	HQ203403	HQ203524	HQ203310	HQ203249	HQ203640
6	*Cyphastrea chalcidicum*	G61902	HQ203404	HQ203525	HQ203311	HQ203250	
7	*Cyphastrea chalcidicum*	S103	HQ203405	HQ203526	HQ203312	FJ345415	
8	*Cyphastrea microphthalma*	S069	HQ203406	HQ203527		FJ345416	
9	*Cyphastrea serailia*	G61889	HQ203407	HQ203528	HQ203313	HQ203251	
10	*Cyphastrea serailia*	S024	HQ203408	HQ203529	HQ203314	EU371659	
11	*Cyphastrea serailia*	P120	HQ203409	HQ203530		HQ203252	
12	*Diploastrea heliopora* (XV)	S048	HQ203410	HQ203531	HQ203315	EU371660	
13	*Echinopora gemmacea*	S120	HQ203411	HQ203532	HQ203316	FJ345418	FJ345457
14	***Echinopora horrida***	G61907	HQ203412	HQ203533	HQ203317	HQ203253	HQ203641
15	*Echinopora lamellosa*	S109	HQ203413	HQ203534	HQ203318	FJ345419	FJ345458
16	***Echinopora mammiformis***	G61884	HQ203414	HQ203535	HQ203319	HQ203254	HQ203642
17	*Echinopora pacificus*	S110	HQ203415	HQ203536	HQ203320	FJ345420	FJ345459
18	*Favia danae*	G61885	HQ203416	HQ203537	HQ203321		HQ203643
19	*Favia danae*	S092	HQ203417	HQ203538		EU371663	FJ345476
20	*Favia favus*	G61880	HQ203418	HQ203539	HQ203322	HQ203255	HQ203644
21	*Favia favus*	G61915	HQ203419	HQ203540	HQ203323	HQ203256	HQ203645
22	*Favia favus*	S003	HQ203420	HQ203541	HQ203324	EU371710	FJ345511
23	*Favia favus*	S025	HQ203421	HQ203542		EU371664	FJ345465
24	*Favia favus*	S040	HQ203422	HQ203543	HQ203325	EU371665	FJ345466
25	*Favia favus*	P105	HQ203423	HQ203544		HQ203257	HQ203646
26	*Favia fragum* (XXI)		AF549222			AB117222	
27	*Favia* cf. *laxa*	S013	HQ203424	HQ203545		EU371707	FJ345508
28	*Favia* cf. *laxa*	S014	HQ203425	HQ203546	HQ203326	EU371708	FJ345509
29	*Favia lizardensis*	G61872	HQ203426	HQ203547	HQ203327		HQ203647
30	*Favia lizardensis*	S072	HQ203427	HQ203548	HQ203328	EU371668	FJ345484
31	*Favia lizardensis*	P136	HQ203428	HQ203549			HQ203648
32	***Favia* cf. *maritima***	G61912	HQ203429	HQ203550	HQ203329	HQ203258	HQ203649
33	*Favia matthaii*	G61881	HQ203430	HQ203551	HQ203330		
34	*Favia matthaii*	G61883	HQ203431	HQ203552	HQ203331	HQ203259	HQ203650
35	*Favia matthaii*	S005	HQ203432	HQ203553	HQ203332	EU371669	FJ345471
36	*Favia matthaii*	S029	HQ203433	HQ203554	HQ203333	EU371671	FJ345473
37	*Favia maxima*	S052	HQ203434	HQ203555	HQ203334	EU371674	
38	*Favia maxima*	P142	HQ203435	HQ203556		HQ203260	HQ203651
39	*Favia* cf. *maxima*	P134	HQ203436	HQ203557	HQ203335	HQ203261	HQ203652
40	*Favia pallida*	G61898	HQ203437	HQ203558	HQ203336		HQ203653
41	*Favia pallida*	S036	HQ203438	HQ203559	HQ203337	EU371675	FJ345482
42	***Favia rosaria***	G61911	HQ203439	HQ203560	HQ203338	HQ203262	HQ203654
43	*Favia rotumana*	S068	HQ203440	HQ203561	HQ203339	FJ345427	FJ345485
44	***Favia rotundata***	G61874	HQ203441	HQ203562	HQ203340	HQ203263	
45	***Favia rotundata***	P132	HQ203442	HQ203563			
46	*Favia speciosa*	S001	HQ203443	HQ203564	HQ203341	EU371677	FJ345505
47	*Favia speciosa*	S026	HQ203444	HQ203565		EU371680	FJ345506
48	*Favia speciosa*	P103	HQ203445	HQ203566	HQ203342	HQ203264	HQ203655
49	*Favia stelligera*	P141	HQ203446	HQ203567	HQ203343	HQ203265	HQ203656
50	***Favia truncatus***		HQ203447	HQ203568	HQ203344	HQ203266	HQ203657
51	***Favites abdita***	S002	HQ203448	HQ203569	HQ203345	HQ203267	
52	*Favites chinensis*	S084	HQ203449	HQ203570	HQ203346	HQ203268	
53	*Favites complanata*	S007	HQ203450	HQ203571	HQ203347	EU371689	
54	***Favites flexuosa***	P116	HQ203451	HQ203572	HQ203348	HQ203269	
55	*Favites halicora*	S115	HQ203452	HQ203573	HQ203349	HQ203270	

Table 3.1: Species and DNA sequences examined in this study, continued.

No.	Species	Voucher	28S rDNA	histone H3	ITS rDNA	mt COI	mt IGR
56	*Favites paraflexuosa*	S100	HQ203453	HQ203574	HQ203350	EU371694	FJ345521
57	*Favites pentagona*	S086	HQ203454	HQ203575	HQ203351	EU371695	
58	*Favites pentagona*	P111	HQ203455	HQ203576		HQ203271	
59	***Favites russelli***	G61895	HQ203456	HQ203577	HQ203352	HQ203272	HQ203658
60	***Favites stylifera***	P128	HQ203457	HQ203578	HQ203353	HQ203273	HQ203659
61	*Goniastrea aspera*	S107	HQ203458	HQ203579	HQ203354	FJ345430	FJ345487
62	*Goniastrea australensis*	G61876	HQ203459	HQ203580	HQ203355	HQ203274	HQ203660
63	*Goniastrea australensis*	S088	HQ203460	HQ203581	HQ203356	FJ345431	FJ345490
64	*Goniastrea australensis*	S098	HQ203461	HQ203582		EU371696	FJ345491
65	*Goniastrea edwardsi*	S045	HQ203462	HQ203583	HQ203357	EU371697	FJ345492
66	*Goniastrea edwardsi*	S117	HQ203463	HQ203584		FJ345432	FJ345493
67	*Goniastrea favulus*	G61877	HQ203464	HQ203585	HQ203358		HQ203661
68	*Goniastrea favulus*	S022	HQ203465	HQ203586		EU371698	FJ345494
69	*Goniastrea palauensis*	S021	HQ203466	HQ203587	HQ203359	EU371699	FJ345488
70	*Goniastrea pectinata*	G61879	HQ203467	HQ203588	HQ203360		HQ203662
71	*Goniastrea pectinata*	S043	HQ203468	HQ203589		FJ345434	FJ345489
72	*Goniastrea pectinata*	P110	HQ203469	HQ203590			HQ203663
73	*Goniastrea retiformis*	S083	HQ203470	HQ203591	HQ203361	EU371700	FJ345527
74	*Goniastrea retiformis*	P119	HQ203471	HQ203592		HQ203275	HQ203664
75	*Hydnophora exesa* (Merulinidae)	P127	HQ203472	HQ203593	HQ203362	HQ203276	HQ203665
76	***Hydnophora microconos*** (Merulinidae)	P121	HQ203473	HQ203594	HQ203363	HQ203277	HQ203666
77	***Hydnophora pilosa*** (Merulinidae)	P138	HQ203474	HQ203595	HQ203364	HQ203278	HQ203667
78	*Leptoria irregularis*	P133	HQ203475	HQ203596		HQ203279	HQ203668
79	*Leptoria phrygia*	S081	HQ203476	HQ203597	HQ203365	EU371705	FJ345529
80	*Lobophyllia corymbosa* (XIX; Mussidae)		AF549237			AB117241	
81	*Merulina ampliata* (Merulinidae)	P106	HQ203477	HQ203598		HQ203280	HQ203669
82	*Merulina scabricula* (Merulinidae)	P114	HQ203478	HQ203599	HQ203366	HQ203281	HQ203670
83	*Montastraea annularis*	A622	HQ203479	HQ203600	HQ203367	HQ203282	
84	*Montastraea* cf. *annuligera*	P117	HQ203481	HQ203602	HQ203369		HQ203671
85	*Montastraea cavernosa* (XVI)	A005	HQ203480	HQ203601	HQ203368	HQ203283	
86	***Montastraea colemani***	P118	HQ203482	HQ203603		HQ203284	
87	*Montastraea curta*	G61882	HQ203483	HQ203604	HQ203370	HQ203285	
88	*Montastraea curta*	P122	HQ203484	HQ203605		HQ203286	
89	*Montastraea magnistellata*	G61896	HQ203485	HQ203606	HQ203371	HQ203287	
90	*Montastraea magnistellata*	P109	HQ203486	HQ203607		HQ203288	
91	***Montastraea multipunctata***	P131	HQ203487	HQ203608	HQ203372	HQ203289	
92	***Montastraea salebrosa***	P139	HQ203488	HQ203609	HQ203373	HQ203290	HQ203672
93	*Montastraea valenciennesi*	G61904	HQ203489	HQ203610		HQ203291	HQ203673
94	*Montastraea valenciennesi*	S006	HQ203490	HQ203611	HQ203374	EU371713	FJ345514
95	*Montastraea valenciennesi*	S008	HQ203491	HQ203612		EU371714	FJ345515
96	*Montastraea valenciennesi*	P102	HQ203492	HQ203613	HQ203375	HQ203292	
97	***Moseleya latistellata***	G61909	HQ203493	HQ203614	HQ203376	HQ203293	HQ203674
98	*Mussa angulosa* (XXI; Mussidae)		AF549236		AB441402	NC_008163	
99	*Mycedium elephantotus* (Pectiniidae)	S121	HQ203494	HQ203615	HQ203377	HQ203294	HQ203675
100	***Mycedium robokaki*** (Pectiniidae)	S126	HQ203495	HQ203616	HQ203378	HQ203295	HQ203676
101	*Oulophyllia bennettae*	G61873	HQ203496	HQ203617		HQ203296	HQ203677
102	*Oulophyllia bennettae*	S033	HQ203497	HQ203618	HQ203379	FJ345436	FJ345497
103	*Oulophyllia* aff. *bennettae*	P140	HQ203498	HQ203619	HQ203380	HQ203297	
104	*Oulophyllia crispa*	S055	HQ203499	HQ203620	HQ203381	EU371721	FJ345500
105	*Pectinia alcicornis* (Pectiniidae)	P124	HQ203500	HQ203621	HQ203382	HQ203298	HQ203678
106	***Pectinia ayleni*** (Pectiniidae)	S122	HQ203501	HQ203622	HQ203383	HQ203299	HQ203679
107	***Pectinia lactuca*** (Pectiniidae)	P115	HQ203502	HQ203623	HQ203384	HQ203300	HQ203680
108	*Pectinia paeonia* (Pectiniidae)	P126	HQ203503	HQ203624	HQ203385	HQ203301	HQ203681
109	***Platygyra acuta***	P123	HQ203504	HQ203625	HQ203386		HQ203682
110	***Platygyra contorta***	P112	HQ203505	HQ203626	HQ203387		HQ203683
111	*Platygyra daedalea*	G61878	HQ203506	HQ203627			HQ203684
112	*Platygyra daedalea*	S116	HQ203507	HQ203628	HQ203388	FJ345440	FJ345530
113	*Platygyra lamellina*	G61887	HQ203508	HQ203629	HQ203389	HQ203302	HQ203685
114	*Platygyra lamellina*	S114	HQ203509	HQ203630		FJ345441	FJ345531
115	*Platygyra pini*	G61899	HQ203510	HQ203631	HQ203390	HQ203303	HQ203686
116	*Platygyra pini*	S035	HQ203511	HQ203632	HQ203391	FJ345443	FJ345535
117	***Platygyra ryukyuensis***	P101	HQ203512	HQ203633	HQ203392	HQ203304	HQ203687
118	*Platygyra sinensis*	S118	HQ203513	HQ203634	HQ203393	FJ345442	FJ345534
119	*Platygyra sinensis*	P130	HQ203514	HQ203635		HQ203305	HQ203688

Table 3.1: Species and DNA sequences examined in this study, continued.

No.	Species	Voucher	28S rDNA	histone H3	ITS rDNA	mt COI	mt IGR
120	*Platygyra* cf. *verweyi*	S037	HQ203515	HQ203636	HQ203394	EU371722	FJ345532
121	*Plesiastrea versipora* (XIV)	S127	HQ203397	HQ203518	HQ203307	HQ203246	
122	*Plesiastrea versipora* (XIV)	P137	HQ203398	HQ203519		HQ203247	
123	*Scapophyllia cylindrica* (Merulinidae)	S060	HQ203516	HQ203637	HQ203395	FJ345444	FJ345502
124	*Trachyphyllia geoffroyi* (Trachyphylliidae)	J001	HQ203517	HQ203638	HQ203396	HQ203306	HQ203689

acronym; 4M guanidine thiocyanate, 0.1% N-lauroyl sarcosine sodium, 10mM Tris pH 8, 0.1M 2-mercaptoethanol) for at least three days at room temperature before DNA extraction using a phenol-chloroform based method with a phenol extraction buffer (100 mM TrisCl pH 8, 10 mM EDTA, 0.1% SDS) (Sargent et al., 1986; Fukami et al., 2004b; Huang et al., 2008; 2009). For specimens from Australia and the Philippines, genomic DNA was extracted from the tissues preserved in ethanol using the Qiagen DNeasy kit, following the manufacturer's instructions.

The rest of the colony was sprayed with a powerful water jet to remove as much tissue as possible before being bleached in 5–10% sodium hypochlorite solution. The skeletons were rinsed in fresh water, dried, and deposited in the Raffles Museum of Biodiversity Research (Singapore), Seto Marine Biological Laboratory (Wakayama, Japan), Museum of Tropical Queensland (Australia), and De La Salle University (Manila, The Philippines) (Table 3.1).

PCR amplification and sequencing

A total of five molecular markers were amplified for a majority of the samples (Tables 3.1, 3.2). They consist of three nuclear and two mitochondrial loci: (1) 28S rDNA D1 and D2 fragments; (2) histone H3; (3) internal transcribed spacers 1 and 2, including 5.8S rDNA (ITS in short); (4) cytochrome oxidase subunit I (COI); and (5) noncoding intergenic region situated between COI and the formylmethionine transfer RNA gene (IGR in short) (Cuif et al., 2003; Fukami et al., 2004a,b; Colgan et al., 1998; Takabayashi et al., 1998a).

The mitochondrial intergenic region (IGR) was too variable to be aligned across

Table 3.2: Molecular markers utilised for phylogenetic reconstruction.

Marker	Primer pairs	Total characters (informative)	Model
28S rDNA	C1': 5'–ACC CGC TGA ATT TAA GCA T–3' D2MAD: 5'–GAC GAT CGA TTT GCA CGT CA–3'	861 (135)	HKY + G
histone H3	H3F: 5'–ATG GCT CGT ACC AAG CAG ACV GC–3' H3R: 5'–ATA TCC TTR GGC ATR ATR GTG AC–3'	374 (73)	HKY + G
ITS rDNA	A18S: 5'–GATCGAACGGTTTAGTGAGG–3' ITS-4: 5'–TCCTCCGCTTATTGATATGC–3'	1137 (425)	SYM + G
mt COI	MCOIF: 5'–TCTACAAATCATAAAGACATAGG–3' MCOIR: 5'–GAGAAATTATACCAAAACCAGG–3'	719 (71)	HKY + I
mt IGR	MNC1f: 5'–GAGCTGGGCTTCTTTAGAGTG–3' MNC1r: 5'–GTGAGACTCGAACTCACTTTTC–3'	1509 (763)	SYM + I

the entire clade, so only alignable sequences were included in the analysis. ITS comprises multiple copies in the nuclear genome, but the primers we used have shown high fidelity for a single copy, precluding the need to clone the amplicons (Takabayashi et al., 1998a,b; 2003; van Oppen et al., 2000; Lam and Morton, 2003; Mangubhai et al., 2007; Knittweis et al., 2009). Nevertheless, in the unlikely case that paralogs were sequenced, our analyses could be confused by incomplete lineage sorting (van Oppen et al., 2001). We therefore sequenced the ITS locus from at most one representative of each species, unless analyses of the other four markers did not recover its sequences as a clade. In the latter case, sequences may actually belong to separate cryptic species that have been obscured by gross morphological similarities. For COI, not all specimens of each species were necessarily sequenced since intraspecific variation of this gene is limited (Huang et al., 2008; 2009).

PCR products were purified with ExoSAP-IT (GE Healthcare, Uppsala, Sweden) and sequencing was performed by Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) at the University of Hawaii at Manoa using the Applied Biosystems BigDye Terminator kit and an ABI 3730XL sequencer. New sequences were deposited in GenBank under accession numbers HQ203246–HQ203689 (Table 3.1).

Phylogenetic analyses

Sequences were organised into five separate data matrices using Mesquite 2.72 (Maddison and Maddison, 2011), and each aligned with the accurate alignment option (E-INS-i) in MAFFT 6.7 (Katoh et al., 2002; 2009; Katoh and Toh, 2008) under default parameters. Substitution saturation of protein-coding genes was assessed via DAMBE

(Xia and Xie, 2001; Xia et al., 2003), where we found histone H3 and COI to be unsaturated at the third codon positions for tree inference. Consequently, we concatenated the five gene matrices into a single partitioned matrix consisting of 4600 characters, 1467 of which were parsimony informative. This was analysed using maximum parsimony, Bayesian likelihood, and maximum likelihood methods. We also carried out these analyses on a four-gene dataset omitting the ITS partition to determine if the phylogenetic reconstruction was sensitive to the ITS sampling strategy.

Under a maximum parsimony framework, we utilised new search technologies (Goloboff, 1999; Nixon, 1999) in the software TNT 1.1 (Goloboff et al., 2008). Tree searches consisted of 50000 random addition sequence replicates under the default sectorial, ratchet, drift and tree fusing parameters. Gaps were treated as missing data and clade stability was inferred using 1000 bootstrap replicates each employing 100 random addition sequences.

For maximum likelihood, neighbour-joining and Bayesian analyses, we determined the most suitable model of molecular evolution for each gene partition and the concatenated matrix using jModelTest 0.1.1 (Posada, 2008; Guindon and Gascuel, 2003) to test for a total of 24 models, following the Akaike Information Criterion (AIC). The maximum likelihood tree for each partition and the combined dataset was inferred using RAxML 7.2.3 (Stamatakis, 2006; Stamatakis et al., 2008) at the Cyberinfrastructure for Phylogenetic Research (CIPRES; www.phylo.org), employing the GTRGAMMA model. The proportion of invariable sites and gamma distribution shape parameter for variable sites were estimated during the maximum likelihood analysis. Multiparametric bootstrap analysis was carried out using 1000 bootstrap replicates. Maximum likelihood analysis was also carried out with PhyML 3.0 (Guindon and Gascuel, 2003; Guindon et al., 2005) on the combined data, utilising the AIC-chosen model (GTR + I + G), and generating 1000 bootstrap replicates. The neighbour-joining tree of the combined data was calculated in PAUP*4.0b10 (Swofford, 2003) with 1000 bootstrap replicates, employing the evolutionary model selected above.

Bayesian inference was carried out in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), using the resources of the Computational Biology Service Unit from Cornell University, with each partition modeled (Table 3.2) but unlinked for separate parameter estimations. Four Markov chains of 10 million generations were implemented in twelve runs, saving a tree every 100th generation. MCMC convergence among the runs was monitored using Tracer 1.5 (Rambaut and Drummond, 2009), where we ascertained that only four of the twelve runs converged on the shortest trees (only two runs converged for the four-gene analysis; see Brown et al., 2010; Marshall, 2010; Schwartz and Mueller, 2010), and the first 40001 trees were to be discarded as burn-in.

Additionally, compensatory base changes because of the secondary structure of the ITS rDNA loci may lead to non-independence and increased homoplasy of characters (Dixon and Hillis, 1993; Baldwin et al., 1995; Alvarez and Wendel, 2003). Hence, analysis of the secondary structure of this region may result in a more rigorous phylogeny (Müller et al., 2007; Keller et al., 2008; Coleman, 2009; Schultz and Wolf, 2009). Using the ITS2 segment of each ITS sequence, secondary structure was predicted by searching the ITS2 database (Koetschan et al., 2010) for the best match template and then modelling its structure based on free energy minimisation. The ITS2 sequences and their associated structural information were aligned using 4SALE 1.5 (Seibel et al., 2006; 2008), and then exported for analysis in ProfDistS 0.9.8 (Müller et al., 2004; Friedrich et al., 2005; Wolf et al., 2008). The profile neighbour-joining algorithm was executed with 10000 bootstrap replicates on the RNA structural alignment, using the GTR model and rate matrix 'Q_ITS2.txt' for distance correction. ITS2 could not be amplified from *Hydnophora microconos, H. pilosa* and *Merulina scabricula*. Consequently these species were excluded from the analysis.

RESULTS AND DISCUSSION

In this study, the evolutionary history of the 'Bigmessidae' corals was robustly reconstructed using five genes. Relations among other clade representatives chosen as outgroups were also inferred. The maximum likelihood reconstructions carried out by RAxML 7.2.3 and PhyML 3.0 had log likelihood values of –36224.67 and –36995.48, respectively. As they were identical when considering nodes with bootstrap values ≥ 50, we present the RAxML tree that garnered a higher likelihood score (Figures 3.1, 3.2). A total of 182 most parsimonious trees (tree length = 6178) were obtained. No conflicts between tree optimisation procedures (including Bayesian inference and the neighbour-joining algorithm) were apparent when considering only the supported nodes (bootstrap ≥ 50 and posterior probability ≥ 0.9). Analyses excluding the ITS partition also gave congruent results. Several clades were consistent and well supported among maximum likelihood, parsimony and Bayesian inferences. We named some of these groups within clade XVII from A to I, consistent with the classification in Budd and Stolarski (2011). On the other hand, the neighbour-joining method generated a relatively unresolved tree—subclades A, C, F and I did not achieve bootstrap values of ≥ 50.

The combined five-gene data yielded the most resolved phylogeny hitherto of clade XVII, with most branches garnering high support values. However, most partitions gave fairly unresolved trees when analysed individually. By examining the support of subclades among trees obtained via different partitions, we found that nuclear markers contributed a greater extent to the final tree topology (Table 3.3). Histone H3, for instance, supported all higher-level groupings and all subclades except D/E (Figure 3.1). The 28S and ITS rDNA gene trees had moderate resolution within clade XVII, with only two unresolved subclades each. Surprisingly, the tree based on ITS2 rDNA secondary structure had less resolution than the primary sequence alignment. Indeed, the former has demonstrated potential for resolving intrageneric phylogenies in other anthozoans (Grajales et al., 2007; Sánchez and Dorado, 2008), but it is less informative for relationships at higher taxonomic levels (Chen et al., 2004; Wei et al., 2006). Evidently, the COI tree was poorly resolved, with ≥ 50 bootstrap support for few relationships among major clades and only one subclade. The slow evolution of the mitochondrial COI gene among anthozoans is certainly the reason behind this (Shearer et al., 2002; Hellberg, 2006; Huang et al., 2008). While the intergenic marker (IGR) adjacent to COI on the mitochondrial genome has shown promise for phylogenetic reconstruction among Faviidae and Mussidae (Huang et al., 2009; Fukami et al., 2004b; Nunes et al., 2008), it cannot be unambiguously aligned between the major clades. We urge the development of more nuclear phylogenetic markers that can be reliably applied across diverse scleractinian clades.

Most relationships among clades XV to XXI obtained in this study corroborate

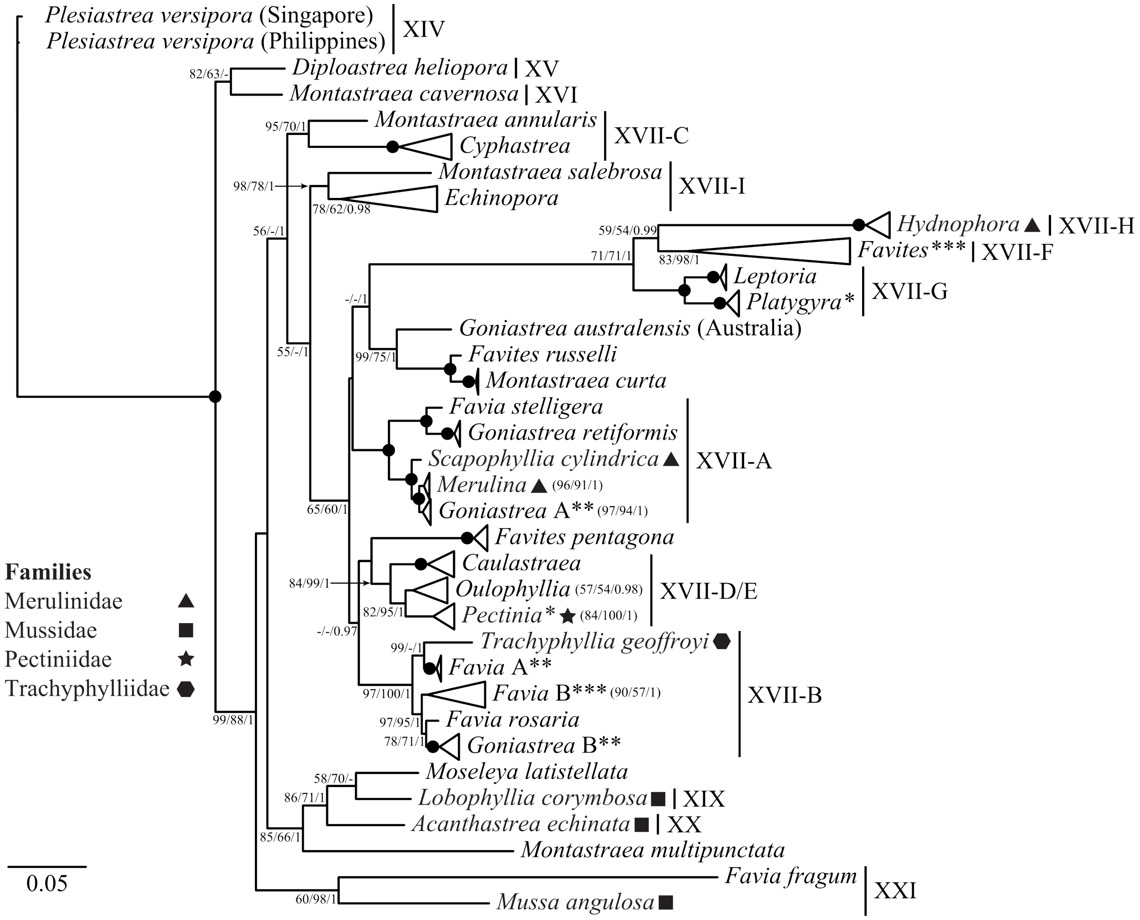

Figure 3.1: Maximum likelihood tree of the combined molecular data. Species have been summarised into genera where possible. One asterisk denotes paraphyletic genus, two asterisks polyphyly, and three represents a genus that is both para- and polyphyletic. All taxa from conventional family Faviidae unless otherwise indicated. Clade designations XIV to XXI shown; clade XVII divided into well-supported subclades. Numbers adjacent to branches/taxa are support values (maximum likelihood bootstrap ≥ 50, maximum parsimony bootstrap ≥ 50, followed by Bayesian posterior probability ≥ 0.9). Filled circles indicate well-supported clades (bootstrap values ≥ 98 and posterior probability of 1).

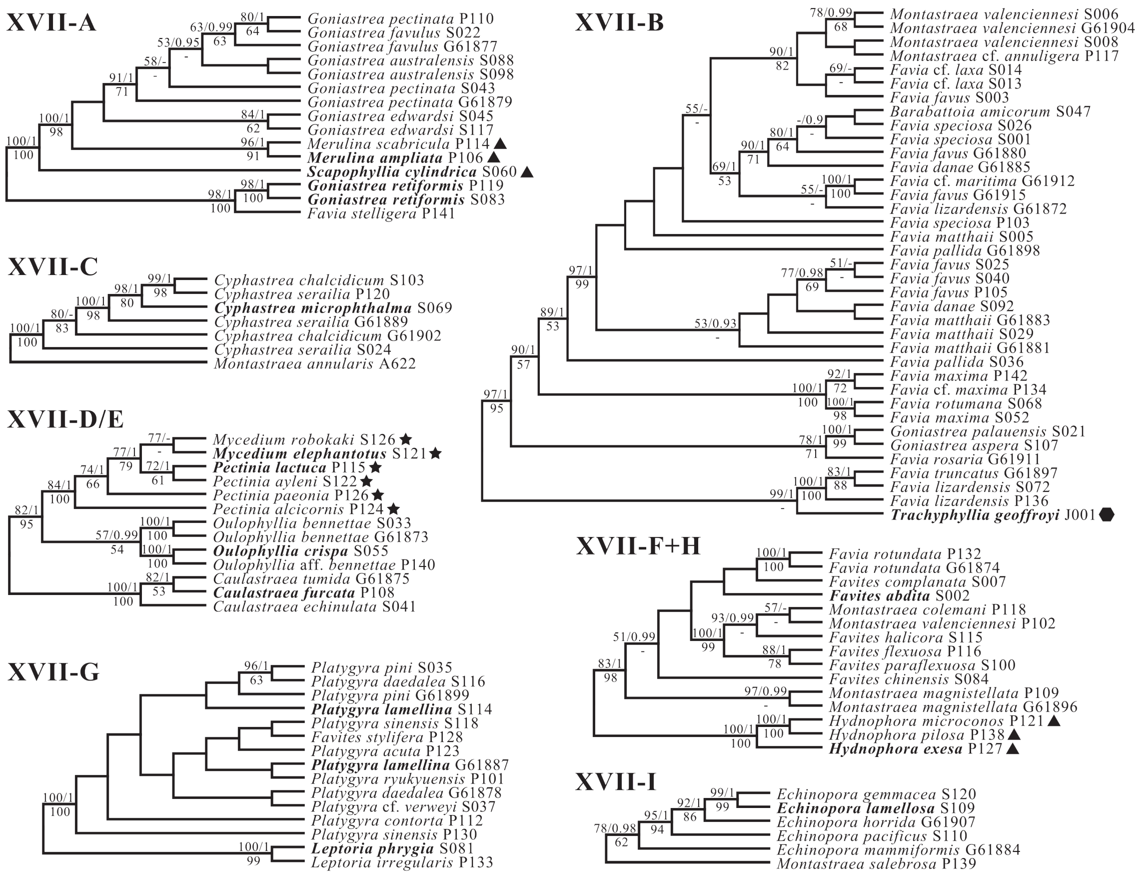

Figure 3.2: Maximum likelihood topologies of each subclade. Numbers above branches are maximum likelihood bootstrap ≥ 50 and Bayesian posterior probability ≥ 0.9, while number below denotes maximum parsimony bootstrap ≥ 50. Family classification follows definitions given for Figure 3.1. Type species of genera are in bold.

Table 3.3: Clades supported by maximum likelihood analysis for each partition. '√√': clade present with ≥ 50 bootstrap support; '√': clade present but not supported (< 50 bootstrap); 'XX': contradicted clade with ≥ 50 bootstrap support; and 'X': contradicted clade not supported. Empty cells indicate insufficient data. Note that *Montastraea multipunctata* and *Moseleya latistellata* are herein considered as part of clade XIX + XX, and subclade I is expanded to include *Montastraea salebrosa*.

Clade	**nuclear DNA**	**mt DNA**	**28S rDNA**	**histone H3**	**ITS sequence**	**ITS structure**	**mt COI**	**mt IGR**
XV to XXI	√√	√√	√√	√√	√√	√√	√√	
XV + XVI	√√	X	√√	√√	√	√√	XX	
XVII to XXI	√√	√√	√	√√	√√	√	√√	
XXI	√√	√√	√				√√	
XIX + XX	√√	√	√	√√	X	√√	√	
XVII	√√	X	√	√√	√	X	X	√√
XVII-A	√√	X	√√	√√	√√	X	X	X
XVII-B	√√	X	X	√√	√√	√√	X	√
XVII-C	√√	XX	√√	√√	√√	X	X	
XVII-D/E	√√	XX	X	X	√√	√	XX	√√
XVII-F	√√	X	√√	√√	X	√√	XX	
XVII-G	√√	√√	√√	√√	X	X	√	√√
XVII-H	√√	X	√√	√√	√√		√√	√√
XVII-I	√√	X	√√	√√	√√	√	X	X

results of Fukami et al. (2008) (Figure 3.1). The only difference occurs in the sister grouping of *Diploastrea heliopora* (XV) and *Montastraea cavernosa* (XVI) (supported by all analyses except Bayesian likelihood) that form a grade in Fukami et al. (2008). The monophyly of the clade XVII + XIX + XX (Pacific faviids and mussids) is recovered but not well supported. *Montastraea multipunctata* and *Moseleya latistellata* are Pacific faviids, and therefore presumably in clade XVII. But as a result of superficial similarities, they have historically been associated with the Pacific mussids *Blastomussa merleti* (clade XIV) (Hodgson, 1985) and *Acanthastrea hillae* (clade XVIII) (Veron et al., 1977; Veron, 1986), respectively. Here, we find them to be more closely related to clades XIX and XX instead, revealing a taxonomic situation more challenging than anticipated. Pacific faviids other than *Diploastrea heliopora* can no longer be restricted to clade XVII, and the possibility exists that yet-to-be sampled taxa provisionally placed in clade XVII—particularly the monotypic genera, *Australogyra*, *Erythrastrea*, *Boninastrea* and *Paraclavarina*—have unexpected affinities.

Nested within clade XVII are four conventional families—Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae (Figure 3.1). Two Pectiniidae genera, *Pectinia* and *Mycedium* (XVII-E) form the sister clade to *Oulophyllia*. This is a similar relationship to the results of Fukami et al. (2008), although here we also show with reasonable support that *Oulophyllia* is monophyletic, and *Caulastraea* is an outgroup rather than nested within *Oulophyllia* (XVII-D). Merulinidae is represented by *Hydnophora*, *Merulina* and *Scapophyllia*. *Hydnophora* is more closely related to *Favites* and Pacific *Montastraea* spp. than *Merulina* and *Scapophyllia*, which form a grade within the clade dominated by *Goniastrea*. The monospecific Trachyphylliidae is nested within the clade consisting primarily of *Favia* spp., and is sister to *Favia lizardensis* and *F. truncatus* (Figure 3.2). Work is ongoing to redescribe clade XVII by incorporating the above families and applying a new taxon name since the type species of Faviidae, *Favia fragum* (Esper, 1797), belongs to clade XXI (Fukami et al., 2008).

The genetic affiliation of *Hydnophora* and *Trachyphyllia* with Faviidae has previously been proposed by Fukami et al. (2004a; 2008). However, this is not exclusively a molecular hypothesis. Based on a combination of colony, corallite and subcorallite characters (e.g. polyp budding; wall, septal and columellar structures), Vaughan and Wells (1943) placed the two taxa within Faviidae. But later, Chevalier (1975) attempted to distinguish *Trachyphyllia* from Faviidae based on minor differences in wall and septal structures by elevating it to the rank of family. Correspondingly, Veron (1985) moved *Hydnophora* into Merulinidae because of *Hydnophora* species' macromorphological similarities (i.e. colony growth form and polyp structure) with *Merulina ampliata* and *Scapophyllia cylindrica*, which are genetically in the same lineage (subclade A) as several *Goniastrea* spp. and *Favia stelligera* (Figures 3.1, 3.2; see also Fukami et al., 2004a; 2008).

Montastraea annularis and likely other members of the species complex (*M. faveolata* and *M. franksi*) are the only Atlantic species in clade XVII (see also Fukami et al., 2004a; 2008). Most significantly here, *M. annularis* is sister to *Cyphastrea*, forming clade XVII-C (Figure 3.1). This placement may seem bizarre in the context of traditional macromorphological characters used to classify scleractinians (e.g. Wells, 1956; Vaughan and Wells, 1943). However, recent work at the microstructural scale (centers of rapid accretion and thickening deposits) has suggested that their septothecal walls (formed by fusion of outer margins of septa) may unite the two taxa (Budd and Stolarski, 2011; see also Budd and Stolarski, 2009). These subcorallite features appear to be appropriate synapomorphies for other subclades. For instance, clade XVII-A consists of *Merulina*, *Scapophyllia*, *Goniastrea* A and *Favia stelligera* (Figure 3.2). At the corallite level, these corals cannot be reconciled within the same taxon, since *Favia stelligera* corallites have single centers with separate walls (plocoid), *Goniastrea* spp. have fused walls (cerioid) and may form valleys (meandroid), while *Merulina* and *Scapophyllia* are composed predominantly of elongated valleys. On the other hand, they share the apomorphy of having septothecal walls with abortive septa (thin bands between normal septa with their own centers of rapid accretion).

The use of macromorphology for identifying 'Bigmessidae' species is known for being problematic as most of these characters are homoplasious (Budd and Smith, 2005; Budd and Stolarski, 2009; Huang et al., 2009). The ability to distinguish clades based on microstructural features is encouraging for scleractinian systematics. Micromorphology, at the scale of septal teeth and granules, has also exhibited promise as phylogenetic characters (Stolarski and Roniewicz, 2001; Stolarski and Russo, 2002; Cuif et al., 2003; Stolarski and Vertino, 2007; Zlatarski, 2008; Budd and Stolarski, 2009). Interestingly, in light of recent molecular hypotheses, other biological traits, in particular, sexuality and to a lesser extent, breeding mode appear highly conserved and could be further developed as phylogenetic markers (Baird et al., 2009; Kerr et al., 2011).

Prior to the use of molecular data to build evolutionary trees, it was a great challenge to determine which morphological characters could be useful for classification, given their intraspecific variability (Mangubhai et al., 2007; Budd, 1990) and phenotypic plasticity (Foster, 1979; Budd, 1988; Todd et al. 2004a,b,c; Todd, 2008). Indeed, the general anthozoan body plan is relatively simple, and scleractinians in particular have few discrete morphological characters that are known to be phylogenetically informative at the polyp level (Wells, 1956; Budd et al., 1994; Wallace and Willis, 1994; Daly et al., 2007). As a result of the recent disarray in coral systematics, morphological taxonomies of scleractinians have been heavily criticised (e.g. Fukami et al., 2004a; 2008; Veron et al., 1996; Knowlton and Budd, 2001). Molecular characters, which are much more numerous and arguably neutrally evolving, can certainly aid our understanding of evolutionary relationships. However, morphological evidence supporting various molecular clades in the present analysis suggests that morphology at novel scales will play an essential role in the taxonomy of 'Bigmessidae' (Budd and Stolarski, 2009).

Widespread sampling in this study has shown that corals thought to belong to the same species across the central Indo-Pacific are actually from distinct lineages. Consider *Goniastrea australensis* (Milne Edwards and Haime, 1857), which occurs in two clades (Figures 3.1, 3.2). Since this species was first described from Australia, the Australian specimen that clustered with *Favites russelli* and *Montastraea curta* should be considered *G. australensis*, while the two specimens from Singapore (S088 and S098, subclade A) probably represent new species yet to be described. This is certainly not an isolated case. A similar situation is revealed for *Montastraea valenciennesi*. Specimens from Australia (G61904) and Singapore (S006 and S008) are in subclade B of mostly *Favia* spp., while the representative from the Philippines (P102) is in subclade F, a distant clade comprising mainly *Favites* species. Interestingly, two reproductively isolated morphotypes of *M. valenciennesi* were recently found to co-occur in Wakayama (Japan), distinguished by the degree of wall fusion among corallites (Fukami and Nomura, 2009). Chevalier (1971) upon examination of the holotype, placed the species in *Favia* on the basis of corallites possessing separate walls and budding intratentacularly (see also Matthai, 1914; Crossland, 1952; Wells, 1954; Nemenzo, 1959; Wijsman-Best, 1972; 1974a). This suggests that the name *Favia valenciennesi* (Milne Edwards and Haime, 1848) could be applied to the Australian and Singaporean specimens in subclade B, while P102 (subclade F) is a new species.

Less extensive issues occur among *Goniastrea* and *Favia* species. For instance, *G. pectinata* (subclade A), collected from three locations, is clearly paraphyletic, with *G. australensis* and *G. favulus* nested within them (Figure 3.2). For *Favia* (subclade B), of six *F. favus* specimens collected from three localities, only three of these form a supported clade while the rest are dispersed within clade XVII-B with no apparent biogeographical pattern. The nesting of *Barabattoia amicorum* among *Favia* spp. has been consistently recovered in recent molecular phylogenies (Fukami et al., 2008; Huang et al., 2009), but this affinity was in fact the dominant hypothesis (Veron et al., 1977; Wijsman-Best, 1972; 1974a; Scheer and Pillai, 1983) until Veron, 1986, included the species in its current genus. Conversely, *Favia rotundata* clusters with *Favites* spp. rather than its congeners, but it was indeed originally described as *Favites rotundata* Veron, Pichon and Wijsman-Best, 1977 (see also Scheer and Pillai, 1983; Nemenzo, 1981).

The polyphyly of most 'Bigmessidae' genera seems to confer a bleak outlook for revisionary work. However, as we have shown in Figure 3.1, several genera can be clearly grouped as clades with limited name changes. For instance, subclade F is composed of species from *Favites* Link, 1807, *Montastraea* de Blainville, 1830, and

Favia Ehrenberg, 1834 (Figure 3.2). While the remaining *Favites* spp. (i.e. *F. pentagona*, *F. russelli*, and *F. stylifera*) are not included within this subclade, the type species of this genus is *Favites abdita* (Ellis and Solander, 1786, type locality “probablement les mers des Grandes-Indes” according to Lamarck, 1816, p. 265). The representative of the latter we used falls well within subclade F. Since no other type species were recovered and with *Favites* Link, 1807, being the oldest valid genus in the subclade, *Favites* should be expanded to include the other species, while *F. pentagona*, *F. russelli* and *F. stylifera* will have to be subsumed within other genera. Several other multi-species genera in fact appear stable: *Caulastraea*, *Cyphastrea*, *Echinopora*, *Hydnophora*, *Leptoria*, *Merulina* and *Oulophyllia*. Name changes are certainly not necessary for *Favites* and *Platygyra*, since they host their respective type species in the subclades shown in Figure 3.2.

CONCLUSIONS

Numerous instances of cryptic taxa determined in this study support the assertion that coral diversity estimates have been fraught with errors (Fukami et al., 2004a). Traits relating to the gross skeletal morphology of corals are unreliable for species description and identification because of their potential for intraspecific variability (Mangubhai et al., 2007; Budd, 1990) and environment-induced plasticity (Foster, 1979; Budd, 1988; Todd et al., 2004a,b,c; Todd, 2008). Yet, these characters have served as the foundation for scleractinian taxonomy (e.g. Wells, 1956; Veron et al., 1977). Fortunately, using molecular data, the recovery of most genera within the 'Bigmessidae' with only minor degrees of paraphyly spells hope for impending taxonomic amendments. Our results show that most genera only require slight revisions, and most major changes are necessary only at the level of the major clades described in Fukami et al. (2008). Certainly, broad taxonomic sampling within Faviidae has revealed more species with unexpected affinities, such as *Moseleya latistellata* and *Montastraea multipunctata*. Clade XVII may consequently have to be redefined to exclude them.

Nevertheless, 'Bigmessidae' subclades are well defined and will no doubt provide a robust framework for taxonomic revisions. The fact that microstructural features support 'Bigmessidae' subclades also offers hope for the morphological approach. Evolutionary relationships among subclades are still provisional due to insufficient statistical support, but they can be clarified with further sampling of nuclear sequences. Eventually, a well-resolved tree of a redescribed clade XVII will be available to reconstruct the morphological evolution of 'Bigmessidae' at various scales.

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CHAPTER 4

Evolution of coral morphology in Merulinidae, and revision of *Merulina* Ehrenberg, 1834, and *Goniastrea* Milne Edwards and Haime, 1848

INTRODUCTION

In the last decade, scleractinian coral taxonomy has been greatly advanced by the integration of genetic data and new morphological characters (Budd et al., 2010). Molecular phylogenetic studies have provided solid evidence that conventional taxonomy based on easily-observed morphological traits fails to organise coral taxa based on their evolutionary histories (Fukami et al., 2004a; Fukami et al., 2008; Kitahara et al., 2010). On the other hand, recent investigations into subcorallite morphology (i.e. small and/or internal features of the polyp's skeleton that are not directly observable with the naked eye) via palaeontological approaches have shown that several clades possess unique characteristics yet to be used for delineation and description of taxa (Budd and Stolarski, 2009; 2011).

