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Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia)

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Modern coral taxonomy has begun to resolve many long-standing problems in traditional systematics stemming from its reliance on skeletal macromorphology. By integrating examinations of colony, corallite, and subcorallite morphology with the molecular sequence data that have proliferated in the last decade, many taxa spread across the scleractinian tree of life have been incorporated into a rigorous classification underpinned by greater phylogenetic understanding. This monograph focuses on one of the most challenging clades recovered to date – its disarray epitomized by the informal name 'Bigmessidae'. This group of predominantly Indo-Pacific species previously comprised families Merulinidae, Faviidae, Pectiniidae, and Trachyphylliidae, but in a recent study these have been incorporated within Merulinidae. We studied 84 living merulinid species by examining morphological traits at three different scales of coral skeletal structure – macromorphology, micromorphology, and microstructure – to construct a morphological matrix comprising 44 characters. Data were analysed via maximum parsimony and also transformed onto a robust molecular phylogeny under the parsimony and maximum likelihood criteria. Comparisons amongst morphological character types suggest that although many characters at every scale are homoplastic, some to a greater extent than others, several can aid in distinguishing genus-level clades. Our resulting trees and character analyses form the basis of a revised classification that spans a total of 139 species contained within 24 genera. The tree topologies necessitate the synonymization of *Barabattoia* as *Dipsastraea*, and *Phymastrea* as *Favites*. Furthermore, *Astrea* and *Coelastrea* are resurrected, and one new genus, ***Paramontastraea*** Huang & Budd **gen. nov.**, is described. All the genera in Merulinidae, along with the monotypic Montastraeidae and Diploastraeidae, are diagnosed based on the characters examined. The integrative classification system proposed here will form the framework for more accurate biodiversity estimates and guide the taxonomic placement of extinct species.

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ADDITIONAL KEYWORDS: Faviidae – Faviina – Indo-Pacific – integrative taxonomy – morphological phylogenetics – Pectiniidae – systematics – Trachyphylliidae.

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INTRODUCTION

In the last decade, coral taxonomy has been greatly advanced by the integration of genetic data and new morphological characters (Frank & Mokady, 2002; Budd *et al*., 2010). Molecular phylogenetic studies have provided solid evidence that conventional taxonomy based on easily observed morphological traits (i.e. macromorphology) fails to organize coral taxa based on their evolutionary histories (Fukami *et al*., 2004a, 2008). In contrast to the five to seven macromorphology-based suborders (Vaughan & Wells, 1943; Wells, 1956), it is now widely accepted that Scleractinia Bourne, 1900 comprises three highly divergent clades, the 'basal' (*sic*; see Krell & Cranston, 2004), 'complex', and 'robust' corals (Romano & Palumbi, 1996, 1997; Romano & Cairns, 2000; Chen, Wallace & Wolstenholme, 2002; Cuif *et al*., 2003; Le Goff-Vitry, Rogers & Baglow, 2004; Kerr, 2005; Fukami *et al*., 2008; Kitahara *et al*., 2010; Stolarski *et al*., 2011; Huang, 2012). None of the traditional suborders are monophyletic. However, recent investigations into subcorallite morphology (i.e. small and/or internal features of the coral skeleton that are not directly observable with the naked eye) have shown that several clades possess unique characteristics (Stolarski & Roniewicz, 2001; Stolarski, 2003; Budd & Stolarski, 2009, 2011), which are only beginning to be used for delineation and description of taxa (Budd *et al*., 2012).

Taxonomic revisions based on this new integrated approach have commenced (e.g. Wallace *et al*., 2007; Gittenberger, Reijnen & Hoeksema, 2011; Benzoni *et al*., 2012b; Schmidt-Roach *et al*., 2014), albeit at a slow pace. Without exception, thorough systematic treatments of problematic coral taxa require long-term effort by many scientists. For instance, the genus *Psammocora* Dana, 1846, took workers at least five years to demonstrate its nonmonophyly (Benzoni *et al*., 2007), reconstruct a robust species phylogeny supported by molecular and morphological data (Stefani *et al*., 2008a, b), and comprehensively resolve taxonomic names for 23 nominal species (Stefani *et al*., 2008a; Benzoni *et al*., 2010, 2012a). Several factors contribute to the difficulty in resolving relationships amongst corals despite the burgeoning amounts of molecular data that have emerged. These include morphological convergence between distinct species even amongst the newly derived traits (Budd & Stolarski, 2009), the inherently plastic nature of coral anatomy (Foster, 1977, 1979, 1980; Todd, Sidle & Lewin-Koh, 2004; Todd *et al*., 2004a, b; Todd, 2008; Hoeksema, 2012), and recent speciation (Miller, 1992; Wolstenholme, Wallace & Chen, 2003; Wolstenholme, 2004; Mangubhai, Souter & Grahn, 2007; Huang *et al*., 2009).

The present study consolidates the large amount of phylogenetic data that has been generated recently, in conjunction with a detailed characterization of corallite and subcorallite morphologies, to advance the goal of a phylogenetic-based taxonomic classification of Scleractinia. This is the second in a series of monographs focusing on modern reef (i.e. zooxanthellate) corals that have traditionally been placed in the suborder Faviina *sensu* Vaughan & Wells (1943) and Wells (1956), or Faviina + Meandriina *sensu* Veron (1995). This grouping includes eight extant families (Vaughan & Wells, 1943; Wells, 1956) that are generally nested within the 'robust' group, all of which have been shown to be nonmonophyletic (Fukami *et al*., 2008; Kitahara *et al*., 2010; Stolarski *et al*., 2011; Huang, 2012; Huang & Roy, 2013). A few genera conventionally assigned to these families even belong to the 'complex' clade (e.g. *Ctenella* Matthai, 1928, and *Galaxea* Milne Edwards & Haime, 1857). The first monograph of this series by Budd *et al*. (2012) resolved this issue by moving these genera into the 'complex' family Euphylliidae Alloiteau, 1952.

For five of these eight families that consist entirely of reef corals (Meandrinidae Gray, 1847, Merulinidae Verrill, 1865, Mussidae Ortmann, 1890, Faviidae Gregory, 1900, and Pectiniidae Vaughan & Wells, 1943), Budd *et al*. (2012) carried out a complete reorganization at the genus level based primarily on the molecular phylogeny of Fukami *et al*. (2008). They noted that the large clade XVII *sensu* Fukami *et al*. (2008), also referred to as the 'Bigmessidae' (Budd, 2009), required additional morphological and molecular work. It comprises Faviidae (including Trachyphylliidae Verrill, 1901), Merulinidae, and Pectiniidae (Huang *et al*., 2011), with species distributed mainly in the Indo-Pacific. Molecular phylogenetic analyses unequivocally showed that these families are not monophyletic (Fukami *et al*., 2008; Huang *et al*., 2011). For instance, *Trachyphyllia geoffroyi*, the only extant Trachyphylliidae species, groups with Indo-Pacific *Favia*, whereas two of the Indo-Pacific 'faviid' species analysed, *Montastrea multipunctata* Hodgson, 1985, and *Moseleya latistellata* Quelch, 1884, are nested alongside Indo-Pacific 'mussids' (Huang *et al*., 2011). More critically, the Atlantic faviids are more closely related to mussids of the same ocean basin (Fukami *et al*., 2004a, 2008), and species of Merulinidae and Pectiniidae belong to multiple divergent subclades within the 'Bigmessidae'.

On the basis of molecular phylogenies by Fukami *et al*. (2008), and to a lesser extent Huang *et al*. (2011), Budd *et al*. (2012) expanded Merulinidae to include all members of the 'Bigmessidae' clade (Fig. 1), demoting Faviidae to the subfamily Faviinae as a group limited to the Atlantic (see also Schwartz, Budd & Carlon, 2012), and regarding Pectiniidae and Trachyphylliidae as junior synonyms of Merulinidae. The reason for restricting Faviinae to the Atlantic species, excluding the Indo-Pacific taxa, lies in the split of Faviidae (*sensu* Vaughan & Wells, 1943; Wells, 1956)

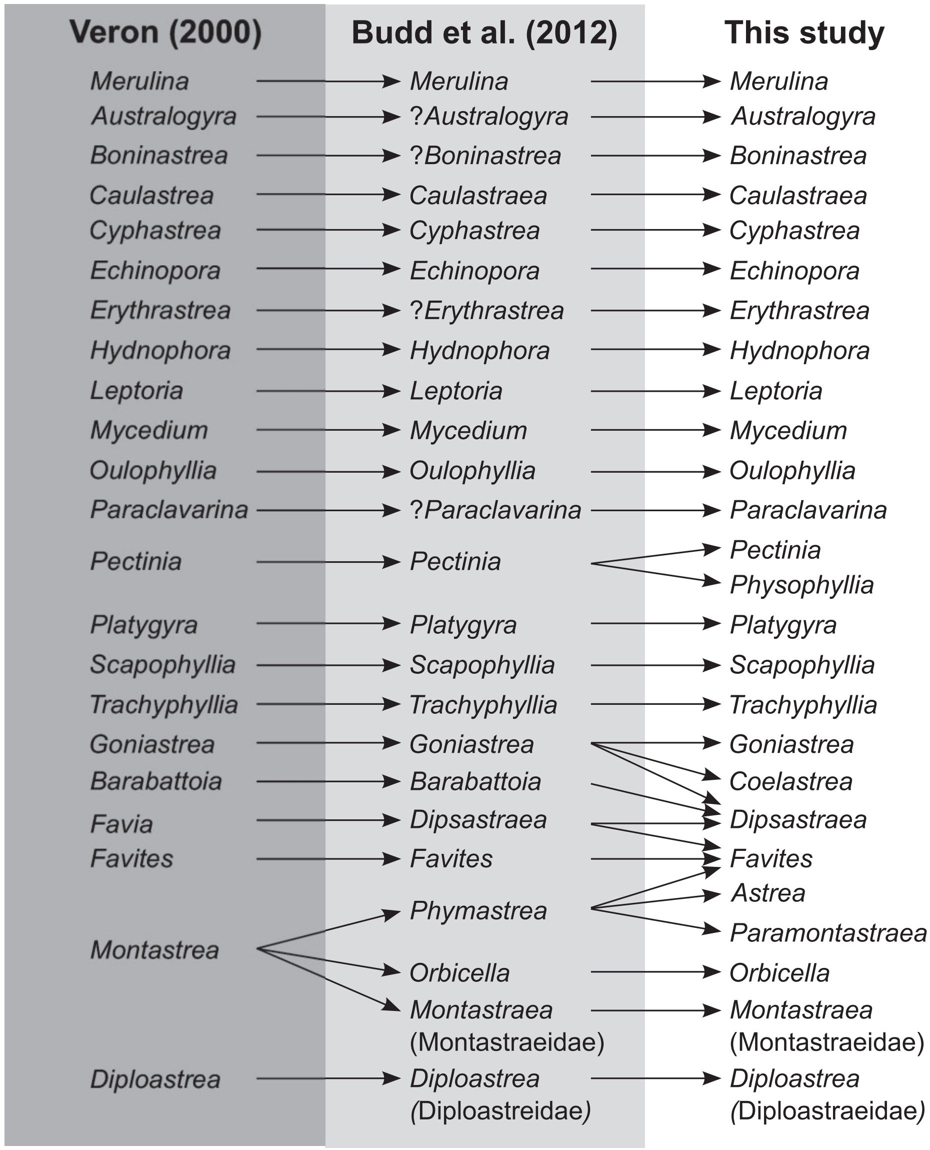


Figure 1. Comparisons amongst recent classifications of reef corals examined in this study. Family level taxonomy follows Budd *et al*. (2012). See Stolarski & Roniewicz (2001) for comparisons with Vaughan & Wells (1943), Wells (1956), Alloiteau (1952), and Chevalier & Beauvais (1987).

into two major clades (XVII and XXI, *sensu* Fukami *et al*., 2008), with its type species *Favia fragum* (Esper, 1795) and close relatives present only in the Atlantic. Aided by detailed observations and phylogenetic analyses of coral morphology at the corallite and subcorallite scales (Budd & Stolarski, 2009, 2011), Budd *et al*. (2012) redefined Mussidae to incorporate Mussinae Ortmann, 1890 (Atlantic mussids) and Faviinae Gregory, 1900. The Pacific 'mussid' species (clades XVIII–XX) have also been placed in the new family Lobophylliidae Dai & Horng, 2009: 59 (= Lobophylliidae Fukami, Budd & Knowlton in Budd *et al*., 2012; see also Licuanan, 2009: 135), whereas the phylogenetically distinct *Diploastrea heliopora* (clade XV; Indo-Pacific) and *Montastraea cavernosa* (clade XVI; Atlantic) have been separated into two families monotypic for extant taxa – Diploastraeidae Chevalier & Beauvais, 1987, and Montastraeidae Yabe & Sugiyama, 1941 respectively.

As a result of these revisions, multiple merulinid species (*sensu* Budd *et al*., 2012) have been excluded from the well-known genera *Favia* and *Montastraea* (Fig. 1). The attempt to restore order at the genus level by resurrecting *Dipsastraea* de Blainville, 1830, for Indo-Pacific *Favia*, *Phymastrea* Milne Edwards & Haime, 1848a, for Indo-Pacific *Montastraea* (excluding *Montastraea cavernosa*), and *Orbicella* Dana, 1846, for the Atlantic '*Montastraea*' *annularis* complex (Budd *et al*., 2012) is necessary yet inadequate because *Dipsastraea* and *Phymastrea* remain polyphyletic (Huang *et al*., 2011; Arrigoni *et al*., 2012).

To date, analyses of Merulinidae have called into question the use of traditional morphological characters for defining species within the group (Fukami *et al*., 2008; Huang *et al*., 2009; Arrigoni *et al*., 2012; see also Budd & Smith, 2005). Yet, most merulinid genera are monophyletic (the exceptions being *Dipsastraea*, *Favites*, *Goniastrea*, and *Phymastrea*) (Huang *et al*., 2011), and well-defined genus-level subclades denoted as 'A' to 'I' (Fig. 2A) appear to be supported by subcorallite morphological features (Budd & Stolarski, 2011). These characters have clearly demonstrated potential in resolving the problematic genera. For instance, *Dipsastraea* (Indo-Pacific '*Favia*') is polyphyletic partly because *Dipsastraea stelligera* (Dana, 1846) is more closely related to *Goniastrea* than to its congenerics. Transverse thin sections of the corallite wall reveal that this species possesses abortive septa (i.e. septa forming between normal septa but not protruding into the calice) similar to *Goniastrea* species and in particular *Goniastrea retiformis*, to which it is a sister taxon. In contrast, all other *Dipsastraea* spp. form walls that are paraseptothecal (Budd & Stolarski, 2011). Three-dimensional characteristics of calicular surfaces, imaged via scanning electron microscopy, are also differentiating these subclades to some extent, but are more compelling for distinguishing the Indo-Pacific merulinids (irregular septal teeth) from Atlantic Faviinae species (regular teeth) (Budd & Stolarski, 2009, 2011). More importantly, these subcorallite traits have served as a basis for the revision of Mussidae (Budd *et al*., 2012).