Taxonomic revisions based on this new integrated approach have commenced, albeit at a very slow pace. For the genus *Psammocora* for instance, it took about a dozen biologists more than five years to realise its non-monophyly (Benzoni et al., 2007), reconstruct a robust species phylogeny supported by molecular and morphological data (Stefani et al., 2008a,b), and eventually resolve taxonomic names for 23 nominal species (Stefani et al., 2008a; Benzoni et al., 2010; 2012). Several factors contribute to the difficulty in resolving relationships among corals despite the burgeoning amount of data that have emerged. These include morphological convergence between distinct species even among the newly-derived traits (Budd and Stolarski, 2009), the inherently plastic nature of coral anatomy (Todd et al., 2004a,b,c; Todd, 2008; Ow and Todd, 2010), and recent speciation (Miller, 1992; Wolstenholme et al., 2003; Wolstenholme, 2004; Mangubhai et al., 2007; Huang et al., 2009).

One group plagued with all of the above issues is a clade popularly known as 'Bigmessidae' (Budd, 2009), comprising four conventional living families—Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae—found primarily in the Indo-Pacific (Huang et al., 2011). Molecular phylogenetic analyses unequivocally showed that these families were not monophyletic (Fukami et al., 2008; Huang et al., 2011). For instance, *Trachyphyllia geoffroyi*, the only extant Trachyphylliidae species, grouped with Pacific *Favia*, while species of Merulinidae belonged to two separate subclades within 'Bigmessidae'. These results called into question the use of traditional morphological characters for defining taxa within the group. Yet, most 'Bigmessidae' genera were monophyletic (the exceptions being *Favia*, *Favites*, *Goniastrea* and *Montastraea*) (Huang et al., 2011), and well-defined genus-level subclades appeared to be supported by subcorallite morphological features (Budd and Stolarski, 2011).

On the basis of molecular phylogenies by Fukami et al. (2008) and Huang et al. (2011), as well as detailed examinations of coral morphology at the corallite and subcorallite scales (Budd and Stolarski, 2011), Merulinidae Verrill, 1865, was expanded to include all members of 'Bigmessidae', Faviidae was demoted to the subfamily Faviinae as a group limited to the Atlantic, and the remaining two families were synonymised (Budd et al., in press). The seniority of the name Merulinidae relative to the other families justified this modification under the International Code of Zoological

Nomenclature (hereafter referred to as the Code). Yet its type genus *Merulina* was initially placed in the family Daedalina Ehrenberg along with other traditional Faviidae taxa such as *Favia* and *Platygyra* (Ehrenberg, 1834). It was only later that Verrill (1865) recognised the family-level morphological distinction between *Merulina* and the Faviidae taxa, concurred by Vaughan and Wells (1943) and Wells (1956). However, the evolutionary affinity between Merulinidae and Faviidae *sensu* Wells (1956) was never doubted, and the affiliation of the genus *Hydnophora* Fischer de Waldheim to either family was unclear (see Vaughan and Wells, 1943; Wells, 1956; Chevalier, 1975; Veron et al., 1977; Veron and Pichon, 1980; Veron, 1986; 2000). Furthermore, Trachyphylliinae Wells, 1956, was a subfamily within Faviidae, and Pectiniidae Vaughan and Wells, 1943, was hypothesised to be very closely related. As these taxa were historically linked to a large extent, incorporation of the entire 'Bigmessidae' clade under Merulinidae should hardly be surprising.

At the genus level, on the other hand, the polyphyly of the genera *Favia*, *Favites*, *Goniastrea* and *Montastraea* as traditionally delineated appeared to be a considerable hurdle for taxonomic revisions (Huang et al., 2011). Order was beginning to be restored to some extent with the resurrection of *Dipsastraea* Blainville, 1830 (Pacific *Favia*), *Phymastrea* Milne Edwards and Haime, 1848 (Pacific *Montastraea*), and *Orbicella* Dana, 1846 (*'Montastraea' annularis* complex) (Budd et al., in press), as well as detailed study of several *Dipsastraea* species (Kongjandtre et al., 2012). However, the examination of type species of the above polyphyletic genera is paramount for revisions at this taxonomic level since they bear the genus names (Article 42.3 of the Code). Particularly for the resolution of *Goniastrea*, members of which were recovered in subclades A and B

(Figures 3.1, 3.2), the placement of its type *Goniastrea retiformis* (Lamarck, 1816) is of significance. Unfortunately, terminals used in the phylogenetic reconstructions of Merulinidae to date were mostly samples collected outside of species' type localities. Given that Fukami et al. (2008) and Huang et al. (2009; 2011) recovered different relationships in some instances, it is possible that species identifications were inconsistent and names had been erroneously applied to the samples collected by one or the other team.

In this study, we presented a detailed analysis of Merulinidae based on characters associated with species' corallite and subcorallite skeletal structures to infer the morphological evolution of the clade with respect to its phylogenetic history. We then carried out a formal taxonomic revision of subclade A within Merulinidae (*Merulina* + *Goniastrea*; see Figure 3.1) based on a robust molecular phylogenetic analysis of key species in the group. We took positive steps in circumventing the above-mentioned problems associated with the type concept by including type species of genera and samples collected from type localities, as well as comparing the present collection with type specimens.

MATERIALS AND METHODS

Morphological analysis of Merulinidae

Based on specimens collected by Huang et al. (2011), morphological traits from three different scales of skeletal structure—macromorphology, micromorphology and microstructure according to Budd and Stolarski (2011)—were examined to construct a morphological matrix consisting of 47 characters (Table 4.1). First, characterisation of

Table 4.1: Morphological characters from three different scales of coral skeletal structure examined in this study. Characters are based on Budd and Stolarski (2011).

Character	States	Parsimony model
Macromorphology		
Intracalicular budding	Absent Present	Unordered
Extracalicular budding	Absent Present	Unordered
Polymorphism	Absent Present	Unordered
Corallite integration	Solitary-discrete (1–3 mouths) Uni-/multi-serial Organically united	Unordered
Coenosteum structure	Costate Spinose Vesicular/solid	Unordered
Coenosteum amount	Absent (void) Fused walls Limited (includes double wall) Moderate (< corallite diameter) Extensive (> corallite diameter)	Ordered
Calice or valley width	Small (< 4 mm) Medium (4–10 mm) Large (10–15 mm) Very large (> 15 mm)	Ordered
Calice relief	Low (< 2 mm) Medium (2–4 mm) High (4–10 mm) Very high (> 10 mm)	Ordered
Continuity of costosepta	Not confluent Sometimes confluent Mostly confluent	Ordered

Table 4.1: Morphological characters examined in this study, continued.

Character	**States**	**Parsimony model**
Number of septa	< 3 cycles (< 24) 3 cycles (24–36) 4 cycles (36–60) 5 cycles (> 60)	Ordered
Minor septa (i.e. free septa)	Absent Irregular Regular	Ordered
Septa spacing (per 5 mm)	< 6 6–12 > 12	Ordered
Relative costosepta thickness or height	Equal Slightly unequal Unequal	Ordered
Columella continuity	Absent Continuous (trabecular linkage) Discontinuous (lamellar linkage)	Unordered
Columella structure	Lamellar Trabecular, compact (1–3 threads) Trabecular, spongy (> 3 threads)	Unordered
Columella size (relative to calice width)	≤ 1/4 1/3 1/2	Ordered
Septal lobes	Absent Present	Unordered
Epitheca	Absent Reduced Well-developed	Ordered
Endotheca	Sparse Low-moderate/tabular Abundant/vesicular	Ordered

Table 4.1: Morphological characters examined in this study, continued.

Character	States	Parsimony model
Paliform lobes (height)	Absent Weak Well-developed	Ordered
Paliform lobes (number)	Absent ≤ 6 6 or more	Ordered
Micromorphology		
Tooth outline (mid-septum)	Elliptical Circular	Unordered
Tooth orientation (mid-septum)	Absent (parellel to septum) Perpendicular	Unordered
Tooth axes (mid-septum)	One (spine) 3–5 (fan) > 5 (multidirectional)	Ordered
Tooth shape (mid-septum)	Regular Irregular	Unordered
Tooth height (first order septum)	Low (< 0.3 mm) Medium (0.3–0.6 mm) High (0.6–1 mm) Very high (> 1 mm)	Ordered
Tooth spacing (first order septum)	Narrow (< 0.3 mm) Medium (0.3–0.6 mm) High (0.6–1 mm) Very high (> 1 mm)	Ordered
Number of teeth per septum	Few (< 6) Medium (6–10) Many (> 10)	Ordered
Granule distribution	Diffuse Evenly scattered Organised in lines	Unordered

Table 4.1: Morphological characters examined in this study, continued.

Character	States	Parsimony model
Granule shape	Pointed (spikes) Pointed (low spikes) Rounded knobs	Ordered
Interarea	Horizontal bands Smooth Palisade	Unordered
Third vs. first order costa tooth shape	Equal Unequal	Unordered
Third vs. first order costa tooth size	Equal Unequal	Unordered
Wall vs. septum tooth size	Equal Unequal	Unordered
Microstructure		
Synapticulotheca	Absent Present	Unordered
Septotheca	Absent Partial Dominant (= septothecal)	Ordered
Abortive septa	Absent Present	Unordered
Trabeculotheca	Absent Partial Dominant (= trabeculothecal)	Ordered
Paratheca	Absent Partial Dominant (= parathecal)	Ordered
Overall wall thickness	Thin (< 0.5 mm) Intermediate (0.5–2 mm) Thick (> 2 mm)	Ordered

Table 4.1: Morphological characters examined in this study, continued.

Character	**States**	**Parsimony model**
Thickening deposits	Fibrous Thick fibrous or layered Concentric rings (extensive stereome)	Ordered
Costa centers	No lines Weak lines Lines	Ordered
Distance between costa clusters	< 0.3 mm 0.3–0.5 mm 0.5–1 mm > 1 mm	Ordered
Costa lines (shape)	Absent Straight Undulating/zigzag	Unordered
Septum centers	Clustered Aligned (weak lines) Aligned (strong lines)	Ordered
Perpendicular crosses	Absent Clusters Carinae	Ordered
Columella centers	Clustered Aligned (weak lines) Aligned (strong lines)	Ordered

macromorphology involved the examination of traditional diagnostic traits related to colony form, and the structure and development of the calice, septa, columella, theca and coenosteum (Vaughan and Wells, 1943; Wells, 1956). Observations were made using a light microscope, and data obtained for 21 characters. Second, micromorphology was visualised at the scale of the shapes of teeth along the wall, septa, columella and septal face granulations. We examined 13 characters employing this method. Each calice was mounted on stubs and observations were carried out via scanning electron microscopy (SEM) at magnifications lower than 200× (Budd and Stolarski, 2009; 2011). Third, the study of coral microstructure involved examinations of the arrangements of rapid accretion deposits and thickening deposits or fibres (Stolarski, 2003; Nothdurft and Webb, 2007; Brahmi et al., 2010) within the wall, septa and columella, using thin sections and observing at magnifications < 100×. Thirteen characters were studied in this manner. Each calice was cut transversely, impregnated with epoxy, and sectioned to a thickness of ~30 µm prior to visualisation under a stereo microscope (Budd and Stolarski, 2009; 2011).

To infer the morphological evolution of Merulinidae, we mapped the resultant 47 characters onto an 83-species molecular phylogeny represented by 124 terminals presented in the previous chapter (Figure 3.1). This tree spanned clades XIV to XXI (sensu Fukami et al., 2008). With the aid of Mesquite 2.75 (Maddison and Maddison, 2011), we examined possible apomorphies at both the corallite and subcorallite levels by performing character transformations on the full phylogeny. Ancestral states were inferred according to maximum parsimony as well as maximum likelihood based on the Mk1 model (Lewis, 2001). To determine morphological traits that were diagnostic of subclades within Merulinidae, we computed consistency and retention indices (CI and RI) based on a tree trimmed of the 10 outgroup terminals.

Molecular analysis of *Merulina* and *Goniastrea*

Corals were sampled from Singapore, the Great Barrier Reef (Queensland, Australia) and Talim Bay (Batangas, The Philippines) in the Indo-West Pacific; Djibouti, Mayotte and the Seychelles in the Indian Ocean; and Fiji and New Caledonia in the Pacific. Species identifications follow Veron et al. (1977), Veron and Pichon (1980), and Veron (1986; 2000; 2002), based upon the phylogenetic (diagnosable) species concept (Nelson and Platnick, 1981; Cracraft, 1983; Nixon and Wheeler, 1990; see also de Queiroz, 2005a,b,c; 2007). In total, 74 specimens spanning 12 species in subclade A according to Huang et al. (2011) were collected for this study (Table 4.2). 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 ~2cm^2 of tissue preserved in 100% ethanol or CHAOS solution (Sargent et al., 1986; Fukami et al., 2004b; Huang et al., 2008). The rest of the colony sample was cleaned with a powerful water jet prior to being bleached in 5–10% sodium hypochlorite. The skeletons were rinsed in fresh water, dried, and deposited at the Raffles Museum of Biodiversity Research (vouchers with HD code; Singapore), Museum of Tropical Queensland (vouchers with GB code; Australia), De La Salle University (vouchers with TB code; The Philippines), Seto Marine Biological Laboratory (vouchers with JP code; Japan), Museo di Storia Naturale di Milano (vouchers with DJ, MY and NC codes; Italy) and Scripps Institution of Oceanography Benthic Collection (vouchers with FJ and SC codes; U.S.A.) (Table 4.2).

Table 4.2: Data for the 91 specimens examined in this study of subclade A. See text for details of repositories and molecular markers. New sequence data are denoted with 'X'.

Morphospecies	Sub-clade	Location	Voucher No.	Repository	GenBank accession no.		
					histone H3	ITS	IGR
Favia stelligera	A	Suva	FJ009	SIO	X	X	X
Favia stelligera	A	Moturiki	FJ038	SIO	X	X	X
Favia stelligera	A	Moturiki	FJ044	SIO	X	X	X
Favia stelligera	A	Naviti	FJ055	SIO	X	X	X
Favia stelligera	A	Batangas	TB141	DLSU	HQ203567	HQ203343	HQ203656
Goniastrea australensis	A	Singapore	HD088	RMBR	HQ203581	HQ203356	FJ345490
Goniastrea australensis	A	Singapore	HD098	RMBR	HQ203582	X	FJ345491
Goniastrea edwardsi	A	Djibouti	DJ126	MSNM	X	X	
Goniastrea edwardsi	A	Djibouti	DJ279	MSNM	X	X	
Goniastrea edwardsi	A	Beqa	FJ019	SIO	X	X	X
Goniastrea edwardsi	A	Queensland	GB034	MTQ	X	X	X
Goniastrea edwardsi	A	Singapore	HD045	RMBR	HQ203583	HQ203357	FJ345492
Goniastrea edwardsi	A	Singapore	HD117	RMBR	HQ203584	X	FJ345493
Goniastrea edwardsi	A	Mahé	SC001	SIO	X	X	
Goniastrea edwardsi	A	Mahé	SC005	SIO	X	X	X
Goniastrea edwardsi	A	Mahé	SC014	SIO	X	X	
Goniastrea edwardsi	A	Mahé	SC024	SIO	X	X	X
Goniastrea edwardsi	A	Mahé	SC029	SIO	X	X	X
Goniastrea favulus	A	Djibouti	DJ054	MSNM	X	X	X
Goniastrea favulus	A	Djibouti	DJ118	MSNM	X	X	X
Goniastrea favulus	A	Suva	FJ010	SIO	X	X	X
Goniastrea favulus	A	Beqa	FJ018	SIO	X	X	X
Goniastrea favulus	A	Moturiki	FJ034	SIO	X	X	X
Goniastrea favulus	A	Caqalai	FJ039	SIO	X	X	X
Goniastrea favulus	A	Moturiki	FJ041	SIO	X	X	X
Goniastrea favulus	A	Moturiki	FJ043	SIO	X	X	X
Goniastrea favulus	A	Vitogo	FJ064	SIO	X	X	X
Goniastrea favulus	A	Queensland	GB006	MTQ	HQ203585	HQ203358	HQ203661
Goniastrea favulus	A	Singapore	HD022	RMBR	HQ203586	X	FJ345494
Goniastrea favulus	A	Singapore	HD091	RMBR	X	X	FJ345495
Goniastrea favulus	A	Mayotte	MY180	MSNM	X	X	X
Goniastrea minuta	A	Mahé	SC002	SIO	X	X	X
Goniastrea minuta	A	Mahé	SC011	SIO	X	X	X
Goniastrea minuta	A	Mahé	SC021	SIO	X	X	X
Goniastrea pectinata	A	Queensland	GB008	MTQ	HQ203588	HQ203360	HQ203662
Goniastrea pectinata	A	Queensland	GB023	MTQ	X	X	X
Goniastrea pectinata	A	Queensland	GB030	MTQ	X	X	X
Goniastrea pectinata	A	Queensland	GB035	MTQ	X	X	X
Goniastrea pectinata	A	Queensland	GB037	MTQ	X	X	X
Goniastrea pectinata	A	Singapore	HD043	RMBR	HQ203589	X	FJ345489
Goniastrea pectinata	A	Batangas	TB110	DLSU	HQ203590	X	HQ203663
Goniastrea retiformis	A	Djibouti	DJ193	MSNM	X	X	X
Goniastrea retiformis	A	Djibouti	DJ278	MSNM	X	X	X
Goniastrea retiformis	A	Suva	FJ012	SIO	X	X	X
Goniastrea retiformis	A	Singapore	HD083	RMBR	HQ203591	HQ203361	FJ345527
Goniastrea retiformis	A	Singapore	HD094	RMBR	X	X	FJ345528
Goniastrea retiformis	A	Singapore	HD131	RMBR	X	X	X
Goniastrea retiformis	A	Mayotte	MY179	MSNM	X	X	X
Goniastrea retiformis	A	Mahé	SC022	SIO	X	X	X
Goniastrea retiformis	A	Mahé	SC023	SIO	X	X	X
Goniastrea retiformis	A	Mahé	SC025	SIO	X	X	X
Goniastrea retiformis	A	Batangas	TB119	DLSU	HQ203592	X	HQ203664
Goniastrea sp.	A	Mayotte	MY338	MSNM	X		

Table 4.2: Data for the 91 specimens examined in this study of subclade A, continued.

Morphospecies	Sub-clade	Location	Voucher No.	Repository	GenBank accession no.		
					histone H3	**ITS**	**IGR**
Merulina ampliata	A	Djibouti	DJ258	MSNM	X	X	X
Merulina ampliata	A	Suva	FJ008	SIO	X	X	
Merulina ampliata	A	Singapore	HD134	RMBR	X	X	X
Merulina ampliata	A	Mayotte	MY327	MSNM	X	X	X
Merulina ampliata	A	New Caledonia	NC867	MSNM	X	X	X
Merulina ampliata	A	Batangas	TB106	DLSU	HQ203598	X	
Merulina scabricula	A	Beqa	FJ020	SIO	X	X	X
Merulina scabricula	A	Beqa	FJ021	SIO	X	X	X
Merulina scabricula	A	Beqa	FJ022	SIO	X	X	X
Merulina scabricula	A	Leleuvia	FJ031	SIO	X	X	X
Merulina scabricula	A	Naviti	FJ052	SIO	X	X	X
Merulina scabricula	A	Vitogo	FJ063	SIO	X	X	X
Merulina scabricula	A	Singapore	HD135	RMBR	X	X	X
Merulina scabricula	A	New Caledonia	NC849	MSNM	X	X	X
Merulina scabricula	A	Batangas	TB114	DLSU	HQ203599	X	HQ203670
Merulina scheeri	A	Djibouti	DJ006	MSNM	X	X	X
Merulina scheeri	A	Djibouti	DJ140	MSNM	X	X	X
Merulina scheeri	A	Djibouti	DJ246	MSNM	X	X	X
Scapophyllia cylindrica	A	Singapore	HD060	RMBR	HQ203637	HQ203395	FJ345502
Scapophyllia cylindrica	A	Singapore	HD132	RMBR	X	X	X
Barabattoia amicorum	B	Singapore	HD047	RMBR	HQ203521	HQ203309	FJ345480
Favia favus	B	Queensland	GB009	MTQ	HQ203539	HQ203322	HQ203644
Favia lizardensis	B	Singapore	HD072	RMBR	HQ203548	HQ203328	FJ345484
Favia rosaria	B	Queensland	GB040	MTQ	HQ203560	HQ203338	HQ203654
Goniastrea aspera	B	Queensland	GB017	MTQ	X	X	X
Goniastrea aspera	B	Singapore	HD107	RMBR	HQ203579	HQ203354	FJ345487
Goniastrea palauensis	B	Singapore	HD021	RMBR	HQ203587	HQ203359	FJ345488
Montastraea valenciennesi	B	Singapore	HD006	RMBR	HQ203611	HQ203374	FJ345514
Trachyphyllia geoffroyi	B	Wakayama	JP001	SMBL	HQ203638	HQ203396	HQ203689
Caulastraea tumida	D	Queensland	GB004	MTQ	HQ203524	HQ203310	HQ203640
Oulophyllia crispa	D	Singapore	HD055	RMBR	HQ203620	HQ203381	FJ345500
Mycedium elephantotus	E	Singapore	HD121	RMBR	HQ203615	HQ203377	HQ203675
Pectinia lactuca	E	Batangas	TB115	DLSU	HQ203623	HQ203384	HQ203680
Echinopora gemmacea	I	Singapore	HD120	RMBR	HQ203532	HQ203316	FJ345457
Echinopora horrida	I	Queensland	GB036	MTQ	HQ203533	HQ203317	HQ203641
Montastraea salebrosa	I	Batangas	TB139	DLSU	HQ203609	HQ203373	HQ203672
Favites russelli	?	Queensland	GB024	MTQ	HQ203577	HQ203352	HQ203658
Goniastrea australensis	?	Queensland	GB005	MTQ	HQ203580	HQ203355	HQ203660

DNA extraction and polymerase chain reaction (PCR) protocols followed Huang et al. (2011). Three molecular markers were amplified from the samples, namely the nuclear histone H3 (Colgan et al., 1998), nuclear internal transcribed spacers 1 and 2 (ITS; including 5.8S rDNA) (Takabayashi et al., 1998a,b), and mitochondrial (mt) noncoding intergenic region (IGR; between COI and the formylmethionine transfer RNA gene) (Fukami et al., 2004b). Sequences were organised into three separate data matrices using Mesquite 2.75 (Maddison and Maddison, 2011). The histone H3 dataset was supplemented with all sequences from Huang et al. (2011), while 17 other species across the Merulinidae clade were included as outgroups for the ITS and IGR datasets (Table 4.2). Alignments were carried out using the E-INS-i option in MAFFT 6.8 (Katoh et al., 2002; 2009; Katoh and Toh, 2008) under default parameters. Phylogenetic reconstructions were performed separately for each marker, and then concatenated for combined analyses. ITS and IGR could not be amplified from an unidentified *Goniastrea* sp. from Mayotte, so the sample (MY338) was omitted from the combined dataset.

Three phylogenetic optimisation criteria were employed. First, maximum likelihood trees were inferred using RAxML 7.2.8 (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, under the maximum parsimony framework, heuristic searches in PAUP* 4.0b10 (Swofford, 2003) were carried out with 10^5 random additions and nodal supports were assessed using 1000 bootstrap replicates (100 random additions per replicate). Third, for Bayesian analyses, we determined the most suitable model of molecular evolution for each gene partition using jModelTest 0.1.1 (Posada, 2008; Guindon and Gascuel, 2003), testing for a total of

24 models based on the Akaike Information Criterion (AIC). Bayesian inferences were carried out in MrBayes 3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003; Ronquist et al., 2012). Each partition was modelled separately and unlinked during parameter estimations for the concatenated dataset. Four Markov chains of 10 million generations were implemented in four runs, logging one tree per 100 generations. MCMC convergence among the runs was monitored using Tracer 1.5 (Rambaut and Drummond, 2009), where it was determined that the first 10% of trees from each analysis were to be discarded as burn-in.

RESULTS AND DISCUSSION

Morphological analysis of Merulinidae

On the basis of the full 83-species phylogeny including the outgroups (Figure 3.1), microstructural characters showed the lowest levels of homoplasy (mean RI [retention index] = 0.704 ± S.D. 0.203), while macro- and micromorphology were more homoplastic (respectively, mean RI = 0.654 ± S.D. 0.162 and 0.676 ± 0.196). Using the most parsimonious transformations, four characters were found to be apomorphies of Merulinidae. The first, pertaining to macromorphology, was the compact trabecular columella (1–3 threads), with eight reversals to a spongy structure (> 3 threads) and one change to the lamellar form (*Leptoria phrygia*). Second, the distance between costa clusters was < 0.3 mm, the shortest range among all clades, but there were at least four instances of an increase (reversal) in distance to ≥ 0.3 mm. Two micromorphological characters associated with the mid-septal teeth were also apomorphic—the circular tooth outline with a reversal to an elliptical shape in the clade leading to *Goniastrea* *australensis*, *Montastraea curta* and *Favites russelli*, and the irregular tooth shape with multidirectional axes (> 5). The latter was extremely labile within the Merulinidae clade, with reduced axes in several subclades.

All the above apomorphies were supported by the Mk1 model, with the exception of the compact trabecular columella, predicted to have evolved with a higher likelihood (+ 0.0417 proportional likelihood) prior to the origin of Merulinidae. No synapomorphies were detected according to our data.

Our results supported Budd and Stolarski's (2011) assertion that there were few diagnostic characters for Merulinidae. We however added one macromorphological (compact trabecular columella), one microstructural (< 0.3 mm between costa clusters) and one micromorphological (circular tooth outline) trait to the apomorphy they identified (irregular, multidirectional tooth). Most other characters were plesiomorphies that were shared with outgroups such as discrete corallites (1–3 mouths), costate coenosteum, and moderate amount of coenosteum.

Focusing on the Merulinidae clade (see Figure 3.1), we found that corallite characters (mean RI = 0.694 ± S.D. 0.172) exhibited more homoplasy overall than subcorallite ones (microstructure mean RI = 0.734 ± S.D. 0.213; micromorphology mean RI = 0.808 ± S.D. 0.132), but several corallite traits such as the presence of intracalicular budding (RI = 0.929) and corallite polymorphism (RI = 1) showed limited or no homoplasy (Figure 4.1). The four corallite characters with the highest RI clearly could be used to diagnose subclades (Figures 4.2, 4.3). Most of them were apomorphies for the least inclusive clade containing subclades A and B, thus distinguishing subclades C and I within Merulinidae. No other subclades except E were supported by these characters.

Interestingly, these traits were diagnostic of Pectiniidae Vaughan and Wells, 1943, in which subclade E members, *Pectinia* and *Mycedium,* were classed prior to revision by Budd et al. (in press). Even though the above groups could be easily identified based on some aspects of macromorphology, more traits were needed for the rest of Merulinidae.

Micromorphology offered many diagnostic characters for Merulidae subclades. Indeed, merely four septal traits at this level (RI > 0.75) provided sufficient distinction for each subclade (Figures 4.4, 4.5). For instance, the placement of *Favia rotundata* and *Montastraea* spp. in *Favites*-dominated subclade F was supported by their fan-like teeth, 0.3–0.6 mm tooth spacing, low pointed granules and smooth interarea between teeth. The interarea in subclade B, in which most other *Favia* spp. were found, was palisade. Conversely, corallite wall integration, the traditional macromorphological character separating *Favia* and *Favites* (Vaughan and Wells, 1943; Wells, 1956; Veron et al., 1977; Veron, 1986; 2000), was inadequate as *Favia rotundata* and *Montastraea* spp. may have separate walls but were still be more closely related to *Favites* species that possessed fused walls. Furthermore, most *Goniastrea* spp., previously thought to be a close relative of *Favites* because of their fused walls (Veron, 1986; Veron et al., 1977), were in subclade A, and differed from subclade F in all four of the above traits.

Most subclades were also distinguished based on the dominance of different wall microstructural characteristics. Species were dominant in at least one type of wall morphology formed by different configurations of the rapid accretion deposits and fibres (for details, see Figure 3 in Budd and Stolarski, 2011), but may have partial formation of another wall structure (Figures 4.6, 4.7). For example, species in subclade B possessed walls formed predominantly by dissepiments (paratheca), but may also have some

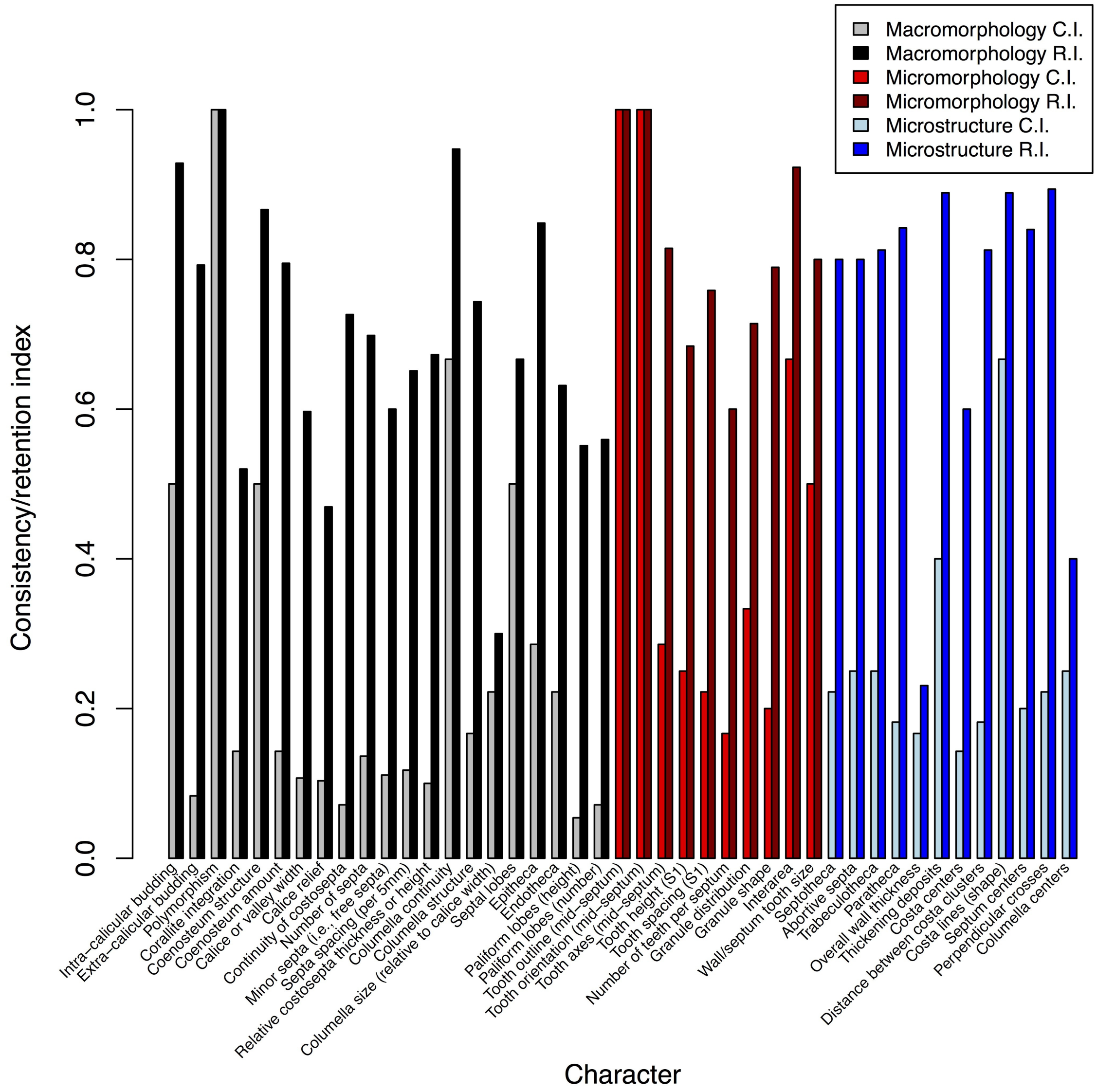

Figure 4.1: Consistency and retention indices for 21 macromorphological, 10 micromorphological and 12 microstructural characters transformed onto Merulinidae tree. The remaining four of the 47 characters examined were not variable and hence were omitted from the plot.

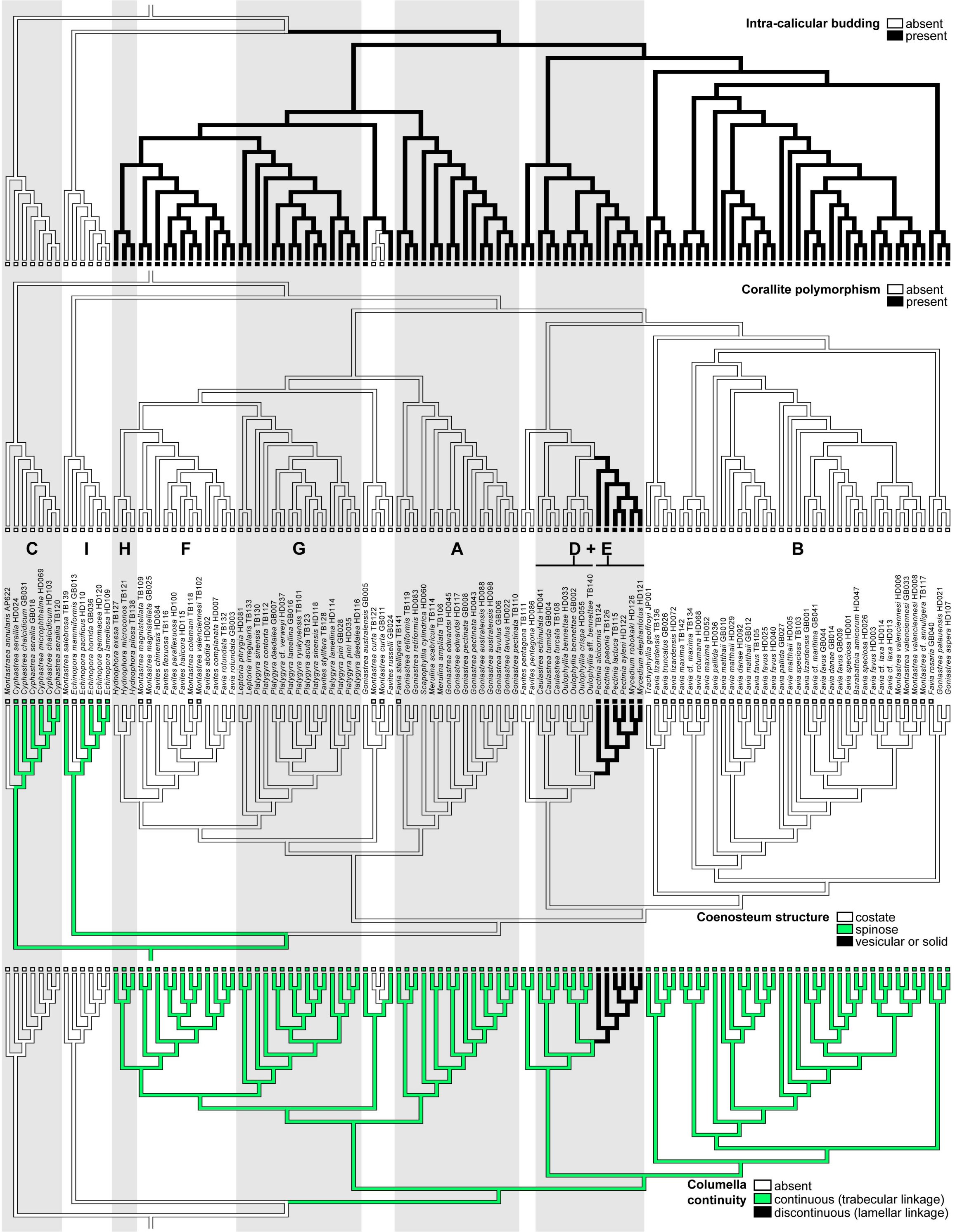

Figure 4.2: Four macromorphological characters with the highest retention index transformed onto Merulinidae tree.

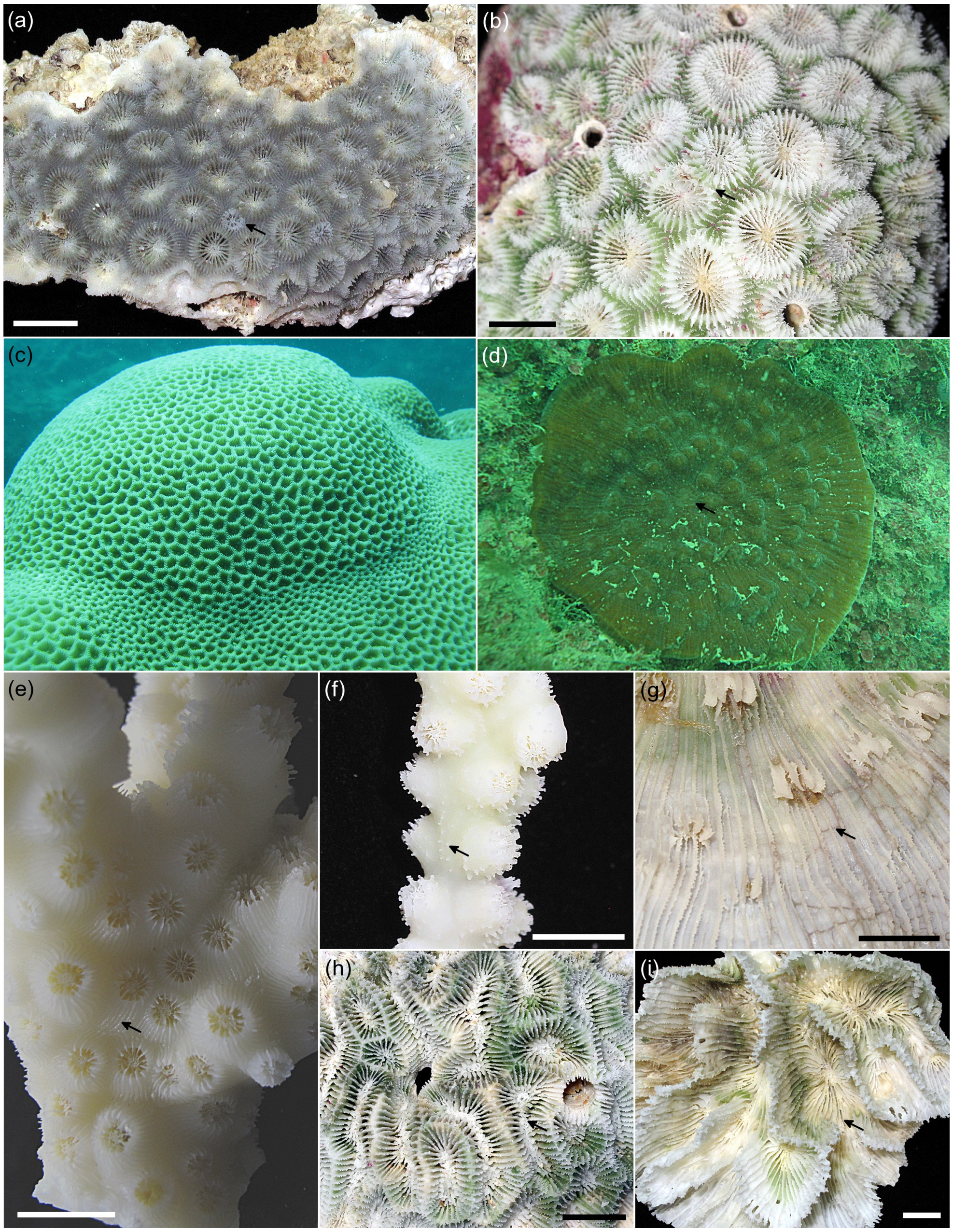

Figure 4.3: Images of coral colonies showing corallite macromorphological character states (black arrows). (a) *Montastraea curta* (TB122), extracalicular budding; (b) *Favia favus* (GB009; subclade B), intracalicular budding; (c) *Goniastrea favulus* (GB006; subclade A), no corallite polymorphism; (d) *Mycedium robokaki* (HD126; subclade E), corallite polymorphism; (e) *Echinopora mammiformis* (GB013; subclade I), costate coenosteum and absence of columella continuity; (f) *Echinopora horrida* (GB036; subclade I), spinose coenosteum; (g) *Mycedium robokaki* (HD126; subclade E), vesicular coenosteum; (h) *Goniastrea australensis* (GB005), continuous columella and trabecular linkage; (i) *Pectinia lactuca* (TB115; subclade E), discontinuous columella and lamellar linkage. Scale 1 cm in length.

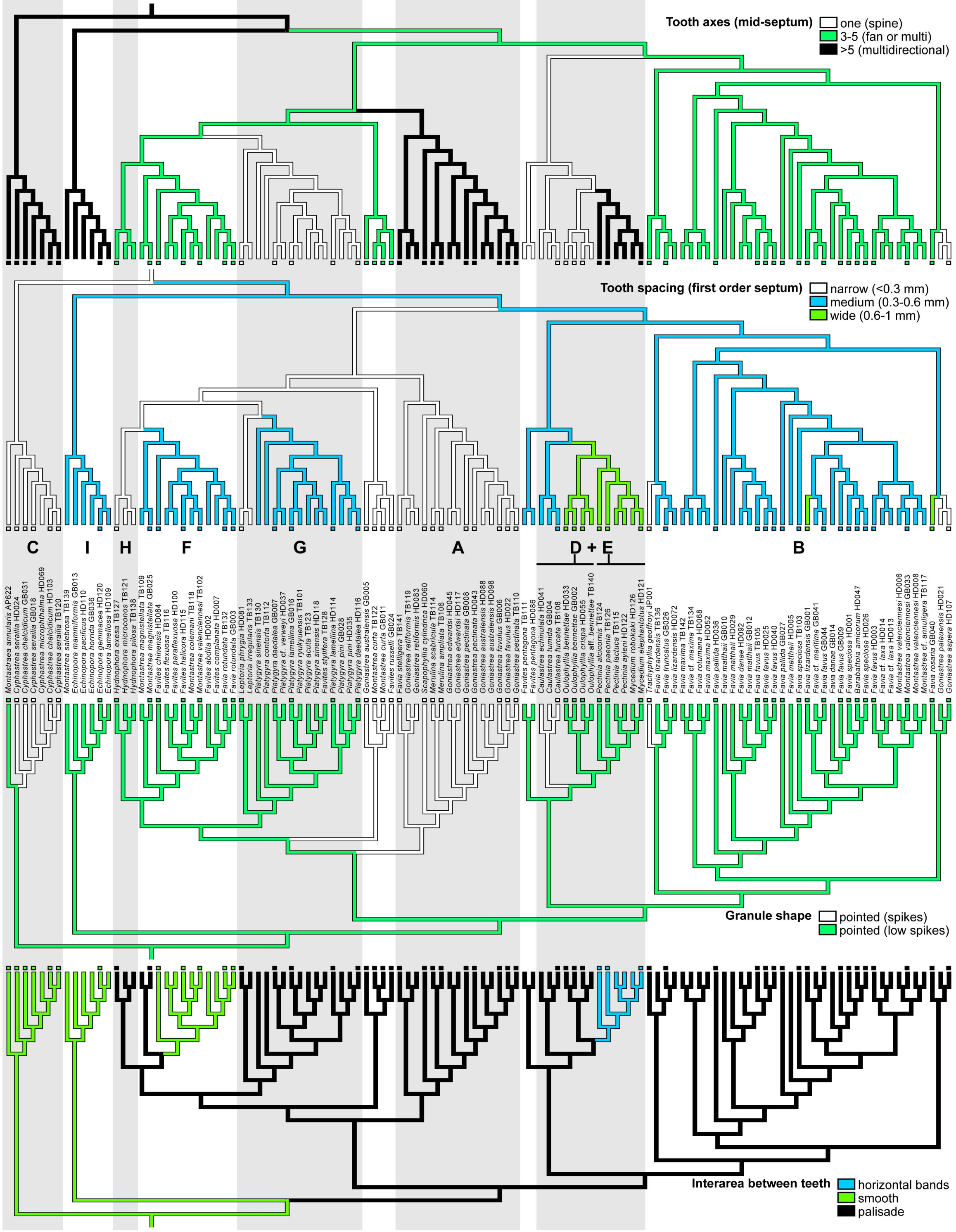

Figure 4.4: Four diagnostic septal micromorphological characters transformed onto Merulinidae tree.