Here, we follow the precedent set by work carried out on the Atlantic family Mussidae in the first monograph and present a detailed analysis of Merulinidae, Montastraeidae, and Diploastraeidae by characterizing these subcorallite characters at the species level. Macromorphological characters are also examined for they appear to delineate most merulinid genera and may be even more effective when coded appropriately. We compare these results with a comprehensive molecular phylogeny encompassing the three families (Fig. 2A; Huang *et al*., 2011) and reconstruct ancestral morphological states for genus-level clades. Finally, we provide an account of all the genera of Merulinidae, Montastraeidae, and Diploastraeidae, formally revising parts of the merulinid classification where necessary to achieve a phylogenetic-based taxonomy.

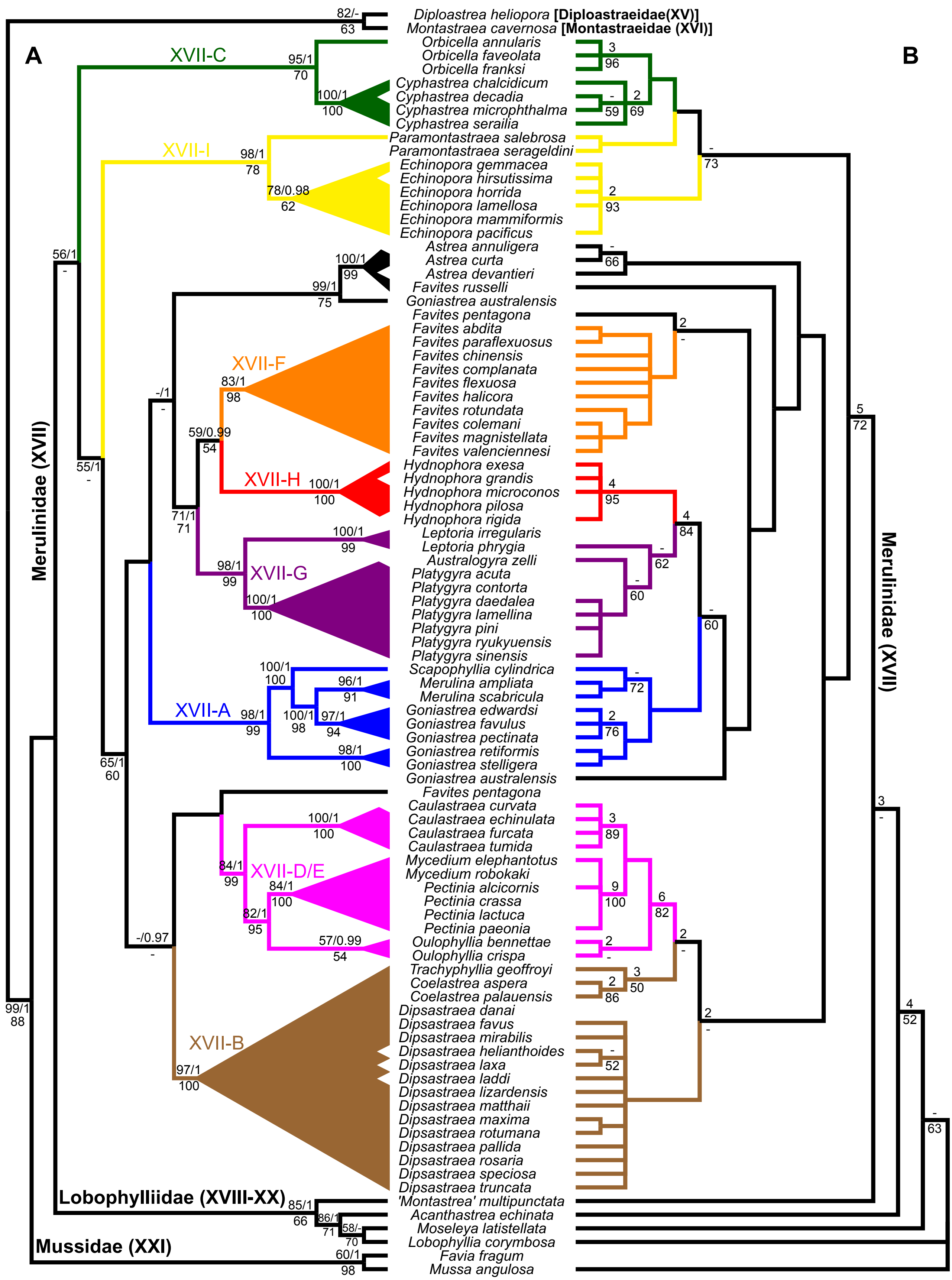
Our revised classification for Merulinidae, in summary, inventorizes a total of 139 species contained within 24 genera (Fig. 1). Two genera are resurrected: *Astrea* Lamarck, 1801, to consist of *Madrepora rotulosa* Ellis & Solander, 1786, *Astrea annuligera* Milne Edwards & Haime, 1849b, *Astrea curta* Dana, 1846, and *Plesiastrea devantieri* Veron, 2000; and *Coelastrea* Verrill, 1866, to consist of *Coelastrea tenuis* Verrill, 1866, *Goniastrea aspera* Verrill, 1866, and *Favia palauensis* Yabe & Sugiyama, 1936. We describe a new genus, *Paramontastraea* Huang & Budd to comprise *Plesiastrea salebrosa* Nemenzo, 1959, *Favites peresi* Faure & Pichon, 1978, and *Montastrea serageldini* Veron, 2000. Two genera are synonymized: *Barabattoia* Yabe & Sugiyama, 1941, as a junior synonym of *Dipsastraea* de Blainville, 1830, resulting in the new combinations *Dipsastraea amicorum* (Milne Edwards & Haime, 1849b), *Dipsastraea laddi* (Wells, 1954), and *Dipsastraea mirabilis* (Yabe & Sugiyama, 1941); and *Phymastrea* Milne Edwards & Haime, 1848a as a junior synonym of *Favites* Link, 1807, resulting in new combinations *Favites colemani* (Veron, 2000), *Favites magnistellata* (Chevalier, 1971), and *Favites valenciennesi* (Milne Edwards & Haime, 1849b). Furthermore, we revert *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977 to its original generic placement and transfer *Astrea* (*Orbicella*) *stelligera* Dana, 1846, into *Goniastrea* Milne Edwards & Haime, 1848a.

MATERIAL AND METHODS

TAXA STUDIED

We analysed the morphology of 84 species within clade XVII *sensu* Fukami *et al*. (2008), including 69 species that have been positively placed within the molecular phylogeny of Huang *et al*. (2011; Fig. 2A). These represent 20 of the 24 genera in Merulinidae that comprise 17 genera listed by Budd *et al*. (2012; Fig. 1) [*Merulina* (two species), *Australogyra* (one species), *Caulastraea* (four species), *Cyphastrea* (five species), *Dipsastraea* (14 species), *Echinopora* (six species), *Favites*

Figure 2. Phylogenetic reconstructions of the reef coral families Diploastraeidae, Montastraeidae, Merulinidae, Lobophylliidae, and Mussidae (clades XV–XXI *sensu* Fukami *et al*., 2008). Molecular subclades within Merulinidae (XVII) are differentiated by colour. A, maximum likelihood tree based on three nuclear and two mitochondrial markers, with numbers adjacent to branches showing support values (upper: maximum likelihood bootstrap ≥ 50, Bayesian posterior probability ≥ 0.9; lower: maximum parsimony bootstrap ≥ 50), after Huang *et al*. (2011). B, one of eight maximum parsimony trees (= strict consensus topology) based on 44 morphological characters analysed in this study, with numbers indicating support (upper: Bremer decay index ≥ 2; lower: maximum parsimony bootstrap ≥ 50).



A
B
Diploastrea heliopora [Diploastraeidae(XV)]
Montastraea cavernosa [Montastraeidae (XVI)]
XVII-C
Orbicella annularis
Orbicella faveolata
Orbicella franksi
Cyphastrea chalcidicum
Cyphastrea decadia
Cyphastrea microphthalma
Cyphastrea serailia
XVII-I
Paramontastraea salebrosa
Paramontastraea serageldini
Echinopora gemmacea
Echinopora hirsutissima
Echinopora horrida
Echinopora lamellosa
Echinopora mammiformis
Echinopora pacificus
Astrea annuligera
Astrea curta
Astrea devantieri
Favites russelli
Goniastrea australensis
Favites pentagona
XVII-F
Favites abdita
Favites paraflexuosus
Favites chinensis
Favites complanata
Favites flexuosa
Favites halicora
Favites rotundata
Favites colemani
Favites magnistellata
Favites valenciennesi
XVII-H
Hydnophora exesa
Hydnophora grandis
Hydnophora microconos
Hydnophora pilosa
Hydnophora rigida
XVII-G
Leptoria irregularis
Leptoria phrygia
Australogyra zelli
Platygyra acuta
Platygyra contorta
Platygyra daedalea
Platygyra lamellina
Platygyra pini
Platygyra ryukyuensis
Platygyra sinensis
XVII-A
Scapophyllia cylindrica
Merulina ampliata
Merulina scabricula
Goniastrea edwardsi
Goniastrea favulus
Goniastrea pectinata
Goniastrea retiformis
Goniastrea stelligera
Goniastrea australensis
Favites pentagona
XVII-D/E
Caulastraea curvata
Caulastraea echinulata
Caulastraea furcata
Caulastraea tumida
Mycedium elephantotus
Mycedium robokaki
Pectinia alcicornis
Pectinia crassa
Pectinia lactuca
Pectinia paeonia
Oulophyllia bennettae
Oulophyllia crispa
XVII-B
Trachyphyllia geoffroyi
Coelastrea aspera
Coelastrea palauensis
Dipsastraea danai
Dipsastraea favus
Dipsastraea mirabilis
Dipsastraea helianthoides
Dipsastraea laxa
Dipsastraea laddi
Dipsastraea lizardensis
Dipsastraea matthaii
Dipsastraea maxima
Dipsastraea rotumana
Dipsastraea pallida
Dipsastraea rosaria
Dipsastraea speciosa
Dipsastraea truncata
Lobophylliidae (XVIII-XX)
'Montastrea' multipunctata
Acanthastrea echinata
Moseleya latistellata
Lobophyllia corymbosa
Mussidae (XXI)
Favia fragum
Mussa angulosa
Merulinidae (XVII)
Merulinidae (XVII)

(12 species), *Goniastrea* (six species), *Hydnophora* (five species), *Leptoria* (two species), *Mycedium* (two species), *Orbicella* (three species), *Oulophyllia* (two species), *Pectinia* (four species), *Platygyra* (seven species), *Scapophyllia* (one species), and *Trachyphyllia* (one species)], two resurrected genera [*Astrea* (three species), *Coelastrea* (two species)] and one new genus [*Paramontastraea* (two species)].

The remaining four genera not analysed phylogenetically are the monotypic *Boninastrea*, *Erythrastrea*, *Paraclavarina*, and *Physophyllia*. Molecular and subcorallite morphology data are not yet available for these taxa, but their type materials were studied and the genera rediagnosed based on macromorphology. The same examinations were carried out for 17 species that have not been analysed in any phylogenetic context.

We also included as outgroups eight species from the families Diploastraeidae (*Diploastrea heliopora*), Montastraeidae (*Montastraea cavernosa*), Lobophylliidae (*Lobophyllia corymbosa*, *Acanthastrea echinata*, '*Montastrea*' *multipunctata*, and *Moseleya latistellata*), and Mussidae (*Favia fragum* and *Mussa angulosa*) (*sensu* Budd *et al*., 2012), the former two of which are given a full systematic account below. Over 400 specimens examined in this monograph are listed in Appendix S1.

Taxonomy at the species level was based primarily on Veron (2000, 2002), along with new species described thereafter (Ditlev, 2003; Latypov, 2006, 2013; Mondal, Raghunathan & Venkataraman, 2013). We were able to locate and photograph nearly all of the name-bearing type specimens of genera and species within Merulinidae, Montastraeidae, and Diploastraeidae, many of which are figured here (Figs 3–28). Specimens that are not name-bearing and figured for the first time are indicated as hypotypes. Type material used to describe the genera *Hydnophora* Fischer von Waldheim, 1807, *Mycedium* Milne Edwards & Haime, 1851, and *Pectinia* de Blainville, 1825 were verified to be lost, so neotypes have been designated.

We note that Veron (2000) described 103 new scleractinian species without designating type material or type localities, rendering them to be *nomina nuda*. These were redescribed in Veron (2002) and a 'holotype' was designated for each species. Following ICZN (2011), the Veron (2000) publication was validated as an available taxonomic work. The species named in Veron (2000) are therefore valid, but the type specimens designated in Veron (2002) are not (see Wallace, Done & Muir, 2012). Twenty-six of these species are in Merulinidae. Based on Veron (2000) and Veron (2002), it is evident that Dr J. E.N. Veron used more than one specimen when describing each species, e.g. at least three for *Favia truncata* Veron, 2000 (Veron, 2002: 142, figs 260–263; ICZN, 2011: 164). Except for the 'holotype' of *Favites bestae* Veron, 2000, a junior synonym of *Favites melicerum* (Ehrenberg, 1834), each of these specimens should be regarded as part of a syntype series. We therefore regard Dr Veron's intent for 25 of the 26 Merulinidae 'holotypes' listed in Veron (2002) to be lectotypes chosen subsequent to the original descriptions of the syntype series based on Veron (2000).

Geographical distributions of genera were obtained from Veron (2000), with updates from Veron *et al*. (2009, 2011). Other distributional data are specifically cited.