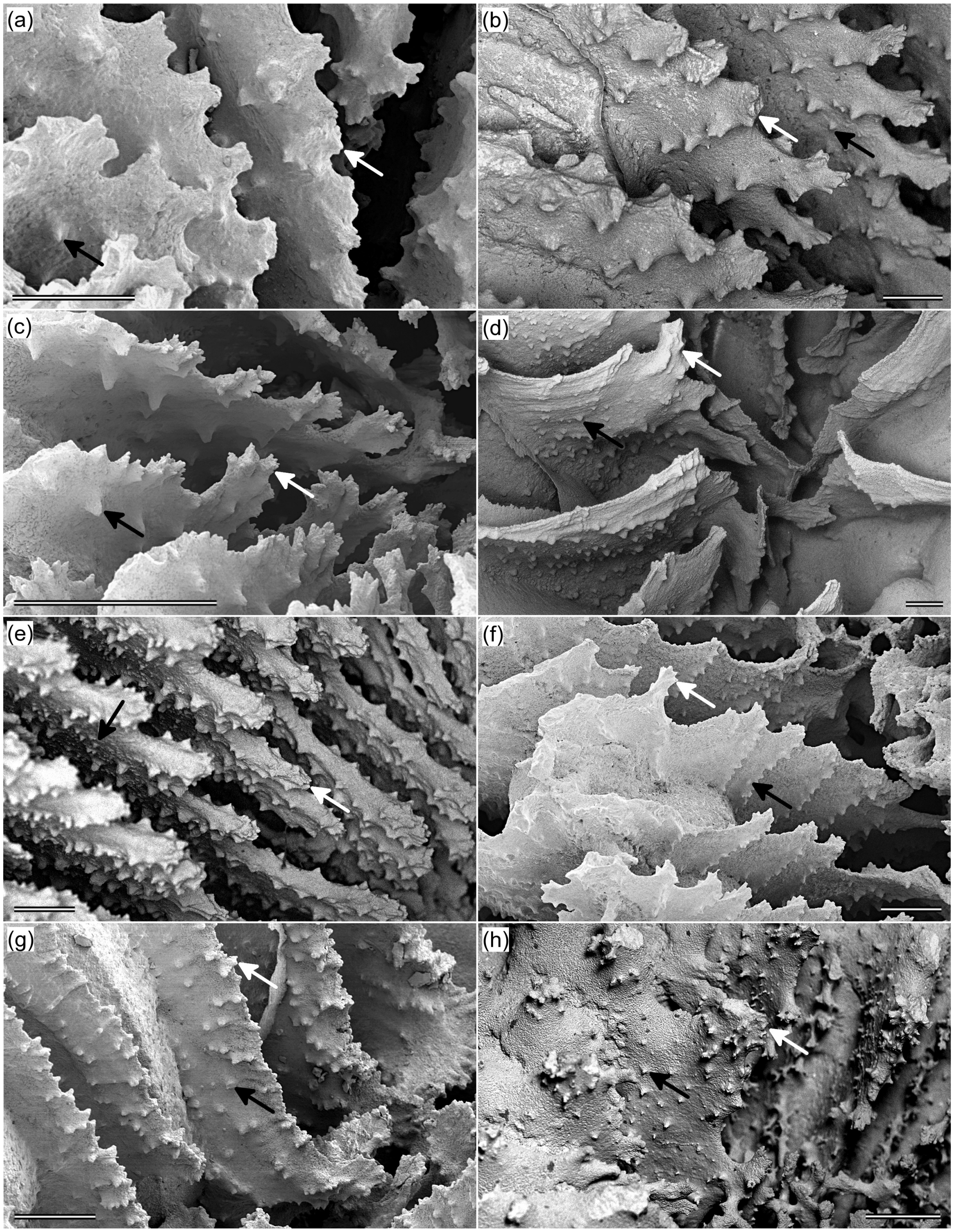

Figure 4.5: Scanning electron micrographs of coral septa showing micromorphological character states as traced on the phylogeny in Figure 4.4. Septal teeth and granulations indicated by white and black arrows respectively. (a) *Merulina ampliata* (subclade A); (b) *Favia rosaria* (GB040; subclade B); (c) *Cyphastrea chalcidicum* (subclade C); (d) *Pectinia paeonia* (subclade E); (e) *Favia rotundata* (GB003; subclade F); (f) *Platygyra lamellina* (subclade G); (g) *Hydnophora exesa* (subclade H); (h) *Echinopora gemmacea* (subclade I). Scale 500 μm in length.

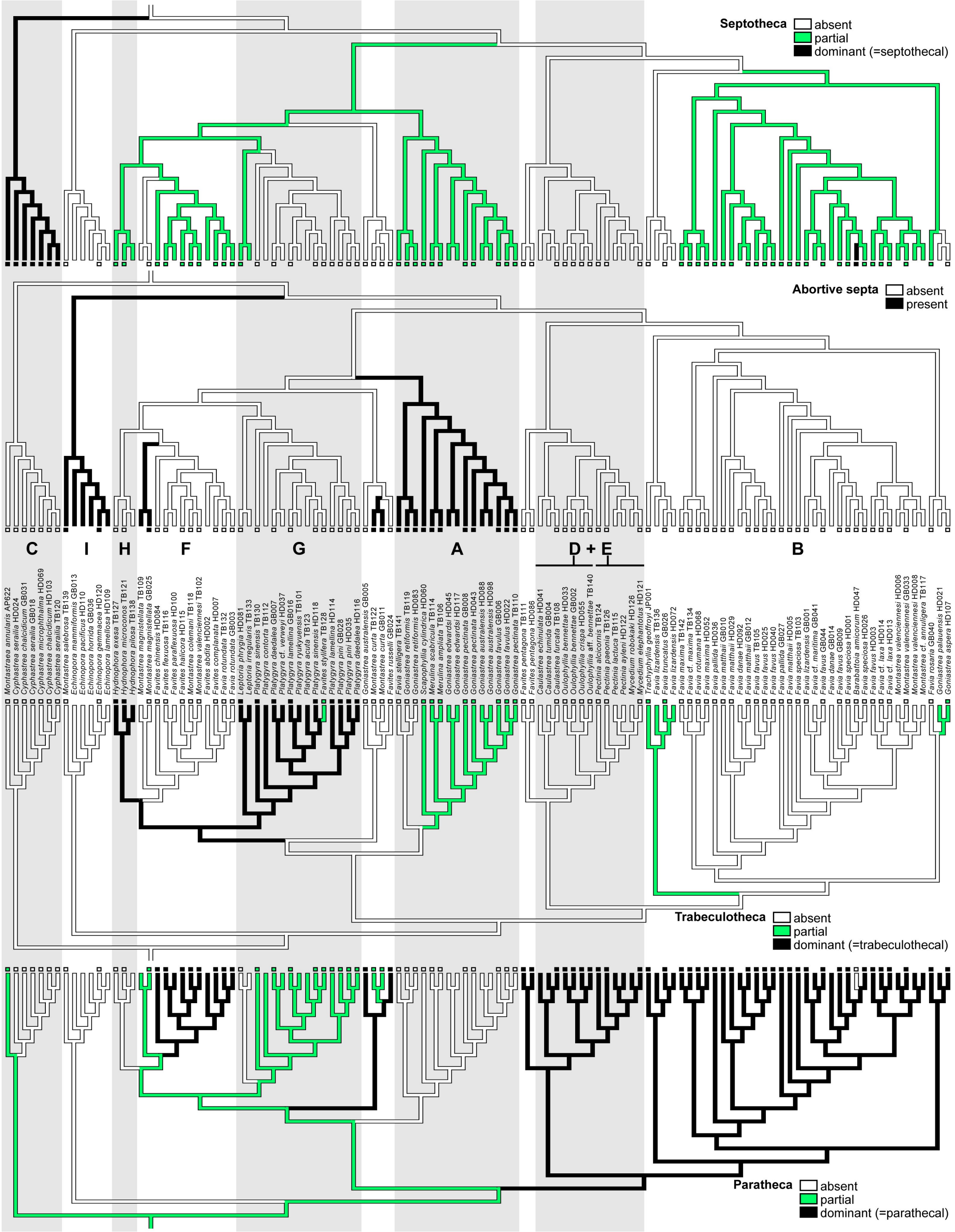

Figure 4.6: Four diagnostic wall microstructural characters transformed onto Merulinidae tree.

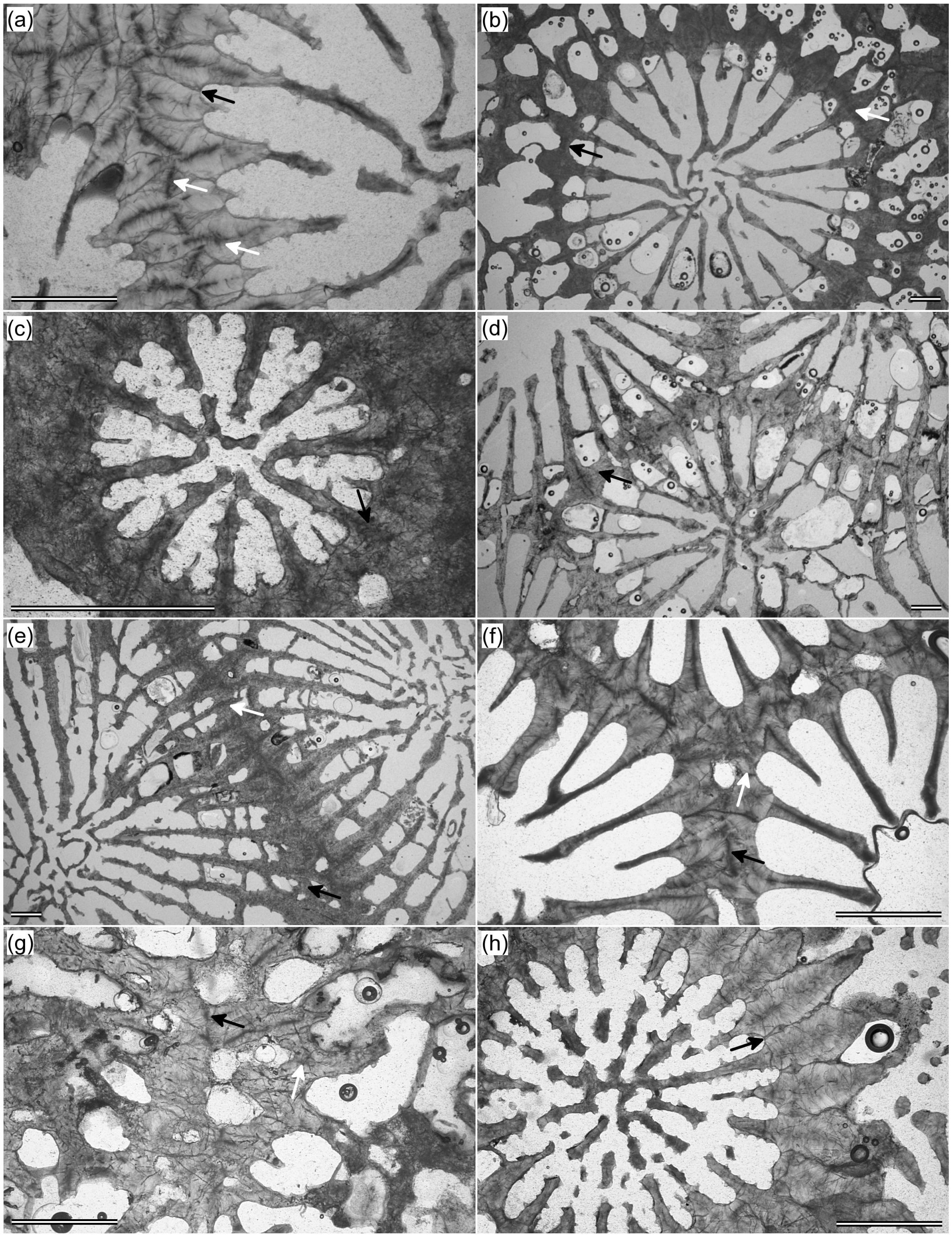

Figure 4.7: Thin section micrographs of corallite walls showing microstructural character states as traced on the phylogeny in Figure 4.6. Dominant and partial wall structures indicated by black and white arrows respectively. (a) *Goniastrea favulus* (GB006; subclade A); (b) *Favia lizardensis* (GB001; subclade B); (c) *Cyphastrea microphthalma* (subclade C); (d) *Oulophyllia bennettae* (GB002; subclade D); (e) *Favia rotundata* (GB003; subclade F); (f) *Platygyra sinensis* (subclade G); (g) *Hydnophora microconos* (TB121; subclade H); (h) *Montastraea salabrosa* (TB139; subclade I). Scale 1 mm in length.

elements of septal thickening (septotheca) or thickening perpendicular to the septa (trabeculotheca). Interestingly, while there was considerable signal associated with each of these characters, there were nonetheless instances of convergence at this level of morphology. Abortive septa had evolved four times and other characters also typically showed no gradual increase or decrease in dominance of the respective wall structures (Figure 4.6). Partial features evolved on some branches and full structures on others for septotheca, trabeculotheca and paratheca.

Our results indicated that, although most morphologic characters at both corallite and subcorallite scales were convergent, some to a greater extent than others, many were effective at distinguishing subclades and tracing their evolution. However, the actual biomineralisation processes associated with the microstructural and micromorphological features were still unclear. Differences observed between zooxanthellate and azooxanthellate corals in, for instance, the regularity of bands formed in the thickening deposits encasing the rapid accretion deposits suggested that these characteristics may be taxonomically conserved (Stolarski, 2003). However, as these two ecological groups were not separate clades (Kitahara et al., 2010), phylogenetic signal might have been limited for these traits. At an even smaller scale, *Hydnophora exesa* appeared to have a distinct chemical component present in the soluble organic matrix compared to *H. microconos*, *H. rigida* and *Merulina scabricula*, and mineralisation patterns were well varied among the four species (Dauphin et al., 2008). Evidently, these features were useful in diagnosing individual species, but the evolutionary implications at the subclade level appeared to be more complicated.

Molecular analysis of *Merulina* and *Goniastrea*

The more detailed phylogenetic analysis of subclade A based on an expanded taxon sampling clearly reinforced the notion that congenerics were not monophyletic. Our broad-based histone H3 tree recovered the same groups as before (Huang et al., 2011), including clade XVII (Figure 4.8), which was known as 'Bigmessidae' until Budd et al. (in press) expanded Merulinidae Verrill 1865 to encompass the clade.

Merulina ampliata (Ellis and Solander, 1786), the name-bearing type of the family fell within subclade A, a well-supported group. Analyses based on the mt IGR marker recovered two deeply divergent clades of subclade A, with *Goniastrea retiformis/minuta* and *Favia stelligera* within one, and all other species in the second (Figure 4.9). The latter, present in both the mt IGR and the nuclear ITS trees (Figures 4.9 and 4.10), contained *Merulina*, *Scapophyllia* and four species of *Goniastrea* (*G. australensis*, *G. edwardsi*, *G. favulus* and *G. pectinata*). The relationships among these species varied depending on the marker used—*Merulina* was paraphyletic on the mitochondrial tree and *Goniastrea* was paraphyletic on the nuclear tree but the latter relationship was not supported by bootstrap analyses or the Bayesian posterior distribution.

On all inferred trees, *Goniastrea edwardsi*, *G. favulus* and *G. pectinata* were more closely related to *Merulina* spp. than the type species of *Goniastrea*, *G. retiformis*. On the basis of the combined data (Figure 4.11), we propose to move these three species into the type genus as *Merulina edwardsi* (Chevalier, 1971) new combination, *M. favulus* (Dana, 1846) new combination and *M. pectinata* (Ehrenberg, 1834) new combination. Note that our analysis incorporated samples from the type localities for *Goniastrea edwardsi*

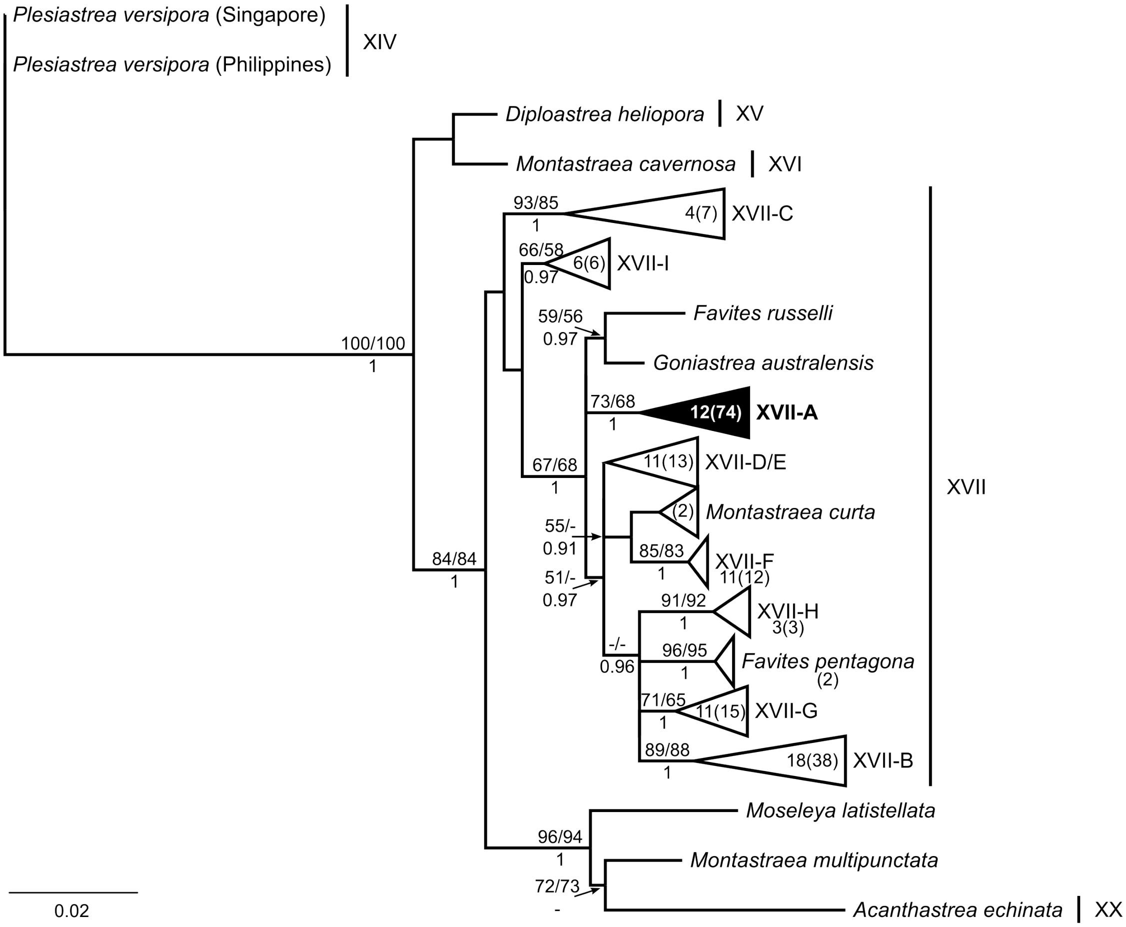

Figure 4.8: Maximum likelihood phylogram of corals from clades XIV to XX based on the nuclear histone H3 gene. Subclades within Merulinidae (clade XVII) grouped for clarity, with number of species analysed (and specimens in parenthesis) shown for each subclade. Subclade A, the focus of this revision, is highlighted. Numbers associated with each branch indicate support values from maximum likelihood and parsimony bootstrap analyses (above), as well as Bayesian posterior probabilities (below).

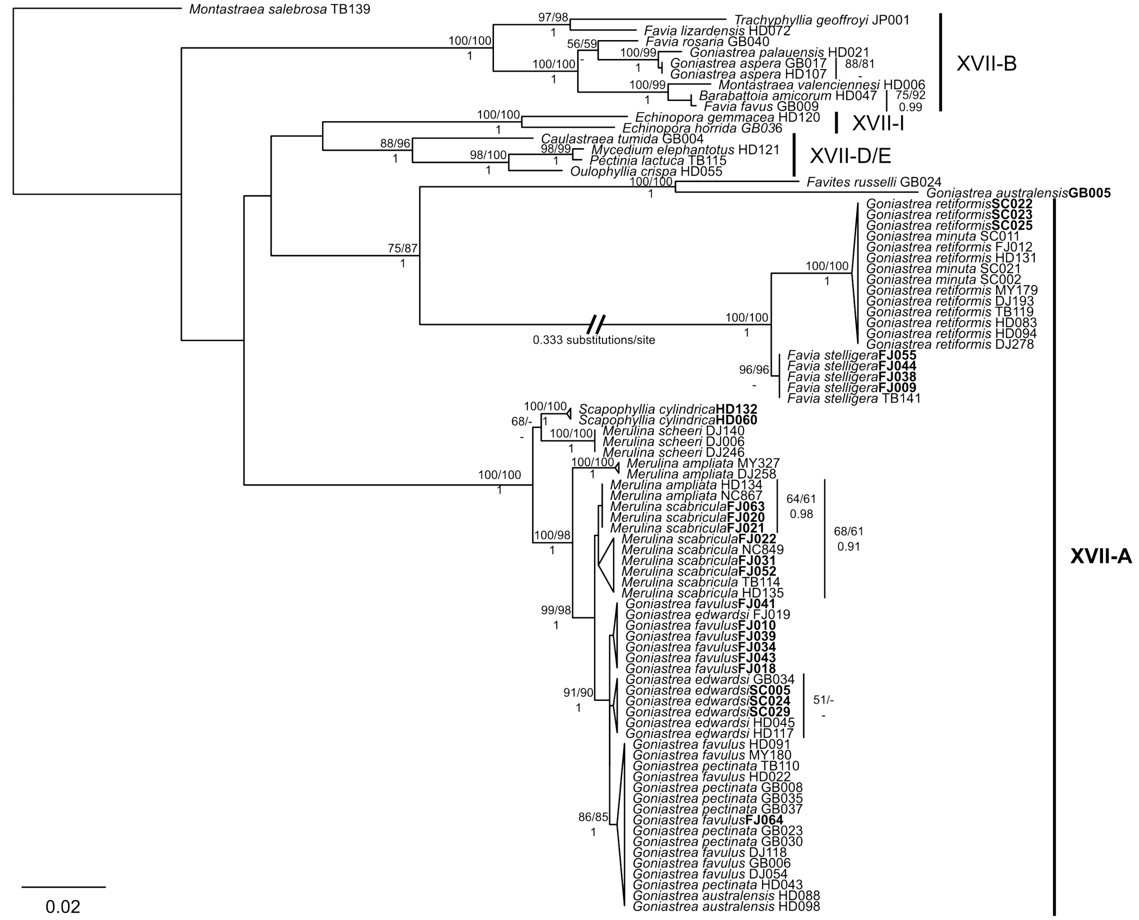

Figure 4.9: Maximum likelihood phylogram of Merulinidae corals focusing on subclade A based on the mitochondrial intergenic region (IGR). Specimen numbers follow species names, and those from type localities are in bold. Numbers associated with each branch indicate support values displayed as in Figure 4.8.

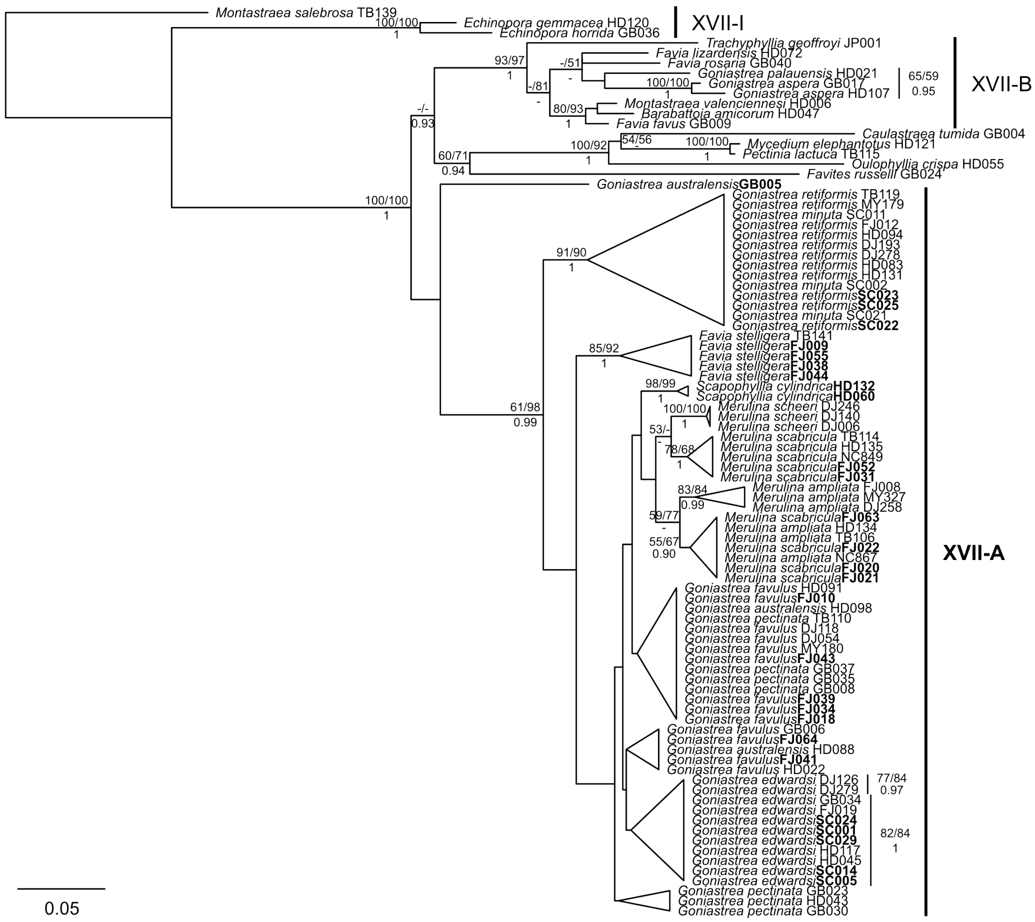

Figure 4.10: Maximum likelihood phylogram of Merulinidae corals focusing on subclade A based on the nuclear internal transcribed spacers 1 and 2 (ITS; including 5.8S rDNA). Specimen numbers follow species names, and those from type localities are in bold. Numbers associated with each branch indicate support values displayed as in Figure 4.8.

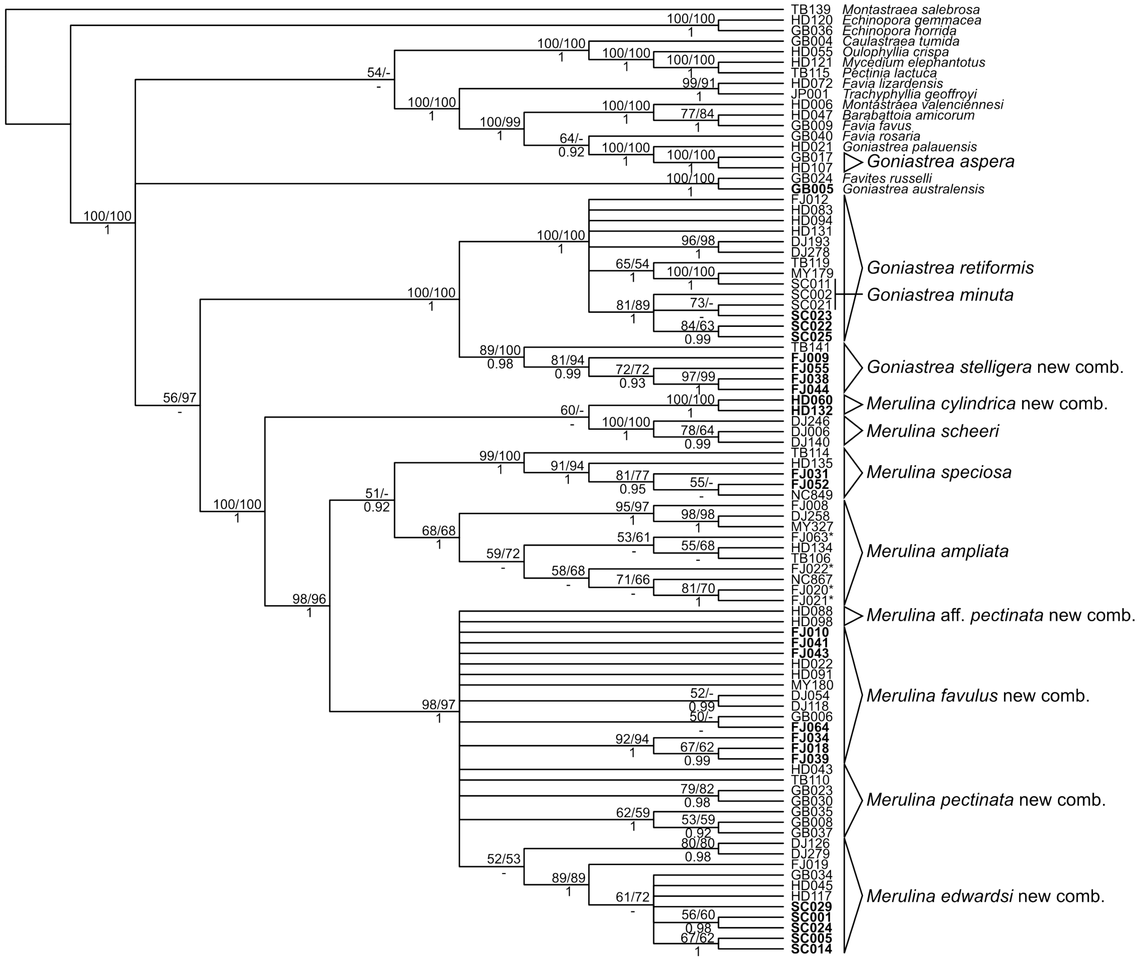

Figure 4.11: Maximum likelihood cladogram of Merulinidae corals based on concatenated dataset comprising histone H3, ITS and IGR. Specimen numbers follow species names, and those from type localities are in bold. Names according to revised taxonomy proposed in this study. Numbers associated with each branch indicate support values displayed as in Figure 4.8.

(Seychelles; Chevalier, 1971) and *G. favulus* (Fiji; Dana, 1846). Two specimens in the same clade (HD088 and HD098) were identified as *Goniastrea australensis* (Milne Edwards and Haime, 1857) (see also clade XVII-A in Figure 3.2), but evidently, this name should apply to the specimen GB005 collected from Australia, type locality of the species. Specimens HD088 and HD098 from Singapore were consequently reidentified as *Merulina* aff. *pectinata* (Figure 4.11). Unfortunately, the present study did not generate more certainty in the placement of *G. australensis*.

The recognition of the monotypic genus *Scapophyllia* was deemed unnecessary, since *S. cylindrica* showed an even greater affinity to *Merulina* on the basis of molecular data placing the monospecific genus as the sister group to *Merulina scheeri.* Note however that this was not well supported (Figure 4.11). As specimens analysed here were collected from Singapore, within the likely type locality of “les mers de la Chine?” (p. 278, Milne Edwards and Haime, 1848b), we were confident of our use of the species name, and thus propose the change to *Merulina cylindrica* (Milne Edwards and Haime, 1848) new combination. These changes would result in a well-supported *Merulina* clade that differed from its sister group (*Goniastrea retiformis/minuta* + *Favia stelligera*) in having partial trabeculotheca in addition to the abortive septa that defined the microstructure of subclade A.

All inferred trees further demonstrated the paraphyly of species within this clade. *Merulina favulus* and *M. pectinata* were not recovered as clades in both mitochondrial and nuclear trees (Figures 4.9, 4.10), and only *M. edwardsi* appeared to be monophyletic according to the combined data (Figure 4.11). We preserve these species groups as they did form distinct morphotypes in our present collection.

On the other hand, it is necessary to clarify the species boundaries of *M. ampliata*, in part because of its type status, but also since the closely-related *M. scabricula* collected from the type locality of Fiji was nested among its representatives. The syntype of *M. scabricula* Dana, 1846, is a branching colony with “obtuse truncate extremities of the branches, as broad as below” (p. 275, Dana, 1846). None of the photographs and descriptions depicting this species in Veron's (1986; 2000) monographs displayed such a morphology (see also Veron, 1992), resulting in widespread confusion regarding this genus.

The branching specimens closest to the description above (FJ020, FJ021, FJ022 and FJ063) formed a clade with *M. ampliata* that was moderately supported in the combined and nuclear ITS analysis (Figures 4.10 and 4.11). The mt IGR phylogeny showed FJ022 grouping with a clade comprising other *M. scabricula* sequences but this was not supported by any optimisation method (Figure 4.9). It is worth noting that taxonomists have had much difficulty differentiating these two species, e.g. “les différences entre *M. scabricula* et *M. ampliata* n'ont pas été définies avec précision” (p. 225, Chevalier, 1975). The branching species *Paraclavarina triangularis* (Veron and Pichon, 1980), originally described in the context of currently-synonymised genus *Clavarina* Verrill, 1864, had affinities to *M. scabricula*, but Veron (1985) deemed *P. triangularis* to be distinct from *Merulina*. We were unable to test Veron's (1985) hypothesis without sampling this species, and had assumed that it is a valid genus and species. We argue that the specimens nested within *M. ampliata* represented the correct application of the name *Merulina scabricula* Dana, 1846, because of similarities with the syntype. On the basis of the combined analysis, we propose to synonymise *Merulina* *scabricula* as *M. ampliata* (Ellis and Solander, 1786).

The other *Merulina* specimens identified according to more recent descriptions (Veron, 1986; 2000), including specimens from Fiji, New Caledonia, Philippines and Singapore, formed a well-supported clade sister to *M. ampliata* in all analyses. Interestingly, their morphotypes resembled a broad range of explanate species described by Dana, 1846 , including *M. regalis*, *M. speciosa* and *M. crispa*. The commonalities among them, the thin and delicate theca and septa, contrasted with the thicker and coarser skeleton of *M. ampliata* (Veron, 2000). Since *M. scabricula* is now a junior synonym of *M. ampliata*, and Dana's (1846) *M. scabricula* syntype does not have thin and fine skeletal structures, we propose the resurrection of *Merulina speciosa* Dana, 1846, to refer to this sister clade of *M. ampliata*.

Our preference for *M. speciosa* over the other names in the 'explanate' group (i.e. *M. regalis* and *M. crispa*) was supported by colonial characteristics of our samples, which were all “very thin explanate”, mostly unifacial, and if present, folia were “1–3 inches broad” (p. 273–274, Dana, 1846). There was limited coalescence of folia leading to bifacial fronds, present in *M. crispa*, and no formation of broad folia that were more than 3 inches, as in *M. regalia*. Two of our specimens (FJ031 and TB114) resembled *M. regalia* in forming “hemispherical clumps, sometimes four feet in diameter” (p. 273, Dana, 1846), but did not possess folia that were more than 3 inches. Position precedence only applies when designating the type species for a genus (Recommendation 69A.10 of the Code), so we were not obliged to use *M. regalia*, mentioned first in Dana, 1846, even if none of the three names was preferred based on the original descriptions.

Goniastrea retiformis (Lamarck, 1816), the type species of *Goniastrea* Milne-

Edwards and Haime, 1848, was distinct from all other congeneric species, except *G. minuta*. Its sequences, including those collected from the type locality of Seychelles, were closely allied with those of *Favia stelligera*, including samples from the type locality, Fiji. This placement was contributed primarily by the mitochondrial DNA data, with a very long branch subtending from the tree (Figure 4.9), but the combined analysis also showed a well supported clade of the two species with *G. minuta* (Figure 4.11). The nuclear ITS tree recovered a paraphyly but the *F. stelligera* + *Merulina* clade was not supported (Figure 4.10). The new combination *Goniastrea stelligera* (Dana, 1846) is hereby proposed.

Goniastrea retiformis and *G. minuta* were indistinguishable from each other on the phylogeny. The main morphological character used by Veron (2000; 2002) to separate the two species was 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 (pers. obs.). It is noteworthy that Milne Edwards and Haime, 1848 , described Lamarck's (1816) holotype of *Astrea retiformis* as “grande diagonale des calices, 3 millimètres environ” (p. 161). Their and our observations indicated that *Goniastrea retiformis* may possess small corallites comparable to *G. minuta* that Veron (2000; 2002) described. As it was likely that the type of *Astrea 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 a clade comprising both *G. retiformis* and *G. minuta* (Figure 4.11). Nevertheless, on the basis that we did not examine *G. minuta* specimens from its type locality of Milne Bay, Papua New Guinea, we preserve its name until further studies of these two morphotypes falsify the hypothesis that they are separate species.

The placement of *Goniastrea aspera* and *G. palauensis* sequences in subclade B, grouping with most *Favia* spp., was well supported for all three markers. *Goniastrea palauensis* was originally described as a *Favia* species (Yabe et al., 1936), so this result was not entirely surprising. However, we were unable to obtain specimens from their type localities (Ryukyu Islands and Palau respectively), and thus refrained from revising their generic identity here.

Overall, we have presented a framework for diagnosing subclades within Merulinidae, and taken the first steps in revising its constituent genera. We posit that an evolutionary perspective of coral morphology, when integrated with genetic analysis of critical species derived from their type localities, will help resolve the extreme polyphyly of traditionally-defined genera such as *Goniastrea*. The type material of centuries-old species may not warrant molecular phylogenetic investigation, but examination of new material comparable to these specimens in terms of morphology and locality can certainly be illuminating.

SYSTEMATICS

***Merulina* Ehrenberg, 1834**

Synonym. *Clavarina* Verrill, 1864, p. 56.

Type species. *Madrepora ampliata* Ellis and Solander, 1786, p. 157, pl. 41, fig. 1, 2; original designation Ehrenberg, 1834, p. 328.

Original description. “Fere pedalis, frondibus liberis, subflabellatis, e ramulis coalitis dichotome colliculatis, collibus lamelloso-serratis, asperrimis, vix lineam altis, stellis in seriebus dichotomis saepe confluentibus positis, sulcis lineam latis, parietibus turgidis, 2''' distantibus.” (p. 328, Ehrenberg, 1834).

Subsequent descriptions. Dana, 1846, p. 271–272; Milne Edwards and Haime, 1857, vol. 2, p. 628; Verrill, 1864, p. 56; Vaughan, 1918, p. 126; Hickson, 1924, p. 60–61; Hoffmeister, 1925, p. 31; Faustino, 1927, p. 163–164; Matthaii, 1928, p. 125–127; Vaughan and Wells, 1943, p. 190; Crossland, 1952, p. 151; Wells, 1956, p. F416; Nemenzo, 1959, p. 125; Chevalier, 1975, p. 208; Veron and Pichon, 1980, p. 216; Scheer and Pillai, 1983, p. 143; Veron, 1986, p. 434–435; Chevalier and Beauvais, 1987, p. 720–721; Sheppard, 1990, p. 14; Veron, 2000, vol. 2, p. 376.

Diagnosis (apomorphies in italics). Colonial, with intracalicular budding, and absence of polymorphic corallites. Corallites discrete with 1–3 mouths, uni- or multiserial. Walls fused. Calice or valley up to 10 mm, relief up to 4 mm from columella. Costosepta may be confluent. Septa in < 3 or 3 equal cycles, with up to 36 septa per individual, between 6–12 per 5 mm. Minor septa, if present, may be regular or irregular. Columellae trabecular and compact (1–3 threads), continuous with trabecular linkage, and at most one-quarter of calice width. Septal lobes absent. Epitheca may be well developed. Alveoli absent. Endotheca sparse to low-moderate or tabular. Paliform lobes well developed (weak in *M. cylindrica*), in variable numbers. Tooth at mid-septum outline circular, parallel to septum. Tooth shape irregular, axes multidirectional (> 5). First-order septa tooth height low (< 0.3 mm), narrowly spaced (< 0.3 mm), with 6–10 teeth per septum. Granules pointed like spikes, evenly scattered on septal face. Interarea between teeth palisade. Ratio of wall to septum tooth size variable. Walls formed by abortive septa, with *partial trabeculothecal* and septothecal elements. Intermediate (0.5–2.0 mm) wall thickness. Thickening deposits thick fibrous or layered. *Costa centers aligned as lines*, in undulating or zigzag pattern, with clusters < 0.3 mm apart. Septum centers aligned as weak lines. Perpendicular structures absent on septa. Columella centers clustered.

Species included. (1) *Merulina ampliata* (Ellis and Solander, 1786, p. 157, pl. 41, fig. 1, 2); holotype: GLAHM 104015 (The Hunterian Museum and Art Gallery, University of Glasgow), dried specimen; type locality: “les mers de l'Inde” (p. 243, Lamarck, 1816). (2) *Merulina pectinata* (Ehrenberg, 1834, p. 320); holotype: lost, but Klunzinger (1879, p. 34–35, pl. 4, fig. 6) figured a specimen studied by Ehrenberg derived from the Red Sea that Chevalier (1971, p. 246) considered as the holotype (ZMB Cni 726; Museum für Naturkunde, Humboldt-Universität zu Berlin); type locality: Red Sea. (3) *Merulina favulus* (Dana, 1846, p. 245, pl. 13, fig. 7); syntype: USNM 66 (National Museum of Natural History, Smithsonian Institution), dried specimen; type locality: Fiji. (4) *Merulina speciosa* Dana, 1846, p. 273–274, pl. 16, fig. 1; syntype: USNM 149 (National Museum of Natural History, Smithsonian Institution), dried specimen; type locality: Fiji. (5) *Merulina edwardsi* (Chevalier, 1971, p. 240–246, pl. 27, fig. 2; pl. 28, fig. 6, 7; pl. 29, fig. 5, 6); holotype: *Goniastrea solida* collected by Milne Edwards, and described by Milne Edwards and Haime (1848b, vol. 4, p. 160–161, pl. 9, fig. 7) (Museum national d'Histoire naturelle, Paris), dried specimen; type locality: Seychelles. (6) *Merulina scheeri* Head, 1983, p. 420–425, fig. 1–6; holotype: 1981.4.1.1 (Natural History Museum, London), dried specimen; paratypes: 1981.4.1.2, 1981.4.1.3 (Natural History Museum, London), dried specimens; type locality: West Harvey, Sudan, Red Sea, 23 m depth.

Remarks. The genus was first described as part of the taxon Daedalina Ehrenberg 1834, and subsequently Astraeidae Dana, 1846, which incorporated a diversity of genera including *Lobophyllia* de Blainville, 1830, *Favia* Oken, 1815, and *Mycedium* Oken, 1815 (Ehrenberg, 1834). The designation of *Merulina* as the type of Merulinidae Verrill, 1865, was unclear since the family name was only listed and not defined (Verrill, 1865, p. 146), but this had thereafter been assumed. Even as Daedalina's constituent genera were redistributed into newly erected families such as Mussidae Ortmann, 1890, Faviidae Gregory, 1900, Trachyphylliidae Verrill, 1901, and Pectiniidae Vaughan and Wells, 1943, the placement of *Merulina* remained ambiguous according to some authors (Vaughan, 1918; Hoffmeister, 1925), while Hickson (1924), Faustino (1927) and Matthai (1928) continued to recognise Dana's (1846) Astraeidae. The separation of *Merulina* from Faviidae Gregory, 1900, was only complete in the comprehensive treatise by Vaughan and Wells (1943).

Molecular data supported *Merulina* as being closely related to *Goniastrea*, but neither genus was monophyletic with conventional taxonomy as the basis (Fukami et al., 2004a; Fukami et al., 2008; Kitahara et al., 2010; Huang et al., 2011). As a consequence of the revisions proposed in this study, *Merulina* is now a monophyletic group sister to *Goniastrea*. We included all three species of *Merulina* as previously defined, but it is possible that more of the remaining unsampled *Goniastrea* spp. would fall within this clade.

There were few apomorphies for this genus: presence of partial trabeculotheca, and costa centers aligned as strong lines, although lines were weaker in *Merulina pectinata*. As most of the subcorallite character transitions occurred at the most recent common ancestor of *Merulina* and *Goniastrea*, a majority of states were therefore plesiomorphic.

***Goniastrea* Milne Edwards and Haime, 1848**

Synonyms. *Coelastrea* Verrill, 1866, p. 32; *Morchellastraea* Alloiteau, 1941, p. 25–26; *Morchellastrea* Reig Oriol, 1990, p. 24.

Type species. *Astrea retiformis* Lamarck, 1816, p. 265; original designation Milne Edwards and Haime, 1848a, p. 495.

Original description. “Multiplication par fissiparité. Murailles compactes et directement soudées entre elles. Cloisons finement denticulées, et portant des palis bien marqués. Columelle peu développée, mince à la partie inférieure des chambres.” (p. 495, Milne Edwards and Haime, 1848a)

Subsequent descriptions. Milne Edwards and Haime, 1857, vol. 2, p. 444; Gardiner, 1899, p. 746; Matthai, 1914, p. 115–117; Vaughan, 1918, p. 113–114; Hickson, 1924, p. 53–54; Faustino, 1927, p. 139; Vaughan and Wells, 1943, p. 167–168; Alloiteau, 1952, p.

617; Crossland, 1952, p. 132–133; Wells, 1956, p. F402; Nemenzo, 1959, p. 97; Chevalier, 1971, p. 231; Veron et al., 1977, p. 79; Scheer and Pillai, 1983, p. 119; Veron, 1986, p. 478–479; Chevalier and Beauvais, 1987, p. 714; Sheppard, 1990, p. 10; Veron, 2000, vol. 3, p. 156–157.