MORPHOLOGICAL CHARACTERS

Morphological traits from three different scales of coral skeletal structure – macromorphology, micromorphology, and microstructure according to Budd & Stolarski (2009, 2011) – were examined to construct a morphological matrix consisting of 44 characters (Table 1; Appendix S2). In particular, we followed closely the characters used by Budd *et al*. (2012) in their revision of Mussidae. Here, we summarize these character types and highlight the characters that were added, omitted, or coded differently from Budd *et al*. (2012; see especially their appendix S3).

First, characterization of 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 & Wells, 1943; Wells, 1956; Beauvais *et al*., 1993; Johnson, 1998; Wallace, 1999; Budd & Smith, 2005; Huang *et al*., 2009). Observations were carried out using a stereo microscope, and data obtained for 21 characters. Second, micromorphology was visualized at the scale of the shapes of teeth along the wall, septa, columella, and septal face granulations (Hoeksema, 1989; Beauvais *et al*., 1993; Cuif & Perrin, 1999; Cuif *et al*., 2003; Budd & Smith, 2005). We examined nine characters employing this method. Each calice was mounted on stubs, and observations were carried out via scanning electron microscopy at magnifications lower than 200 × (Budd & Stolarski, 2009, 2011). Third, the study of coral microstructure involved examinations of the arrangements of rapid accretion deposits and thickening deposits or fibres within the wall, septa, and columella, using thin sections (Alloiteau, 1952; Chevalier & Beauvais, 1987; Beauvais *et al*., 1993; Stolarski & Roniewicz, 2001; Cuif *et al*., 2003; Stolarski, 2003; Nothdurft & Webb, 2007; Brahmi *et al*., 2010; Cuif, 2010). Fourteen characters were studied in this manner. Each calice was cut transversely, impregnated with epoxy, and sectioned to a thickness of ~30 μm prior to visualization under transmitted light at magnifications < 100 × (Budd & Stolarski, 2009, 2011).

We added the character 'monticules' with two states, absent or present (character 4). This feature refers to

Table 1. List of characters and states

No.	Type	Character	States	Parsimony model	Molecular tree Steps	Molecular tree CI	Molecular tree RI	Morphology tree Steps	Morphology tree CI	Morphology tree RI
1	Macromorphology	Intracalicular budding	0 = absent 1 = present	Unordered	4	0.250	0.750	2	0.500	0.938
2	Macromorphology	Extracalicular budding	0 = absent 1 = present	Unordered	6	0.167	0.815	3	0.333	0.935
3	Macromorphology	Polymorphism	0 = absent 1 = present	Unordered	1	1.000	1.000	1	1.000	1.000
4	Macromorphology	Monticules	0 = absent 1 = present	Unordered	1	1.000	1.000	1	1.000	1.000
5	Macromorphology	Corallite integration	0 = discrete (1–3 centres) 1 = uni- or multiserial 2 = organically united	Ordered	10	0.200	0.704	7	0.286	0.737
6	Macromorphology	Coenosteum amount	0 = fused walls 1 = limited (includes double wall) 2 = moderate (< corallite diameter) 3 = extensive (≥ corallite diameter) 4 = phaceloid	Ordered	31	0.129	0.700	23	0.174	0.782
7	Macromorphology	Coenosteum structure	0 = costate 1 = spinose	Unordered	4	0.250	0.625	2	0.500	0.909
8	Macromorphology	Calice width	0 = small (< 4 mm) 1 = medium (4–15 mm) 2 = large (> 15 mm)	Ordered	11	0.182	0.471	9	0.222	0.611
9	Macromorphology	Calice relief	0 = low (< 3 mm) 1 = medium (3–6 mm) 2 = high (> 6 mm)	Ordered	10	0.200	0.692	7	0.286	0.821
10	Macromorphology	Continuity of costosepta	0 = not confluent 1 = confluent	Unordered	7	0.143	0.786	5	0.200	0.818
11	Macromorphology	Number of septa	0 = < 3 cycles (< 24) 1 = 3 cycles (24–36) 2 = ≥ 4 cycles (≥ 48)	Ordered	9	0.222	0.781	6	0.333	0.857
12	Macromorphology	Free septa	0 = absent 1 = irregular 2 = regular	Ordered	8	0.250	0.667	6	0.333	0.833
13	Macromorphology	Septa spacing (per 5 mm)	0 = < 6 1 = 6–11 2 = > 11	Ordered	9	0.222	0.750	5	0.400	0.893
14	Macromorphology	Relative costosepta thickness	0 = unequal 1 = equal	Unordered	7	0.143	0.833	5	0.200	0.882
15	Macromorphology	Columella linkage	0 = continuous (trabecular linkage) 1 = discontinuous (lamellar linkage)	Unordered	2	0.500	0.889	3	0.333	0.667

Table 1. *Continued*

No.	Type	Character	States	Parsimony model	Molecular tree Steps	Molecular tree CI	Molecular tree RI	Morphology tree Steps	Morphology tree CI	Morphology tree RI
16	Macromorphology	Columella structure	0 = lamellar 1 = trabecular, compact (1–3 threads) 2 = trabecular, spongy (> 3 threads)	Unordered	5	0.400	0.800	4	0.500	0.895
17	Macromorphology	Columella size (relative to calice width)	0 = < 1/4 1 = ≥ 1/4	Unordered	4	0.250	0.625	2	0.500	0.857
18	Macromorphology	Development of paliform lobes	0 = absent 1 = weak or moderate 2 = well developed	Ordered	13	0.154	0.744	8	0.250	0.860
19	Macromorphology	Development of septal lobes	0 = absent 1 = weak or moderate 2 = well developed	Ordered	8	0.250	0.571	5	0.400	0.786
20	Macromorphology	Epitheca	0 = absent 1 = reduced 2 = well developed	Ordered	10	0.200	0.771	8	0.250	0.813
21	Macromorphology	Endotheca	0 = sparse 1 = low–moderate (tabular) 2 = abundant (vesicular)	Ordered	7	0.286	0.821	5	0.400	0.889
22	Micromorphology	Tooth base outline (midcalice)	0 = elliptical–parallel 1 = elliptical–perpendicular 2 = circular	Unordered	4	0.500	0.500	2	0.500	0.500
23	Micromorphology	Tooth tip outline (midcalice)	0 = regular (pointed) 1 = irregular	Unordered	1	1.000	1.000	1	1.000	0.000
24	Micromorphology	Tooth tip orientation (midcalice)	0 = parallel 1 = perpendicular 2 = multiaxial	Unordered	2	1.000	1.000	2	1.000	1.000
25	Micromorphology	Tooth height (S1)	0 = low (< 0.3 mm) 1 = medium (0.3–0.6 mm) 2 = high (> 0.6 mm)	Ordered	9	0.222	0.767	6	0.333	0.897
26	Micromorphology	Tooth spacing (S1)	0 = narrow (< 0.3 mm) 1 = medium (0.3–1 mm) 2 = wide (> 1 mm)	Ordered	9	0.222	0.611	5	0.400	0.870
27	Micromorphology	More than 6 teeth per septum	0 = absent 1 = present	Unordered	2	0.500	0.667	2	0.500	0.667
28	Micromorphology	Granule distribution	0 = aligned 1 = scattered	Unordered	4	0.250	0.667	3	0.333	0.818
29	Micromorphology	Granule shape	0 = weak (rounded) 1 = strong (pointed) 2 = irregular	Unordered	6	0.333	0.714	5	0.400	0.769
30	Micromorphology	Interarea	0 = horizontal bands 1 = smooth 2 = palisade	Unordered	4	0.500	0.875	4	0.500	0.889