Diagnosis (apomorphies in italics). Colonial, with intracalicular budding and extracalicular budding. Corallites monomorphic, discrete with 1–3 mouths. Walls fused or with moderate amount of costate coenosteum (< corallite diameter). Calice diameter smaller than 4 mm, low relief (< 2 mm). *Costosepta not confluent.* Septa in < 3 cycles, with at least 6 per 5 mm. Irregular minor septa may be present. Columellae trabecular and compact (1–3 threads), continuous with trabecular linkage, and at most one-quarter of calice width. Septal lobes absent. Epitheca well developed. Alveoli absent. Endotheca low-moderate or tabular. Paliform lobes well developed, more than 6 per corallite. Tooth at mid-septum outline circular, parallel to septum. Tooth shape irregular, axes multidirectional (> 5). First-order septa tooth height low (< 0.3 mm), narrowly spaced (< 0.3 mm), with > 10 teeth per septum. Granules pointed like spikes, evenly scattered on septal face. Interarea between teeth palisade. Wall and septum tooth size equal. Walls formed by abortive septa with septothecal elements. Intermediate (0.5–2.0 mm) wall thickness. Thickening deposits thick fibrous or layered. Costa centers aligned as weak lines, in undulating or zigzag pattern, with clusters < 0.3 mm apart. Septum centers aligned as weak lines. Perpendicular structures (crosses) absent on septa. Columella centers clustered.

Species included. (1) *Goniastrea retiformis* (Lamarck, 1816, p. 265); holotype; MNHN 86 (Museum national d'Histoire naturelle, Paris), dried specimen; type locality: “les iles Seychelles” (p. 161, Milne Edwards and Haime, 1848b, vol. 4). (2) *Goniastrea stelligera* (Dana, 1846, p. 216, pl. 10, fig. 9); syntype: USNM 55 (National Museum of Natural History, Smithsonian Institution), dried specimen; type locality: Fiji. (3) *Goniastrea columella* Crossland, 1948, p. 191–192, pl. 8, 10a; holotype: G11C (Natal Museum South Africa), dried specimen; type locality: Umpangazi, South Africa. (4) *Goniastrea deformis* Veron, 1990, p. 142–144, fig. 48–50, 83; holotype: G32487 (Museum of Tropical Queensland), dried specimen; type locality: Kushimoto, Japan, 4 m depth. (5) *Goniastrea minuta* Veron, 2000, vol. 3, p. 158–159, fig. 1–5 (see also Veron, 2002, p. 153–155, fig. 283–285); 'holotype': G55825, which appeared to be lost (Museum of Tropical Queensland), dried specimen; 'paratype': G60250 (Museum of Tropical Queensland), dried specimen; type locality: Milne Bay, Papua New Guinea, 4 m depth. (6) *Goniastrea ramosa* Veron, 2000, vol. 3, p. 160, fig. 1–2 (see also Veron, 2002, p. 155–157, fig. 286–288); 'holotype': G55803 (Museum of Tropical Queensland), dried specimen; type locality: Flores, Indonesia, 1 m depth. (7) *Goniastrea thecata* Veron, DeVantier and Turak, 2000 (Veron, 2000, vol. 3, p. 169, fig. 5; see also Veron, 2002, p. 157–158, fig. 289–291); 'holotype': G55837 (Museum of Tropical Queensland), dried specimen; type locality: northern Red Sea coast of Saudi Arabia, 1 m depth.

Remarks. *Goniastrea* Milne Edwards and Haime, 1848, accumulated new species gradually since the description of its type in the genus *Astrea* Lamarck, 1816, until as recent as the year 2000, in which three species were added (Veron, 2000). The genus was thought to have affinities with *Favia* and *Favites* (Chevalier, 1971; Veron et al., 1977), but molecular phylogenies consistently placed its type species, *G. retiformis*, within the clade sister to *Merulina* (Huang et al. 2011; this study). This analysis only managed to include two other species, *G. minuta* and *G. stelligera*. While it is likely that *G. deformis*, as analysed by Fukami et al. (2008), could fall within this clade, other species may not be closely related. Due to the recovery of *Goniastrea aspera* and *G. palauensis* in subclade B, and the uncertain placement of *G. australensis*, we declare them *incertae sedis* until revisions are performed for taxa that contain them.

Molecular data strongly supported this genus as a clade, particularly by the mitochondrial loci used in this study that was over 300 bp shorter than *Merulina* sequences. The long branch subtending from the base of the tree was also shown with other mitochondrial markers such as cytochrome oxidase subunit 1 (Fukami et al., 2008; Huang et al., 2011).

The only unequivocal apomorphy of *Goniastrea* found here was the discontinuity of the costosepta among corallites. No subcorallite characters were diagnostic, although the absence of trabeculothecal elements was in contrast with its sister clade, *Merulina*. The monocentric (single mouth) corallites in the three species examined here—*Goniastrea retiformis*, *G. stelligera* and *G. minuta*—generally differed from the long or short valleys in *Merulina*, except *M. edwardsi*. The remaining four species were a mix of monocentric and short valley (≤ 3 mouths) species. The amount of coenosteum was variable among species, unlike in *Merulina* spp. that displayed fused walls. *Goniastrea stelligera* was clearly plocoid (separate walls) with moderate coenosteum, *G. deformis* may have walls separated by 'groove and tubercle' formations, and the other species were cerioid (fused walls).

Incertae sedis. (1) *Goniastrea australensis* (Milne Edwards and Haime, 1857, p. 520); holotype: status unknown (Museum national d'Histoire naturelle, Paris); type locality: Australia. (2) *Goniastrea aspera* Verrill, 1866, p. 32; syntypes: USNM 402, 403 (National Museum of Natural History, Smithsonian Institution), dried specimen; type locality: Ryukyu Islands, Japan. (3) *Goniastrea palauensis* (Yabe and Sugiyama, 1936, p. 30, pl. 19, fig. 5, 6); holotype: 56631 (Tôhoku Imperial University, Sendai), dried specimen; type locality: Palau.

CHAPTER 5

Threatened reef corals of the world

INTRODUCTION

Worldwide, ocean-scale effects of sea surface warming and acidification are subjecting reef corals to severe stresses, resulting in intensified bleaching and disease, as well as declining calcification rates (Hughes et al., 2003; Bruno et al., 2007; Hoegh-Guldberg et al., 2007; Knowlton and Jackson, 2008; De'ath et al., 2009; Veron et al., 2009). Local anthropogenic impacts such as overfishing and pollution have also forced coral reefs through regime shifts toward macroalgal domination (Hughes, 1994; McCook, 1999; Pandolfi et al., 2005; Hughes et al., 2007; Knowlton and Jackson, 2008). Alarmingly, 32.8% of all zooxanthellate reef-building coral species are considered to be threatened with global extinction (Carpenter et al., 2008a; see also Polidoro et al., 2011).

Limited resources constrain scientists and managers to focus their efforts on a subset of the world's coral reefs to minimise extinction risk (Roberts et al., 2002). Consequently, the decision-making process associated with assignment of funds and manpower has become a major research focus in conservation biology (Vane-Wright et al., 1991; Margules and Pressey, 2000; Myers et al., 2000; Murdoch et al., 2007; Arponen, 2012). One of the most widely-used frameworks for assessing threats to species and setting conservation priorities is the International Union for Conservation of Nature (IUCN) Categories and Criteria (IUCN, 2001; Mace et al., 2008). Indeed, the identification and design of protected areas are often guided by the distribution of species with the highest risk of extinction, and in particular, the most threatened species of the

IUCN Red List (Rodrigues et al., 2004; 2006; Hoffmann et al., 2008).

Extinction probabilities aside, species are not equal. Rather, evolutionary processes render each species unique with a characteristic history that can be quantified for the purpose of conservation prioritisation (May, 1990; Altschul and Lipman, 1990; Vane-Wright et al., 1991; Witting and Loeschcke, 1995; Mace et al., 2003). Assessments that integrate phylogenetic distinctiveness and extinction threat have been performed mainly for mammalian groups, drawing attention to extraordinary species from lesser known localities and lineages (i.e. lines of ancestry and descent according to de Queiroz, 2011) (Pavoine et al., 2005; Isaac et al., 2007; Agnarsson et al., 2010; Kuntner et al., 2011; Collen et al., 2011; May-Collado and Agnarsson, 2011). The dire situation of reef corals necessitates an equivalent treatment.

The utility of phylogenetic trees extends beyond the recognition of distinct lineages that are at risk. Due to the hierarchical nature of phylogenies, random losses of species rarely perturb the branches of evolutionary history (Nee and May, 1997), but concentration of threatened species or risk factors in particular parts of the phylogeny can imperil entire clades (McKinney, 1997; Russell et al., 1998; Purvis et al., 2000; Purvis, 2008). Threats to reef corals have traditionally been generalised based on species' taxonomic memberships (Loya et al., 2001; van Woesik et al., 2011). The family Faviidae, for instance, is reputed to be resilient to environmental disturbances (Bellwood and Hughes, 2001), but the extreme polyphyly of the group has called into question such inferences (Fukami et al., 2008; see also Díaz and Madin, 2011). Considering evolutionary history in the analysis of extinction risk will certainly aid in the development of informed conservation strategies against threats facing corals of the world today.

The aim of this study is to apply the phylogenetic approach on all reef corals of the order Scleractinia to identify, first, the most endangered coral lineages, and second, evolutionary patterns associated with extinction probability and various threats. To rank corals according to both distinctiveness and imperilment, I use the EDGE (evolutionarily distinct and globally endangered) metric (Isaac et al., 2007), which combines a unique measure of phylogenetic diversity (Faith, 1992) with the conservation status of each species. Data for the latter are based on the IUCN Red List that includes 827 reef-building scleractinians assessed by the world's leading coral experts in 2006 and 2007 (Carpenter et al., 2008a). Of the 688 species not deemed Data Deficient (DD), 32.7% are considered threatened. These comprise—in decreasing likelihood of extinction—four Critically Endangered (CR), 23 Endangered (EN) and 198 Vulnerable (VU) corals. The remaining species are categorised as Near Threatened (NT; 174 species) or of Least Concern (LC; 289 species).

METHODS

Phylogenetic data and analyses

To reconstruct the scleractinian phylogeny, 827 species from the IUCN Red List dataset (Carpenter et al., 2008a), five previously omitted corals, five new species described since the assessment (Forsman and Birkeland, 2009; Hoeksema, 2009; Wallace et al., 2011), and 65% of non-reef corals (Cairns, 2009) were included in the analysis (see Appendix). The supertree approach (Baum, 1992; Ragan, 1992) was used to combine data from molecular, morphologic and taxonomic sources. Unlike Kerr (2005), the last published Scleractinia supertree, I reanalysed the molecular data rather than use available phylogenies because several DNA markers were utilised repeatedly in different studies (e.g. Romano and Palumbi, 1996, and Romano and Cairns, 2000). Using these phylogenies as source trees would result in data duplication (Bininda-Emonds et al., 2002; Bininda-Emonds, 2004).

Mitochondrial DNA markers each with coverage of > 40 species were obtained from GenBank to assemble a 463-species dataset (365 reef, 98 non-reef). The seven markers used were 12S small subunit ribosomal RNA (12S), 16S ribosomal RNA (16S), ATP synthase F0 subunit 6 (AT6), cytochrome c oxidase subunit I (COI), control region (CTR), cytochrome b (CYB) and NADH dehydrogenase subunit 5 (ND5) (see Appendix). Corallimorphs *Discosoma* and *Ricordea florida* were included as outgroups. Matrices were aligned with MAFFT 6.8 (Katoh et al., 2002; Katoh and Toh, 2008) and concatenated for analysis under the maximum likelihood criterion, using RAxML 7.2.8 (Stamatakis, 2006; Stamatakis et al., 2008) implemented at the Cyberinfrastructure for Phylogenetic Research (http://www.phylo.org) (Miller et al., 2010). Tree searches were carried out in 1000 alternate runs from distinct parsimony starting trees, utilising the partitioned GTRGAMMA model. Nodal supports were assessed via 1000 bootstrap replicates.

Thirteen morphological datasets were used to obtain source trees for the supertree reconstruction (Budd and Smith, 2005; Cairns, 1997; 2001; Daly et al., 2003; Hoeksema, 1989; 1993; Pandolfi, 1992; Pires and Castro, 1997; Wallace, 1999) (Table 5.1). All except one (Budd and Smith, 2005) were included in Kerr's (2005) study. Congeners were assumed monophyletic unless otherwise shown in recent phylogenies (see remarks,

Table 5.1: Morphological data used as source matrices for supertree reconstruction. Numbers in bold represent the taxonomic levels of analyses performed in the original studies.

Taxon	**No. of genera**	**No. of species**	**Analysis parameters**	**Reference**
Faviina	11	**26**	equal weights; unordered	Budd and Smith (2005)
Turbinoliidae	**22**	57	characters weighted; one character ordered	Cairns (1997)
Dendrophylliidae	**20**	164	characters weighted; two characters ordered	Cairns (2001)
Scleractinia	**29**	440	equal weights; unordered	Daly et al. (2003)
Fungiidae	15	**40**	equal weights; unordered	Hoeksema (1989)
Pleuractis	1	**6**	equal weights; unordered	Hoeksema (1993)
Mussidae	**12**	44	characters weighted; Lundberg rooting	Pandolfi (1992)
Lobophyllia + *Symphyllia*	2	**10**	characters weighted	Pandolfi (1992)
Siderastreidae	**6**	29	characters weighted; Lundberg rooting	Pandolfi (1992)
Coscinaraea + *Psammocora*	2	**14**	characters weighted	Pandolfi (1992)
Scleractinia + Corallimorpharia	38	**47**	includes two outgroups	Pires and Castro (1997)
Acroporidae	**6**	291	equal weights; unordered	Wallace (1999)
Acropora + *Isopora*	2	**139**	10 sister species grafted post-analysis	Wallace (1999)

Appendix). Maximum parsimony analyses were performed in PAUP* 4.0b10 (Swofford, 2003) using the branch-and-bound algorithm for matrices with ≤ 25 terminals and heuristic searches (10^5 random additions with a rearrangement limit of 10^7 per replicate) for larger datasets. Nodal supports were determined with 1000 bootstrap replicates (100 random additions per replicate for heuristic searches). For 145 reef species with no available data, a source tree was used to represent likely sister relationships based on a review of literature, favouring the more recent hypotheses in cases of conflict (Benzoni et al., 2007; 2010; Best and Hoeksema, 1987; Chevalier, 1971; Claereboudt, 1990; Claereboudt and Al-Amri, 2004; Ditlev, 2003; Fenner, 1993; Gittenberger et al., 2011; Head, 1983; Huang et al., 2011; Kitahara et al., 2010; Lin et al., 2011; Locke et al., 2007; Moll and Best, 1984; Scheer and Pillai, 1983; Vaughan, 1901; Veron et al., 1977; Veron and Pichon, 1980; Veron, 1986; 1990; 2000; 2002; Wallace et al., 2007; Wells, 1937; Wijsman-Best, 1972; Yabe and Sugiyama, 1941).

Including the molecular phylogeny, 1293 scleractinian species (837 reef, 456 non-reef) were analysed. All source trees were coded into bootstrap percentage-weighted matrix representation with parsimony using SuperMRP 1.2.1 (Bininda-Emonds et al., 2005). To ensure that analyses were driven primarily by data, weights of nodes derived from taxonomic information were each set at one. Maximum parsimony analysis of the 792-character dataset was carried out as above (rearrangement limit of 10^8 per replicate) to obtain 18978 minimum length trees.

The molecular data were then fitted to the strict consensus supertree using RAxML (1000 replicate runs) to derive the best branch length estimates (Jones et al., 2005). Polytomies in the supertree were randomly resolved to generate 1000 different resolutions. Species with no available DNA sequence data were assigned a terminal branch length of zero, though still represented by their ancestral branches based on topology. This procedure yielded estimates for the lower limit of distinctiveness, a conservative approach given the lack of data. Calculations that followed were carried out for each of the 1000 resolutions; reported results are means over all randomly resolved trees.

Determining species priorities

For each reef species in the Scleractinia supertree, Tuatara 1.01 (Maddison and Mooers, 2007) was used to evaluate evolutionary distinctiveness (ED) by summing the terminal branch length and its species-weighted allocation of ancestral branches. ED was then multiplied by extinction probability (PE) to obtain the EDGE score, a measure of expected loss of evolutionary history (Isaac et al., 2007; Redding and Mooers, 2006). PE was calculated based on the IUCN100 transformation of the IUCN categories (Mooers et al., 2008). LC species' PE was set at 0.001, assuming that at most about one of the 289 LC corals would go extinct in 100 years; NT corals were given an intermediate PE of 0.01. For the 149 DD species, a PE value in between the lowest Red List categories (LC and NT) was assigned (May-Collado and Agnarsson, 2011). The 'Isaac' and 'Pessimistic' transformations of Mooers et al. (2008) led to an LC species consistently achieving the top two highest scores, an overly conservative result that is not discussed (available in Appendix). Species were ranked according to their EDGE scores. Analyses repeated exclusively for the reef species show that incomplete sampling of Scleractinia (i.e. the non-reef corals) had minimal effect (mean rank variation: top 30 species = 1.5, all 837 species = 12.8).

Testing for phylogenetic signal

Phylogenetic signal of PE was tested using a randomisation procedure (Blomberg et al., 2003) in R package Picante 1.3 (Kembel et al., 2010) that determined whether the actual phylogeny better fits a set of continuous data relative to data that had been randomly permuted across the tips of the tree (1000 replicates per supertree; K = 0 for random traits). For binary traits, Fritz and Purvis' (Fritz and Purvis, 2010b) D was computed in CAIC 1.0.4 (Orme et al., 2008). This metric was based on the trait's sum of sister-clade disparities on the tree (D = 0 for clumped traits, D = 1 for random traits). The phylogenetic patterns of three extinction risk levels, EN and above, VU and above and at least NT, were determined. In addition, eight species-specific binary traits assessed by Carpenter et al. (2008a) were tested for phylogenetic signal (Table 5.2).

Two potential confounding factors associated with the above analyses were investigated. First, species assembled in the supertree differ in the degree of representation among source trees. It may be argued that poorly-sampled species are generally placed, unresolved, outside of clades with well-sampled species, leading to bias in calculations. The 1000 random resolutions of the strict consensus supertree should circumvent this problem, but to be sure, the tests were repeated for two reduced datasets with species present in at least two and three source trees respectively. Second, the level of phylogenetic signal inferred for each trait may be influenced by variation in species abundances, hence the analyses were also performed separately for species that are considered common (including one abundant taxon), uncommon and rare (data from

Table 5.2: Phylogenetic signal of IUCN categories and traits of reef corals. Results based on D, a measure of total sister-clade disparities on the phylogeny (± S.D.; 0 for clumped traits, 1 for random traits). Numbers in bold denote non-significant results (i.e. not different from 0 or 1).

Category/trait	**Proportion of species**	**D**	**P for H_0: D = 0**	**P for H_0: D = 1**
Endangered and above	0.032	1.096 ± 0.063	< 0.001	**0.780**
Vulnerable and above	0.269	0.960 ± 0.023	< 0.001	**0.167**
Near Threatened and above	0.477	0.853 ± 0.018	< 0.001	< 0.001
moderately or highly susceptible to bleaching	0.419	0.229 ± 0.010	< 0.001	< 0.001
moderately or highly resistant to bleaching	0.116	0.300 ± 0.023	0.001	< 0.001
moderately or highly susceptible to disease	0.310	0.124 ± 0.012	0.024	< 0.001
moderately or highly resistant to disease	0.058	-0.172 ± 0.015	**0.887**	< 0.001
recovers quickly from bleaching or disease	0.134	0.125 ± 0.013	**0.068**	< 0.001
moderately or highly susceptible to crown-of-thorns seastar predation	0.273	0.052 ± 0.011	**0.180**	< 0.001
restricted or highly fragmented range	0.124	1.136 ± 0.037	< 0.001	**0.973**
reported collection of > 1000 pieces per year	0.157	0.630 ± 0.021	< 0.001	< 0.001

Carpenter et al., 2008a). Phylogenetic signal of the trait 'reported collection of > 1000 pieces per year' for the 'rare' dataset could not be computed as it is represented by just two species.

Carpenter et al. (2008a) also found that several taxa that are susceptible to bleaching also appear to be heavily impacted by disease and predation by the crown-of-thorns seastar, *Acanthaster planci*. To ascertain if this relationship holds with the incorporation of phylogenetic information, I tested for correlation among traits associated with coral bleaching, disease and predation using phylogenetically independent contrasts (Felsenstein, 1985). This was implemented in APE 2.7 (Paradis et al., 2004), with statistical significance evaluated based on fit to a linear model.

Finally, I determined whether the decrease in phylogenetic diversity (PD) (Faith, 1992) under various extinction scenarios was different from a null model of random extinction. PD was compared between rarefied trees based on threat status (EN and above, VU and above, NT and above) and 1000 randomly pruned trees with the same species richness, using the one-sample t-test (Fritz and Purvis, 2010a). This analysis was also carried out for 30 species with the highest EDGE scores.

RESULTS

Integrating the diverse data types using a supertree approach yields a 1293-species phylogeny of Scleractinia that includes all 837 reef-building corals (Figures 5.1, 5.2, 5.3). Despite the vast increase in taxon sampling over previous phylogenies (Fukami et al., 2008; Kitahara et al., 2010), the present analysis recovers a highly similar topology. In particular, all 21 clades recognised by Fukami et al. (2008) (labelled I to XXI) are present

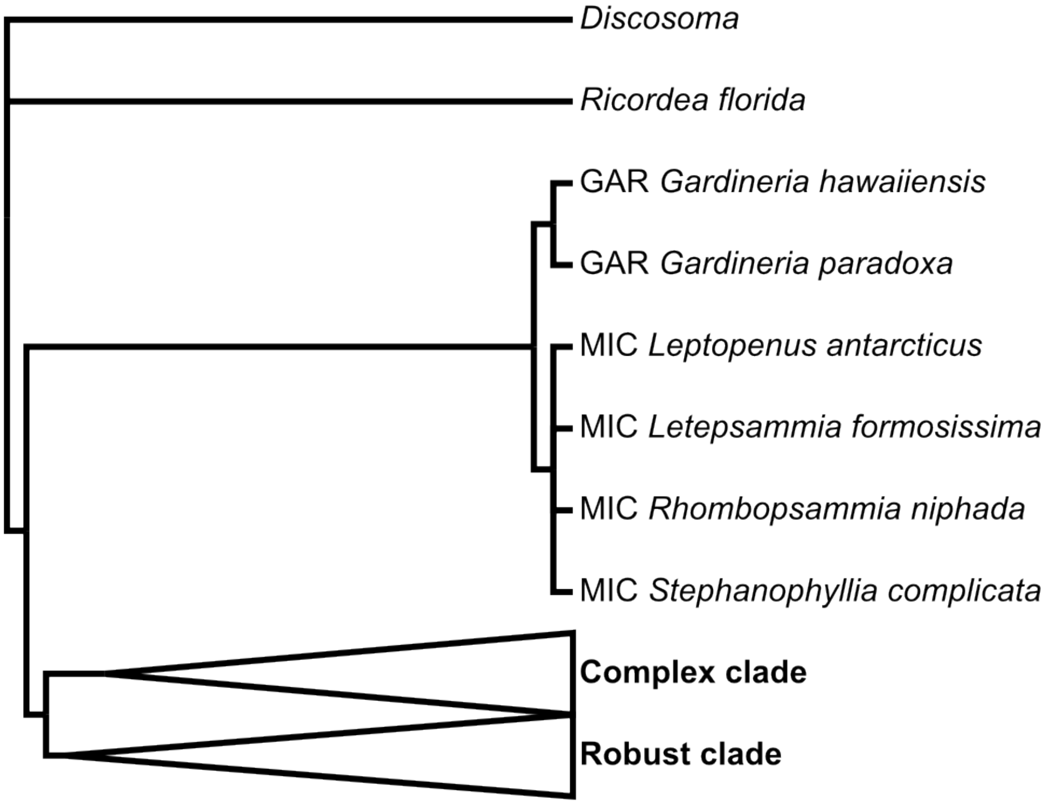

Figure 5.1: Supertree of Scleractinia with corallimorph outgroups *Discosoma* and *Ricordea florida*. Cladogram of 1293 corals inferred by maximum parsimony analysis of the 792-character dataset assembled using 15 source trees (13 morphological, one molecular and one taxonomic). Complex and robust clades shown in Figures 5.2 and 5.3 respectively. GAR: Gardineriidae, MIC: Micrabaciidae.

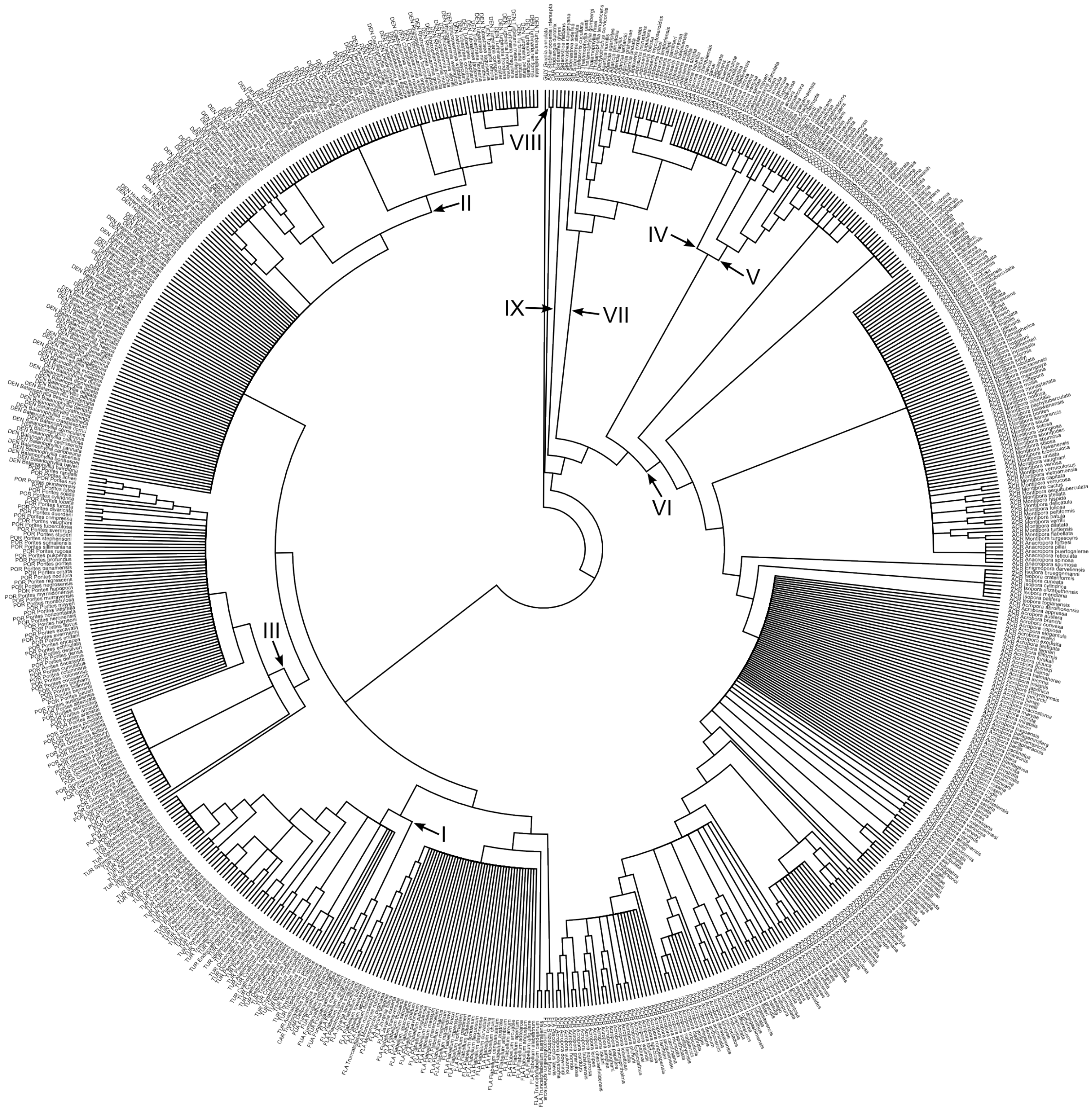

Figure 5.2: Cladogram of scleractinian corals in the complex clade. A total of 735 corals, including 462 reef species, are represented on this maximum parsimony cladogram that is part of the scleractinian supertree (Figure 5.1). Roman numerals denote clades based on the phylogeny in Fukami et al. (2008). ACR: Acroporidae, AGA: Agariciidae, AST: Astrocoeniidae, CAR: Caryophylliidae, DEN: Dendrophylliidae, EUP: Euphylliidae, FLA: Flabellidae, FUA: Fungiacyathidae, GUY: Guyniidae, MEA: Meandrinidae, OCU: Oculinidae, POR: Poritidae, SID: Siderastreidae, TUR: Turbinoliidae.

Figure 5.3: Cladogram of scleractinian corals in the robust clade. A total of 552 corals, including 375 reef species, are represented on this maximum parsimony cladogram that is part of the scleractinian supertree (Figure 5.1). Roman numerals denote clades based on the phylogeny in Fukami et al. (2008). ANT: Anthemiphyllidae, AST: Astrocoeniidae, CAR: Caryophylliidae, EUP: Euphylliidae, FAV: Faviidae, FUN: Fungiidae, MEA: Meandrinidae, MER: Merulinidae, MUS: Mussidae, OCU: Oculinidae, PEC: Pectiniidae, POC: Pocilloporidae, RHI: Rhizangiidae, SID: Siderastreidae, STE: Stenocyathidae, TRC: Trachyphylliidae.

in the supertree.

The analysis of EDGE scores has produced a priority list of reef-building corals that are both phylogenetically unique and facing elevated extinction risk (Figure 5.4; for full ranking, see Appendix). Conservation of these endangered lineages is critical for the preservation of evolutionary diversity. The priority scores of the top 30 species exceed the mean of all reef corals by at least an order of magnitude, and a significantly greater than random loss of phylogenetic diversity would occur should these species go extinct ($P < 0.001$).

Extinction probability of corals exhibits negligible phylogenetic signal since the hypothesis that there is no signal cannot be rejected given the data, i.e. non-zero K values are only non-zero by chance ($P = 0.745$, $K = 1.584 \times 10^{-11}$). Threatened species (EN and above, and VU and above) are randomly distributed on the phylogeny, while species given a minimum status of NT are only slightly more clumped than random (Figure 5.5, Table 5.2). The datasets with reduced species sampling in source trees and different abundances show very similar patterns, indicating that these factors have limited influence on phylogenetic signal strength (Figure 5.6). Gains in statistical significance (more clumped than random) are recorded for corals in the VU category and above with $\geq$ 3 source trees, as well as for taxa considered at least VU and NT for the uncommon species, but values of D remain close to one (random). Simulated extinction scenarios of reef corals based solely on threat status result in smaller than random losses of PD ($P < 0.001$, EN and above, VU and above, NT and above, all significantly less than random loss).

The tests for phylogenetic signal show that species susceptible to bleaching,

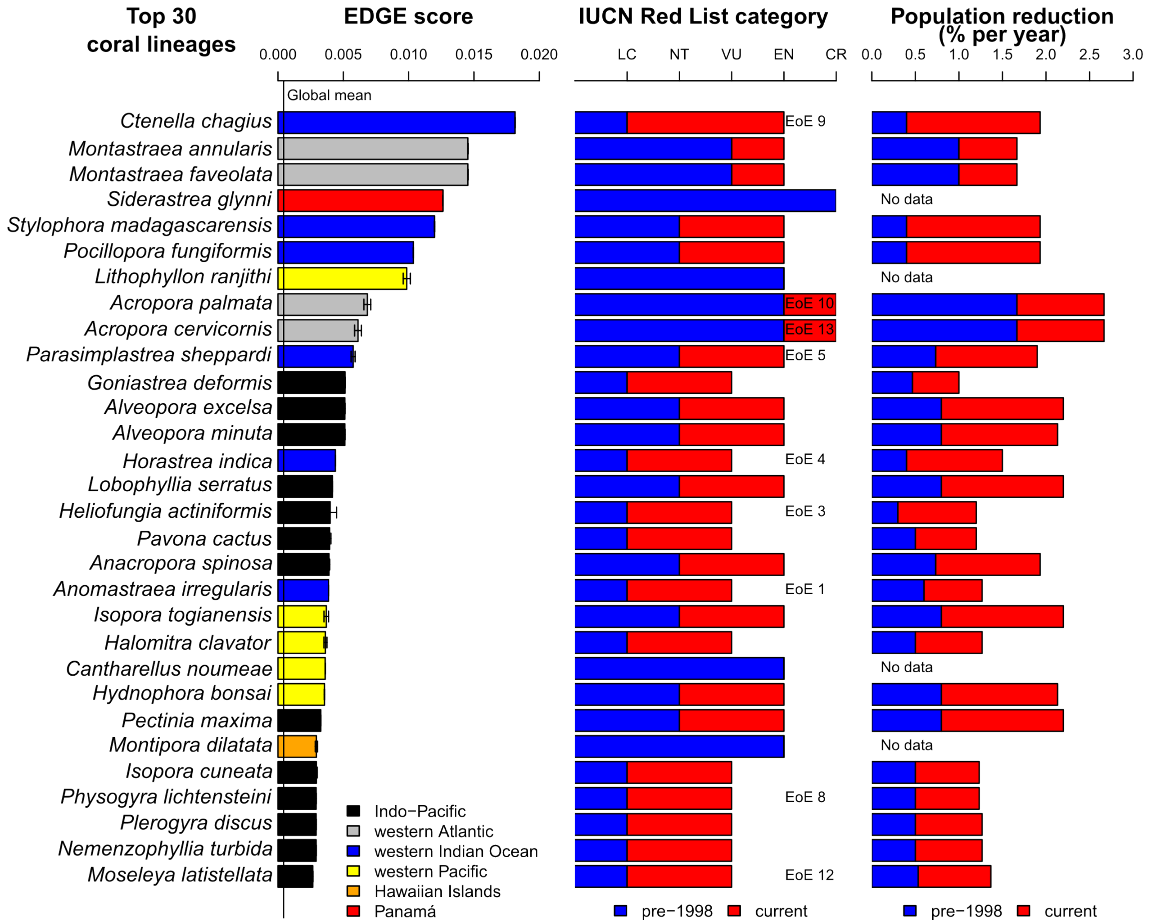

Figure 5.4: Top 30 reef corals ranked according to EDGE scores. List of corals representing high evolutionary distinctiveness and extinction risk. Left panel shows the EDGE score for each species. Global mean score for all 837 reef corals denoted by vertical line through bars, which are coloured to indicate respective geographic ranges. Error bars represent standard deviation. Middle panel shows pre-1998 and present IUCN Red List categories, as well as ranks according to the EDGE of Existence (EoE) programme. Right panel shows pre-1998 and present rates of global population reduction. IUCN Red List and population reduction data derived from Carpenter et al. (2008a).

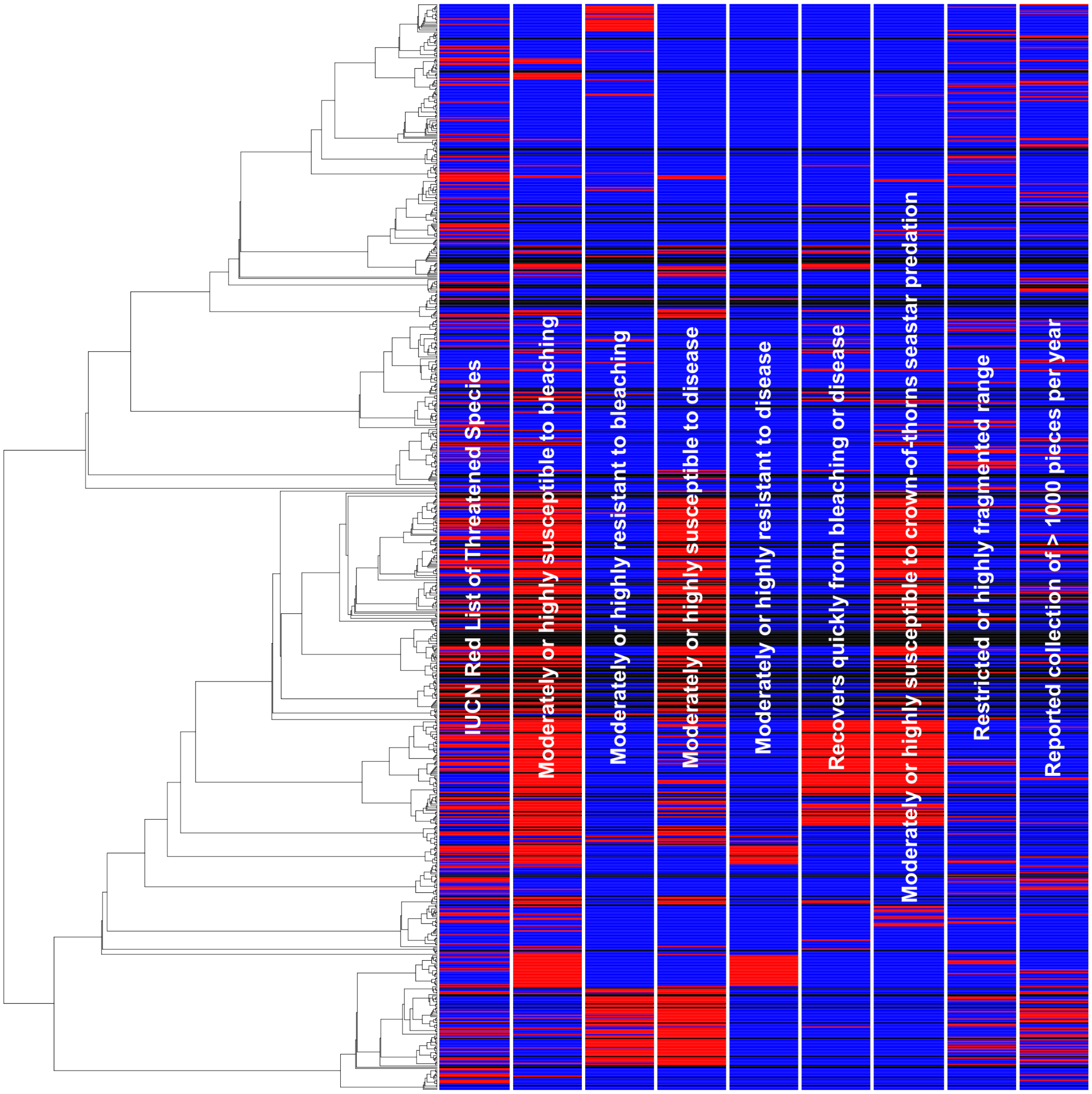

Figure 5.5: Cladogram of reef corals illustrating phylogenetic signal of traits. This tree represents the first of 1000 random resolutions of the strict consensus supertree. Vertical bars illustrate, in red, degrees of clumping among species classified as Vulnerable (VU) and above, susceptible and/or resistant to specific threats, and those recovering quickly from bleaching and disease. Taxa absent for the above traits are in blue. Data Deficient (DD) species, which are not phylogenetically clumped, are in black.

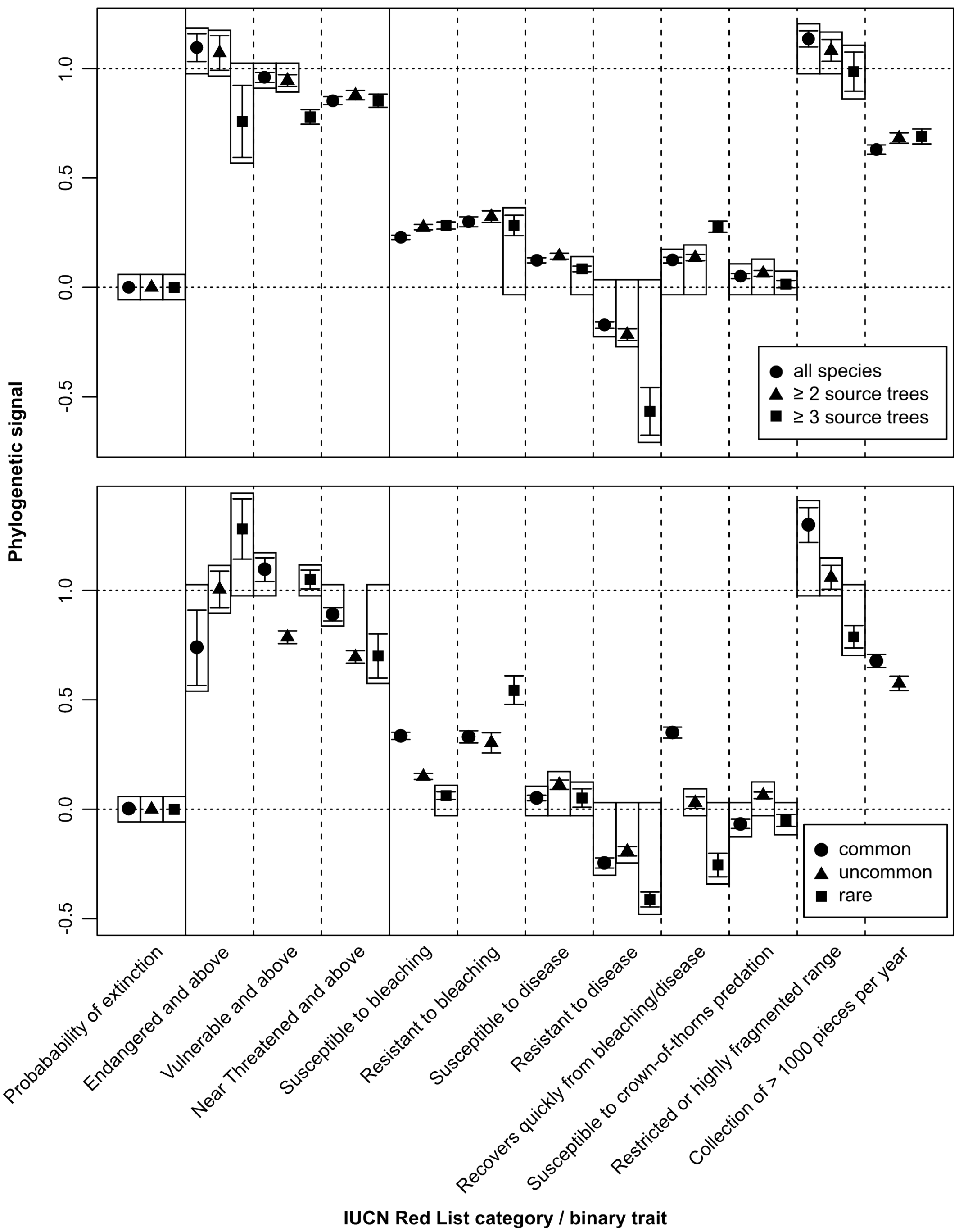

Figure 5.6: Species' source tree representation and abundances show limited effect on phylogenetic signal strength. Measure of phylogenetic signal based on K for probability of extinction (K = 0 for random continuous traits) and D for all other traits (D = 0 for clumped and D = 1 for random binary traits). Upper and lower panels show levels of phylogenetic signal for datasets with varying degrees of source tree representation and abundance respectively. Error bars represent standard deviation. Means not significantly different from zero or one are enclosed by boxes with those values.

disease, and predation by *Acanthaster planci*, as well as those resistant to and recovering quickly from bleaching and disease (i.e. resilient according to Nyström et al., 2008) are at least moderately clumped on the coral tree (Figure 5.5, Table 5.2; see Fritz and Purvis, 2010b). Species' source tree representation and abundances have negligible effects on these inferences (Figure 5.6). In fact, phylogenetic signal increases among taxa represented by at least three source trees for the traits 'resistant to bleaching', 'susceptible to disease' and 'resistant to disease'. It should be noted that in the dataset comprising only rare corals, species resistant to bleaching display relatively low signal ($D = 0.545 \pm$ S.D. 0.065), but are still significantly more clustered than random on the phylogeny ($P = 0.016$). Among lineages, correlations are evident between susceptibilities to bleaching events and disease ($P = 0.001$), as well as susceptibilities to bleaching and predation ($P < 0.001$). Negative linear relationships are present between susceptibility and resistance for both bleaching ($P < 0.001$) and disease ($P < 0.001$), although there is a positive correlation between susceptibility to disease and quick recovery from bleaching/disease ($P = 0.025$).

DISCUSSION

Using the most comprehensive coral phylogeny to date, this study has quantified the expected loss of evolutionary history for reef species based on the EDGE (evolutionarily distinct and globally endangered) measure. The ranking provided here, the first of its kind for corals, has been successful in identifying distinct lineages that warrant the highest conservation attention.

The top-30 list captures three of four CR species and 16 of the 23 EN species, the majority of which have restricted ranges (Figure 5.4). In particular, the most endangered lineage represented by *Ctenella chagius* is known only from the Chagos Archipelago, Mauritius and La Réunion, while *Siderastrea glynni*, fourth on the list, is endemic to Panamá in the tropical eastern Pacific (Veron, 2000). The remaining 11 species are of VU status and could be accorded lower conservation priority based upon extinction risk alone. Five of these, *Horastrea indica*, *Heliofungia actiniformis*, *Anomastraea irregularis*, *Physogyra lichtensteini* and *Moseleya latistellata* have only recently been highlighted by the EDGE of Existence programme (http://www.edgeofexistence.org/coral_reef) that aims to identify evolutionarily distinct and globally endangered species. Yet it has failed to recognise 21 of the 30 corals shown here to be of top priority; neither the 'Isaac' nor 'Pessimistic' transformation increases its representation of high EDGE-scoring species (22 and 24 species overlooked respectively). The programme's methodology remains unknown, but likely utilisation of an incomplete phylogeny may have precluded a comprehensive listing (see also materials and methods in Isaac et al., 2007).

Distinctiveness metrics such as ED often account for a greater proportion of total PD than expected (Redding et al., 2008). Recent evidence also suggests that evolutionarily distinct species and high PD represent a broader distribution of ecological diversity and higher ecosystem function than expected (Maherali and Klironomos, 2007; Cadotte et al., 2008; 2009; Redding et al., 2010; Connolly et al., 2011; Flynn et al., 2011; but see Fritz and Purvis, 2010a). If the preservation of biological diversity is a goal of reef conservation, then such phylogenetically-informed rankings would shore up priority setting efforts that currently focus on species richness, rarity and connectivity (Hughes et al., 2002; Roberts et al., 2002; Beger et al., 2003; Almany et al., 2009; Carpenter et al., 2011).

Despite the heightened risk in a larger fraction of corals relative to birds and mammals (Carpenter et al., 2008a), groups that exhibit phylogenetic clustering of threat status (Davies et al., 2008; Fritz and Purvis, 2010b), extinction probability and threatened species of corals show negligible signal associated with phylogeny (Figure 5.5). That species facing elevated extinction risk are not concentrated in particular parts of the phylogeny is no cause for optimism, however, as recent simulations have shown that other factors are involved in determining the magnitude of PD loss during extinctions (Parhar and Mooers, 2011). In particular, trees derived from real data generally have asymmetric topologies (Mooers, 1995; Mooers and Heard, 1997; Purvis and Agapow, 2002; Blum and François, 2006; Purvis et al., 2011); the coral supertree is no exception ($P < 0.001$, Colless' (1982) index significantly greater than predicted by the Yule model). Under this circumstance, even random exterminations of species can lead to disproportionate losses of PD (Nee and May, 1997; Heard and Mooers, 2000; Parhar and Mooers, 2011). High average extinction probability among reef corals (Carpenter et al., 2008a) may also exacerbate this pattern (Parhar and Mooers, 2011). Indeed, random extinction scenarios of coral species lead to larger declines in PD compared to extinctions based on IUCN Red List threat status. In other words, while none of the 20 major clades of reef corals are in immediate danger of complete obliteration, the unbalanced phylogeny and high mean extinction risk suggest that any extinction event can substantially reduce overall PD.

Bleaching, disease, and predation by *A. planci* are three of the most serious stressors affecting coral health today (Bellwood et al., 2004; Bruno and Selig, 2007). Tests for phylogenetic signal show that species susceptible to these threats, as well as those resistant and resilient to bleaching and disease are clustered on the tree, indicating that the aggravation of these risk factors can result in disproportionately large PD declines. More worrying is the finding that lineages vulnerable to bleaching events are also more likely to be susceptible to disease and predation. These threats often impact similar sets of species (Marshall and Baird, 2000; Miller et al., 2006; Carpenter et al., 2008a; Brandt and McManus, 2009; Yee et al., 2011), yet this relationship holds even after controlling for effects of shared common ancestry.

The value of investigating extinction risk in the phylogenetic context has been emphasised in considerable detail elsewhere (Weitzman, 1998; Mace et al., 2003; Redding and Mooers, 2006; Isaac et al., 2007; Purvis, 2008; Faith et al., 2010; Collen et al., 2011). Specifically for corals, confusion surrounding traditional taxonomy makes it difficult to accurately generalise traits exhibited by species to higher level taxa (Fukami et al., 2008). For instance, following the massive bleaching event in 1998, the family Faviidae, including *Leptastrea purpurea* and *L. transversa*, has been declared a 'winner' in the recovery process at Sesoko Island, Japan (Loya et al., 2001; van Woesik et al., 2011). Yet phylogenies inferred in the last 15 years have unequivocally demonstrated that *Leptastrea* is more closely related to members of Fungiidae rather than Faviidae (Romano and Palumbi, 1996; 1997; Romano and Cairns, 2000; Fukami et al., 2008; Kitahara et al., 2010; see also Fukami et al., 2004a; Budd et al., 2010), recovered within clade X with corals that are resistant to or recover quickly from bleaching (Figures 5.3, 5.5). Results here suggest that these traits are conserved on the evolutionary tree, irrespective of species' taxonomic affiliations.

Vulnerabilities of reef corals to bleaching and disease appear to be mediated by the same physiological mechanisms, and immune responses against these threats tend to be similar among close relatives, with Acroporidae and *Porites* (Poritidae) possessing the lowest and highest immunity levels respectively (Palmer et al., 2010). Consequently, the enhanced susceptibility of *Alveopora* to bleaching (Carpenter et al., 2008a) is better understood in the context of recent phylogenies that show the genus being placed within Acroporidae (clade VI) rather than, traditionally, Poritidae (clade III) (Fukami et al., 2008; Kitahara et al., 2010). It is clear that, conventional taxonomy notwithstanding, close relatives are likely to share similar levels of susceptibility, resistance and resilience to various risk factors, underscoring the utility of phylogenetic approaches in understanding specific responses of corals to environmental perturbations.

Subsequent analyses will utilise these results in distinguishing reef regions that make the greatest contribution to evolutionary history, in comparison to the most species-rich areas (Veron et al., 2009). A biogeographically-weighted evolutionary distinctiveness (ED) metric has the potential for regional prioritisation (Cadotte and Davies, 2010), but a probabilistic approach that accounts for future extinctions of related species may be more suitable than the static allocation of conservation value afforded by the ED measure (Steel et al., 2007; Faith, 2008; Collen et al., 2011).

Analyses demonstrating phylogenetic clustering of susceptibilities, resistance and resilience to various risk factors rely on accurate and precise species-specific data. The conservation status of Data Deficient species clearly needs to be assessed while regular updates are necessary for all corals (Knowlton and Nunes, 2008; Carpenter et al., 2008b).

Increasingly, recent research is revealing a wider range of species responses to environmental threats than before (Maynard et al., 2008; Fabricius et al., 2011; Pandolfi et al., 2011; Rodolfo-Metalpa et al., 2011). Given that these threats exhibit considerable phylogenetic signal, the coral tree of life will prove an excellent framework for investigating these variabilities.

This chapter is a reproduction of the material as it appears in PLoS ONE 2012. Huang, Danwei, PLoS, 2012. The dissertation author was the primary investigator and author of this paper.

CHAPTER 6

General conclusions

The convoluted history of coral taxonomy has hindered the implementation of a classification system based upon phylogeny, yet the last few years have seen a concerted effort by coral biologists to develop such a scheme (e.g. Benzoni et al., 2007; 2010; Stefani et al., 2008a,b; this study). The basic approach employed by current taxonomists can be described as a five-step process: (1) inferring a broad-based scleractinian phylogeny (Fukami et al., 2008; Kitahara et al., 2010); (2) performing morphological character transformations on the tree to infer apomorphies of higher-level taxa (Budd and Stolarski, 2009; 2011; this study); (3) revising and redescribing suprageneric taxa (Budd et al., in press); (4) reconstructing the phylogeny with increased number of representatives for each species, wider geographic sampling, as well as including type species of genera and type locality samples of species to be revised (Huang et al., 2011; this study); and (5) revising and redescribing genera and species by comparing the studied collection with type material (this study). This process should ideally be iteratively repeated to include more species from Scleractinia and to retest the taxonomic hypotheses generated at every stage. Certainly, the ultimate goal of this exercise is to infer the coral tree of life that informs taxonomic decisions.

At present, one round of this process has been completed for Fungiidae (Gittenberger et al., 2011), Mussidae (Budd et al., in press) and Merulinidae (this study), but up to 40% of all species in the latter taxon have not been analysed. More extensive sampling may reveal unexpected placements. For instance, *Montastraea multipunctata* and *Moseleya latistellata*, previously presumed to be within Merulinidae, have been shown to be more closely related to Lobophylliidae (Huang et al., 2011; Budd et al., in press).

A second round of the above process has recently commenced for corals in the robust clade with the publication of a comprehensive phylogeny that focused on samples from the Indian Ocean, Gulf of Aden and the Red Sea (Arrigoni et al., 2012). On the basis of molecular markers COI and ITS, the authors found several novel relationships, such as the distinctiveness of *Acanthastrea maxima* (Lobophylliidae) from its congenerics and the unexpected Merulinidae subclade I placement of *Favites peresi*, previously presumed to be in subclade F (see Figures 3.1, 3.2). Intraspecific interoceanic divergences were also detected in several species such as *Favites complanata* and *F. halicora*, suggesting that they may constitute cryptic species and/or misidentification with respect to the type material. In motivating the next course of action, the authors stated that these relationships have to be corroborated by known and novel morphologic traits to support formal taxonomic modifications (Arrigoni et al., 2012).

Complete molecular sampling of all species is unlikely in the near future due to the rarity of many coral species such as *Montipora porites* Veron, 2000, and *Oxypora egyptensis* Veron, 2000. However, as more species are studied in a phylogenetic context, particularly using genetic data, the prospect of an accurate portrayal of evolutionary history improves with the aid of the supertree approach. A complete phylogeny has proved extremely useful for the estimation of various aspects of coral ecology and conservation with respect to evolution, as evidenced in chapter 5. Further work is planned to address more fundamental questions regarding the phylogenetic conservatism of extinction risk and biogeographic origins of coral diversity throughout the world. Preliminary results suggest that phylogenetically clustered threats can obliterate a considerable amount of reef corals' evolutionary history (Huang and Roy, in prep.).

This dissertation demonstrates the power of phylogenetic inferences in supporting taxonomic and conservation decisions. In particular, I provided the molecular and morphological foundation that justified the revision of Faviidae Gregory, 1900 (chapter 2), and more broadly the 'Bigmessidae' (chapter 3). I formally revised the type genus of Merulinidae Verrill, 1865 (*Merulina*), and *Goniastrea* (chapter 4), and finally uncovered the threatened reef coral lineages of the world based on a comprehensive supertree (chapter 5). I strongly believe that these findings will be of long-term significance to the study of coral evolution—if not for its specific content, at least in terms of the general approach presented.

APPENDIX

Reef and non-reef coral species included in the phylogenetic analysis of Scleractinia performed in chapter 5. For each species, the IUCN Red List category and ranks according to the EDGE of Existence (EoE) programme and the present study are shown where appropriate. Transformations according to Mooers et al. (2008)—A: IUCN100; B: Isaac et al. (2007); C: 'Pessimistic' by Mooers et al. (2008). Species not assessed indicated as N/A. GenBank accession numbers are provided for DNA sequences (see text for names of markers).

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Acroporidae									
Acropora abrolhosensis	Yes	VU	N/A	157	310	309	ND5: EU533959	Wallace, 1999	
Acropora abrotanoides	Yes	LC	N/A	793	725	725	CTR: FJ899068	Wallace, 1999	
Acropora aculeus	Yes	VU	N/A	189	427	419		Wallace, 1999	
Acropora acuminata	Yes	VU	N/A	234	527	527	ND5: EU533969	Wallace, 1999	
Acropora akajimensis	Yes	DD	N/A	459	553	553		Wallace, 1999	Junior synonym of A. donei (Wallace, 1999)
Acropora anthocercis	Yes	VU	N/A	231	523	523	ND5: EU533970	Wallace, 1999	
Acropora appressa	Yes	NT	N/A	528	723	723		Wallace, 1999	
Acropora arabensis	Yes	NT	N/A	449	606	606		Wallace, 1999	Sister species to A. valida (Wallace, 1999)
Acropora aspera	Yes	VU	N/A	82	116	107	CTR: EU918267; CYB: FJ391987	Wallace, 1999	
Acropora austera	Yes	NT	N/A	266	158	147	CTR: EU918228; CYB: FJ391989	Wallace, 1999	
Acropora awi	Yes	VU	N/A	256	567	567		Wallace, 1999	
Acropora batunai	Yes	VU	N/A	85	134	123	CTR: EU918250; ND5: EU533971	Wallace, 1999	
Acropora bifurcata	Yes	DD	N/A	579	726	726		Wallace, 1999	Junior synonym of A. hyacinthus (Wallace, 1999)
Acropora branchi	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora bushyensis	Yes	LC	N/A	788	708	708	ND5: EU533975	Wallace, 1999	
Acropora cardenae	Yes	DD	N/A	467	582	582		Wallace, 1999	
Acropora carduus	Yes	NT	N/A	416	531	531	ND5: EU533976	Wallace, 1999	
Acropora caroliniana	Yes	VU	N/A	61	74	69	CTR: EU918274	Wallace, 1999	
Acropora cerealis	Yes	LC	N/A	796	729	729	CTR: EU918248; CYB: AF099652; ND5: EU533979	Wallace, 1999	
Acropora cervicornis	Yes	CR	13	9	28	174	12S: EF597094; COI: AY451340; CTR: EU918257; CYB: AF099654; ND5: EU533960	Wallace, 1999	
Acropora chesterfieldensis	Yes	LC	N/A	602	428	420	CTR: EU918262; ND5: EU533981	Wallace, 1999	
Acropora clathrata	Yes	LC	N/A	819	816	816		Wallace, 1999	
Acropora convexa	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. millepora (Wallace, 1999)
Acropora cophodactyla	Yes	DD	N/A	601	749	749		Wallace, 1999	Junior synonym of A. humilis (Wallace, 1999)
Acropora copiosa	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. muricata (Wallace, 1999)

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Acropora cytherea	Yes	LC	N/A	711	584	584	12S: AF333054; 16S: L75995; CTR: AY083876; CYB: FJ391995	Wallace, 1999	
Acropora dendrum	Yes	VU	N/A	230	522	522	ND5: EU533983	Wallace, 1999	Sister species to A. loisetteae (Wallace, 1999)
Acropora derawanensis	Yes	VU	N/A	35	31	25	CTR: EU918263; ND5: EU533984	Wallace, 1999	
Acropora desalwii	Yes	VU	N/A	153	292	291		Wallace, 1999	
Acropora digitifera	Yes	NT	N/A	335	363	355	12S: AF333051; AT6: AB033199; CTR: EU918261; CYB: AB033184	Wallace, 1999	
Acropora divaricata	Yes	NT	N/A	377	440	432	CTR: AY026432; ND5: EU533985	Wallace, 1999	
Acropora donei	Yes	VU	N/A	77	96	90	AT6: AB033195; CYB: AB033180	Wallace, 1999	
Acropora downingi	Yes	LC	N/A	746	637	637		Wallace, 1999	Sister species to A. polystoma (Wallace, 1999)
Acropora echinata	Yes	VU	N/A	39	39	34	CYB: FJ391985; ND5: EU533986	Wallace, 1999	
Acropora efflorescens	Yes	DD	N/A	595	739	739		Wallace, 1999	Junior synonym of A. cytherea (Wallace, 1999)
Acropora elegans	Yes	VU	N/A	232	524	524	ND5: EU533990	Wallace, 1999	
Acropora elegantula	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora elseyi	Yes	LC	N/A	766	669	669	ND5: EU533991	Wallace, 1999	
Acropora exquisita	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora fastigata	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora fenneri	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora filiformis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora florida	Yes	NT	N/A	440	599	599	AT6: AB033197; CTR: AY026435; CYB: AB033182; ND5: EU533993	Wallace, 1999	
Acropora forskali	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora gemmifera	Yes	LC	N/A	786	705	705	AT6: AB033198; CTR: EU918277; CYB: AB033183	Wallace, 1999	
Acropora glauca	Yes	NT	N/A	528	723	723		Wallace, 1999	
Acropora globiceps	Yes	VU	N/A	190	429	421	CTR: EF206433	Wallace, 1999	Sister species to A. humilis (Wallace, 1999)
Acropora gomezi	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora grandis	Yes	LC	N/A	809	804	804	ND5: EU533994	Wallace, 1999	
Acropora granulosa	Yes	NT	N/A	416	531	531	ND5: EU533995	Wallace, 1999	
Acropora haimei	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora halmaherae	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora hemprichii	Yes	VU	N/A	80	101	94	16S: AF550359	Wallace, 1999	Sister species to A. austera (Wallace, 1999)
Acropora hoeksemai	Yes	VU	N/A	236	534	534		Wallace, 1999	
Acropora horrida	Yes	VU	N/A	99	169	161	ND5: EU533998	Wallace, 1999	
Acropora humilis	Yes	NT	N/A	437	586	586	16S: L75996; CTR: EU918282; CYB: EF363316	Wallace, 1999	
Acropora hyacinthus	Yes	NT	N/A	396	479	473	12S: AF333053; CTR: AY083877; CYB: FJ391988; ND5: EU534002	Wallace, 1999	
Acropora indonesia	Yes	VU	N/A	228	514	514	ND5: EU534003	Wallace, 1999	
Acropora inermis	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. horrida (Wallace, 1999)
Acropora insignis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora intermedia	Yes	LC	N/A	685	533	533	CTR: AY026451; ND5: EU533965	Wallace, 1999	Senior synonym of A. nobilis (Wallace, 1999)
Acropora irregularis	Yes	DD	N/A	553	682	682		Wallace, 1999	Junior synonym of A. abrotanoides (Wallace, 1999)

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Acropora jacquelineae	Yes	VU	N/A	119	210	204	CTR: EU918284; ND5: EU534012	Wallace, 1999	
Acropora japonica	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora khayranensis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora kimbeensis	Yes	VU	N/A	113	191	183	CTR: EU918214	Wallace, 1999	
Acropora kirstyae	Yes	VU	N/A	164	332	330	CTR: EU918215; ND5: EU534015	Wallace, 1999	
Acropora kosurini	Yes	VU	N/A	236	534	534		Wallace, 1999	
Acropora lamarcki	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora latistella	Yes	LC	N/A	610	436	428	CTR: AY026443; CYB: AF099656	Wallace, 1999	
Acropora lianae	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora listeri	Yes	VU	N/A	192	439	431	ND5: EU533966	Wallace, 1999	
Acropora loisetteae	Yes	VU	N/A	114	202	195	CTR: EU918222	Wallace, 1999	
Acropora lokani	Yes	VU	N/A	109	183	175	CTR: EU918270	Wallace, 1999	
Acropora longicyathus	Yes	LC	N/A	808	803	803	CTR: EU918220; ND5: EU534017	Wallace, 1999	
Acropora loripes	Yes	NT	N/A	401	510	507	CTR: EU918227; ND5: EU534020	Wallace, 1999	
Acropora lovelli	Yes	VU	N/A	259	570	570		Wallace, 1999	
Acropora lutkeni	Yes	NT	N/A	378	449	441	ND5: EU534023	Wallace, 1999	
Acropora macrostoma	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. tenuis (Wallace, 1999)
Acropora maryae	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora massawensis	Yes	DD	N/A	569	709	709		Wallace, 1999	Junior synonym of A. polystoma (Wallace, 1999)
Acropora microclados	Yes	VU	N/A	137	237	234	ND5: EU534024	Wallace, 1999	
Acropora microphthalma	Yes	LC	N/A	759	653	653	CTR: EU918203; CYB: FJ391986; ND5: EU534026	Wallace, 1999	
Acropora millepora	Yes	NT	N/A	477	656	656	CTR: EU918207; CYB: AF099653; ND5: EU534029	Wallace, 1999	
Acropora minuta	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora mirabilis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora monticulosa	Yes	NT	N/A	438	588	588	CTR: EF206487	Wallace, 1999	
Acropora multiacuta	Yes	VU	N/A	195	446	438	CTR: EF206546	Wallace, 1999	
Acropora muricata	Yes	NT	N/A	402	511	508	12S: AF177042; CYB: AF099651	Wallace, 1999	Type species of Acropora (Wallace, 1999)
Acropora nana	Yes	NT	N/A	393	473	467	ND5: EU534031	Wallace, 1999	
Acropora nasuta	Yes	NT	N/A	466	650	650	AT6: AB033200; CTR: EU918229; CYB: AB033185; ND5: EU534032	Wallace, 1999	
Acropora natalensis	Yes	DD	N/A	598	741	741		Wallace, 1999	Junior synonym of A. solitaryensis (Wallace, 1999)
Acropora navini	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora ocellata	Yes	DD	N/A	552	670	670		Wallace, 1999	Senior synonym of A. lutkeni (Wallace, 1999)
Acropora orbicularis	Yes	DD	N/A	599	742	742		Wallace, 1999	Junior synonym of A. clathrata (Wallace, 1999)
Acropora pagoensis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora palmata	Yes	CR	10	8	21	150	12S: EF597092; COI: AB441246; CTR: AF507217; CYB: AB441331; ND5: EU533962	Wallace, 1999	
Acropora palmerae	Yes	VU	N/A	188	423	415		Wallace, 1999	
Acropora paniculata	Yes	VU	N/A	229	518	518		Wallace, 1999	
Acropora papillare	Yes	VU	N/A	32	27	20	CTR: EU918211	Wallace, 1999	
Acropora paragemmifera	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora parahemprichii	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora parapharaonis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora parilis	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. horrida (Wallace, 1999)
Acropora pectinatus	Yes	DD	N/A	622	762	762		Wallace, 1999	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Acropora pharaonis	Yes	VU	N/A	259	570	570		Wallace, 1999	
Acropora pichoni	Yes	NT	N/A	322	325	323	CTR: EU918206; ND5: EU534033	Wallace, 1999	Sister species to A. elegans (Wallace, 1999)
Acropora pinguis	Yes	DD	N/A	553	682	682		Wallace, 1999	Junior synonym of A. robusta (Wallace, 1999)
Acropora plana	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. tenuis (Wallace, 1999)
Acropora plantaginea	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora plumosa	Yes	VU	N/A	259	570	570		Wallace, 1999	
Acropora polystoma	Yes	VU	N/A	87	138	128	ND5: EU533964	Wallace, 1999	
Acropora prostrata	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. millepora (Wallace, 1999)
Acropora proximalis	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora pruinosa	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora pulchra	Yes	LC	N/A	760	654	654	CTR: EU918230; ND5: EU533967	Wallace, 1999	
Acropora rambleri	Yes	DD	N/A	596	740	740		Wallace, 1999	Junior synonym of A. speciosa (Wallace, 1999)
Acropora retusa	Yes	VU	N/A	147	280	278	CTR: EF206535	Wallace, 1999	
Acropora ridzwani	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora robusta	Yes	LC	N/A	789	718	718	CTR: FJ899064	Wallace, 1999	
Acropora rongelapensis	Yes	DD	N/A	422	447	439	CTR: EU918210	Wallace, 1999	
Acropora rosaria	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora roseni	Yes	EN	N/A	69	360	511		Wallace, 1999	
Acropora rudis	Yes	EN	N/A	69	360	511		Wallace, 1999	
Acropora rufus	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora russelli	Yes	VU	N/A	153	292	291		Wallace, 1999	
Acropora samoensis	Yes	LC	N/A	762	658	658	CTR: AY364095; CYB: FJ391994	Wallace, 1999	
Acropora sarmentosa	Yes	LC	N/A	797	737	737	CTR: AY026455; ND5: EU534034	Wallace, 1999	
Acropora scherzeriana	Yes	DD	N/A	567	706	706		Wallace, 1999	Junior synonym of A. gemmifera (Wallace, 1999)
Acropora schmitti	Yes	DD	N/A	512	636	636		Wallace, 1999	Junior synonym of A. digitifera (Wallace, 1999)
Acropora secale	Yes	NT	N/A	479	660	660		Wallace, 1999	
Acropora sekiseiensis	Yes	DD	N/A	622	762	762		Wallace, 1999	Junior synonym of A. horrida (Wallace, 1999)
Acropora selago	Yes	NT	N/A	477	656	656	CTR: AB361179; ND5: EU534035	Wallace, 1999	
Acropora seriata	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora simplex	Yes	VU	N/A	194	442	434		Wallace, 1999	
Acropora solitaryensis	Yes	VU	N/A	233	525	525	ND5: EU534039	Wallace, 1999	
Acropora spathulata	Yes	LC	N/A	798	738	738	CTR: EU918209; ND5: EU534040	Wallace, 1999	
Acropora speciosa	Yes	VU	N/A	37	35	29	CTR: EU918245	Wallace, 1999	
Acropora spicifera	Yes	VU	N/A	175	398	390	CTR: AY083881; ND5: EU534041	Wallace, 1999	
Acropora squarrosa	Yes	LC	N/A	767	685	685		Wallace, 1999	Sister species to A. loripes (Wallace, 1999)
Acropora stoddarti	Yes	DD	N/A	603	753	753		Wallace, 1999	Junior synonym of A. divaricata (Wallace, 1999)
Acropora striata	Yes	VU	N/A	259	570	570		Wallace, 1999	
Acropora subglabra	Yes	LC	N/A	834	833	833	ND5: EU534042	Wallace, 1999	
Acropora subulata	Yes	LC	N/A	763	659	659		Wallace, 1999	
Acropora suharsonoi	Yes	EN	N/A	68	359	510		Wallace, 1999	
Acropora sukarnoi	Yes	DD	N/A	471	587	587		Wallace, 1999	
Acropora tanegashimensis	Yes	DD	N/A	564	686	686		Wallace, 1999	Sister species to A. hyacinthus (Wallace, 1999)
Acropora tenella	Yes	VU	N/A	97	167	159	CTR: EU918240	Wallace, 1999	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Acropora tenuis	Yes	NT	N/A	297	250	247	12S: AF338425; 16S: AF338425; AT6: AF338425; COI: AF338425; CTR: AF338425; CYB: AF338425; ND5: AF338425	Wallace, 1999	
Acropora teres	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora tizardi	Yes	DD	N/A	603	753	753		Wallace, 1999	Junior synonym of A. cerealis (Wallace, 1999)
Acropora torihalimeda	Yes	DD	N/A	467	582	582		Wallace, 1999	
Acropora torresiana	Yes	DD	N/A	622	762	762		Wallace, 1999	
Acropora tortuosa	Yes	LC	N/A	545	324	322	CTR: EU918238	Wallace, 1999	
Acropora tumida	Yes	DD	N/A	603	753	753		Wallace, 1999	Junior synonym of A. valida (Wallace, 1999)
Acropora turaki	Yes	VU	N/A	256	567	567		Wallace, 1999	
Acropora tutuilensis	Yes	DD	N/A	553	682	682		Wallace, 1999	Junior synonym of A. abrotanoides (Wallace, 1999)
Acropora valenciennesi	Yes	LC	N/A	835	834	834		Wallace, 1999	
Acropora valida	Yes	LC	N/A	747	638	638	CTR: EU918235; CYB: AF099658; ND5: EU534047	Wallace, 1999	
Acropora variabilis	Yes	DD	N/A	603	753	753		Wallace, 1999	Junior synonym of A. valida (Wallace, 1999)
Acropora variolosa	Yes	LC	N/A	835	834	834		Wallace, 1999	Sister species to A. rudis (Wallace, 1999)
Acropora vaughani	Yes	VU	N/A	83	125	115	CTR: EU918224	Wallace, 1999	
Acropora vermiculata	Yes	DD	N/A	575	722	722		Wallace, 1999	Junior synonym of A. sarmentosa (Wallace, 1999)
Acropora verweyi	Yes	VU	N/A	259	570	570		Wallace, 1999	
Acropora walindii	Yes	VU	N/A	75	90	84	CTR: EU918234	Wallace, 1999	Sister species to A. tenella (Wallace, 1999)
Acropora wallaceae	Yes	DD	N/A	551	668	668		Wallace, 1999	Junior synonym of A. samoensis (Wallace, 1999)
Acropora willisae	Yes	VU	N/A	256	567	567		Wallace, 1999	
Acropora yongei	Yes	LC	N/A	818	815	815	ND5: EU534048	Wallace, 1999	
Anacropora forbesi	Yes	LC	N/A	461	196	188	COI: AB441251; CYB: AB441336	Wallace, 1999	
Anacropora matthai	Yes	VU	N/A	59	72	67	12S: AY903295; 16S: AY903295; AT6: AY903295; COI: AY903295; CTR: AY903295; CYB: AY903295; ND5: AY903295	Wallace, 1999	
Anacropora pillai	Yes	DD	N/A	447	488	482		Wallace, 1999	
Anacropora puertogalerae	Yes	VU	N/A	138	243	240		Wallace, 1999	
Anacropora reticulata	Yes	VU	N/A	138	243	240		Wallace, 1999	
Anacropora spinosa	Yes	EN	N/A	18	98	198		Wallace, 1999	
Anacropora spumosa	Yes	DD	N/A	447	488	482		Wallace, 1999	
Astreopora acroporina	Yes	DD	N/A	541	663	663		Wallace, 1999	New species (Wallace et al., 2011)
Astreopora cenderawasih	Yes	DD	N/A	541	663	663		Wallace, 1999	New species (Wallace et al., 2011)
Astreopora cucullata	Yes	VU	N/A	176	399	391		Wallace, 1999	
Astreopora eliptica	Yes	DD	N/A	541	663	663		Wallace, 1999	
Astreopora expansa	Yes	NT	N/A	450	613	613		Wallace, 1999	
Astreopora gracilis	Yes	LC	N/A	799	743	743		Wallace, 1999	
Astreopora incrustans	Yes	VU	N/A	176	399	391		Wallace, 1999	
Astreopora listeri	Yes	LC	N/A	799	743	743		Wallace, 1999	
Astreopora macrostoma	Yes	NT	N/A	450	613	613		Wallace, 1999	
Astreopora montiporina	Yes	DD	N/A	541	663	663		Wallace, 1999	New species (Wallace et al., 2011)
Astreopora moretonensis	Yes	VU	N/A	176	399	391		Wallace, 1999	
Astreopora myriophthalma	Yes	LC	N/A	446	164	156	12S: AF177046; AT6: AB033186; COI: AB441253; CYB: AB441338	Wallace, 1999	
Astreopora ocellata	Yes	LC	N/A	799	743	743		Wallace, 1999	

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Astreopora randalli	Yes	LC	N/A	799	743	743		Wallace, 1999	
Astreopora scabra	Yes	LC	N/A	799	743	743		Wallace, 1999	
Astreopora suggesta	Yes	LC	N/A	799	743	743		Wallace, 1999	
Enigmopora darveliensis	Yes	DD	N/A	682	806	806			Closest to Acropora (prior to elevation of Isopora) (Ditlev, 2003)
Isopora brueggemanni	Yes	VU	N/A	93	151	141	12S: AF333048; AT6: AB033193; COI: AB441247; CYB: AB441332; ND5: EU534004	Wallace, 1999	
Isopora crateriformis	Yes	VU	N/A	169	369	361		Wallace, 1999	
Isopora cuneata	Yes	VU	N/A	26	16	11	12S: AF333049; CTR: AY026429; ND5: EU534006	Wallace, 1999	
Isopora cylindrica	Yes	DD	N/A	514	639	639		Wallace, 1999	
Isopora elizabethensis	Yes	DD	N/A	514	639	639		Wallace, 1999	
Isopora meridiana	Yes	DD	N/A	514	639	639		Wallace, 1999	Junior synonym of Acropora brueggemanni (Wallace, 1999)
Isopora palifera	Yes	NT	N/A	309	294	293	12S: AF177044; 16S: AF265593; AT6: AB033194; COI: AB441248; CYB: AB441333; ND5: EU534010	Wallace, 1999	
Isopora togianensis	Yes	EN	N/A	20	107	214	12S: AF333050; COI: AB441249; CYB: AB441334; ND5: EU534008	Wallace, 1999	Morphological coding updated (Wallace et al., 2007)
Montipora aequituberculata	Yes	LC	N/A	726	610	610	12S: AF333045; AT6: AB033187; CTR: AY313548; CYB: AB033172	Wallace, 1999	
Montipora altasepta	Yes	VU	N/A	58	70	65	AT6: AB033190; CTR: AY313572; CYB: AB033175	Wallace, 1999	
Montipora angulata	Yes	VU	N/A	74	89	83	CTR: AY313563	Wallace, 1999	
Montipora aspergillus	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora australiensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora cactus	Yes	VU	N/A	90	145	135	12S: AY903296; 16S: AY903296; AT6: AY903296; COI: AY903296; CTR: AY903296; CYB: AY903296; ND5: AY903296	Wallace, 1999	
Montipora calcarea	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora caliculata	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora capitata	Yes	NT	N/A	338	367	359	16S: HQ246709; AT6: HQ246686; COI: HQ246613; CTR: HQ246520; CYB: HQ246516	Wallace, 1999	
Montipora capricornis	Yes	VU	N/A	76	94	88	CTR: AY313583	Wallace, 1999	
Montipora cebuensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora circumvallata	Yes	LC	N/A	276	13	9	16S: AF550368	Wallace, 1999	
Montipora cocosensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora confusa	Yes	NT	N/A	300	265	263	CTR: AY313551	Wallace, 1999	
Montipora corbettensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora crassituberculata	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora cryptus	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora danae	Yes	LC	N/A	609	435	427	CTR: AY313549	Wallace, 1999	
Montipora delicatula	Yes	VU	N/A	118	209	203	CTR: AY313566	Wallace, 1999	

Species	Reef	Red	EoE	EDGE rank			Molecular	Morphology	Remarks
		List	rank	A	B	C	sources	sources	
Montipora digitata	Yes	LC	N/A	768	687	687	12S: AF177045; 16S: L75993; AT6: AB033188; CTR: AY313579; CYB: AB033173	Wallace, 1999	
Montipora dilatata	Yes	EN	N/A	25	156	282	16S: HQ246702; AT6: HQ246678; COI: HQ246605; CTR: HQ246554; CYB: HQ246508	Wallace, 1999	
Montipora echinata	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora efflorescens	Yes	NT	N/A	253	136	126	AT6: AB033189; CYB: AB033174	Wallace, 1999	
Montipora effusa	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora flabellata	Yes	VU	N/A	155	299	298	16S: HQ246698; AT6: HQ246674; COI: HQ246601; CTR: HQ246561; CYB: HQ246504	Wallace, 1999	
Montipora florida	Yes	VU	N/A	81	105	98	CTR: AY313562	Wallace, 1999	
Montipora floweri	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora foliosa	Yes	NT	N/A	239	133	122	CYB: FJ392003	Wallace, 1999	
Montipora foveolata	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora friabilis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora gaimardi	Yes	VU	N/A	72	87	81	CTR: AY313565	Wallace, 1999	
Montipora grisea	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora hemispherica	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora hirsuta	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora hispida	Yes	LC	N/A	663	454	446	CTR: AY313553; CYB: FJ392005	Wallace, 1999	
Montipora hodgsoni	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora hoffmeisteri	Yes	LC	N/A	770	689	689	CTR: AY313580	Wallace, 1999	
Montipora incrassata	Yes	NT	N/A	324	330	328	16S: HQ246710; AT6: HQ246687; COI: HQ246614; CTR: HQ246593; CYB: HQ246517	Wallace, 1999	Montipora cf. incrassata in GenBank
Montipora informis	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora kellyi	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora lobulata	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora mactanensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora malampaya	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora meandrina	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora millepora	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora mollis	Yes	LC	N/A	785	704	704	CTR: AY313552	Wallace, 1999	
Montipora monasteriata	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora niugini	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora nodosa	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora orientalis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora pachytuberculata	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora palawanensis	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora patula	Yes	VU	N/A	117	208	202	16S: HQ246691; AT6: HQ246667; COI: HQ246595; CTR: HQ246573; CYB: HQ246497	Wallace, 1999	
Montipora peltiformis	Yes	NT	N/A	363	420	412	CTR: AY313550	Wallace, 1999	
Montipora porites	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora samarensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora saudii	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora setosa	Yes	EN	N/A	52	311	461		Wallace, 1999	
Montipora spongiosa	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora spongodes	Yes	LC	N/A	769	688	688	CTR: AY313547	Wallace, 1999	
Montipora spumosa	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora stellata	Yes	LC	N/A	726	610	610	CTR: AY313587	Wallace, 1999	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Montipora stilosa	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora taiwanensis	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora tuberculosa	Yes	LC	N/A	810	807	807		Wallace, 1999	
Montipora turgescens	Yes	LC	N/A	765	662	662	16S: HQ246704; AT6: HQ246681; COI: HQ246608; CTR: HQ246564; CYB: HQ246511	Wallace, 1999	Montipora cf. turgescens in GenBank
Montipora turtlensis	Yes	VU	N/A	156	308	307	CTR: AY313574	Wallace, 1999	
Montipora undata	Yes	NT	N/A	286	221	216	CTR: AY313569	Wallace, 1999	
Montipora vaughani	Yes	DD	N/A	587	730	730		Wallace, 1999	
Montipora venosa	Yes	NT	N/A	489	671	671		Wallace, 1999	
Montipora verrilli	Yes	DD	N/A	436	472	465	16S: HQ246695; AT6: HQ246671; COI: HQ246598; CTR: HQ246582; CYB: HQ246501	Wallace, 1999	
Montipora verrucosa	Yes	LC	N/A	719	601	601	12S: EF597090; CTR: AY313584	Wallace, 1999	
Montipora verruculosus	Yes	VU	N/A	204	491	488		Wallace, 1999	
Montipora vietnamensis	Yes	VU	N/A	204	491	488		Wallace, 1999	
Agariciidae									
Agaricia agaricites	Yes	LC	N/A	617	443	435	12S: EF597079; COI: AY451366	Pires and Castro, 1997	
Agaricia fragilis	Yes	DD	N/A	313	222	217	12S: EF597077	Pires and Castro, 1997	
Agaricia grahamae	Yes	LC	N/A	684	526	526	12S: EF597078		
Agaricia humilis	Yes	LC	N/A	540	318	316	12S: DQ643831; 16S: DQ643831; AT6: DQ643831; COI: DQ643831; CYB: DQ643831; ND5: DQ643831		
Agaricia lamarcki	Yes	VU	N/A	51	61	56	12S: EF597076; COI: AY451369		
Agaricia tenuifolia	Yes	NT	N/A	323	327	325	12S: EF597081; COI: AY451370		
Agaricia undata	Yes	DD	N/A	397	393	385	12S: EF597075		
Coeloseris mayeri	Yes	LC	ED	674	477	471			Closest to Pavona (Veron, 1986)
Gardineroseris planulata	Yes	LC	N/A	556	338	336	12S: EF597084; COI: AB441218; CYB: AB441303		
Helioseris cucullata	Yes	LC	N/A	370	71	66	COI: AB441220; CYB: AB441305	Pires and Castro, 1997	
Leptoseris amitoriensis	Yes	NT	N/A	353	403	395			Leptoseris monophyly assumed; closest to L. papyracea (Veron, 1990)
Leptoseris cailleti	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed; closest to L. papyracea (Veron, 2000)
Leptoseris explanata	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed
Leptoseris foliosa	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed; closest to L. mycetoseroides (Veron, 1986)
Leptoseris gardineri	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed; closest to L. papyracea (Veron, 1986)
Leptoseris hawaiiensis	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed; closest to L. scabra (Veron, 1986)
Leptoseris incrustans	Yes	VU	N/A	123	223	219	16S: L76012		
Leptoseris mycetoseroides	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed
Leptoseris papyracea	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed
Leptoseris scabra	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed
Leptoseris solida	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed; closest to L. scabra (Veron, 2000)

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Leptoseris striata	Yes	NT	N/A	353	403	395			Leptoseris monophyly assumed; closest to L. scabra (Veron, 2002)
Leptoseris tubulifera	Yes	LC	N/A	735	621	621			Leptoseris monophyly assumed
Leptoseris yabei	Yes	VU	N/A	129	229	225			Leptoseris monophyly assumed; closest to L. mycetoseroides (Veron, 1986)
Pachyseris foliosa	Yes	LC	N/A	686	536	536			Pachyseris monophyly assumed; closest to P. involuta (Veron, 1990)
Pachyseris gemmae	Yes	NT	N/A	278	197	190			Pachyseris monophyly assumed; closest to P. rugosa and P. speciosa (Veron, 2000)
Pachyseris involuta	Yes	VU	N/A	98	168	160			Pachyseris monophyly assumed
Pachyseris rugosa	Yes	VU	N/A	57	69	64			Pachyseris monophyly assumed
Pachyseris speciosa	Yes	LC	N/A	380	83	78	COI: AB441222; CYB: AB441307		
Pavona bipartita	Yes	VU	N/A	124	224	220		Daly et al., 2003	
Pavona cactus	Yes	VU	N/A	17	10	6	16S: AF550370; COI: AB441217; CYB: AB441302	Daly et al., 2003	
Pavona chiriquiensis	Yes	LC	N/A	730	616	616		Daly et al., 2003	
Pavona clavus	Yes	LC	N/A	570	368	360	12S: DQ643836; 16S: DQ643836; AT6: DQ643836; COI: DQ643836; CYB: DQ643836; ND5: DQ643836	Daly et al., 2003	
Pavona danai	Yes	VU	N/A	124	224	220		Daly et al., 2003	
Pavona decussata	Yes	VU	N/A	124	224	220		Daly et al., 2003	
Pavona diffluens	Yes	VU	N/A	124	224	220		Daly et al., 2003	
Pavona duerdeni	Yes	LC	N/A	730	616	616		Daly et al., 2003	
Pavona explanulata	Yes	LC	N/A	730	616	616		Daly et al., 2003	
Pavona frondifera	Yes	LC	N/A	517	284	283	12S: AF333055	Daly et al., 2003	
Pavona gigantea	Yes	LC	N/A	730	616	616		Daly et al., 2003	
Pavona maldivensis	Yes	LC	N/A	730	616	616		Daly et al., 2003	
Pavona minuta	Yes	NT	N/A	352	402	394		Daly et al., 2003	
Pavona varians	Yes	LC	N/A	669	464	456	12S: EF597083; 16S: L76016	Daly et al., 2003	
Pavona venosa	Yes	VU	N/A	124	224	220		Daly et al., 2003	
Pavona xarifae	Yes	DD	N/A	439	480	474		Daly et al., 2003	
Anthemiphyllidae									
Anthemiphyllia dentata	No	N/A	N/A	N/A	N/A	N/A	COI: HM018603	Daly et al., 2003	
Anthemiphyllia frustum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Anthemiphyllia macrolobata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Anthemiphyllia multidentata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Anthemiphyllia pacifica	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Anthemiphyllia patera	No	N/A	N/A	N/A	N/A	N/A	COI: HM018604	Daly et al., 2003	
Anthemiphyllia spinifera	No	N/A	N/A	N/A	N/A	N/A	16S: AF265596	Daly et al., 2003	
Astrocoeniidae									
Madracis asanoi	Yes	DD	N/A	252	81	76	COI: HM018656		
Madracis asperula	Yes	DD	N/A	273	113	105			Closest to M. asanoi (Veron, 2000)
Madracis auretenra	Yes	LC	N/A	469	207	201	12S: EU400212; 16S: EU400212; AT6: EU400212; COI: EU400212; CYB: EU400212		Probably M. mirabilis in GenBank (Locke et al., 2007)
Madracis carmabi	Yes	DD	N/A	292	166	158	12S: EF596980		
Madracis decactis	Yes	LC	N/A	482	251	248	12S: EF596982	Pires and Castro, 1997	
Madracis formosa	Yes	LC	N/A	463	200	193	12S: EF596981		
Madracis kirbyi	Yes	LC	N/A	483	252	249			Closest to M. decactis (Veron, 2000)
Madracis pharensis	Yes	LC	N/A	462	198	191	12S: EF596983		