Table 1. *Continued*

No.	Type	Character	States	Parsimony model	Molecular tree Steps	Molecular tree CI	Molecular tree RI	Morphology tree Steps	Morphology tree CI	Morphology tree RI
31	Microstructure	Synapticulotheca	0 = absent 1 = present	Unordered	1	–	–	0	–	–
32	Microstructure	Septotheca	0 = absent 1 = partial 2 = dominant (= septothecal)	Ordered	5	0.400	0.769	3	0.667	0.933
33	Microstructure	Abortive septa	0 = absent 1 = weak 2 = strong	Ordered	5	0.400	0.842	4	0.500	0.900
34	Microstructure	Trabeculotheca	0 = absent 1 = partial 2 = dominant (= trabeculothecal)	Ordered	8	0.250	0.727	5	0.400	0.893
35	Microstructure	Paratheca	0 = absent 1 = partial 2 = dominant (= parathecal)	Ordered	12	0.167	0.792	5	0.400	0.942
36	Microstructure	Thickening deposits/ structure	0 = microfibrous 1 = thick fibrous 2 = concentric rings (extensive stereome)	Ordered	3	0.667	0.833	3	0.667	0.800
37	Microstructure	Costa centre clusters	0 = not distinct 1 = weak 2 = strong	Ordered	6	0.333	0.879	4	0.500	0.941
38	Microstructure	Distance between costa clusters	0 = < 0.3 mm 1 = 0.3–0.6 mm 2 = > 0.6 mm	Ordered	6	0.333	0.789	2	1.000	1.000
39	Microstructure	Costa medial lines	0 = absent 1 = weak 2 = strong	Ordered	6	0.333	0.714	2	0.500	0.933
40	Microstructure	Septum centre clusters	0 = not distinct 1 = weak 2 = strong	Ordered	3	0.667	0.889	2	1.000	1.000
41	Microstructure	Distance between septum clusters	0 = < 0.3 mm 1 = 0.3–0.5 mm 2 = > 0.5 mm	Ordered	7	0.286	0.821	3	0.667	0.970
42	Microstructure	Septum medial lines	0 = absent 1 = weak 2 = strong	Ordered	6	0.333	0.826	6	0.333	0.833
43	Microstructure	Transverse crosses	0 = absent 1 = present	Unordered	4	0.250	0.897	4	0.250	0.906
44	Microstructure	Columella centres	0 = clustered 1 = aligned	Unordered	3	0.333	0.714	1	1.000	1.000

CI, consistency index (Kluge & Farris, 1969); RI, retention index (Farris, 1989).

the mound-like structures protruding from the corallum surface, around which corallite centres are arranged (Wells, 1956). Monticules were only found to be present in *Hydnophora* species amongst all the taxa examined in this study.

We generalized the character 'coenosteum amount' to five ordered states (character 6) – fused walls, limited, moderate, extensive, or phaceloid – and limited the character 'coenosteum structure' to two states (character 7) – costate or spinose. Budd *et al*. (2012) coded the absence of coenosteum in both of these characters, although 'coenosteum amount' was not included in their phylogenetic analysis. To avoid replicating the absence in both characters, we interpreted 'coenosteum amount' (character 6) more generally and ordered the states to reflect the level of integration between walls of adjacent corallites. Walls can be fused, and hence have no coenosteum at all, but they can be separated to four varying degrees. Coenosteum can be present as limited (includes double wall), moderate (< corallite diameter), or extensive (> corallite diameter), but it can again be absent in the extreme case of wall separation by void space, in which a branch is formed by each corallite (i.e. phaceloid) or a series of corallites (i.e. flabello-meandroid). The character 'coenosteum structure' (character 7) was only coded for species that have coenosteum in the first place (i.e. limited, moderate, or extensive for character 6), for which it can be constructed by radially arranged plates known as costae (costate) or by spines (spinose). We omitted the state 'vesicular or solid' because species that possess such coenosteum (i.e. *Mycedium* and *Pectinia*) are also costate.

The character 'septal spacing (per 5 mm)' with three ordered states (character 13) was adjusted to account for several instances of variation occurring at the range of 12–13 septa per 5 mm (e.g. *Echinopora* and *Orbicella* spp.) – fewer than six, six to 11, or > 11 septa per 5 mm.

We found it unnecessary under the present set of study taxa to group species into three states for the character 'relative costosepta thickness' (character 14). Species either have unequal or equal thickness, and were thus coded as such. The height variable used by Budd *et al*. (2012) was also not as informative here because of high intraspecific variability amongst merulinids.

The character 'columella linkage' with two states (character 15) – continuous or discontinuous – was derived from 'corallite centre linkage' of Budd *et al*. (2012). Because only species with 'extracalicular budding' could have no linkage between corallite centres, the state of absence was omitted to avoid dependence between these two characters.

We made a distinction between 'development of paliform lobes' (character 18) and 'septal lobes' (character 19) that were combined as 'internal lobes' in Budd *et al*. (2012). This was necessary because some taxa (e.g. *Caulastraea*) have both types of lobes that appear to be of independent origins. These features were each characterized in three ordered states, as absent, weak, or moderate, or well developed.

We clarified the character 'tooth tips' in Budd *et al*. (2012) by recognizing that the outline of a tooth tip at midcalice may first and foremost be regular (pointed) or irregular. If the tip is not pointed, it would be shaped in more than one axis, which we define as irregular. Then we characterized its shape in more detail based on its orientation with respect to the septal outline. Thus, the characters introduced in place of 'tooth tips' are 'tooth tip outline (midcalice)' with two states (character 23) – regular (pointed) or irregular – and 'tooth tip orientation (midcalice)' with three unordered states (character 24) – parallel, perpendicular, or multiaxial.

None of the ingroup taxa have very wide (> 2 mm) tooth spacing. Only one outgroup (*Lobophyllia corymbosa*) possesses it as an autapomorphy, so the character 'tooth spacing (S1)' was limited to three ordered states (character 26) – narrow, medium, or wide – with the same ranges as Budd *et al*. (2012) for these categories.

Species differ in the number of teeth present on the major septa (i.e. septa whose proximal margins fuse with the columella). Most species either have several more than six or fewer than six, so we added to the data set a character 'more than six teeth per septum' with two states (character 27) – absent or present.

We redefined the character 'granule shape and distribution' in Budd *et al*. (2012) as two separate characters 'granule distribution' with two states (character 28) – aligned or scattered – and 'granule shape' with three unordered states (character 29) – weak, strong, or irregular. These states were used by Budd *et al*. (2012) in fixed combinations with irregular as a single state. We found that irregular granules are present in a majority of the ingroup, yet they may either be aligned or scattered. Weak granules may also be scattered but this was not a possible state in the previous analysis. The feature concerning granules that are enveloped by thickening deposits is only present in few of the outgroups, so this state was omitted.

We excluded the characters 'cs3/cs1 tooth shape' and 'wall/septum tooth size' in Budd *et al*. (2012) because these were only unequal in the outgroups *Lobophyllia corymbosa* and *Moseleya latistellata*, and not informative for the ingroup.