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Madracis senaria	Yes	LC	N/A	464	201	194	12S: EF596979		
Palauastrea ramosa	Yes	NT	N/A	275	175	166			Closest to Madracis (Yabe and Sugiyama, 1941)
Stephanocoenia intersepta	Yes	LC	ED	321	33	27	12S: EF597072; COI: AB441228; CYB: AB441313	Pires and Castro, 1997	Senior synonym of S. michelinii
Stylocoeniella armata	Yes	LC	N/A	503	264	262			Stylocoeniella monophyly assumed; closest to S. guentheri (Veron, 2000)
Stylocoeniella cocosensis	Yes	VU	N/A	54	66	61			Stylocoeniella monophyly assumed
Stylocoeniella guentheri	Yes	LC	N/A	389	92	86	COI: AB441225; CYB: AB441310		
Stylocoeniella muscosus	Yes	DD	N/A	328	256	254			Stylocoeniella monophyly assumed
Caryophylliidae									
Caryophyllia abrupta	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia abyssorum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia alaskensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia alberti	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia ambrosia	No	N/A	N/A	N/A	N/A	N/A	16S: AF550362	Daly et al., 2003; Pires and Castro, 1997	
Caryophyllia antarctica	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia antillarum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia arnoldi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia aspera	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia atlantica	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788113; COI: HM018613	Daly et al., 2003	
Caryophyllia balanacea	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia barbadensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia berteriana	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia calveri	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia cincticulatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia concreta	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia cornulum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia corona	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia corrugata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia crosnieri	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia crypta	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia cyathus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia decamera	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia dentata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia diomedeae	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788115; COI: HM018614	Daly et al., 2003	
Caryophyllia eltaninae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia ephyala	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia foresti	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia grandis	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788117	Daly et al., 2003	
Caryophyllia grayi	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788119; COI: HM018615	Daly et al., 2003	
Caryophyllia hawaiiensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia horologium	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia huinayensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia inornata	No	N/A	N/A	N/A	N/A	N/A	12S: EF597042; 16S: AF265599	Daly et al., 2003	
Caryophyllia japonica	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia jogashimaensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia karubarica	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia laevigata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia lamellifera	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788120; COI: HM018616	Daly et al., 2003	
Caryophyllia mabahithi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia marmorea	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia oblonga	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Caryophyllia octonaria	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia octopali	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia paradoxus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia paucipalata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia perculta	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia planilamellata	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788121	Daly et al., 2003	
Caryophyllia polygona	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia profunda	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia protei	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia quadragenaria	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia quangdongensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia ralphae	No	N/A	N/A	N/A	N/A	N/A	COI: HM018617	Daly et al., 2003	
Caryophyllia rugosa	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788123; COI: HM018618	Daly et al., 2003	
Caryophyllia sarsiae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia scobinosa	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788124	Daly et al., 2003	
Caryophyllia secta	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia seguenzae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia sewelli	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia smithii	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia solida	No	DD	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia spinicarens	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia spinigera	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia squiresi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia stellula	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia tangaroae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia transversalis	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788125	Daly et al., 2003	
Caryophyllia unicristata	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788127	Daly et al., 2003	
Caryophyllia valdiviae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia versicolorata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia zanzibarensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Caryophyllia zopyros	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Ceratotrochus magnaghii	No	N/A	N/A	N/A	N/A	N/A	16S: AF265597		
Conotrochus funicolumna	No	N/A	N/A	N/A	N/A	N/A	COI: HM018621		
Crispatotrochus cornu	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus curvatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus foxi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus galapagensis	No	DD	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus gregarius	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus inornatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus irregularis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus niinoi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus rubescens	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus rugosus	No	N/A	N/A	N/A	N/A	N/A	12S: EF597041; 16S: AF265600	Daly et al., 2003	
Crispatotrochus septumdentatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus squiresi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Crispatotrochus woodsi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Dactylotrochus cervicornis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018624		
Dasmosmilia lymani	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788130; COI: HM018625	Pires and Castro, 1997	Dasmosmilia cf. lymani in GenBank
Dasmosmilia variegata	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	Dasmosmilia monophyly assumed
Deltocyathus calcar	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	Deltocyathus monophyly assumed
Deltocyathus eccentricus	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	Deltocyathus monophyly assumed
Deltocyathus inusitatus	No	N/A	N/A	N/A	N/A	N/A	COI: HM018626		
Deltocyathus italicus	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	
Deltocyathus magnificus	No	N/A	N/A	N/A	N/A	N/A	COI: HM018627		

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Deltocyathus ornatus	No	N/A	N/A	N/A	N/A	N/A	COI: HM018628		
Deltocyathus rotulus	No	N/A	N/A	N/A	N/A	N/A	COI: HM018629		
Deltocyathus sarsi	No	N/A	N/A	N/A	N/A	N/A	COI: HM018630		
Deltocyathus suluensis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018631		
Desmophyllum dianthus	No	N/A	N/A	N/A	N/A	N/A	12S: GQ868667; 16S: GQ868690		
Heterocyathus aequicostatus	Yes	LC	N/A	790	719	719			Heterocyathus monophyly assumed; Caryophylliidae clade (M.V. Kitahara, pers comm)
Heterocyathus alternatus	Yes	LC	N/A	790	719	719			Heterocyathus monophyly assumed; Caryophylliidae clade (M.V. Kitahara, pers comm)
Heterocyathus sulcatus	Yes	LC	N/A	790	719	719			Heterocyathus monophyly assumed; Caryophylliidae clade (M.V. Kitahara, pers comm)
Hoplangia durotrix	No	N/A	N/A	N/A	N/A	N/A	12S: EF597064		
Lophelia pertusa	No	N/A	N/A	N/A	N/A	N/A	12S: FR821799; 16S: FR821799; AT6: FR821799; COI: FR821799; CYB: FR821799		
Paracyathus andersoni	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus arcuatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus cavatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus conceptus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus coronatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus darwinensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus ebonensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus fulvus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus humilis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus indicus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus lifuensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus molokensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus monteryensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus parvulus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus persicus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus porcellanus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus profundus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus pruinosus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus pulchellus	No	N/A	N/A	N/A	N/A	N/A	12S: EF597027; 16S: AF265603	Daly et al., 2003	
Paracyathus rotundatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus stearnsii	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus stokesii	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Paracyathus vittatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia americana	No	N/A	N/A	N/A	N/A	N/A	12S: EF597022; 16S: AF265605	Daly et al., 2003; Pires and Castro, 1997	
Phyllangia consagensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia dispersa	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia echinosepes	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia granulata	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia hayamaensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Phyllangia papuensis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018660	Daly et al., 2003	
Phyllangia pequegnatae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus andamanensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus atlanticus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus difficilis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus fulvus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus furanaensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus fuscomarginatus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus hodgsoni	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus hondaensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus isabela	No	VU	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus marigondoni	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Polycyathus mayae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus muellerae	No	N/A	N/A	N/A	N/A	N/A	12S: EF597026; 16S: AF265606	Daly et al., 2003	
Polycyathus norfolkensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus octuplus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus palifera	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus persicus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus senegalensis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Polycyathus verrilli	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Premocyathus cornuformis	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	Revised from Caryophyllia cornuformis
Rhizosmilia maculata	No	N/A	N/A	N/A	N/A	N/A	12S: EF597023; 16S: AF265602	Pires and Castro, 1997	
Rhizosmilia robusta	No	N/A	N/A	N/A	N/A	N/A	COI: HM018664		
Solenosmilia variabilis	No	N/A	N/A	N/A	N/A	N/A	16S: HM015348		
Stephanocyathus platypus	No	N/A	N/A	N/A	N/A	N/A	16S: HM015352		
Stephanocyathus spiniger	No	N/A	N/A	N/A	N/A	N/A	16S: HM015359; COI: HM018665		
Stephanocyathus weberianus	No	N/A	N/A	N/A	N/A	N/A	16S: AF265594		
Tethocyathus virgatus	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788131		
Thalamophyllia gasti	No	N/A	N/A	N/A	N/A	N/A	12S: EF597086; 16S: AF265590	Daly et al., 2003	
Thalamophyllia gombergi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Thalamophyllia riisei	No	N/A	N/A	N/A	N/A	N/A	12S: EF597087	Daly et al., 2003	
Thalamophyllia tenuescens	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Trochocyathus efateensis	No	N/A	N/A	N/A	N/A	N/A	16S: FJ788132; COI: HM018667		
Trochocyathus rhombocolumna	No	N/A	N/A	N/A	N/A	N/A	COI: HM018668		
Vaughanella concinna	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Vaughanella margaritata	No	N/A	N/A	N/A	N/A	N/A	16S: AF265595	Daly et al., 2003	Vaughanella sp. in GenBank; terminal branch shared with conspecifics
Vaughanella multipalifera	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Vaughanella oreophila	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Dendrophylliidae									
Astroides calycularis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Balanophyllia bairdiana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia bayeri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia bonaespei	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia capensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia caribbeana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia carinata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia cedrosensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia cellulosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia chnous	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia corniculans	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia cornu	No	N/A	N/A	N/A	N/A	N/A	COI: HM018605	Cairns, 2001; Daly et al., 2003	
Balanophyllia crassiseptum	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia crassitheca	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia cumingii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Balanophyllia cyathoides	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia dentata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia desmophyllioides	No	N/A	N/A	N/A	N/A	N/A	COI: HM018607	Cairns, 2001; Daly et al., 2003	
Balanophyllia diademata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia diffusa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia dilatata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia dineta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia diomedeae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia dubia	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia elegans	No	N/A	N/A	N/A	N/A	N/A	COI: DQ445805	Cairns, 2001; Daly et al., 2003	
Balanophyllia europaea	Yes	DD	N/A	756	836	836		Cairns, 2001; Daly et al., 2003; Pires and Castro, 1997	
Balanophyllia floridana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia galapagensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia gemma	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia gemmifera	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia generatrix	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia gigas	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia hadros	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia helenae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia imperialis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia iwayamaensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia japonica	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia kalakauai	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia laysanensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia malouinensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia merguiensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia palifera	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia parallela	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia parvula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia pittieri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia profundicella	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia rediviva	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Balanophyllia regalis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia regia	No	N/A	N/A	N/A	N/A	N/A	12S: EF597047; 16S: AF265587	Cairns, 2001; Daly et al., 2003	
Balanophyllia scabra	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia scabrosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia serrata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia spongiosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia stimpsonii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	Balanophyllia (Eupsammia)
Balanophyllia striata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia taprobanae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia tenuis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia thalassae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia vanderhorsti	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia wellsi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Balanophyllia yongei	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Bathypsammia falloscoialis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Bathypsammia tintinnabulum	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Cladopsammia echinata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Cladopsammia eguchii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Cladopsammia gracilis	No	N/A	N/A	N/A	N/A	N/A	12S: EF597049; 16S: AF265588	Cairns, 2001	
Cladopsammia manuelensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Cladopsammia rolandi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Cladopsammia willeyi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia aculeata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia alcocki	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia alternata	No	N/A	N/A	N/A	N/A	N/A	16S: AF550366	Cairns, 2001	
Dendrophyllia arbuscula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia boschmai	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia californica	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia carleenae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia cecilliana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia cladonia	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia cornigera	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia cribrosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia dilatata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia florulenta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia fotojiku	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia granosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia ijimai	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia incisa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia indica	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia johnsoni	No	DD	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia laboreli	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia minima	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia minuscula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia oldroydae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia paragracilis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia radians	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia ramea	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia robusta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Dendrophyllia suprarbuscula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dendrophyllia velata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Dichopsammia granulosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Duncanopsammia axifuga	Yes	NT	N/A	445	603	603		Cairns, 2001	
Eguchipsammia cornucopia	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia fistula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia gaditana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia japonica	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia serpentina	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia strigosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Eguchipsammia wellsi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Enallopsammia profunda	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Enallopsammia pusilla	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Enallopsammia rostrata	No	N/A	N/A	N/A	N/A	N/A	16S: U40294; COI: HM018632	Cairns, 2001; Daly et al., 2003	
Endopachys bulbosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Endopachys grayi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Endopsammia philippensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Endopsammia pourtalesi	No	DD	N/A	N/A	N/A	N/A		Cairns, 2001	
Endopsammia regularis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Heteropsammia cochleata	Yes	LC	N/A	837	837	837	12S: EF597050	Cairns, 2001	Heteropsammia sp. in GenBank; terminal branch shared with conspecifics
Heteropsammia eupsammides	Yes	NT	N/A	670	832	832		Cairns, 2001	
Heteropsammia moretonensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Leptopsammia britannica	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia chevalieri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia columna	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia crassa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia formosa	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia poculum	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia pruvoti	No	N/A	N/A	N/A	N/A	N/A	12S: EF597068; 16S: AF265579	Cairns, 2001; Daly et al., 2003	
Leptopsammia queenslandiae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia stokesiana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Leptopsammia trinitatis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Notophyllia etheridgi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Notophyllia hecki	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Notophyllia piscacauda	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Notophyllia recta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Pourtalopsammia togata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Rhizopsammia annae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia bermudensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia compacta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia goesi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia minuta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Rhizopsammia nuda	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia pulchra	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia verrilli	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia wellingtoni	No	CR	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Rhizopsammia wettsteini	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Thecopsammia elongata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Thecopsammia socialis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Trochopsammia infundibulum	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001	
Tubastraea coccinea	No	N/A	N/A	N/A	N/A	N/A	12S: EF597045; 16S: L76022; COI: DQ445806	Cairns, 2001; Daly et al., 2003	
Tubastraea diaphana	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Tubastraea faulkneri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Tubastraea floreana	No	CR	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Tubastraea micranthus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Tubastraea tagusensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 2001; Daly et al., 2003	
Turbinaria bifrons	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Turbinaria conspicua	Yes	LC	N/A	805	750	750		Cairns, 2001; Daly et al., 2003	
Turbinaria crater	Yes	DD	N/A	547	667	667		Cairns, 2001; Daly et al., 2003	Previously excluded (Carpenter et al., 2008a)
Turbinaria frondens	Yes	LC	N/A	805	750	750		Cairns, 2001; Daly et al., 2003	
Turbinaria heronensis	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Turbinaria irregularis	Yes	LC	N/A	805	750	750		Cairns, 2001; Daly et al., 2003	
Turbinaria mesenterina	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Turbinaria patula	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Turbinaria peltata	Yes	VU	N/A	34	30	24	12S: EF597044; COI: AB441240; CYB: AB441325	Cairns, 2001; Daly et al., 2003	
Turbinaria radicalis	Yes	NT	N/A	454	634	634		Cairns, 2001; Daly et al., 2003	
Turbinaria reniformis	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Turbinaria stellulata	Yes	VU	N/A	179	410	402		Cairns, 2001; Daly et al., 2003	
Euphylliidae									
Catalaphyllia jardinei	Yes	VU	6	53	65	60	12S: EF596997; 16S: L76000	Daly et al., 2003	
Euphyllia ancora	Yes	VU	N/A	41	43	38	12S: JF825139; 16S: JF825139; AT6: JF825139; COI: JF825139; CYB: JF825139; ND5: JF825139		
Euphyllia cristata	Yes	VU	N/A	62	78	73			Closest to E. glabrescens (Chevalier, 1971)
Euphyllia divisa	Yes	NT	N/A	202	106	99	COI: AB441203; CYB: AB441288		

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				A	B	C			
Euphyllia glabrescens	Yes	NT	N/A	196	85	80	COI: AB441206; CYB: AB441291		
Euphyllia paraancora	Yes	VU	N/A	43	45	40			Closest to E. ancora and E. divisa (Lin et al., 2011)
Euphyllia paradivisa	Yes	VU	N/A	62	78	73			Closest to E. glabrescens (Veron, 1990)
Euphyllia paraglabrescens	Yes	VU	N/A	62	78	73			Closest to E. glabrescens (Lin et al., 2011)
Euphyllia yaeyamaensis	Yes	NT	N/A	255	141	131			Closest to E. divisa (Veron, 2000)
Nemenzophyllia turbida	Yes	VU	N/A	29	20	14			Closest to Plerogyra (Veron, 1986)
Physogyra lichtensteini	Yes	VU	8	27	18	12	12S: EF597030; COI: AB289562; CYB: AB289564	Pires and Castro, 1997	
Plerogyra cauliformis	Yes	DD	N/A	270	108	100			Plerogyra monophyly assumed; closest to P. simplex (Ditlev, 2003)
Plerogyra diabolotus	Yes	DD	N/A	270	108	100			Plerogyra monophyly assumed
Plerogyra discus	Yes	VU	N/A	28	19	13			Plerogyra monophyly assumed; closest to P. sinuosa (Veron, 2002)
Plerogyra multilobata	Yes	DD	N/A	270	108	100			Plerogyra monophyly assumed; closest to P. diabolotus (Ditlev, 2003)
Plerogyra simplex	Yes	NT	N/A	185	62	57			Plerogyra monophyly assumed
Plerogyra sinuosa	Yes	NT	N/A	185	62	57	COI: HM018663		Plerogyra sp. in GenBank; ancestral branch shared with conspecifics
Faviidae									
Australogyra zelli	Yes	VU	N/A	144	267	265			Closest to Platygyra (Veron et al., 1977)
Barabattoia amicorum	Yes	LC	N/A	689	539	539	COI: AB441193; CYB: AB441278		
Barabattoia laddi	Yes	VU	N/A	101	172	164			Clade VII-B monophyly shown (Huang et al., 2011); Barabattoia monophyly assumed
Caulastraea connata	Yes	VU	N/A	111	188	180			Closest to C. tumida (Veron, 2000)
Caulastraea curvata	Yes	VU	N/A	136	236	233			Closest to C. furcata (Wijsman-Best, 1972)
Caulastraea echinulata	Yes	VU	N/A	79	99	92	COI: FJ345414		
Caulastraea furcata	Yes	LC	N/A	745	635	635	12S: EF597035; 16S: L75997; COI: AB117274; CYB: AB117355		
Caulastraea tumida	Yes	NT	N/A	306	282	280	COI: HQ203249		
Cladocora arbuscula	Yes	LC	N/A	580	388	380	COI: AB117292; CYB: AB117377	Daly et al., 2003; Pires and Castro, 1997	
Cladocora caespitosa	Yes	DD	N/A	274	117	108	12S: EF597017; 16S: AF265612	Daly et al., 2003	
Cladocora debilis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003; Pires and Castro, 1997	
Cladocora pacifica	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Colpophyllia amaranthus	Yes	DD	N/A	368	357	352		Budd and Smith, 2005	Previously excluded (Carpenter et al., 2008a)
Colpophyllia breviserialis	Yes	DD	N/A	368	357	352		Budd and Smith, 2005	Previously excluded (Carpenter et al., 2008a)
Colpophyllia natans	Yes	LC	N/A	666	457	449	12S: DQ643833; 16S: DQ643833; AT6: DQ643833; COI: DQ643833; CYB: DQ643833	Budd and Smith, 2005	
Cyphastrea agassizi	Yes	VU	N/A	100	171	163			Cyphastrea monophyly shown (Huang et al., 2011)

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Cyphastrea chalcidicum	Yes	LC	N/A	420	137	127	COI: AB117259; CYB: AB117336		
Cyphastrea decadia	Yes	LC	N/A	687	537	537			Cyphastrea monophyly shown (Huang et al., 2011); closest to C. japonica (Moll and Best, 1984)
Cyphastrea hexasepta	Yes	VU	N/A	42	44	39			Cyphastrea monophyly shown (Huang et al., 2011); closest to C. microphthalma (Veron, 2002)
Cyphastrea japonica	Yes	LC	N/A	687	537	537			Cyphastrea monophyly shown (Huang et al., 2011)
Cyphastrea microphthalma	Yes	LC	N/A	430	152	142	COI: FJ345416		
Cyphastrea ocellina	Yes	VU	N/A	96	162	154	12S: EF596996; 16S: L76132		
Cyphastrea serailia	Yes	LC	N/A	423	142	132	COI: AB117258; CYB: AB117334		
Diploastrea heliopora	Yes	NT	ED	167	40	35	COI: AB117290; CYB: AB117375		
Diploria clivosa	Yes	LC	N/A	667	458	450	12S: EF597001; COI: AB117226; CYB: AB117304	Budd and Smith, 2005	
Diploria labyrinthiformis	Yes	LC	N/A	668	459	451	12S: EF597002; COI: AB117224; CYB: AB117302	Budd and Smith, 2005	
Diploria strigosa	Yes	LC	N/A	597	424	416	12S: EF597003; COI: AB117225; CYB: AB117303	Budd and Smith, 2005	
Echinopora ashmorensis	Yes	VU	N/A	115	203	196			Echinopora monophyly shown (Huang et al., 2011); closest to E. lamellosa (Veron, 1990)
Echinopora forskaliana	Yes	NT	N/A	413	528	528			Echinopora monophyly shown (Huang et al., 2011)
Echinopora fruticulosa	Yes	NT	N/A	413	528	528			Echinopora monophyly shown (Huang et al., 2011)
Echinopora gemmacea	Yes	LC	N/A	456	192	184	COI: AB117263; CYB: AB117342		
Echinopora grandicula	Yes	DD	N/A	484	631	631			Echinopora monophyly shown (Huang et al., 2011)
Echinopora hirsutissima	Yes	LC	N/A	787	707	707			Echinopora monophyly shown (Huang et al., 2011)
Echinopora horrida	Yes	NT	N/A	165	36	30	COI: HQ203253		
Echinopora irregularis	Yes	DD	N/A	484	631	631			Echinopora monophyly shown (Huang et al., 2011); closest to E. hirsutissima (Veron, 2002)
Echinopora lamellosa	Yes	LC	N/A	584	397	389	16S: L76003; COI: FJ345419		
Echinopora mammiformis	Yes	NT	N/A	193	77	72	COI: HQ203254		
Echinopora pacificus	Yes	NT	N/A	191	76	71	COI: AB117262; CYB: AB117341		
Echinopora robusta	Yes	VU	N/A	166	334	332			Echinopora monophyly shown (Huang et al., 2011); closest to E. forskaliana (Veron, 2002)
Echinopora taylorae	Yes	NT	N/A	413	528	528			Echinopora monophyly shown (Huang et al., 2011)
Echinopora tiranensis	Yes	DD	N/A	484	631	631			Echinopora monophyly shown (Huang et al., 2011)
Erythrastrea flabellata	Yes	NT	N/A	373	432	424			Closest to Caulastraea (Scheer and Pillai, 1983)
Favia albidus	Yes	NT	N/A	361	419	411			Clade VII-B monophyly shown (Huang et al., 2011); closest to F. matthaii (Veron, 2002)
Favia danae	Yes	LC	N/A	713	594	594	COI: EU371663		
Favia favus	Yes	LC	N/A	619	448	440	12S: AF177048; COI: AB117267; CYB: AB117346		

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Favia fragum	Yes	LC	N/A	712	589	589	12S: EF597005; 16S: U40295; COI: AB117222; CYB: AB117301	Budd and Smith, 2005	
Favia gravida	Yes	DD	N/A	421	444	436		Budd and Smith, 2005	Previously excluded (Carpenter et al., 2008a)
Favia helianthoides	Yes	NT	N/A	342	378	370			Clade VII-B monophyly shown (Huang et al., 2011); closest to F. laxa (Veron, 2000)
Favia lacuna	Yes	NT	N/A	409	520	520			Clade VII-B monophyly shown (Huang et al., 2011)
Favia laxa	Yes	NT	N/A	341	377	369	COI: EU371707		Favia cf. laxa in GenBank
Favia leptophylla	Yes	DD	N/A	441	484	478	COI: AB117229; CYB: AB117307	Budd and Smith, 2005; Pires and Castro, 1997	
Favia lizardensis	Yes	NT	N/A	359	417	409	COI: HM018633		
Favia maritima	Yes	NT	N/A	254	140	130	COI: HQ203258		Favia cf. maritima in GenBank
Favia marshae	Yes	NT	N/A	345	384	376			Clade VII-F monophyly shown (Huang et al., 2011); closest to F. rotundata (Veron, 2002)
Favia matthaii	Yes	NT	N/A	360	418	410	COI: HQ203259		
Favia maxima	Yes	NT	N/A	284	219	213	COI: HQ203260		
Favia pallida	Yes	LC	N/A	713	594	594	COI: AB117266; CYB: AB117345		
Favia rosaria	Yes	VU	N/A	151	289	288	COI: HQ203262		
Favia rotumana	Yes	LC	N/A	452	184	176	COI: FJ345427		
Favia rotundata	Yes	NT	N/A	302	269	267	COI: HQ203263		Clade VII-F monophyly shown (Huang et al., 2011)
Favia speciosa	Yes	LC	N/A	683	519	519	COI: AB441194; CYB: AB441279		
Favia stelligera	Yes	NT	N/A	310	296	295	COI: AB117264; CYB: AB117343		
Favia truncatus	Yes	LC	N/A	761	655	655	COI: HQ203266		
Favia veroni	Yes	NT	N/A	334	362	354			Clade VII-B monophyly shown (Huang et al., 2011); closest to F. maxima (Moll and Best, 1984)
Favia vietnamensis	Yes	NT	N/A	409	520	520			Clade VII-B monophyly shown (Huang et al., 2011)
Favites abdita	Yes	NT	N/A	268	160	152	COI: HQ203267	Pires and Castro, 1997	
Favites acuticollis	Yes	NT	N/A	390	469	462			Clade VII-F monophyly shown (Huang et al., 2011)
Favites bestae	Yes	NT	N/A	390	469	462			Clade VII-F monophyly shown (Huang et al., 2011)
Favites chinensis	Yes	NT	N/A	347	387	379	COI: AB117269; CYB: AB117349		
Favites complanata	Yes	NT	N/A	294	245	242	COI: EU371689		
Favites flexuosa	Yes	NT	N/A	289	239	236	COI: HQ203269		
Favites halicora	Yes	NT	N/A	290	240	237	COI: AB117268; CYB: AB117348		
Favites micropentagona	Yes	NT	N/A	277	194	186			Closest to F. pentagona (Veron, 2002)
Favites paraflexuosa	Yes	NT	N/A	226	123	113	COI: EU371694		
Favites pentagona	Yes	LC	N/A	574	373	365	COI: HQ203271		
Favites russelli	Yes	NT	N/A	223	118	109	COI: HQ203272		
Favites spinosa	Yes	VU	N/A	152	291	290			Clade VII-F monophyly shown (Huang et al., 2011)
Favites stylifera	Yes	NT	N/A	235	127	117	COI: HQ203273	Daly et al., 2003	Clade VII-G monophyly shown (Huang et al., 2011)
Favites vasta	Yes	NT	N/A	390	469	462			Clade VII-F monophyly shown (Huang et al., 2011)
Goniastrea aspera	Yes	LC	N/A	709	580	580	COI: AB117271; CYB: AB117351		
Goniastrea australensis	Yes	LC	N/A	500	261	259	COI: HQ203274		
Goniastrea columella	Yes	NT	N/A	349	390	382			Closest to G. pectinata (Veron, 2000)

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				A	B	C			
Goniastrea deformis	Yes	VU	N/A	11	3	2	COI: AB441195; CYB: AB441280		
Goniastrea edwardsi	Yes	LC	N/A	722	605	605	COI: EU371697		
Goniastrea favulus	Yes	NT	N/A	348	389	381	COI: EU371698		
Goniastrea minuta	Yes	NT	N/A	311	297	296			Closest to G. retiformis (Veron, 2002)
Goniastrea palauensis	Yes	NT	N/A	240	135	124	COI: EU371699		Clade VII-B monophyly shown (Huang et al., 2011)
Goniastrea pectinata	Yes	LC	N/A	721	604	604	COI: AB117270; CYB: AB117350		
Goniastrea peresi	Yes	NT	N/A	371	430	422			Closest to G. aspera (Veron, 2000)
Goniastrea ramosa	Yes	VU	N/A	91	146	136			Closest to G. retiformis (Veron, 2002)
Goniastrea retiformis	Yes	LC	N/A	673	476	470	12S: EF597033; COI: HQ203275		
Goniastrea thecata	Yes	NT	N/A	371	430	422			Closest to G. aspera (Veron, 2002)
Leptastrea aequalis	Yes	VU	N/A	71	84	79			Leptastrea + Fungiidae monophyly shown (Kitahara et al., 2010)
Leptastrea bewickensis	Yes	NT	N/A	281	213	207			Leptastrea + Fungiidae monophyly shown (Kitahara et al., 2010)
Leptastrea bottae	Yes	NT	N/A	281	213	207			Leptastrea + Fungiidae monophyly shown (Kitahara et al., 2010)
Leptastrea inaequalis	Yes	NT	N/A	281	213	207			Leptastrea + Fungiidae monophyly shown (Kitahara et al., 2010)
Leptastrea pruinosa	Yes	LC	N/A	502	263	261	COI: AB441196; CYB: AB441281		
Leptastrea purpurea	Yes	LC	N/A	532	301	300	COI: EU371702		
Leptastrea transversa	Yes	LC	N/A	531	300	299	COI: HM018655		
Leptoria irregularis	Yes	VU	N/A	89	144	134	COI: AB117272; CYB: AB117353		
Leptoria phrygia	Yes	NT	N/A	279	205	199	16S: L76011; COI: AB117273; CYB: AB117354		
Manicina areolata	Yes	LC	ED	665	456	448	12S: EF597012; COI: AB117227; CYB: AB117305	Budd and Smith, 2005	
Montastraea annularis	Yes	EN	N/A	2	7	21	12S: AP008973; 16S: AP008973; AT6: AP008973; COI: AP008973; CYB: AP008973		
Montastraea annuligera	Yes	NT	N/A	340	376	368	COI: JN248781		Clade VII-B monophyly shown (Huang et al., 2011)
Montastraea cavernosa	Yes	LC	ED	395	104	97	12S: EF597006; COI: AB117288; CYB: AB117373	Pires and Castro, 1997	
Montastraea colemani	Yes	NT	N/A	288	238	235	COI: HQ203284		Clade VII-F monophyly shown (Huang et al., 2011)
Montastraea curta	Yes	LC	N/A	538	312	310	COI: AB117278; CYB: AB117359		
Montastraea faveolata	Yes	EN	N/A	2	7	21	12S: AP008977; 16S: AP008977; AT6: AP008977; COI: AP008977; CYB: AP008977		
Montastraea franksi	Yes	VU	N/A	36	34	28	12S: AP008976; 16S: AP008976; AT6: AP008976; COI: AP008976; CYB: AP008976		
Montastraea magnistellata	Yes	NT	N/A	326	333	331	COI: AB117279; CYB: AB117360		Clade VII-F monophyly shown (Huang et al., 2011)

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Montastraea multipunctata	Yes	VU	N/A	38	37	32	COI: HQ203289		
Montastraea salebrosa	Yes	VU	N/A	92	149	139	COI: HQ203290		
Montastraea serageldini	Yes	VU	N/A	49	59	54			Closest to M. curta (Veron, 2002)
Montastraea valenciennesi	Yes	NT	N/A	307	283	281	12S: AF333061; COI: AB117280; CYB: AB117361		Clade VII-F monophyly shown (Huang et al., 2011)
Moseleya latistellata	Yes	VU	12	30	24	17	COI: HQ203293		
Oulastrea crispata	Yes	LC	ED	224	2	1	12S: AF333062; COI: AB441197; CYB: AB441282		
Oulophyllia bennettae	Yes	NT	N/A	350	391	383	COI: AB117277; CYB: AB117358		
Oulophyllia crispa	Yes	NT	N/A	351	392	384	COI: AB117276; CYB: AB117357		
Oulophyllia levis	Yes	LC	N/A	725	609	609			Closest to O. crispa (Veron, 2000)
Parasimplastrea sheppardi	Yes	EN	5	10	42	125			Closest to Leptastrea (Veron, 2002)
Platygyra acuta	Yes	NT	N/A	319	316	314	COI: JN248782	Daly et al., 2003	
Platygyra carnosus	Yes	NT	N/A	375	437	429		Daly et al., 2003	
Platygyra contorta	Yes	LC	N/A	681	509	506	COI: JN248783	Daly et al., 2003	
Platygyra crosslandi	Yes	NT	N/A	375	437	429		Daly et al., 2003	
Platygyra daedalea	Yes	LC	N/A	527	295	294	COI: AB117281; CYB: AB117362	Daly et al., 2003; Pires and Castro, 1997	
Platygyra lamellina	Yes	NT	N/A	317	314	312	COI: HQ203302; CYB: AB117363	Daly et al., 2003	
Platygyra pini	Yes	LC	N/A	513	281	279	COI: HQ203303	Daly et al., 2003	
Platygyra ryukyuensis	Yes	NT	N/A	319	316	314	COI: HQ203304	Daly et al., 2003	
Platygyra sinensis	Yes	LC	N/A	755	649	649	12S: AF177047; COI: HQ203305	Daly et al., 2003	
Platygyra verweyi	Yes	NT	N/A	317	314	312	COI: EU371722	Daly et al., 2003	Platygyra cf. verweyi in GenBank
Platygyra yaeyamaensis	Yes	VU	N/A	143	266	264		Daly et al., 2003	
Plesiastrea devantieri	Yes	NT	ED	404	512	509	COI: FR837987		
Plesiastrea versipora	Yes	LC	ED	418	129	119	COI: AB289561; CYB: AB289566		
Solenastrea bournoni	Yes	LC	N/A	487	254	252	COI: AB117291; CYB: AB117376		
Solenastrea hyades	Yes	LC	N/A	429	150	140	COI: FJ966870		
Flabellidae									
Flabellum alabastrum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum angulare	No	N/A	N/A	N/A	N/A	N/A	16S: AF550363	Daly et al., 2003	
Flabellum angustum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum aotearoa	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum apertum	No	N/A	N/A	N/A	N/A	N/A	COI: HM018635	Daly et al., 2003	
Flabellum arcuatile	No	N/A	N/A	N/A	N/A	N/A	COI: HM018636	Daly et al., 2003	
Flabellum areum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum atlanticum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum australe	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum campanulatum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum chunii	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum conuis	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum curvatum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum daphnense	No	DD	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum deludens	No	N/A	N/A	N/A	N/A	N/A	16S: AB510170; COI: HM018638	Daly et al., 2003	
Flabellum flexuosum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum floridanum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum folkesoni	No	N/A	N/A	N/A	N/A	N/A	COI: HM018639	Daly et al., 2003	
Flabellum gardineri	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum hoffmeisteri	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum impensum	No	N/A	N/A	N/A	N/A	N/A	16S: AF265582	Daly et al., 2003	
Flabellum japonicum	No	N/A	N/A	N/A	N/A	N/A	16S: AB510178	Daly et al., 2003	
Flabellum knoxi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum lamellulosum	No	N/A	N/A	N/A	N/A	N/A	COI: HM018640	Daly et al., 2003	
Flabellum lowekeyesi	No	N/A	N/A	N/A	N/A	N/A	COI: HM018641	Daly et al., 2003	
Flabellum macandrewi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Flabellum magnificum	No	N/A	N/A	N/A	N/A	N/A	16S: AB510167; COI: HM018637	Daly et al., 2003	Flabellum cf. magnificum in GenBank
Flabellum marcus	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum marenzelleri	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum messum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum moseleyi	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum ongulense	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum patens	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum pavoninum	No	N/A	N/A	N/A	N/A	N/A	16S: AB510168	Daly et al., 2003	
Flabellum politum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum sexcostatum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum sibogae	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum thouarsii	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum transversale	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Flabellum tuthilli	No	N/A	N/A	N/A	N/A	N/A	COI: HM018643	Daly et al., 2003	
Flabellum vaughani	No	N/A	N/A	N/A	N/A	N/A	COI: HM018644	Daly et al., 2003	
Javania exserta	No	N/A	N/A	N/A	N/A	N/A	COI: HM018651		
Javania fusca	No	N/A	N/A	N/A	N/A	N/A	COI: HM018652		
Javania insignis	No	N/A	N/A	N/A	N/A	N/A	16S: AB510174		
Javania lamprotichum	No	N/A	N/A	N/A	N/A	N/A	COI: HM018653		
Monomyces pygmaea	No	N/A	N/A	N/A	N/A	N/A	16S: AF265583	Daly et al., 2003	
Monomyces rubrum	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Placotrochides scaphula	No	N/A	N/A	N/A	N/A	N/A	COI: HM018661		
Placotrochus laevis	No	N/A	N/A	N/A	N/A	N/A	16S: AF265589	Daly et al., 2003	
Rhizotrochus typus	No	N/A	N/A	N/A	N/A	N/A	16S: AB510175		
Truncatoflabellum australiensis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018670		
Truncatoflabellum candeanum	No	N/A	N/A	N/A	N/A	N/A	COI: HM018671		
Truncatoflabellum macroeschara	No	N/A	N/A	N/A	N/A	N/A	COI: HM018672		
Truncatoflabellum spheniscus	No	N/A	N/A	N/A	N/A	N/A	16S: AB510172		
Fungiacyathidae									
Fungiacyathus fragilis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018645		
Fungiacyathus marenzelleri	No	N/A	N/A	N/A	N/A	N/A	12S: EF597074; 16S: L76004		
Fungiacyathus pusillus	No	N/A	N/A	N/A	N/A	N/A	COI: HM018646		
Fungiacyathus stephanus	No	N/A	N/A	N/A	N/A	N/A	12S: JF825138; 16S: JF825138; AT6: JF825138; COI: JF825138; CYB: JF825138; ND5: JF825138		
Fungiacyathus turbinolioides	No	N/A	N/A	N/A	N/A	N/A	COI: HM018648		
Fungiidae									
Cantharellus doederleini	Yes	LC	N/A	748	642	642		Hoeksema, 1989	
Cantharellus jebbi	Yes	LC	N/A	748	642	642			Cantharellus monophyly assumed
Cantharellus noumeae	Yes	EN	N/A	22	114	218		Hoeksema, 1989	
Ctenactis albitentaculata	Yes	NT	N/A	269	161	153	COI: EU149869	Hoeksema, 1989	
Ctenactis crassa	Yes	LC	N/A	548	328	326	COI: EU149859	Hoeksema, 1989	
Ctenactis echinata	Yes	LC	N/A	546	326	324	COI: EU149879	Hoeksema, 1989	
Cycloseris costulata	Yes	LC	N/A	510	276	274	COI: EU149870	Hoeksema, 1989; Pires and Castro, 1997	Revised from Fungia costulata and C. marginata
Cycloseris curvata	Yes	VU	N/A	141	257	255		Hoeksema, 1989	Revised from Fungia curvata
Cycloseris cyclolites	Yes	LC	N/A	506	271	269	COI: EU202719	Hoeksema, 1989	Revised from Fungia cyclolites
Cycloseris distorta	Yes	LC	N/A	748	642	642		Hoeksema, 1989	Revised from Fungia distorta
Cycloseris fragilis	Yes	LC	N/A	507	272	270	16S: L75998; COI: EU149860	Hoeksema, 1989	Revised from Fungia fragilis
Cycloseris hexagonalis	Yes	LC	N/A	748	642	642		Hoeksema, 1989	Revised from Fungia hexagonalis
Cycloseris mokai	Yes	LC	N/A	504	268	266	COI: EU149877	Hoeksema, 1989; Pires and Castro, 1997	Revised from Lithophyllon mokai

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Cycloseris sinensis	Yes	LC	N/A	505	270	268	COI: EU149900	Hoeksema, 1989; Pires and Castro, 1997	Revised from Fungia sinensis
Cycloseris somervillei	Yes	LC	N/A	748	642	642		Hoeksema, 1989	Revised from Fungia somervillei
Cycloseris tenuis	Yes	LC	N/A	511	277	275	COI: EU149871	Hoeksema, 1989	Revised from Fungia tenuis
Cycloseris vaughani	Yes	LC	N/A	508	273	271	16S: L75999; COI: EU149861	Hoeksema, 1989	Revised from Fungia vaughani
Danafungia horrida	Yes	LC	N/A	693	556	556		Hoeksema, 1989	Revised from Fungia horrida
Danafungia scruposa	Yes	LC	N/A	398	111	103	COI: EU149872	Hoeksema, 1989	Revised from Fungia scruposa
Fungia fungites	Yes	NT	N/A	140	23	16	COI: EU149892	Daly et al., 2003; Hoeksema, 1989; Pires and Castro, 1997	
Halomitra clavator	Yes	VU	N/A	21	12	8	COI: EU149904	Hoeksema, 1989	
Halomitra pileus	Yes	LC	N/A	379	82	77	COI: EU149865	Hoeksema, 1989; Pires and Castro, 1997	
Heliofungia actiniformis	Yes	VU	3	16	9	5	12S: EF596995; COI: EU149885	Hoeksema, 1989	
Heliofungia fralinae	Yes	LC	N/A	394	103	96	COI: EU149901	Hoeksema, 1989	Revised from Fungia fralinae
Herpolitha limax	Yes	LC	N/A	460	195	187	COI: AB441223; CYB: AB441308	Hoeksema, 1989; Pires and Castro, 1997	
Lithophyllon concinna	Yes	LC	N/A	427	147	137	COI: EU149893	Hoeksema, 1989; Pires and Castro, 1997	Revised from Fungia concinna
Lithophyllon puishani	Yes	DD	N/A	301	190	182			Revised from Fungia puishani; closest to L. scabra (Veron, 2002)
Lithophyllon ranjithi	Yes	EN	N/A	7	17	41			Lithophyllon monophyly shown (Gittenberger et al., 2011)
Lithophyllon repanda	Yes	LC	N/A	428	148	138	COI: EU149883	Hoeksema, 1989; Pires and Castro, 1997	Revised from Fungia repanda
Lithophyllon scabra	Yes	LC	N/A	455	187	179	COI: EU149874	Hoeksema, 1989	Revised from Fungia scabra
Lithophyllon spinifer	Yes	LC	N/A	419	130	120	COI: EU149864	Hoeksema, 1989	Revised from Fungia spinifer
Lithophyllon undulatum	Yes	NT	N/A	172	48	44	COI: EU149867	Hoeksema, 1989	
Lobactis scutaria	Yes	LC	N/A	298	22	15	12S: DQ320497; 16S: L76005; COI: AB441224; CYB: AB441309	Hoeksema, 1989	Revised from Fungia scutaria
Pleuractis granulosa	Yes	LC	N/A	472	212	206	COI: EU149884	Hoeksema, 1989; 1993	Revised from Fungia granulosa
Pleuractis gravis	Yes	DD	N/A	305	199	192	COI: EU149910	Hoeksema, 1989; 1993	Previously excluded (Carpenter et al., 2008a); revised from Fungia gravis
Pleuractis moluccensis	Yes	LC	N/A	501	262	260	COI: EU149909	Hoeksema, 1989; 1993	Revised from Fungia moluccensis
Pleuractis paumotensis	Yes	LC	N/A	620	450	442	COI: EU149911	Hoeksema, 1989; 1993	Revised from Fungia paumotensis
Pleuractis seychellensis	Yes	VU	N/A	84	126	116		Hoeksema, 1993	Revised from Fungia seychellensis
Pleuractis taiwanensis	Yes	VU	N/A	56	68	63		Hoeksema, 1993	Revised from Fungia taiwanensis
Podabacia crustacea	Yes	LC	N/A	583	396	388	COI: EU149878	Hoeksema, 1989	
Podabacia kunzmanni	Yes	DD	N/A	366	346	344	COI: EU149908		New species (Hoeksema, 2009)
Podabacia motuporensis	Yes	NT	N/A	238	132	121	COI: EU149868		
Podabacia sinai	Yes	DD	N/A	366	346	344	COI: EU149888		
Polyphyllia novaehiberniae	Yes	NT	N/A	312	303	302		Hoeksema, 1989	
Polyphyllia talpina	Yes	LC	N/A	675	478	472	COI: EU149915	Hoeksema, 1989; Pires and Castro, 1997	
Sandalolitha dentata	Yes	LC	N/A	581	394	386	COI: EU149914	Hoeksema, 1989	
Sandalolitha robusta	Yes	LC	N/A	582	395	387	COI: EU149917	Hoeksema, 1989	
Zoopilus echinatus	Yes	LC	N/A	621	451	443	12S: EF596990; 16S: L76024; COI: EU149916	Daly et al., 2003; Hoeksema, 1989; Pires and Castro, 1997	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Gardineriidae									
Gardineria hawaiiensis	No	N/A	N/A	N/A	N/A	N/A	12S: GQ868660; 16S: GQ868701; COI: GQ868678		
Gardineria paradoxa	No	N/A	N/A	N/A	N/A	N/A	12S: GQ868656; 16S: GQ868700; COI: GQ868681		
Guyniidae									
Guynia annulata	No	N/A	N/A	N/A	N/A	N/A	16S: AF265580		
Meandrinidae									
Ctenella chagius	Yes	EN	9	1	1	10	COI: AB441208; CYB: AB441293		
Dendrogyra cylindrus	Yes	VU	2	50	60	55	12S: EF597024; COI: AB117299; CYB: AB117384		
Dichocoenia stellaris	Yes	DD	N/A	346	304	303		Daly et al., 2003	
Dichocoenia stokesi	Yes	VU	7	60	73	68	12S: EF597020; 16S: AF265607; COI: AB117298; CYB: AB117383	Daly et al., 2003	
Eusmilia fastigiata	Yes	LC	N/A	550	331	329	COI: AB117294; CYB: AB117380		
Gyrosmilia interrupta	Yes	LC	N/A	571	370	362			Closest to Ctenella chagius (Veron, 2000)
Meandrina braziliensis	Yes	DD	N/A	296	173	165	COI: AB117297; CYB: AB117382	Pires and Castro, 1997	
Meandrina danae	Yes	LC	N/A	576	380	372			Closest to M. braziliensis (Vaughan, 1901)
Meandrina meandrites	Yes	LC	N/A	499	260	258	12S: EF597032; COI: AB117296; CYB: AB117381		
Montigyra kenti	Yes	DD	N/A	329	258	256			Closest to Gyrosmilia (Veron, 1986)
Merulinidae									
Boninastrea boninensis	Yes	DD	N/A	426	453	445			Closest to Merulina (Veron, 1986)
Hydnophora bonsai	Yes	EN	N/A	23	121	232		Daly et al., 2003	
Hydnophora exesa	Yes	NT	N/A	303	275	273	12S: AF333059; COI: AB117285; CYB: AB117370	Daly et al., 2003	
Hydnophora grandis	Yes	LC	N/A	480	248	245	COI: AB117286; CYB: AB117371	Daly et al., 2003	
Hydnophora microconos	Yes	NT	N/A	199	100	93	COI: HQ203277	Daly et al., 2003	
Hydnophora pilosa	Yes	LC	N/A	481	249	246	COI: HQ203278	Daly et al., 2003	
Hydnophora rigida	Yes	LC	N/A	729	615	615	12S: EF597000; 16S: L76009	Daly et al., 2003	
Merulina ampliata	Yes	LC	N/A	680	490	484	12S: AF333058; COI: AB117283; CYB: AB117368		
Merulina scabricula	Yes	LC	N/A	710	581	581	16S: L76014; COI: AB117284; CYB: AB117369		
Merulina scheeri	Yes	LC	N/A	690	540	540			Merulina monophyly shown (Huang et al., 2011); closest to M. ampliata (Head, 1983)
Paraclavarina triangularis	Yes	NT	N/A	339	375	367			Closest to Merulina (Veron and Pichon, 1980)
Scapophyllia cylindrica	Yes	LC	N/A	694	557	557	COI: AB441198; CYB: AB441283		
Micrabaciidae									
Leptopenus antarcticus	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	
Letepsammia formosissima	No	N/A	N/A	N/A	N/A	N/A	12S: GQ868663; 16S: GQ868697; COI: GQ868685		