Although the character 'synapticulotheca' with two states (character 31) – absent or present – is most likely an autapomorphy for *Diploastrea* and not informative for relationships within the ingroup, we retained the character in the data set to facilitate diagnosis of the genus.

For microstructural characters relating to the calcification centres, we distinguished between centres that are within the costa (distal section of the costoseptum from the wall structure) and the septum (proximal section of the costoseptum). The three features that define these centres are the distinctiveness of clusters formed by centres within areas of rapid accretion, the distance between the clusters, as well as the distinctiveness of medial lines, also formed by the centres. Between the costa and septum, these features may vary even within a single costoseptum. We also found that all members of the ingroup have intercluster distances that are ≤ 0.6 mm within the costa and ≤ 0.5 mm within the septum. To describe these patterns adequately for Merulinidae, we introduced six characters each with three ordered states (characters 37–42) in place of the three describing costoseptum clusters and medial lines in Budd *et al*. (2012). The states are indistinct, weak, or strong for the centre clusters, separately for costa and septum; < 0.3, 0.3–0.6, or > 0.6 mm for intercluster distances within the costa; < 0.3, 0.3–0.5, or > 0.5 mm for distances within the septum; and absent, weak, or strong for the medial lines, separately for costa and septum.

Finally, we could not differentiate the transverse structures crossing the medial lines as clusters or carinae (lines of centres) amongst most of the specimens that possess them. We thus simplified the character 'transverse crosses' into two states (character 43) – absent or present.

Phylogenetic analyses

We performed maximum parsimony tree searches and rooted the phylogeny with *Mussa angulosa* while omitting *Diploastrea heliopora*, *Montastraea cavernosa*, and *Favia fragum* because of considerable convergence in characters that are clustering these outgroups with merulinid taxa. There is a large body of evidence supporting their distinction from the ingroup and Lobophylliidae (Fukami *et al*., 2008; Barbeitos, Romano & Lasker, 2010; Kitahara *et al*., 2010; Benzoni *et al*., 2011; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012; Huang & Roy, 2013; Marcelino *et al*., 2013). We thus regard their morphological similarities, particularly with merulinid species possessing discrete corallites, as true homoplasy and restricted the analysis to a less inclusive clade (XVII–XX). Also excluded from the analysis are 11 merulinid species for which only macromorphological data were available.

Tree searches were performed in PAUP* 4.0b10 (Swofford, 2003). We ran heuristic searches with 10 000 random addition sequences on the 78-taxon by 44-character data matrix. To assess branch support, 1000 bootstrap pseudoreplicates (Felsenstein, 1985) were carried out based on 100 random additions and a rearrangement limit of 1 000 000 per replicate. We also employed TreeRot 3 (Sorenson & Franzosa, 2007) to evaluate Bremer support (Bremer, 1988; see also Grant & Kluge, 2008) for each node. For this purpose, tree searches were carried out in PAUP* 4.0b10 with 1000 random addition replicates (rearrangement limit of 1 000 000 per replicate) for each constrained analysis.

In conjunction with the morphological tree obtained, we also used a robust molecular phylogeny as a basis for the revised classification of Merulinidae, Montastraeidae, and Diploastraeidae. This tree was inferred by Huang *et al*. (2011) under the optimization procedures of maximum likelihood, parsimony, Bayesian likelihood, and the neighbour-joining algorithm, based on a partitioned matrix consisting of 4600 characters from three nuclear and two mitochondrial loci – respectively, 28S rDNA D1 and D2 fragments (Cuif *et al*., 2003), histone H3 (Colgan *et al*., 1998); internal transcribed spacers 1 and 2 with 5.8S rDNA (Takabayashi *et al*., 1998a, b); cytochrome oxidase subunit I (Fukami *et al*., 2004a; Huang *et al*., 2008); and a noncoding intergenic region (Fukami *et al*., 2004b; Nunes *et al*., 2008). No conflicts were found amongst different methods when considering supported nodes with bootstrap value ≥ 50 and posterior probability ≥ 0.9 (Huang *et al*., 2011).

The maximum likelihood tree of Huang *et al*. (2011) inferred using RAxML 7.2.3 (Stamatakis, 2006; Stamatakis, Hoover & Rougemont, 2008) was first pruned of the two outgroup *Plesiastrea versipora* terminals for which we had no morphological data. As morphological states were consistent amongst conspecifics, it was further trimmed to species level, resulting in a 77-species phylogeny spanning clades XV to XXI (Fig. 2A). Two criteria were used for this operation: (1) the species representative must have been positively identified with type material and/or collected from the type locality; therefore tips with 'cf.' or 'aff.' were excluded; and (2) only the terminal with the best molecular data coverage amongst conspecifics was retained.

To infer the morphological evolution of Merulinidae, we mapped all 44 characters onto both the pruned molecular phylogeny and the inferred morphology tree using Mesquite 2.75 (Maddison & Maddison, 2011). Ancestral states were inferred according to maximum parsimony for both trees, but also with maximum likelihood based on the Markov k 1 (Mk1) model (Lewis, 2001) for the molecular phylogeny. By performing character transformations on each tree, we examined state changes leading to genus-level clades, and conservatively recognized them as apomorphies only when they were present under both molecular and morphological tree topologies.

To determine morphological traits that were diagnostic of monophyletic groups, we computed the consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989) for each character on the molecular and morphological trees. Character comparisons were based only on the RI as the CI does not account for autapomorphies that are uninformative for grouping species on the tree, whereas the RI is generally considered a better measure of synapomorphy (Farris, 1989). We omitted the character 'synapticulotheca' (character 31) from these calculations because it was uninformative on both trees – autapomorphic for *Diploastrea heliopora* based on the molecular reconstruction and invariable on the morphology tree.

Museum abbreviations

AS, Academia Sinica, Taipei, Taiwan; BMRI, Borneo Marine Research Institute, Universiti Malaysia Sabah, Malaysia; FEBRAS, Museum of the Zhirmunsky Institute of Marine Biology, Far East Branch, Russian Academy of Sciences, Vladivostok, Russia; GLAHM, Hunterian Museum and Art Gallery, University of Glasgow, UK; MNHN, Muséum national d'Histoire naturelle de Paris, France; MTQ, Museum of Tropical Queensland, Australia; MZS, Musée Zoologique de la ville de Strasbourg, France; NHMUK, Natural History Museum, London, UK (formerly British Museum of Natural History; BMNH); NSMT, National Museum of Nature and Science, Tokyo, Japan; PMJ, Phyletisches Museum Jena, Germany; RMBR, Raffles Museum of Biodiversity Research, Singapore; RMNH, Naturalis Biodiversity Center, Leiden, the Netherlands (formerly Rijksmuseum van Natuurlijke Historie); SIO, Scripps Institution of Oceanography, La Jolla, California, USA; SUI, Paleontology Repository of the University of Iowa, Iowa City, Iowa, USA; TIU, Tôhoku Imperial University, Sendai, Japan; UF, Florida Museum of National History, University of Florida, Gainesville, Florida, USA; UP, Marine Science Institute, University of the Philippines, Manila, the Philippines; USC, University of San Carlos, Cebu, the Philippines; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA; ZMA, Naturalis Biodiversity Center, Leiden, the Netherlands (formerly Zoological Museum Amsterdam); ZMB, Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum Berlin); ZMTAU, Zoological Museum Tel Aviv University, Tel Aviv, Israel; ZMUC, Zoologisk Museum, University of Copenhagen, Denmark; ZSI/ANRC, Zoological Survey of India, Andaman and Nicobar Regional Centre, Port Blair, India.