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Rhombopsammia niphada	No	N/A	N/A	N/A	N/A	N/A	12S: GQ868661; 16S: GQ868693; COI: GQ868683		
Stephanophyllia complicata	No	N/A	N/A	N/A	N/A	N/A	16S: GQ868689		
Mussidae									
Acanthastrea bowerbanki	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea brevis	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea echinata	Yes	LC	N/A	691	554	554	COI: AB117249; CYB: AB117327	Budd and Smith, 2005; Pandolfi, 1992	
Acanthastrea faviaformis	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea hemprichii	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea hillae	Yes	NT	ED	171	47	43	COI: AB441199; CYB: AB441284		
Acanthastrea ishigakiensis	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea lordhowensis	Yes	NT	N/A	355	405	397		Pandolfi, 1992	
Acanthastrea maxima	Yes	NT	N/A	355	405	397		Pandolfi, 1992	
Acanthastrea regularis	Yes	VU	N/A	130	230	226		Pandolfi, 1992	
Acanthastrea rotundoflora	Yes	NT	N/A	327	336	334	COI: AB117251; CYB: AB117328	Budd and Smith, 2005; Pandolfi, 1992	
Acanthastrea subechinata	Yes	NT	N/A	355	405	397		Pandolfi, 1992	
Australomussa rowleyensis	Yes	NT	N/A	365	421	413		Pandolfi, 1992	
Blastomussa merleti	Yes	LC	ED	412	128	118		Pandolfi, 1992	
Blastomussa wellsi	Yes	NT	ED	86	5	3	COI: AB289563; CYB: AB289565	Pandolfi, 1992	
Cynarina lacrymalis	Yes	NT	N/A	168	41	36	12S: EF597034; COI: AB117246; CYB: AB117323	Pandolfi, 1992	
Indophyllia macassarensis	Yes	DD	N/A	314	241	238			Closest to Cynarina lacrymalis (Best and Hoeksema, 1987)
Isophyllastrea rigida	Yes	LC	N/A	698	561	561		Budd and Smith, 2005; Pandolfi, 1992	
Isophyllia sinuosa	Yes	LC	N/A	672	475	469	COI: AB117238; CYB: AB117315	Budd and Smith, 2005; Pandolfi, 1992	
Lobophyllia corymbosa	Yes	LC	N/A	600	426	418	COI: AB117241; CYB: AB117318	Daly et al., 2003; Pandolfi, 1992	
Lobophyllia dentatus	Yes	VU	N/A	120	216	210		Daly et al., 2003; Pandolfi, 1992	
Lobophyllia diminuta	Yes	VU	N/A	120	216	210		Daly et al., 2003; Pandolfi, 1992	
Lobophyllia flabelliformis	Yes	VU	N/A	120	216	210		Daly et al., 2003; Pandolfi, 1992	
Lobophyllia hataii	Yes	LC	N/A	723	607	607		Daly et al., 2003; Pandolfi, 1992	
Lobophyllia hemprichii	Yes	LC	N/A	577	385	377	12S: EF597013; 16S: L76013; COI: AB117240; CYB: AB117317	Daly et al., 2003; Pandolfi, 1992; Pires and Castro, 1997	
Lobophyllia pachysepta	Yes	NT	N/A	280	206	200	COI: AB117242; CYB: AB117319	Daly et al., 2003; Pandolfi, 1992	
Lobophyllia robusta	Yes	LC	N/A	723	607	607		Daly et al., 2003; Pandolfi, 1992	
Lobophyllia serratus	Yes	EN	N/A	15	86	189		Daly et al., 2003; Pandolfi, 1992	
Micromussa amakusensis	Yes	NT	ED	198	95	89	COI: AB441200; CYB: AB441285		
Micromussa diminuta	Yes	DD	N/A	295	170	162			Micromussa monophyly assumed; closest to M. minuta (Veron, 2002)
Micromussa minuta	Yes	NT	N/A	227	124	114			Micromussa monophyly assumed

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				A	B	C			
Mussa angulosa	Yes	LC	N/A	664	455	447	12S: DQ643834; 16S: DQ643834; AT6: DQ643834; COI: DQ643834; CYB: DQ643834	Budd and Smith, 2005; Pandolfi, 1992	
Mussismilia braziliensis	Yes	DD	P	443	486	480	COI: AB117231; CYB: AB117309	Budd and Smith, 2005; Pandolfi, 1992; Pires and Castro, 1997	
Mussismilia harttii	Yes	DD	N/A	444	487	481	COI: AB117232; CYB: AB117308	Budd and Smith, 2005; Pandolfi, 1992; Pires and Castro, 1997	
Mussismilia hispida	Yes	DD	N/A	442	485	479	COI: AB117233; CYB: AB117310	Budd and Smith, 2005; Pandolfi, 1992; Pires and Castro, 1997	
Mycetophyllia aliciae	Yes	LC	N/A	537	309	308	12S: EF597039; COI: AB117235; CYB: AB117312	Budd and Smith, 2005; Pandolfi, 1992	
Mycetophyllia danaana	Yes	LC	N/A	695	558	558	COI: AB117234; CYB: AB117311	Budd and Smith, 2005; Pandolfi, 1992	
Mycetophyllia ferox	Yes	VU	N/A	94	154	144		Budd and Smith, 2005; Pandolfi, 1992	
Mycetophyllia lamarckiana	Yes	LC	N/A	458	193	185	12S: EF597040	Budd and Smith, 2005; Pandolfi, 1992	
Mycetophyllia reesi	Yes	DD	N/A	358	335	333		Budd and Smith, 2005; Pandolfi, 1992	
Scolymia australis	Yes	LC	N/A	671	474	468		Pandolfi, 1992	
Scolymia cubensis	Yes	LC	N/A	696	559	559	COI: AB117236; CYB: AB117314	Budd and Smith, 2005	Atlantic Scolymia
Scolymia lacera	Yes	LC	N/A	697	560	560		Budd and Smith, 2005	Junior synonym of S. cubensis (Veron, 2000); Atlantic Scolymia
Scolymia vitiensis	Yes	NT	N/A	265	157	146	COI: AB117247; CYB: AB117324	Pandolfi, 1992	
Scolymia wellsi	Yes	DD	N/A	411	425	417		Budd and Smith, 2005; Pires and Castro, 1997	Junior synonym of S. cubensis (Fenner, 1993); Atlantic Scolymia
Symphyllia agaricia	Yes	LC	N/A	702	564	564	COI: AB117243; CYB: AB117320	Pandolfi, 1992	
Symphyllia erythraea	Yes	LC	N/A	703	565	565		Pandolfi, 1992	
Symphyllia hassi	Yes	VU	N/A	110	186	178		Pandolfi, 1992	
Symphyllia radians	Yes	LC	N/A	700	562	562	COI: AB117245; CYB: AB117322	Pandolfi, 1992	
Symphyllia recta	Yes	LC	N/A	701	563	563	COI: AB117244; CYB: AB117321	Pandolfi, 1992	
Symphyllia valenciennesii	Yes	LC	N/A	578	386	378	COI: HM018666	Pandolfi, 1992	
Symphyllia wilsoni	Yes	LC	N/A	703	565	565		Pandolfi, 1992	
Oculinidae									
Cyathelia axillaris	No	N/A	N/A	N/A	N/A	N/A	COI: HM018622		
Galaxea acrhelia	Yes	VU	N/A	78	97	91			Closest to G. horrescens (Veron, 2002)
Galaxea astreata	Yes	VU	N/A	55	67	62	12S: AF333056		
Galaxea cryptoramosa	Yes	VU	N/A	73	88	82			Closest to G. astreata (Veron, 2002)
Galaxea fascicularis	Yes	NT	N/A	304	278	276	16S: L76006; COI: AB441201; CYB: AB441286; ND5: AB109376		
Galaxea horrescens	Yes	LC	N/A	594	416	408	12S: EF597096; 16S: L75994		

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Galaxea longisepta	Yes	NT	N/A	293	242	239			Closest to G. horrescens (Veron, 2002)
Galaxea paucisepta	Yes	NT	N/A	285	220	215			Closest to G. astreata (Claereboudt, 1990)
Madrepora oculata	No	N/A	N/A	N/A	N/A	N/A	16S: AF550369; COI: HM018659		
Oculina diffusa	Yes	LC	N/A	585	408	400	COI: AB117293; CYB: AB117379	Daly et al., 2003	
Oculina patagonica	Yes	LC	N/A	764	661	661	12S: EF597025; 16S: AF265601	Daly et al., 2003; Pires and Castro, 1997	
Oculina profunda	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Oculina robusta	Yes	DD	N/A	325	253	250	COI: FJ966869	Daly et al., 2003	
Oculina tenella	Yes	DD	N/A	473	590	590		Daly et al., 2003	
Oculina valenciennesi	Yes	DD	N/A	473	590	590		Daly et al., 2003	
Oculina varicosa	Yes	VU	11	88	139	129	COI: FJ966875	Daly et al., 2003	
Oculina virgosa	No	N/A	N/A	N/A	N/A	N/A		Daly et al., 2003	
Schizoculina africana	Yes	DD	P	475	592	592			Schizoculina monophyly assumed; closest to Oculina (Wells, 1937)
Schizoculina fissipara	Yes	DD	P	475	592	592			Schizoculina monophyly assumed; closest to Oculina (Wells, 1937)
Simplastrea vesicularis	Yes	DD	P	381	374	366			Closest to Galaxea (Veron, 2000)
Pectiniidae									
Echinomorpha nishihirai	Yes	NT	N/A	337	366	358			Closest to Echinophyllia (Veron, 1990)
Echinophyllia aspera	Yes	LC	N/A	568	364	356	COI: AB117252; CYB: AB117329		
Echinophyllia costata	Yes	VU	N/A	95	155	145			Echinophyllia monophyly shown (Fukami et al., 2008); closest to E. pectinata (Veron, 2002)
Echinophyllia echinata	Yes	LC	N/A	679	483	477			Echinophyllia monophyly shown (Fukami et al., 2008)
Echinophyllia echinoporoides	Yes	LC	N/A	586	409	401	COI: AB117254; CYB: AB117331		
Echinophyllia orpheensis	Yes	LC	N/A	549	329	327	12S: AF333065; COI: AB117253; CYB: AB117330		
Echinophyllia patula	Yes	LC	N/A	608	434	426			Echinophyllia monophyly shown (Fukami et al., 2008); closest to E. aspera (Veron, 2000)
Echinophyllia pectinata	Yes	DD	N/A	388	381	373			Echinophyllia monophyly shown (Fukami et al., 2008)
Mycedium elephantotus	Yes	LC	N/A	728	612	612	12S: AF333057; COI: AB117387; CYB: AB117366		
Mycedium mancaoi	Yes	LC	N/A	753	647	647			Mycedium monophyly shown (Huang et al., 2011); closest to M. elephantotus (Veron, 2000)
Mycedium robokaki	Yes	LC	N/A	758	652	652	COI: HQ203295		
Mycedium spina	Yes	DD	N/A	457	552	552			Mycedium monophyly shown (Huang et al., 2011)
Mycedium steeni	Yes	VU	N/A	146	279	277			Mycedium monophyly shown (Huang et al., 2011); closest to M. robokaki (Veron, 2002)
Mycedium umbra	Yes	LC	N/A	753	647	647			Mycedium monophyly shown (Huang et al., 2011); closest to M. elephantotus (Veron, 2002)
Oxypora convoluta	Yes	DD	N/A	386	379	371			Oxypora monophyly assumed; closest to O. lacera (Veron, 2002)
Oxypora crassispinosa	Yes	LC	N/A	715	596	596			Oxypora monophyly assumed; closest to O. glabra (Veron, 2000)
Oxypora egyptensis	Yes	DD	N/A	425	452	444			Oxypora monophyly assumed; closest to O. glabra (Veron, 2000)
Oxypora glabra	Yes	LC	N/A	715	596	596			Oxypora monophyly assumed

Species	Reef	Red List	EoE rank	EDGE rank A	EDGE rank B	EDGE rank C	Molecular sources	Morphology sources	Remarks
Oxypora lacera	Yes	LC	N/A	539	313	311	COI: AB117255; CYB: AB117332		
Pectinia africanus	Yes	VU	N/A	150	288	287			Pectinia + Mycedium monophyly shown (Huang et al., 2011); closest to P. lactuca (Veron, 2002)
Pectinia alcicornis	Yes	VU	N/A	148	286	285	12S: EF597037; 16S: L76017; COI: AB117385; CYB: AB117364		
Pectinia ayleni	Yes	NT	N/A	382	465	457	COI: HQ203299		
Pectinia crassa	Yes	DD	N/A	465	575	575			Pectinia + Mycedium monophyly shown (Huang et al., 2011)
Pectinia elongata	Yes	NT	N/A	383	466	458			Pectinia + Mycedium monophyly shown (Huang et al., 2011)
Pectinia lactuca	Yes	VU	N/A	149	287	286	COI: HQ203300		
Pectinia maxima	Yes	EN	N/A	24	131	251			Pectinia + Mycedium monophyly shown (Huang et al., 2011); closest to P. lactuca and P. ayleni (Veron, 2000)
Pectinia paeonia	Yes	NT	N/A	308	285	284	COI: AB117386; CYB: AB117365	Pires and Castro, 1997	
Pectinia pygmaeus	Yes	NT	N/A	383	466	458			Pectinia + Mycedium monophyly shown (Huang et al., 2011); closest to P. elongata and P. teres (Veron, 2002)
Pectinia teres	Yes	NT	N/A	383	466	458			Pectinia + Mycedium monophyly shown (Huang et al., 2011); closest to P. elongata (Veron, 2000)
Pocilloporidae									
Pocillopora ankeli	Yes	VU	N/A	44	50	47		Wallace, 1999	
Pocillopora capitata	Yes	LC	N/A	558	340	338		Wallace, 1999	
Pocillopora damicornis	Yes	LC	N/A	518	290	289	12S: EF526302; 16S: EF526302; AT6: EF526302; COI: EF526302; CYB: EF526302	Wallace, 1999	
Pocillopora danae	Yes	VU	N/A	44	50	47		Wallace, 1999	
Pocillopora effusus	Yes	DD	N/A	315	246	243		Wallace, 1999	
Pocillopora elegans	Yes	VU	N/A	44	50	47		Wallace, 1999	
Pocillopora eydouxi	Yes	NT	N/A	200	102	95	12S: EF526303; 16S: EF526303; AT6: EF526303; COI: EF526303; CYB: EF526303	Wallace, 1999	
Pocillopora fungiformis	Yes	EN	N/A	6	15	37		Wallace, 1999	
Pocillopora indiania	Yes	VU	N/A	44	50	47		Wallace, 1999	
Pocillopora inflata	Yes	VU	N/A	44	50	47		Wallace, 1999	
Pocillopora kelleheri	Yes	LC	N/A	558	340	338		Wallace, 1999	
Pocillopora ligulata	Yes	LC	N/A	558	340	338		Wallace, 1999	
Pocillopora meandrina	Yes	LC	N/A	557	339	337	12S: EF596976; 16S: L76018	Wallace, 1999	
Pocillopora molokensis	Yes	DD	N/A	315	246	243		Wallace, 1999	
Pocillopora setichelli	Yes	LC	N/A	558	340	338		Wallace, 1999	
Pocillopora verrucosa	Yes	LC	N/A	424	143	133	COI: AB441230; CYB: AB441315	Wallace, 1999	
Pocillopora woodjonesi	Yes	LC	N/A	558	340	338		Wallace, 1999	
Pocillopora zelli	Yes	LC	N/A	558	340	338		Wallace, 1999	
Seriatopora aculeata	Yes	VU	N/A	33	29	23			Seriatopora monophyly shown (Fukami et al., 2008); closest to S. stellata (Veron, 2000)
Seriatopora caliendrum	Yes	NT	N/A	173	49	45	12S: EF633601; 16S: EF633601; AT6: EF633601; COI: EF633601; CYB: EF633601		

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Seriatopora dendritica	Yes	VU	N/A	31	26	19			Seriatopora monophyly shown (Fukami et al., 2008); closest to S. hystrix (Veron, 2002)
Seriatopora guttatus	Yes	LC	N/A	470	211	205			Seriatopora monophyly shown (Fukami et al., 2008); closest to S. hystrix (Veron, 2002)
Seriatopora hystrix	Yes	LC	N/A	453	185	177	12S: EF633600; 16S: EF633600; AT6: EF633600; COI: EF633600; CYB: EF633600		
Seriatopora stellata	Yes	NT	N/A	197	93	87			Seriatopora monophyly shown (Fukami et al., 2008)
Stylophora danae	Yes	LC	N/A	509	274	272			Stylophora monophyly assumed; closest to S. pistillata (Veron, 2000)
Stylophora kuehlmanni	Yes	LC	N/A	534	305	304			Stylophora monophyly assumed; closest to S. subseriata (Veron, 2000)
Stylophora madagascarensis	Yes	EN	N/A	5	14	31			Stylophora monophyly assumed; closest to S. kuehlmanni and S. subseriata (Veron, 2002)
Stylophora mamillata	Yes	LC	N/A	534	305	304			Stylophora monophyly assumed; not close to other Stylophora (Veron, 2000)
Stylophora pistillata	Yes	NT	N/A	170	46	42	12S: EU400214; 16S: EU400214; AT6: EU400214; COI: EU400214; CYB: EU400214		
Stylophora subseriata	Yes	LC	N/A	534	305	304			Stylophora monophyly assumed
Stylophora wellsi	Yes	NT	N/A	264	153	143			Stylophora monophyly assumed
Poritidae									
Alveopora allingi	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed
Alveopora catalai	Yes	NT	N/A	330	351	346			Alveopora monophyly assumed; closest to A. allingi and A. gigas (Veron, 2000)
Alveopora daedalea	Yes	VU	N/A	102	176	167	12S: EF597088; 16S: AF265592; COI: AB441245; CYB: AB441330		Alveopora sp. in GenBank; ancestral branch shared with conspecifics
Alveopora excelsa	Yes	EN	N/A	12	56	148			Alveopora monophyly assumed
Alveopora fenestrata	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed; closest to A. marionensis and A. verrilliana (Veron, 2000)
Alveopora gigas	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed; closest to A. allingi and A. catalai (Veron, 2000)
Alveopora japonica	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed; closest to A. tizardi (Veron, 2000)
Alveopora marionensis	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed; closest to A. fenestrata and A. verrilliana (Veron, 2000)
Alveopora minuta	Yes	EN	N/A	12	56	148			Alveopora monophyly assumed; closest to A. viridis (Veron, 2002)
Alveopora ocellata	Yes	DD	N/A	403	422	414			Alveopora monophyly assumed
Alveopora spongiosa	Yes	NT	N/A	330	351	346			Alveopora monophyly assumed; closest to A. daedalea (Veron, 2000)
Alveopora tizardi	Yes	LC	N/A	692	555	555			Alveopora monophyly assumed
Alveopora verrilliana	Yes	VU	N/A	102	176	167			Alveopora monophyly assumed
Alveopora viridis	Yes	NT	N/A	330	351	346			Alveopora monophyly assumed
Goniopora albiconus	Yes	VU	N/A	159	319	317		Daly et al., 2003	
Goniopora burgosi	Yes	VU	N/A	159	319	317		Daly et al., 2003	
Goniopora cellulosa	Yes	VU	N/A	159	319	317		Daly et al., 2003	
Goniopora ciliatus	Yes	LC	N/A	771	690	690		Daly et al., 2003	

Species	Reef	Red	EoE	EDGE rank			Molecular	Morphology	Remarks
		List	rank	A	B	C	sources	sources	
Goniopora columna	Yes	NT	N/A	333	354	349	12S: JF825141; 16S: JF825141; AT6: JF825141; COI: JF825141; CYB: JF825141; ND5: JF825141	Daly et al., 2003	
Goniopora djiboutiensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora eclipsensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora fruticosa	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora lobata	Yes	NT	N/A	406	515	515		Daly et al., 2003	
Goniopora minor	Yes	NT	N/A	406	515	515		Daly et al., 2003	
Goniopora norfolkensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora palmensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora pandoraensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora pearsoni	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora pendulus	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora planulata	Yes	VU	N/A	159	319	317		Daly et al., 2003	
Goniopora polyformis	Yes	VU	N/A	159	319	317		Daly et al., 2003	
Goniopora savignyi	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora somaliensis	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora stokesi	Yes	NT	N/A	405	513	513	12S: EF597060; 16S: L76008	Daly et al., 2003	
Goniopora stutchburyi	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora sultani	Yes	LC	N/A	771	690	690		Daly et al., 2003	
Goniopora tenella	Yes	NT	N/A	406	515	515		Daly et al., 2003	
Goniopora tenuidens	Yes	LC	N/A	771	690	690		Daly et al., 2003; Pires and Castro, 1997	
Machadoporites tantillus	Yes	DD	N/A	699	817	817			Closest to Goniopora and Porites (Claereboudt and Al-Amri, 2004)
Porites annae	Yes	NT	N/A	222	115	106	COI: FJ423965	Daly et al., 2003	
Porites aranetai	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites arnaudi	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites astreoides	Yes	LC	N/A	573	372	364	12S: EF597055; COI: AB441242; CYB: AB441327	Daly et al., 2003; Pires and Castro, 1997	
Porites attenuata	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites australiensis	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites baueri	Yes	DD	N/A	611	757	757		Daly et al., 2003	
Porites bernardi	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites branneri	Yes	NT	N/A	267	159	151	12S: EF597059; COI: AY451380	Daly et al., 2003	
Porites brighami	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites cocosensis	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites colonensis	Yes	DD	N/A	201	58	53	COI: FJ423972	Daly et al., 2003	
Porites columnaris	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites compressa	Yes	LC	N/A	677	481	475	12S: EF597053; 16S: L76020; COI: FJ423970	Daly et al., 2003	
Porites cumulatus	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites cylindrica	Yes	NT	N/A	435	585	585	COI: FJ423968	Daly et al., 2003	
Porites decasepta	Yes	DD	N/A	611	757	757		Daly et al., 2003	
Porites deformis	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites densa	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites desilveri	Yes	EN	N/A	65	348	485		Daly et al., 2003	
Porites divaricata	Yes	LC	N/A	607	433	425	12S: EF597058; COI: FJ423969	Daly et al., 2003	
Porites duerdeni	Yes	LC	N/A	677	481	475	COI: FJ423976	Daly et al., 2003	
Porites echinulata	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites ericacea	Yes	DD	N/A	611	757	757		Daly et al., 2003	
Porites eridani	Yes	EN	N/A	65	348	485		Daly et al., 2003	
Porites evermanni	Yes	DD	N/A	291	165	157	COI: FJ423984	Daly et al., 2003	
Porites excavata	Yes	DD	N/A	611	757	757		Daly et al., 2003	
Porites flavus	Yes	DD	N/A	611	757	757		Daly et al., 2003	
Porites furcata	Yes	LC	N/A	618	445	437	COI: FJ423988	Daly et al., 2003	
Porites harrisoni	Yes	NT	N/A	519	710	710		Daly et al., 2003	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Porites heronensis	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites horizontalata	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites latistella	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites lichen	Yes	LC	N/A	757	651	651	COI: FJ423963	Daly et al., 2003	
Porites lobata	Yes	NT	N/A	158	32	26	16S: AF550372; COI: FJ423973	Daly et al., 2003	
Porites lutea	Yes	LC	N/A	794	727	727	COI: AB441243; CYB: AB441328	Daly et al., 2003	
Porites mayeri	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites monticulosa	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites murrayensis	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites myrmidonensis	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites napopora	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites negrosensis	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites nigrescens	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites nodifera	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites okinawensis	Yes	VU	N/A	142	259	257	12S: JF825142; 16S: JF825142; AT6: JF825142; COI: JF825142; CYB: JF825142; ND5: JF825142	Daly et al., 2003	
Porites ornata	Yes	EN	N/A	65	348	485		Daly et al., 2003	
Porites panamensis	Yes	LC	N/A	572	371	363	COI: FJ423990	Daly et al., 2003	
Porites porites	Yes	LC	N/A	533	302	301	12S: DQ643837; 16S: DQ643837; AT6: DQ643837; COI: DQ643837; CYB: DQ643837; ND5: DQ643837	Daly et al., 2003	
Porites profundus	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites pukoensis	Yes	CR	N/A	40	174	466		Daly et al., 2003	
Porites randalli	Yes	DD	N/A	364	337	335	COI: FJ423966	Daly et al., 2003	New species (Forsman and Birkeland, 2009)
Porites rugosa	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites rus	Yes	LC	N/A	616	441	433	COI: FJ423979	Daly et al., 2003	
Porites sillimaniana	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites solida	Yes	LC	N/A	795	728	728	COI: FJ423962	Daly et al., 2003	
Porites somaliensis	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites stephensoni	Yes	NT	N/A	519	710	710		Daly et al., 2003	
Porites studeri	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Porites sverdrupi	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites tuberculosa	Yes	VU	N/A	241	541	541		Daly et al., 2003	
Porites vaughani	Yes	LC	N/A	820	818	818		Daly et al., 2003	
Poritipora paliformis	Yes	VU	N/A	299	681	681			Poritidae monophyly assumed (excluding Alveopora)
Stylaraea punctata	Yes	DD	P	676	805	805			Closest to Porites (Veron, 1986)
Rhizangiidae									
Astrangia poculata	Yes	LC	N/A	720	602	602	12S: DQ643832; AT6: DQ643832; COI: DQ643832; CYB: DQ643832		Astrangia sp. in GenBank; terminal branch shared with conspecifics
Astrangia rathbuni	No	N/A	N/A	N/A	N/A	N/A		Pires and Castro, 1997	
Siderastreidae									
Anomastraea irregularis	Yes	VU	1	19	11	7	COI: AM494870	Pandolfi, 1992	
Coscinaraea columna	Yes	LC	N/A	530	298	297	COI: AB441210; CYB: AB441295	Pandolfi, 1992	
Coscinaraea crassa	Yes	NT	N/A	336	365	357		Pandolfi, 1992	
Coscinaraea exesa	Yes	LC	N/A	705	576	576		Pandolfi, 1992	
Coscinaraea hahazimaensis	Yes	VU	N/A	112	189	181		Pandolfi, 1992	
Coscinaraea marshae	Yes	LC	N/A	705	576	576		Pandolfi, 1992	
Coscinaraea mcneilli	Yes	LC	N/A	705	576	576		Pandolfi, 1992	
Coscinaraea monile	Yes	LC	N/A	705	576	576		Pandolfi, 1992	
Coscinaraea wellsi	Yes	LC	N/A	565	355	350	COI: AM494861		Fungiidae clade (Benzoni et al., 2007)

Species	**Reef**	**Red List**	**EoE rank**	**EDGE rank**			**Molecular sources**	**Morphology sources**	**Remarks**
				A	**B**	**C**			
Craterestrea levis	Yes	LC	N/A	718	600	600			Closest to Coscinaraea (Head, 1983)
Horastrea indica	Yes	VU	4	14	6	4	COI: AM494864	Pandolfi, 1992	
Psammocora albopicta	Yes	DD	N/A	287	163	155	COI: FM865871	Pandolfi, 1992	
Psammocora contigua	Yes	NT	N/A	145	25	18	16S: AF550371; COI: AB441209; CYB: AB441294	Pandolfi, 1992	
Psammocora decussata	Yes	DD	N/A	431	460	452		Pandolfi, 1992	Psammocora monophyly shown (Benzoni et al., 2010)
Psammocora digitata	Yes	NT	N/A	203	112	104	COI: AM494855	Pandolfi, 1992	
Psammocora explanulata	Yes	LC	N/A	565	355	350	COI: AM494845		Fungiidae clade (Benzoni et al., 2007)
Psammocora haimeana	Yes	LC	N/A	488	255	253	COI: FM865874	Pandolfi, 1992	
Psammocora interstinctus	Yes	DD	N/A	431	460	452		Pandolfi, 1992	Psammocora monophyly shown (Benzoni et al., 2010)
Psammocora nierstraszi	Yes	LC	N/A	399	119	110	COI: AM494851	Pandolfi, 1992	
Psammocora obtusangula	Yes	NT	N/A	343	382	374		Pandolfi, 1992	
Psammocora profundacella	Yes	LC	N/A	400	120	111	COI: AM494853	Pandolfi, 1992	
Psammocora ramosa	Yes	DD	N/A	431	460	452		Pandolfi, 1992	Psammocora monophyly shown (Benzoni et al., 2010)
Psammocora stellata	Yes	VU	N/A	116	204	197		Pandolfi, 1992	Psammocora monophyly shown (Benzoni et al., 2010)
Psammocora superficialis	Yes	LC	N/A	717	598	598		Pandolfi, 1992	
Psammocora vaughani	Yes	NT	N/A	343	382	374		Pandolfi, 1992	
Psammocora verrilli	Yes	DD	N/A	431	460	452		Pandolfi, 1992	Psammocora monophyly shown (Benzoni et al., 2010)
Pseudosiderastrea tayami	Yes	NT	ED	174	55	52	COI: AM494866	Pandolfi, 1992	
Siderastrea glynni	Yes	CR	N/A	4	4	46		Pandolfi, 1992	Siderastrea monophyly shown (Kitahara et al., 2010)
Siderastrea radians	Yes	LC	N/A	374	75	70	12S: DQ643838; 16S: DQ643838; AT6: DQ643838; COI: DQ643838; CYB: DQ643838; ND5: DQ643838	Pandolfi, 1992	
Siderastrea savignyana	Yes	LC	N/A	362	64	59	COI: AB441215; CYB: AB441300	Pandolfi, 1992	
Siderastrea siderea	Yes	LC	N/A	387	91	85	12S: EF597067; COI: AB441211; CYB: AB441296	Pandolfi, 1992	
Siderastrea stellata	Yes	DD	N/A	187	38	33	COI: AB441213; CYB: AB441298	Pandolfi, 1992; Pires and Castro, 1997	
Stenocyathidae									
Stenocyathus vermiformis	No	N/A	N/A	N/A	N/A	N/A	COI: HM018619		
Trachyphylliidae									
Trachyphyllia geoffroyi	Yes	NT	ED	225	122	112	COI: AB117287; CYB: AB117372		Clade VII-B monophyly shown (Huang et al., 2011)
Turbinoliidae									
Alatotrochus rubescens	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Australocyathus vincentinus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Conocyathus formosus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Conocyathus gracilis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Conocyathus zelandiae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cryptotrochus brevipalus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cryptotrochus carolinensis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cryptotrochus javanus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cyathotrochus herdmani	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cyathotrochus nascornatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Cyathotrochus pileus	No	N/A	N/A	N/A	N/A	N/A	12S: EF597069; COI: HM018623	Cairns, 1997	
Deltocyathoides orientalis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Deltocyathoides stimpsonii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Dunocyathus parasiticus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Dunocyathus wallaceae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	

Species	Reef	Red List	EoE rank	EDGE rank			Molecular sources	Morphology sources	Remarks
				A	B	C			
Endocyathopora laticostata	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Foveolocyathus alternans	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Foveolocyathus kitsoni	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Foveolocyathus parkeri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Foveolocyathus verconis	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Holcotrochus crenulatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Holcotrochus scriptus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Idiotrochus alatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Idiotrochus emarciatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Idiotrochus kikutii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Kionotrochus suteri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Notocyathus conicus	No	N/A	N/A	N/A	N/A	N/A	12S: EF597061; 16S: AF265584	Cairns, 1997	Notocyathus sp. in GenBank; ancestral branch shared with conspecifics
Notocyathus venustus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Peponocyathus dawsoni	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Peponocyathus folliculus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Peponocyathus minimus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Platytrochus compressus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Platytrochus hastatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Platytrochus laevigatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Platytrochus parisepta	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Pleotrochus venustus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Pleotrochus zibrowii	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Pseudocyathoceras avis	No	DD	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus andrewianus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus aurantiacus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus auritus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus cuneolus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus evexicostatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus excavatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus gardineri	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus gilchristi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus hancocki	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus imbricaticostatus	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus lindstroemi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus ralphae	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Sphenotrochus squiresi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Thrypticotrochus petterdi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Trematotrochus corbicula	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Trematotrochus hedleyi	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Tropidocyathus labidus	No	N/A	N/A	N/A	N/A	N/A	12S: EF597062; 16S: AF265585	Cairns, 1997	
Tropidocyathus lessoni	No	N/A	N/A	N/A	N/A	N/A	COI: HM018669	Cairns, 1997	
Turbinolia stephensoni	No	N/A	N/A	N/A	N/A	N/A		Cairns, 1997	
Outgroups									
Discosoma	N/A	N/A	N/A	N/A	N/A	N/A	12S: DQ643965; 16S: DQ643965; AT6: DQ643965; COI: DQ643965; CYB: DQ643965; ND5: DQ643965	Pires and Castro, 1997	
Ricordea florida	N/A	N/A	N/A	N/A	N/A	N/A	12S: DQ640648; 16S: DQ640648; AT6: DQ640648; COI: DQ640648; CYB: DQ640648; ND5: DQ640648	Pires and Castro, 1997	

REFERENCES

Agapow, P.M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C. and Purvis, A. (2004) The impact of species concept on biodiversity studies. *Quarterly Review of Biology*, **79**, 161–179.

Agnarsson, I., Kuntner, M. and May-Collado, L.J. (2010) Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora. *Molecular Phylogenetics and Evolution*, **54**, 726–745.

Alloiteau, J. (1941) Révision de la collection H. Michelin. Polypiers d'anthozoaires fossiles. I. Crétacé. *Mémoires du Muséum National d'Histoire Naturelle*, **16**, 1–98.

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L. and Williamson, D.H. (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, **28**, 339–351.

Altschul, S.F. and Lipman, D.L. (1990) Equal animals. *Nature*, **348**, 493–494.

Alvarez, I. and Wendel, J.F. (2003) Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution*, **29**, 417–434.

Arponen, A. (2012) Prioritizing species for conservation planning. *Biodiversity and Conservation*, **21**, 875–893.

Arrigoni, R., Stefani, F., Pichon, M., Galli, P. and 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.

Baird, A.H., Guest, J.R. and Willis, B.L. (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 551–571.

Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, C.S. and Donoghue, M.J. (1995) The ITS region of nuclear ribosomal DNA: A valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden*, **82**, 247–277.

Barber, P.H., Erdmann, M.V. and Palumbi, S.R. (2006) Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. *Evolution*, **60**, 1825–1839.

Baum, B.R. (1992) Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon*, **41**, 3–10.

Beagley, C.T., Okada, N.A. and Wolstenholme, D.R. (1996) Two mitochondrial group I introns in a metazoan, the sea anemone *Metridium senile*: one intron contains genes for subunits 1 and 3 of NADH dehydrogenase. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 5619–5623.

Beger, M., Jones, G.P. and Munday, P.L. (2003) Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biological Conservation*, **111**, 53–62.

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

Bellwood, D.R., Hughes, T.P., Folke, C. and Nyström, M. (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.

Benzoni, F., Stefani, F., Stolarski, J., Pichon, M., Mitta, G. and Galli, P. (2007) Debating phylogenetic relationships of the scleractinian *Psammocora*: molecular and morphological evidences. *Contributions to Zoology*, **76**, 35–54.

Benzoni, F., Stefani, F., Pichon, M. and Galli, P. (2010) The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). *Zoological Journal of the Linnean Society*, **160**, 421–456.

Benzoni, F., Arrigoni, R., Stefani, F., Reijnen, B.T., Montano, S. & Hoeksema, B.W. (2012) Phylogenetic position and taxonomy of Cycloseris explanulata and C. wellsi (Scleractinia: Fungiidae): lost mushroom corals find their way home. *Contributions to Zoology*, **81**, 125–146.

Best, M.B. and Hoeksema, B.W. (1987) New observations on scleractinian corals from Indonesia: 1. Free-living species belonging to the Faviina. *Zoologische Mededelingen Leiden*, **61**, 387–403.

Best, M.B., Boekschoten, G.J. and Oosterbaan, A. (1984) Species concept and ecomorph variation in living and fossil Scleractinia. *Palaeontographica Americana*, **54**, 70–79.

Bininda-Emonds, O.R.P. (2004) The evolution of supertrees. *Trends in Ecology and Evolution*, **19**, 315–322.

Bininda-Emonds, O.R.P., Gittleman, J.L. and Purvis, A. (1999) Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews*, **74**, 143–175.

Bininda-Emonds, O.R.P., Gittleman, J.L. and Steel, M.A. (2002) The (super)tree of life: procedures, problems, and prospects. *Annual Review of Ecology and Systematics*, **33**, 265–289.

Bininda-Emonds, O.R.P., Beck, R.M.D. and Purvis, A. (2005) Getting to the roots of matrix representation. *Systematic Biology*, **54**, 668–672.

Blomberg, S.P., Garland, T., Jr and Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, **57**, 717–745.

Blum, M.G.B. and François, O. (2006) Which random processes describe the Tree of Life? A large-scale study of phylogenetic tree imbalance. *Systematic Biology*, **55**, 685–691.

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

Brandt, M.E. and McManus, J.W. (2009) Disease incidence is related to bleaching extent in reef-building corals. *Ecology*, **90**, 2859–2867.

Bromham, L., Woolfit, M., Lee, M.S.Y. and Rambaut, A. (2002) Testing the relationship between morphological and molecular rates of change along phylogenies. *Evolution*, **56**, 1921–1930.

Brown, J.M., Hedtke, S.M., Lemmon, A.R. and Lemmon, E.M. (2010) When trees grow too long: Investigating the causes of highly inaccurate Bayesian branch-length estimates. *Systematic Biology*, **59**, 145–161.

Bruno, J.F. and Selig, E.R. (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE*, **2**, e711.

Bruno, J.F., Selig, E.R., Casey, K.S., Page, C.A., Willis, B.L., Harvell, C.D., Sweatman, H.P.A. and Melendy, A.M. (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*, **5**, e124.

Budd, A.F. (1988) Large-scale evolutionary patterns in the reef-coral *Montastraea*: the role of phenotypic plasticity. *Proceedings of the Sixth International Coral Reef Symposium*, **3**, 393–398.

Budd, A.F. (1990) Longterm patterns of morphological variation within and among species of reef-corals and their relationship to sexual reproduction. *Systematic Botany*, **15**, 150–165.

Budd, A.F. (1993) Variation within and among morphospecies of *Montastraea*. *Courier Forschungsinstitut Senckenberg*, **164**, 241–254.

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

Budd, A.F. and 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. and 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. and 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., Johnson, K.G. and Potts, D.C. (1994) Recognizing morphospecies in colonial reef corals: I. Landmark-based methods. *Paleobiology*, **20**, 484–505.

Budd, A.F., Romano, S.L., Smith, N.D. and Barbeitos, M.S. (2010) Rethinking the phylogeny of scleractinian corals: A review of morphological and molecular data. *Integrative and Comparative Biology*, **50**, 411–427.

Budd, A.F., Fukami, H., Smith, N.D. and Knowlton, N. (in press). Taxonomic classification of the reef coral family. *Zoological Journal of the Linnean Society*.

Cadotte, M.W. and Davies, T.J. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, **16**, 376–385.

Cadotte, M.W., Cardinale, B.J. and Oakley, T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17012–17017.

Cadotte, M.W., Cavender-Bares, J., Tilman, D. and Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, **4**, e5695.

Cairns, S.D. (1997) A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, **591**, 1–55.

Cairns, S.D. (1999) Species richness of Recent Scleractinia. *Atoll Research Bulletin*, **459**, 1–46.

Cairns, S.D. (2001) A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, **615**, 1–75.

Cairns, S.D. (2009) *Phylogenetic list of 722 valid Recent azooxanthellate scleractinian species, with their junior synonyms and depth ranges*. *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats* (ed. by J.M. Roberts, A. Wheeler, A. Freiwald, and S.D. Cairns, pp. 1–28. Cambridge University Press.

Cardillo, M., Bininda-Emonds, O.R.P., Boakes, E. and Purvis, A. (2004) A species-level phylogenetic supertree of marsupials. *Journal of Zoology*, **264**, 11–31.

Carpenter, K.E., Abrar, M., Aeby, G.S., Aronson, R.B., Banks, S., Bruckner, A.W., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L.M., Edgar, G.J., Edwards, A.J., Fenner, D.P., Guzman, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J.C., Sheppard, A., Sheppard, C.R.C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C.C., Weil, E. and Wood, E. (2008a) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, **321**, 560–563.

Carpenter, K.E., Polidoro, B.A., Livingstone, S.R., Aronson, R.B. and Precht, W.F. (2008b) Response to N. Knowlton and F. Nunes' E-Letter. *Science*. http://www.sciencemag.org/content/321/5888/560/reply

Carpenter, K.E., Barber, P.H., Crandall, E.D., Ablan-Lagman, M.C., Ambariyanto, Mahardika, G.N., Manjaji-Matsumoto, B.M., Juinio-Meñez, M.A., Santos, M.D., Starger, C.J. and Toha, A.H.A. (2011) Comparative phylogeography of the Coral Triangle and implications for marine management. *Journal of Marine Biology*, **2011**, 396982.

Chen, C., Dai, C.-F., Plathong, S., Chiou, C.-Y. and Chen, C.A. (2008) The complete mitochondrial genomes of needle corals, *Seriatopora* spp. (Scleractinia : Pocilloporidae): An idiosyncratic atp8, duplicated trnW gene, and hypervariable regions used to determine species phylogenies and recently diverged populations. *Molecular Phylogenetics and Evolution*, **46**, 19–33.

Chen, C.A., Wallace, C.C., Yu, J.-K. and Wei, N.V. (2000) Strategies for amplification by polymerase chain reaction of the complete sequence of the gene encoding nuclear large subunit ribosomal RNA in corals. *Marine Biotechnology*, **2**, 558–570.

Chen, C.A., Wallace, C.C. and Wolstenholme, J.K. (2002) Analysis of the mitochondrial 12S rRNA gene supports a two-clade hypothesis of the evolutionary history of scleractinian corals. *Molecular Phylogenetics and Evolution*, **23**, 137–149.

Chen, C.A., Chang, C.C., Wei, N.V., Chen, C.-H., Lein, Y.T., Lin, H.E., Dai, C.-F. and 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 Francaise (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 Francaise (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. and Beauvais, L. (1987) *Ordre des Scléractiniaires: XI. Systématique. Traité de Zoologie, Tome III. Cnidaires: Anthozoaires* (ed. by P.-P. Grassé and D. Doumenc, pp. 679–764. Masson, Paris.

Claereboudt, M.R. (1990) *Galaxea paucisepta* nom. nov. (for *G. pauciradiata*), rediscovery and redescription of a poorly known scleractinian species (Oculinidae). *Galaxea*, **9**, 1–8.

Claereboudt, M.R. and Al-Amri, I.S. (2004) *Calathiscus tantillus*, a new genus and new species of scleractinian coral (Scleractinia, Poritidae) from the Gulf of Oman. *Zootaxa*, **532**, 1–8.

Coleman, A.W. (2009) Is there a molecular key to the level of "biological species" in eukaryotes? A DNA guide. *Molecular Phylogenetics and Evolution*, **50**, 197–203.

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

Collen, B., Turvey, S.T., Waterman, C., Meredith, H.M.R., Kuhn, T.S., Baillie, J.E.M. and Isaac, N.J.B. (2011) Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2611–2622.

Colless, D.H. (1982) Review of "Phylogenetics: The Theory and Practice of Phylogenetic Systematics." *Systematic Zoology*, **31**, 100–104.

Concepcion, G.T., Crepeau, M.W., Wagner, D., Kahng, S.E. and Toonen, R.J. (2008) An alternative to ITS, a hypervariable, single-copy nuclear intron in corals, and its use in detecting cryptic species within the octocoral genus *Carijoa*. *Coral Reefs*, **27**, 323–336.

Connolly, J., Cadotte, M.W., Brophy, C., Dooley, Á., Finn, J., Kirwan, L., Roscher, C. and Weigelt, A. (2011) Phylogenetically diverse grasslands are associated with pairwise interspecific processes that increase biomass. *Ecology*, **92**, 1385–1392.

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

Crandall, K.A. (1998) Conservation phylogenetics of *Ozark* crayfishes: assigning priorities for aquatic habitat protection. *Biological Conservation*, **84**, 107–117.

Crossland, C. (1952) Madreporaria, Hydrocorallinae, Heliopora and Tubipora. *Great Barrier Reef Expedition (1928-1929) Scientific Reports*, **6**, 85–257.

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

Cuif, J.-P., Lecointre, G., Perrin, C., Tillier, A. and 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.

Daly, M., Brugler, M.R., Cartwright, P., Collins, A.G., Dawson, M.N., Fautin, D.G., France, S.C., McFadden, C.S., Opresko, D.M., Rodriguez, E., Romano, S.L. and Stake, J.L. (2007) The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*, **1668**, 127–182.

Daly, M., Fautin, D.G. and Cappola, V.A. (2003) Systematics of the Hexacorallia (Cnidaria: Anthozoa). *Zoological Journal of the Linnean Society*, **139**, 419–437.

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

Dauphin, Y., Cuif, J.-P. and Williams, C.T. (2008) Soluble organic matrices of aragonitic skeletons of Merulinidae (Cnidaria, Anthozoa). *Comparative Biochemistry and Physiology B-Biochemistry and Molecular Biology*, **150**, 10–22.

Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., Gittleman, J.L., Mace, G.M. and Purvis, A. (2008) Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11556–11563.

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.

de Queiroz, K. (2011) Branches in the lines of descent: Charles Darwin and the evolution of the species concept. *Biological Journal of the Linnean Society*, **103**, 19–35.

De'ath, G., Lough, J.M. and Fabricius, K.E. (2009) Declining coral calcification on the Great Barrier Reef. *Science*, **323**, 116–119.

Diekmann, O.E., Bak, R.P.M., Stam, W.T. and Olsen, J.L. (2001) Molecular genetic evidence for probable reticulate speciation in the coral genus *Madracis* from a Caribbean fringing reef slope. *Marine Biology*, **139**, 221–233.

Ditlev, H. (2003) New scleractinian corals (Cnidaria: Anthozoa) from Sabah, North Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology. *Zoologische Mededelingen Leiden*, **77**, 193–219.

Dixon, M.T. and Hillis, D.M. (1993) Ribosomal RNA secondary structure: Compensatory mutations and implications for phylogenetic analysis. *Molecular Biology and Evolution*, **10**, 256–267.

Díaz, M. and Madin, J.S. (2011) Macroecological relationships between coral species' traits and disease potential. *Coral Reefs*, **30**, 73–84.

Doyle, J.J. (1992) Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany*, **17**, 144–163.

Dustan, P. (1975) Growth and form in the reef-building coral *Montastrea annularis*. *Marine Biology*, **33**, 101–107.

Edgar, R.C. (2004a) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics*, **5**, 1–19.

Edgar, R.C. (2004b) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.

Ehrenberg, C.G. (1834) 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. and Solander, D. (1786) *The Natural History of Many Curious and Uncommon Zoophytes Collected from Various Parts of the Globe*, Benjamin White and Son; and Peter Elmsly, London.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. and Lough, J.M. (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, **1**, 165–169.

Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.

Faith, D.P. (2008) Threatened species and the potential loss of phylogenetic diversity: Conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conservation Biology*, **22**, 1461–1470.

Faith, D.P., Magallón, S., Hendry, A.P., Conti, E., Yahara, T. and Donoghue, M.J. (2010) Evosystem services: an evolutionary perspective on the links between biodiversity and human well-being. *Current Opinion in Environmental Sustainability*, **2**, 66–74.

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

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.

Fenner, D.P. (1993) Species distinctions among several Caribbean stony corals. *Bulletin of Marine Science*, **53**, 1099–1116.

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

Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem function relationships. *Ecology*, **92**, 1573–1581.

Forsman, Z.H. and Birkeland, C. (2009) *Porites randalli*: a new coral species (Scleractinia, Poritidae) from American Samoa. *Zootaxa*, **2244**, 51–59.

Forsman, Z.H., Guzman, H.M., Chen, C.A., Fox, G.E. and 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., Hunter, C.L., Fox, G.E. and Wellington, G.M. (2006) Is the ITS region the solution to the "species problem" in corals? Intragenomic variation, and alignment permutations in *Porites*, *Siderastrea* and outgroup taxa. *Proceedings of the Tenth International Coral Reef Symposium*, 14–23.

Forsskål, P. (1775) *Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium. Quae In Itinere Orientali Observavit Petrus Forskål*, Hauniæ.

Foster, A.B. (1979) Phenotypic plasticity in the reef corals *Montastraea annularis* (Ellis and Solander) and *Siderastrea siderea* (Ellis and Solander). *Journal of Experimental Marine Biology and Ecology*, **39**, 25–54.

Friedrich, J., Dandekar, T., Wolf, M. and Müller, T. (2005) ProfDist: a tool for the construction of large phylogenetic trees based on profile distances.

Bioinformatics, **21**, 2108–2109.

Fritz, S.A. and Purvis, A. (2010a) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 2435–2441.

Fritz, S.A. and Purvis, A. (2010b) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, **24**, 1042–1051.

Fukami, H. and Nomura, K. (2009) Existence of a cryptic species of *Montastraea valenciennesi* (Milne Edwards and Haime, 1848) in Wakayama, southern Honshu, Japan. *Journal of the Japanese Coral Reef Society*, **11**, 25–31.

Fukami, H., Omori, M. and Hatta, M. (2000) Phylogenetic relationships in the coral family Acroporidae, reassessed by inference from mitochondrial genes. *Zoological Science*, **17**, 689–696.

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

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

Fukami, H., Chen, C.A., Chiou, C.-Y. and Knowlton, N. (2007) Novel group I introns encoding a putative homing endonuclease in the mitochondrial cox1 gene of scleractinian corals. *Journal of Molecular Evolution*, **64**, 591–600.

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. and 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.

Funk, D.J. and Omland, K.E. (2003) Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 397–423.

Gardiner, J.S. (1899) On the astræid corals collected by the author in the South Pacific. *Proceedings of the Zoological Society of London*, **67**, 734–764.

Gittenberger, A., Reijnen, B.T. and Hoeksema, B.W. (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits.

Contributions to Zoology, **80**, 107–132.

Goloboff, P.A. (1999) Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics*, **15**, 415–428.

Goloboff, P.A., Farris, J.S. and Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

Grajales, A., Aguilar, C. and Sánchez, J.A. (2007) Phylogenetic reconstruction using secondary structures of Internal Transcribed Spacer 2 (ITS2, rDNA): finding the molecular and morphological gap in Caribbean gorgonian corals. *BMC Evolutionary Biology*, **7**, 90.

Green, E.P. and Hendry, H. (1999) Is CITES an effective tool for monitoring trade in corals? *Coral Reefs*, **18**, 403–407.

Green, E.P. and Shirley, F. (1999) *The Global Trade in Corals*, World Conservation Press.

Gregory, J.W. (1900) The corals. *Palaeontologia Indica, Series IX*, **2**, 1–195.

Grenyer, R. and Purvis, A. (2003) A composite species-level phylogeny of the "Insectivora" (Mammalia: Order Lipotyphla Haeckel, 1866). *Journal of Zoology*, **260**, 245–257.

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

Guindon, S., Lethiec, F., Duroux, P. and Gascuel, O. (2005) PHYML Online—a web server for fast maximum likelihood-based phylogenetic inference. *Nucleic Acids Research*, **33**, W557–W559.

Hatta, M., Fukami, H., Wang, W., Omori, M., Shimoike, K., Hayashibara, T., Ina, Y. and Sugiyama, T. (1999) Reproductive and genetic evidence for a reticulate evolutionary history of mass-spawning corals. *Molecular Biology and Evolution*, **16**, 1607–1613.

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.

Heard, S.B. and Mooers, A.Ø. (2000) Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 613–620.

Hellberg, M.E. (2006) No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. *BMC Evolutionary Biology*, **6**, 8.

Hickson, S.J. (1924) *An Introduction to the Study of Recent Corals*, Manchester University Press, Manchester.

Hodgson, G. (1985) A new species of *Montastrea* (Cnidaria, Scleractinia) from the Philippines. *Pacific Science*, **39**, 283–290.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E.D., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N.A., Bradbury, R.H., Dubi, A. and Hatziolos, M.E. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

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

Hoeksema, B.W. (1993) Historical biogeography of *Fungia* (*Pleuractis*) spp. (Scleractinia: Fungiidae), including a new species from the Seychelles. *Zoologische Mededelingen Leiden*, **67**, 639–654.

Hoeksema, B.W. (2009) Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singapore, including a new species and a new record. *Raffles Bulletin of Zoology*, **S22**, 81–90.

Hoffmann, M., Brooks, T.M., da Fonseca, G.A.B., Gascon, C., Hawkins, A.F.A., James, R.E., Langhammer, P., Mittermeier, R.A., Pilgrim, J.D., Rodrigues, A.S.L. and Silva, J.M.C. (2008) Conservation planning and the IUCN Red List. *Endangered Species Research*, **6**, 113–125.

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**, 90.

Huang, D., Meier, R., Todd, P.A. and 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. and 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. and Fukami, H. (2011) Cleaning up the “Bigmessidae”: molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evolutionary Biology*, **11**, 37.

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

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. and Bollback, J.P. (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, **294**, 2310–2314.

Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**, 1547–1551.

Hughes, T.P., Bellwood, D.R. and Connolly, S.R. (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecology Letters*, **5**, 775–784.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J.A., Lough, J.M., Marshall, P.A., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B.R. and Roughgarden, J. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L.J., Moltschaniwskyj, N.A., Pratchett, M.S., Steneck, R.S. and Willis, B.L. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, **17**, 360–365.

Hunter, C.L., Morden, C.W. and Smith, C.M. (1997) The utility of ITS sequences in assessing relationships among zooxanthellae and corals. *Proceedings of the Eighth International Coral Reef Symposium*, **2**, 1599–1602.

Isaac, N.J.B., Mallet, J. and Mace, G.M. (2004) Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology and Evolution*, **19**, 464–469.

Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. and Baillie, J.E.M. (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE*, **2**, e296.

IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*, IUCN, Gland, Switzerland and Cambridge, UK.

Jones, K.E., Bininda-Emonds, O.R.P. and Gittleman, J.L. (2005) Bats, clocks, and rocks: Diversification patterns in Chiroptera. *Evolution*, **59**, 2243–2255.

Jones, K.E., Purvis, A., MacLarnon, A., Bininda-Emonds, O.R.P. and Simmons, N.B. (2002) A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews*, **77**, 223–259.

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

Katoh, K., Asimenos, G. and Toh, H. (2009) *Multiple alignment of DNA sequences with*

MAFFT. Bioinformatics for DNA Sequence Analysis (ed. by D. Posada, pp. 39–63. Humana Press.

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

Keller, A., Schleicher, T., Förster, F., Ruderisch, B., Dandekar, T., Müller, T. and Wolf, M. (2008) ITS2 data corroborate a monophyletic chlorophycean DO-group (Sphaeropleales). *BMC Evolutionary Biology*, **8**, 218.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. and Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.

Kerr, A.M. (2005) Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony. *Biological Reviews*, **80**, 543–558.

Kerr, A.M., Baird, A.H. and Hughes, T.P. (2011) Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proceedings of the Royal Society B-Biological Sciences*, **278**, 75–81.

Klunzinger, C.B. (1879) Die Korallthiere des Rothen Meeres. II. Die Steinkorallen. II: Die Astraeaceen und Fungiaceen, Verlag der Gutmann'schen Buchhandlung, Berlin.

Kitahara, M.V., Cairns, S.D., Stolarski, J., Blair, D. and Miller, D.J. (2010) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS ONE*, **5**, e11490.

Knittweis, L., Kraemer, W.E., Timm, J. and Kochzius, M. (2009) Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. *Conservation Genetics*, **10**, 241–249.

Knowlton, N. (2001) The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5419–5425.

Knowlton, N. and Budd, A.F. (2001) *Recognizing coral species past and present. Evolutionary Patterns: Growth, Form, and Tempo in the Fossil Record* (ed. by J.B.C. Jackson, S. Lidgard, and F.K. McKinney, pp. 97–119. University Of Chicago Press.

Knowlton, N. and Jackson, J.B.C. (1994) New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? *Trends in Ecology and Evolution*, **9**, 7–9.

Knowlton, N. and Jackson, J.B.C. (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biology*, **6**, e54.

Knowlton, N. and Nunes, F.L.D. (2008) Atlantic corals—least of our concerns? *Science*. http://www.sciencemag.org/content/321/5888/560/reply

Knowlton, N., Weil, E., Weigt, L.A. and Guzman, H.M. (1992) Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. *Science*, **255**, 330–333.

Koetschan, C., Forster, F., Keller, A., Schleicher, T., Ruderisch, B., Schwarz, R., Müller, T., Wolf, M. and Schultz, J. (2010) The ITS2 Database III—sequences and structures for phylogeny. *Nucleic Acids Research*, **38**, D275–D279.

Kongjandtre, N., Ridgway, T., Cook, L.G., Huelsken, T., Budd, A.F. and Hoegh-Guldberg, O. (2012) Taxonomy and species boundaries in the coral genus *Favia* Milne Edwards and Haime, 1857 (Cnidaria: Scleractinia) from Thailand revealed by morphological and genetic data. *Coral Reefs*, **31**, 581–601.

Krajewski, C. (1991) *Conservation Phylogenetics: A Focal Role for Molecular Systematics in the Biodiversity Crisis*, Southern Illinois University.

Krajewski, C. (1994) Phylogenetic measures of biodiversity: a comparison and critique. *Biological Conservation*, **69**, 33–39.

Kuntner, M., May-Collado, L.J. and Agnarsson, I. (2011) Phylogeny and conservation priorities of afrotherian mammals (Afrotheria, Mammalia). *Zoologica Scripta*, **40**, 1–15.

Lam, K.K.Y. and Morton, B. (2003) Morphological and ITS1, 5.8S, and partial ITS2 ribosomal DNA sequence distinctions between two species *Platygyra* (Cnidaria: Scleractinia) from Hong Kong. *Marine Biotechnology*, **5**, 555–567.

Lamarck, J.-B.P. (1816) *Histoire Naturelle des Animaux sans Vertèbres*, Verdière.

Lang, J.C. (1984) Whatever works: the variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. *Palaeontographica Americana*, **54**, 18–44.

Le Goff-Vitry, M.C., Rogers, A.D. and Baglow, D. (2004) A deep-sea slant on the molecular phylogeny of the Scleractinia. *Molecular Phylogenetics and Evolution*, **30**, 167–177.

Levitan, D.R., Fukami, H., Jara, J., Kline, D.I., McGovern, T.M., McGhee, K.E., Swanson, C.A. and Knowlton, N. (2004) Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution*, **58**, 308–323.

Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, **50**, 913–925.

Lin, M.-F., Luzon, K.S., Licuanan, W.Y., Ablan-Lagman, M.C. and Chen, C.A. (2011) Seventy-four universal primers for characterizing the complete mitochondrial genomes of scleractinian corals (Cnidaria; Anthozoa). *Zoological Studies*, **50**, 513–524.

Linnaeus, C. (1758) *Systema Naturæ per Regna Tria Naturæ: Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*, Holmiæ.

Locke, J.M., Weil, E. and Coates, K.A. (2007) A newly documented species of *Madracis* (Scleractinia: Pocilloporidae) from the Caribbean. *Proceedings of the Biological Society of Washington*, **120**, 214–226.

Lopez, J.V. and Knowlton, N. (1997) Discrimination of species in the *Montastraea annularis* complex using multiple genetic loci. *Proceedings of the Eighth International Coral Reef Symposium*, **2**, 1613–1618.

Lopez, J.V., Kersanach, R., Rehner, S.A. and Knowlton, N. (1999) Molecular determination of species boundaries in corals: genetic analysis of the *Montastraea annularis* complex using amplified fragment length polymorphisms and a microsatellite marker. *Biological Bulletin*, **196**, 80–93.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H. and van Woesik, R. (2001) Coral bleaching: the winners and the losers. *Ecology Letters*, **4**, 122–131.

Mace, G.M., Gittleman, J.L. and Purvis, A. (2003) Preserving the tree of life. *Science*, **300**, 1707–1709.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. and Stuart, S.N. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–1442.

Maddison, W.P. and Maddison, D.R. (2011) *Mesquite: A Modular System for Evolutionary Analysis*. http://mesquiteproject.org

Maddison, W.P. and Mooers, A.Ø. (2007) *Tuatara: Conservation Priority in a Phylogenetic Context. Version 1.0*. http://mesquiteproject.org/packages/tuatara

Maherali, H. and Klironomos, J.N. (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, **316**, 1746–1748.

Mangubhai, S., Souter, P. and Grahn, M. (2007) Phenotypic variation in the coral *Platygyra daedalea* in Kenya: morphometry and genetics. *Marine Ecology-*

Progress Series, **345**, 105–115.

Manica, A. and Carter, R.W. (2000) Morphological and fluorescence analysis of the *Montastraea annularis* species complex in Florida. *Marine Biology*, **137**, 899–906.

Margules, C.R. and Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Marquez, L.M., van Oppen, M.J.H., Willis, B.L., Reyes, A. and Miller, D.J. (2002) The highly cross-fertile coral species, *Acropora hyacinthus* and *Acropora cytherea*, constitute statistically distinguishable lineages. *Molecular Ecology*, **11**, 1339–1349.

Marquez, L.M., Miller, D.J., MacKenzie, J.B. and van Oppen, M.J.H. (2003) Pseudogenes contribute to the extreme diversity of nuclear ribosomal DNA in the hard coral *Acropora*. *Molecular Biology and Evolution*, **20**, 1077–1086.

Marshall, D.C. (2010) Cryptic failure of partitioned Bayesian phylogenetic analyses: lost in the land of long trees. *Systematic Biology*, **59**, 108–117.

Marshall, P.A. and Baird, A.H. (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, **19**, 155–163.

Matthai, G. (1914) A revision of the Recent colonial Astræidæ possessing distinct corallites. *Transactions of the Linnean Society of London*, **17**, 1–140.

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

May, R.M. (1990) Taxonomy as destiny. *Nature*, **347**, 129–130.

May-Collado, L.J. and Agnarsson, I. (2011) Phylogenetic analysis of conservation priorities for aquatic mammals and their terrestrial relatives, with a comparison of methods. *PLoS ONE*, **6**, e22562.

Maynard, J.A., Baird, A.H. and Pratchett, M.S. (2008) Revisiting the Cassandra syndrome; the changing climate of coral reef research. *Coral Reefs*, **27**, 745–749.

McCook, L.J. (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, **18**, 357–367.

McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, **28**, 495–516.

Medina, M., Weil, E. and Szmant, A.M. (1999) Examination of the *Montastraea annularis* species complex (Cnidaria: Scleractinia) using ITS and COI sequences. *Marine Biotechnology*, **1**, 89–97.

Medina, M., Collins, A.G., Takaoka, T.L., Kuehl, J.V. and Boore, J.L. (2006) Naked corals: skeleton loss in Scleractinia. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 9096–9100.

Meier, R., Kwong, S., Vaidya, G. and 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.

Miller, J., Waara, R., Muller, E. and Rogers, C.S. (2006) Coral bleaching and disease combine to cause extensive mortality on reefs in US Virgin Islands. *Coral Reefs*, **25**, 418.

Miller, K.J. (1992) Morphological variation in the scleractinian coral *Platygyra daedalea* (Ellis and Solander, 1786)—genetically or environmentally determined? *Proceedings of the Seventh International Coral Reef Symposium*, **1**, 550–556.

Miller, K.J. and Babcock, R.C. (1997) Conflicting morphological and reproductive species boundaries in the coral genus *Platygyra*. *Biological Bulletin*, **192**, 98–110.

Miller, K.J. and Benzie, J.A.H. (1997) No clear genetic distinction between morphological species within the coral genus *Platygyra*. *Bulletin of Marine Science*, **61**, 907–917.

Miller, M.A., Pfeiffer, W. and Schwartz, T. (2010) *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*. pp. 1–7. Gateway Computing Environments Workshop, New Orleans, 14 November 2010.

Milne Edwards, H. and Haime, J. (1857a) *Histoire Naturelle des Coralliaires, ou Polypes Proprement Dits. Tome Premier*, Roret, Paris.

Milne Edwards, H. and Haime, J. (1857b) *Histoire Naturelle des Coralliaires, ou Polypes Proprement Dits. Tome Second*, Roret, Paris.

Milne Edwards, H. and Haime, J. (1860) *Histoire Naturelle des Coralliaires, ou Polypes Proprement Dits. Tome Troisième*, Roret, Paris.

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

Milne Edwards, H. and Haime, J. (1848b) Recherches sur les polypiers. *Annales des Sciences Naturelles 3e Série*.

Moll, H. and Best, M.B. (1984) New scleractinian corals (Anthozoa: Scleractinia) from the Spermonde Archipelago, South Sulawesi, Indonesia. *Zoologische Mededelingen Leiden*, **58**, 47–58.

Mooers, A.Ø. (1995) Tree balance and tree completeness. *Evolution*, **49**, 379–384.

Mooers, A.Ø. and Heard, S.B. (1997) Inferring evolutionary process from phylogenetic tree shape. *Quarterly Review of Biology*, **72**, 31–54.

Mooers, A.Ø., Faith, D.P. and Maddison, W.P. (2008) Converting endangered species categories to probabilities of extinction for phylogenetic conservation prioritization. *PLoS ONE*, **3**, e3700.

Murdoch, W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P. and Shaw, R. (2007) Maximizing return on investment in conservation. *Biological Conservation*, **139**, 375–388.

Müller, T., Rahmann, S., Dandekar, T. and Wolf, M. (2004) Accurate and robust phylogeny estimation based on profile distances: a study of the Chlorophyceae (Chlorophyta). *BMC Evolutionary Biology*, **4**, 20.

Müller, T., Philippi, N., Dandekar, T., Schultz, J. and Wolf, M. (2007) Distinguishing species. *RNA*, **13**, 1469–1472.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nee, S. and May, R.M. (1997) Extinction and the loss of evolutionary history. *Science*, **278**, 692–694.

Nee, S., Mooers, A.Ø. and Harvey, P.H. (1992) Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences of the United States of America*, **89**, 8322–8326.

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

Nemenzo, F. (1959) Systematic studies on Philippine shallow water scleractinians. II. Suborder Faviida. *Natural and Applied Science Bulletin*, **16**, 73–135.

Nemenzo, F. (1981) Studies on the systematics of scleractinian corals in the Philippines. *Proceedings of the Fourth International Coral Reef Symposium*, **1**, 25–32.

Nixon, K.C. (1999) The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics*, **15**, 407–414.

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

Nothdurft, L.D. and 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. and Knowlton, N. (2008) Re-evaluation of the systematics of the endemic corals of Brazil by molecular data. *Coral Reefs*, **27**, 423–432.

Nyström, M., Graham, N.A.J., Lokrantz, J. and Norström, A.V. (2008) Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs*, **27**, 795–809.

Odorico, D.M. and Miller, D.J. (1997) Variation in the ribosomal internal transcribed spacers and 5.8S rDNA among five species of *Acropora* (Cnidaria; Scleractinia): patterns of variation consistent with reticulate evolution. *Molecular Biology and Evolution*, **14**, 465–473.

Oken, L. (1815) *Lehrbuch der Naturgeschichte. III Zoologie*, A. Schmid, Leipzig, Jena.

Orme, C.D.L., Freckleton, R.P., Thomas, G., Petzoldt, T. and Fritz, S.A. (2008) *CAIC: Comparative Analyses Using Independent Contrasts. R Package Version 1.0.4-94*. http://r-forge.r-project.org/projects/caic

Ow, Y.X. and Todd, P.A. (2010) Light-induced morphological plasticity in the scleractinian coral *Goniastrea pectinata* and its functional significance. *Coral Reefs*, **29**, 797–808.

Palmer, C.V., Bythell, J.C. and Willis, B.L. (2010) Levels of immunity parameters underpin bleaching and disease susceptibility of reef corals. *FASEB Journal*, **24**, 1935–1946.

Palumbi, S.R. (1997) Molecular biogeography of the Pacific. *Coral Reefs*, **16**, S47–S52.

Pandolfi, J.M. (1992) Successive isolation rather than evolutionary centres for the origination of Indo-Pacific reef corals. *Journal of Biogeography*, **19**, 593–609.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D.A., McClenachan, L.E., Newman, M.J.H., Paredes, G., Warner, R.R. and Jackson, J.B.C. (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*, **301**, 955–958.

Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P., Kappel, C.V., Micheli, F., Ogden, J.C., Possingham, H.P. and Sala, E. (2005) Are U.S. coral reefs on the slippery slope to slime? *Science*, **308**, 1742–1743.

Pandolfi, J.M., Connolly, S.R., Marshall, D.J. and Cohen, A.L. (2011) Projecting coral reef futures under global warming and ocean acidification. *Science*, **333**, 418–422.

Paradis, E., Claude, J. and Strimmer, K. (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

Parhar, R.K. and Mooers, A.Ø. (2011) Phylogenetically clustered extinction risks do not substantially prune the Tree of Life. *PLoS ONE*, **6**, e23528.

Pavoine, S., Ollier, S. and Dufour, A.B. (2005) Is the originality of a species measurable? *Ecology Letters*, **8**, 579–586.

Pérez-Losada, M., Jara, C.G., Bond-Buckup, G. and Crandall, K.A. (2002) Conservation phylogenetics of Chilean freshwater crabs *Aegla* (Anomura, Aeglidae): assigning priorities for aquatic habitat protection. *Biological Conservation*, **105**, 345–353.

Pichon, M., Chuang, Y.-Y. and Chen, C.A. (2012) *Pseudosiderastrea formosa* sp. nov. (Cnidaria: Anthozoa: Scleractinia) a new coral species endemic to Taiwan. *Zoological Studies*, **51**, 93–98.

Pires, D.O. and Castro, C.B. (1997) Scleractinia and Corallimorpharia: An analysis of cnidae affinity. *Proceedings of the Eighth International Coral Reef Symposium*, **2**, 1581–1586.

Polidoro, B.A., Elfes, C.T., Sanciangco, J.C., Pippard, H. and Carpenter, K.E. (2011) Conservation status of marine biodiversity in Oceania: An analysis of marine species on the IUCN Red List of Threatened Species. *Journal of Marine Biology*, **2011**, 247030.

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

Posada, D. and Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Powers, D.A. and Rohlf, F.J. (1972) A numerical taxonomic study of Caribbean and Hawaiian reef corals. *Systematic Zoology*, **21**, 53–64.

Purvis, A. (1995) A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **348**, 405–421.

Purvis, A. (2008) Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 301–319.

Purvis, A. and Agapow, P.M. (2002) Phylogeny imbalance: taxonomic level matters. *Systematic Biology*, **51**, 855–854.

Purvis, A., Agapow, P.M., Gittleman, J.L. and Mace, G.M. (2000) Nonrandom extinction and the loss of evolutionary history. *Science*, **288**, 328–330.

Purvis, A., Fritz, S.A., Rodríguez, J., Harvey, P.H. and Grenyer, R. (2011) The shape of mammalian phylogeny: patterns, processes and scales. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2462–2477.

Ragan, M.A. (1992) Phylogenetic inference based on matrix representation of trees. *Molecular Phylogenetics and Evolution*, **1**, 53–58.

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

Redding, D.W. and Mooers, A.Ø. (2006) Incorporating evolutionary measures into conservation prioritization. *Conservation Biology*, **20**, 1670–1678.

Redding, D.W., Hartmann, K., Mimoto, A., Bokal, D., DeVos, M. and Mooers, A.Ø. (2008) Evolutionarily distinctive species often capture more phylogenetic diversity than expected. *Journal of Theoretical Biology*, **251**, 606–615.

Redding, D.W., DeWolff, C.V. and Mooers, A.Ø. (2010) Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conservation Biology*, **24**, 1052–1058.

Reimer, J.D., Takishita, K., Ono, S. and Maruyama, T. (2007a) Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) based on nuclear ITS-rDNA. *Coral Reefs*, **26**, 399–410.

Reimer, J.D., Takishita, K., Ono, S., Tsukahara, J. and Maruyama, T. (2007b) Molecular evidence suggesting interspecific hybridization in *Zoanthus* spp. (Anthozoa : Hexacorallia). *Zoological Science*, **24**, 346–359.

Reimer, J.D., Ono, S., Tsukahara, J. and Iwase, F. (2008) Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa : Hexacorallia) and associated zooxanthellae (*Symbiodinium* spp.) from Japan. *Marine Biology*, **153**, 351–363.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M.D., Wells, F., Vynne, C. and Werner, T.B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295**, 1280–1284.

Roberts, D.L. and Solow, A.R. (2008) The effect of the Convention on International Trade in Endangered Species on scientific collections. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 987–989.

Rodolfo-Metalpa, R., Houlbrèque, F., Tambutté, E., Boisson, F., Baggini, C., Patti, F.P., Jeffree, R., Fine, M., Foggo, A., Gattuso, J.-P. and Hall-Spencer, J.M. (2011)

Coral and mollusc resistance to ocean acidification adversely affected by warming. *Nature Climate Change*, **1**, 308–312.

Rodrigues, A.S.L., Akçakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. and Yan, X. (2004) Global gap analysis: Priority regions for expanding the global protected-area network. *Bioscience*, **54**, 1092–1100.

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffman, M. and Brooks, T.M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology and Evolution*, **21**, 71–76.

Romano, S.L. and Cairns, S.D. (2000) Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science*, **67**, 1043–1068.

Romano, S.L. and Palumbi, S.R. (1996) Evolution of scleractinian corals inferred from molecular systematics. *Science*, **271**, 640–642.

Romano, S.L. and Palumbi, S.R. (1997) Molecular evolution of a portion of the mitochondrial 16S ribosomal gene region in scleractinian corals. *Journal of Molecular Evolution*, **45**, 397–411.

Ronquist, F. and 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., Hohna, S., Larget, B., Liu, L., Suchard, M.A. and Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542.

Russell, G.J., Brooks, T.M., McKinney, M.M. and Anderson, C.G. (1998) Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biology*, **12**, 1365–1376.

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

Sánchez, J.A. and Dorado, D. (2008) Intragenomic ITS2 variation in Caribbean seafans. *Proceedings of the Eleventh International Coral Reef Symposium*, 1383–1387.

Scheer, G. and Pillai, C.S.G. (1983) Report on the stony corals from the Red Sea. *Zoologica*, **131**, 1–198.

Schultz, J. and Wolf, M. (2009) ITS2 sequence–structure analysis in phylogenetics: A how-to manual for molecular systematics. *Molecular Phylogenetics and Evolution*, **52**, 520–523.

Schwartz, R.S. and Mueller, R.L. (2010) Branch length estimation and divergence dating: estimates of error in Bayesian and maximum likelihood frameworks. *BMC Evolutionary Biology*, **10**, 5.

Seibel, P.N., Müller, T., Dandekar, T., Schultz, J. and Wolf, M. (2006) 4SALE - A tool for synchronous RNA sequence and secondary structure alignment and editing. *BMC Bioinformatics*, **7**, 498.

Seibel, P.N., Müller, T., Dandekar, T. and Wolf, M. (2008) Synchronous visual analysis and editing of RNA sequence and secondary structure alignments using 4SALE. *BMC Research Notes*, **1**, 91.

Shearer, T.L., van Oppen, M.J.H., Romano, S.L. and Wörheide, G. (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology*, **11**, 2475–2487.

Sheppard, C.R.C. (1990) *Generic Guide to Common Corals*, Marine Conservation Society, Ross-on-Wye.

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

Steel, M., Mimoto, A. and Mooers, A.Ø. (2007) Hedging our bets: The expected contribution of species to future phylogenetic diversity. *Evolutionary Bioinformatics*, **3**, 237–244.

Stefani, F., Benzoni, F., Pichon, M., Cancelliere, C. and Galli, P. (2008a) A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). *Zoologica Scripta*, **37**, 71–91.

Stefani, F., Benzoni, F., Pichon, M., Mitta, G. and Galli, P. (2008b) Genetic and morphometric evidence for unresolved species boundaries in the coral genus *Psammocora* (Cnidaria; Scleractinia). *Hydrobiologia*, **596**, 153–172.

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

Stolarski, J. and Russo, A. (2002) Microstructural diversity of the stylophyllid (Scleractinia) skeleton. *Acta Palaeontologica Polonica*, **47**, 651–666.

Stolarski, J. and Vertino, A. (2007) First Mesozoic record of the scleractinian *Madrepora* from the Maastrichtian siliceous limestones of Poland. *Facies*, **53**, 67–78.

Stolarski, J., Kitahara, M.V., Miller, D.J., Cairns, S.D., Mazur, M. and Meibom, A. (2011) The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. *BMC Evolutionary Biology*, **11**, 316.

Stoner, C.J., Bininda-Emonds, O.R.P. and Caro, T. (2003) The adaptive significance of coloration in lagomorphs. *Biological Journal of the Linnean Society*, **79**, 309–328.

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

Szmant, A.M., Weil, E., Miller, M.W. and Colon, D.E. (1997) Hybridization within the species complex of the scleractinan coral *Montastraea annularis*. *Marine Biology*, **129**, 561–572.

Takabayashi, M., Carter, D.A., Loh, W.K.W. and 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. and 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*, 241–248.

Takabayashi, M., Carter, D.A., Lopez, J.V. and Hoegh-Guldberg, O. (2003) Genetic variation of the scleractinian coral *Stylophora pistillata*, from western Pacific reefs. *Coral Reefs*, **22**, 17–22.

Templeton, A.R. (1983) Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution*, **37**, 221–244.

Templeton, A.R. (1987) Nonparametric phylogenetic inference from restriction cleavage sites. *Molecular Biology and Evolution*, **4**, 315–319.

Thompson, J.D., Higgins, D.G. and Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, **22**, 4673–4680.

Todd, P.A. (2008) Morphological plasticity in scleractinian corals. *Biological Reviews*, **83**, 315–337.

Todd, P.A., Sanderson, P.G. and Chou, L.M. (2001) Morphological variation in the polyps of the scleractinian coral *Favia speciosa* (Dana) around Singapore. *Hydrobiologia*, **444**, 227–235.

Todd, P.A., Sidle, R.C. and Chou, L.M. (2002a) Plastic corals from Singapore: 1. *Coral Reefs*, **21**, 391–392.

Todd, P.A., Sidle, R.C. and Chou, L.M. (2002b) Plastic corals from Singapore: 2. *Coral Reefs*, **21**, 407–408.

Todd, P.A., Ladle, R.J., Lewin-Koh, N.J.I. and Chou, L.M. (2004a) Flesh or bone? Quantifying small-scale coral morphology using with-tissue and without-tissue techniques. *Marine Biology*, **145**, 323–328.

Todd, P.A., Ladle, R.J., Lewin-Koh, N.J.I. and Chou, L.M. (2004b) Genotype × environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliopora*. *Marine Ecology-Progress Series*, **271**, 167–182.

Todd, P.A., Sidle, R.C. and Lewin-Koh, N.J.I. (2004c) An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. *Journal of Experimental Marine Biology and Ecology*, **299**, 97–113.

van Oppen, M.J.H. and Gates, R.D. (2006) Conservation genetics and the resilience of reef-building corals. *Molecular Ecology*, **15**, 3863–3883.

van Oppen, M.J.H., Willis, B.L., van Vugt, H.W.J.A. and Miller, D.J. (2000) Examination of species boundaries in the *Acropora cervicornis* group (Scleractinia, Cnidaria) using nuclear DNA sequence analyses. *Molecular Ecology*, **9**, 1363–1373.

van Oppen, M.J.H., Wörheide, G. and Takabayashi, M. (2000) Nuclear markers in evolutionary and population genetic studies of scleractinian corals and sponges. *Proceedings of the Ninth International Coral Reef Symposium*, **1**, 131–138.

van Oppen, M.J.H., McDonald, B.J., Willis, B.L. and Miller, D.J. (2001) The evolutionary history of the coral genus *Acropora* (Scleractinia, Cnidaria) based on a mitochondrial and a nuclear marker: reticulation, incomplete lineage sorting, or morphological convergence? *Molecular Biology and Evolution*, **18**, 1315–1329.

van Oppen, M.J.H., Willis, B.L., Van Rheede, T. and Miller, D.J. (2002) Spawning times, reproductive compatibilities and genetic structuring in the *Acropora aspera* group: evidence for natural hybridization and semi-permeable species boundaries in corals. *Molecular Ecology*, **11**, 1363–1376.

van Oppen, M.J.H., Koolmees, E.M. and Veron, J.E.N. (2004) Patterns of evolution in the scleractinian coral genus *Montipora* (Acroporidae). *Marine Biology*, **144**, 9–18.

van Veghel, M.L.J. (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. I. Gametogenesis and spawning behavior. *Marine Ecology-Progress Series*, **109**, 209–219.

van Veghel, M.L.J. and Bak, R.P.M. (1993) Intraspecific variation of a dominant Caribbean reef building coral, *Montastrea annularis*: genetic, behavioral, and morphometric aspects. *Marine Ecology-Progress Series*, **92**, 255–265.

van Veghel, M.L.J. and Kahmann, M.E.H. (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. II. Fecundity and colony structure. *Marine Ecology-Progress Series*, **109**, 221–227.

van Veghel, M.L.J. and Bak, R.P.M. (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. III. Reproduction in damaged and regenerating colonies. *Marine Ecology-Progress Series*, **109**, 229–233.

van Veghel, M.L.J., Cleary, D.F.R. and Bak, R.P.M. (1996) Interspecific interactions and competitive ability of the polymorphic reef-building coral *Montastrea annularis*. *Bulletin of Marine Science*, **58**, 792–803.

van Woesik, R., Sakai, K., Ganase, A. and Loya, Y. (2011) Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology-Progress Series*, **434**, 67–76.

Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. (1991) What to protect?-Systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.

Vaughan, T.W. (1901) The stony corals of the Porto Rican waters. *Bulletin of the U.S. Fish Commission for 1900*, **2**, 289–320.

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

Vermeij, M.J.A., Diekmann, O.E. and Bak, R.P.M. (2003) A new species of scleractinian coral (Cnidaria, Anthozoa), *Madracis carmabi* n. sp. from the Caribbean. *Bulletin of Marine Science*, **73**, 679–684.

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*, Angus and Robertson, Sydney.

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

Veron, J.E.N. (1992) *Hermatypic Corals of Japan*, Australian Institute of Marine Science, Townsville.

Veron, J.E.N. (1995) *Corals in Space and Time*, UNSW Press, Sydney.

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

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

Veron, J.E.N. and Pichon, M. (1980) *Scleractinia of Eastern Australia. Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae*, Australian Institute of Marine Science, Townsville.

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

Veron, J.E.N., Odorico, D.M., Chen, C.A. and Miller, D.J. (1996) Reassessing evolutionary relationships of scleractinian corals. *Coral Reefs*, **15**, 1–9.

Veron, J.E.N., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., Sheppard, C.R.C., Spalding, M.D., Stafford-Smith, M.G. and Rogers, A.D. (2009) The coral reef crisis: the critical importance of <350 ppm CO2. *Marine Pollution Bulletin*, **58**, 1428–1436.

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

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 Zoology*, **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. *Communications of the Essex Institute*, **3**, 17–50.

Vollmer, S.V. and Palumbi, S.R. (2004) Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Molecular Ecology*, **13**, 2763–2772.

Wallace, C.C. (1997) New species and new records of recently described species of the coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) from Indonesia. *Zoological Journal of the Linnean Society*, **120**, 27–50.

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

Wallace, C.C. and Willis, B.L. (1994) Systematics of the coral genus *Acropora*: implications of new biological findings for species concepts. *Annual Review of Ecology and Systematics*, **25**, 237–262.

Wallace, C.C. and Wolstenholme, J.K. (1998) Revision of the coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in Indonesia. *Zoological Journal of the Linnean Society*, **123**, 199–384.

Wallace, C.C., Chen, C.A., Fukami, H. and Muir, P.R. (2007) Recognition of separate genera within *Acropora* based on new morphological, reproductive and genetic evidence from *Acropora togianensis*, and elevation of the subgenus *Isopora* Studer, 1878 to genus (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs*, **26**, 231–239.

Wallace, C.C., Turak, E. and DeVantier, L.M. (2011) Novel characters in a conservative coral genus: three new species of *Astreopora* (Scleractinia: Acroporidae) from West Papua. *Journal of Natural History*, **45**, 1905–1924.

Wei, N.V., Wallace, C.C., Dai, C.-F., Moothien Pillay, K.R. and Chen, C.A. (2006) Analyses of the ribosomal internal transcribed spacers (ITS) and the 5.8S gene indicate that extremely high rDNA heterogeneity is a unique feature in the scleractinian coral genus *Acropora* (Scleractinia; Acroporidae). *Zoological Studies*, **45**, 404–418.

Weil, E. and Knowlton, N. (1994) A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bulletin of Marine Science*, **55**, 151–175.

Weitzman, M.L. (1992) On diversity. *Quarterly Journal of Economics*, **107**, 363–405.

Weitzman, M.L. (1998) The Noah's Ark problem. *Econometrica*, **66**, 1279–1298.

Wells, J.W. (1937) New genera of Mesozoic and Cenozoic corals. *Journal of Paleontology*, **11**, 73–77.

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

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

Wijsman-Best, M. (1972) Systematics and ecology of New Caledonian Faviinae (Coelenterata – Scleractinia). *Contributions to Zoology*, **42**, 3–90.

Wijsman-Best, M. (1974a) Biological results of the Snellius Expedition. XXV Faviidae collected by the Snellius Expedition. I. The genus *Favia*. *Zoologische Mededelingen Leiden*, **48**, 249–261.

Wijsman-Best, M. (1974b) Habitat-induced modification of reef corals (Faviidae) and its consequences for taxonomy. *Proceedings of the Second International Coral Reef Symposium*, **2**, 217–228.

Wijsman-Best, M. (1976) Biological results of the Snellius Expedition. XXVII. Faviidae collected by the Snellius Expedition. II. The genera *Favites*, *Goniastrea*, *Platygyra*, *Oulophyllia*, *Leptoria*, *Hydnophora* and *Caulastrea*. *Zoologische Mededelingen Leiden*, **50**, 45–63.

Wijsman-Best, M. (1977a) Intra- and extratentacular budding in hermatypic reef corals. *Proceedings of the Third International Coral Reef Symposium*, **1**, 471–475.

Wijsman-Best, M. (1977b) Indo-Pacific coral species belonging to the subfamily Montastreinae Vaughan and Wells, 1943 (Scleractinia-Coelenterata) Part I. The genera *Montastrea* and *Plesiastrea*. *Zoologische Mededelingen Leiden*, **52**, 81–97.

Wijsman-Best, M. (1980) Indo-Pacific coral species belonging to the subfamily Montastreinae Vaughan and Wells, 1943 (Scleractinia-Coelenterata) Part II. The genera *Cyphastrea*, *Leptastrea*, *Echinopora* and *Diploastrea*. *Zoologische Mededelingen Leiden*, **55**, 235–263.

Wilkinson, C. (2004) *Status of Coral Reefs of the World: 2004*, Australian Institute of Marine Science, Townsville, Queensland.

Willis, B.L., Babcock, R.C., Harrison, P.L. and Wallace, C.C. (1997) Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs*, **16**, S53–S65.

Witting, L. and Loeschcke, V. (1995) The optimization of biodiversity conservation. *Biological Conservation*, **71**, 205–207.

Wolf, M., Ruderisch, B., Dandekar, T., Schultz, J. and Müller, T. (2008) ProfDistS: (profile-) distance based phylogeny on sequence-structure alignments. *Bioinformatics*, **24**, 2401–2402.

Wolstenholme, J.K. (2004) Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). *Marine Biology*, **144**, 567–582.

Wolstenholme, J.K., Wallace, C.C. and Chen, C.A. (2003) Species boundaries within the *Acropora humilis* species group (Cnidaria; Scleractinia): a morphological and molecular interpretation of evolution. *Coral Reefs*, **22**, 155–166.

Xia, X. and Xie, Z. (2001) DAMBE: Software package for data analysis in molecular biology and evolution. *Journal of Heredity*, **92**, 371–373.

Xia, X., Xie, Z., Salemi, M., Chen, L. and Wang, Y. (2003) An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution*, **26**, 1–7.

Yabe, H. and 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. and 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.

Yee, S.H., Santavy, D.L. and Barron, M.G. (2011) Assessing the effects of disease and bleaching on Florida Keys corals by fitting population models to data. *Ecological Modelling*, **222**, 1323–1332.

Zlatarski, V.N. (2008) Need for a more integrative approach to scleractinian taxonomy. *Proceedings of the Eleventh International Coral Reef Symposium*, 1406–1410.