RESULTS

Tree searches based on the 78-taxon by 44-character data set reveal eight most parsimonious topologies that all have a tree length of 191 (Appendix S2). One of the trees has the exact same topology as the strict consensus, and thus is the primary result used for character transformations and shown in Figure 2B. The eight trees differ in three parts of the phylogeny internal to the clades of *Echinopora*, *Favites*, and *Hydnophora*, which are ill-resolved regardless. The bootstrap and Bremer support analyses show that only the Merulinidae clade (bootstrap support of 72 and decay index of 5) and nodes close to the tips are supported. The majority of clades at mid depth are only held together by decay indices of 1 and bootstrap values less than 50. Amongst the best-supported clades are the taxa *Hydnophora* (bootstrap 95, decay index 4), *Mycedium* + *Pectinia* (bootstrap 100, decay index 9), and *Orbicella* (bootstrap 96, decay index 3).

Of the eight major subclades named by Budd & Stolarski (2011) on the molecular phylogeny (Fig. 2A; Huang *et al*., 2011), only two were not recovered here (Fig. 2B). Subclade I, consisting of *Echinopora* and *Paramontastraea* – the latter added by Huang *et al*. (2011) – is paraphyletic on the morphology tree. The new genus *Paramontastraea* Huang & Budd introduced here for *Plesiastrea salebrosa* Nemenzo, 1959, and *Montastrea serageldini* Veron, 2000 is morphologically more similar to *Cyphastrea* + *Orbicella* than *Echinopora*, but this is not well supported, with only one character holding this relationship. Subclade B (*Dipsastraea* + *Coelastrea* + *Trachyphyllia*), as expected, does not cluster in the same morphological clade because of numerous traits separating *Dipsastraea* from the free-living *Trachyphyllia* and former *Goniastrea* species (*Coelastrea aspera* and *Coelastrea palauensis*). These traits include, for example, a moderate amount of coenosteum, three cycles of septa, and weak to moderate paliform lobes in *Dipsastraea*, rather than fused, limited walls or phaceloid colonies, ≥ four septal cycles, and well-developed septal lobes in the latter two genera, not to mention several differences in microstructure.

The six molecular subclades retained on the morphological phylogeny are generally well supported, and relationships amongst them differ only slightly (Fig. 2). Subclades C and I form a weak grade based on molecular data, but a relatively strong clade with morphology (bootstrap 73; note low decay index of 1). Subclades A, F, G, and H constitute a clade on both trees, although the morphological dichotomy between the uniserial clade of A + G + H and the discrete-corallite subclade F is in conflict with the molecular topology. The grouping B + D/E is concordant between the trees.

Two species, *Goniastrea australensis* and *Favites pentagona*, have inconsistent placement between the two trees. On the molecular phylogeny, the former species is recovered at a distance from subclade A, where the majority of *Goniastrea* species lie. It is also outside of subclade A on the morphology tree but slightly closer to its congenerics, owing in part to a number of macromorphological symplesiomorphies (e.g. well-developed paliform lobes). *Favites pentagona* renders *Favites* polyphyletic on the molecular phylogeny (sister to subclade D/E), but the genus is monophyletic on the morphology tree (subclade F; excluding *Favites russelli*) with *Favites pentagona* representing the deepest split in the clade. Both these hypotheses concerning *Favites* are not well supported and are in need of further tests.

A novel subclade comprising *Astrea annuligera* Milne Edwards & Haime, 1849b, *Astrea curta* Dana, 1846 and *Plesiastrea devantieri* Veron, 2000, was recovered on the morphology tree albeit with limited support. Only *Astrea annuligera* + *Astrea curta* is supported, with a bootstrap of 66, partly because the data are incomplete for *Plesiastrea devantieri*. *Favites russelli* (Wells, 1954) forms a grade with this group, and together they are part of a peculiar clade with *Goniastrea australensis* supported by molecular data (Huang *et al*., 2011). This relationship needs further study as it is currently supported by very few morphological characters, particularly with *Goniastrea australensis* and *Favites russelli* switching places between the trees.

On the basis of the 77-species molecular phylogeny (Fig. 2A), microstructural characters exhibit the lowest levels of homoplasy (mean RI = 0.807 ± SD 0.063), whereas macro- and micromorphology are more homoplastic (respectively, mean RI = 0.752 ± SD 0.127 and 0.756 ± SD 0.172), but these differences are not significant (Kruskal–Wallis test, $K = 3.39$, $P = 0.18$; all pairwise Wilcoxon tests, $P > 0.07$). Using the most parsimonious transformations, five characters (two micromorphological and three microstructural) were found to be synapomorphies of Merulinidae – perpendicular or multiaxial tooth tip orientation (character 24), irregularly shaped granules (character 29), weak costa centre clusters (character 37), ≤ 0.6 mm separating costa clusters (character 38), and ≤ 0.5 mm separating septum centre clusters (character 41). These are supported by the Mk1 model with likelihoods of at least 0.90. Only three of these (perpendicular or multiaxial tooth tip orientation, ≤ 0.6 mm separating costa clusters, and ≤ 0.5 mm separating septum centre clusters) are nonhomoplastic synapomorphies, as character state changes occur nearer the terminal branches for all other characters. For instance, Merulinidae acquires irregularity in granule shape as a synapomorphy, but granules become strong in *Cyphastrea* and weak in *Leptoria* + *Platygyra*. Similarly, costa centre clusters are weak in the most recent common ancestor of Merulinidae, but they are strengthened in at least two major lineages and become indistinct in another.

Character transformations performed on the morphological tree show that these traits are unambiguously apomorphic for merulinids amongst all inferred phylogenies. Although homoplasy is comparable amongst the three types of morphology on the molecular phylogeny, macromorphological (mean RI = 0.847 ± SD 0.096) and micromorphological (mean RI = 0.712 ± SD 0.305) traits are significantly more homoplastic on the morphology tree (Kruskal–Wallis test, $K = 9.77$, $P < 0.01$), with greater variability for the latter character type. 'Tooth tip outline' (character 23) is an autapomorphy for the outgroup *Mussa angulosa* on this tree and may account for part of this variation (RI = 0). Omitting this character from the calculation lowered the variance of micromorphology RI (SD 0.156), but only raised its mean to 0.801 (Kruskal–Wallis test, $K = 8.75$, $P = 0.01$). Microstructure retains the lowest homoplasy levels (mean RI = 0.927 ± SD 0.062; both pairwise Wilcoxon tests, $P < 0.01$).

Homoplasy is expected to be lower on the morphological phylogeny, simply because the underlying data are the 44 morphological characters. The degree to which homoplasy decreases for each character can be variable, however, because the set of minimum length trees is built with all characters. We find that the marginal tree length for each macromorphological and microstructural character is respectively discounted by 2.38 (7.95 to 5.57) and 2.31 (5.69 to 3.38) on average when going from the molecular to morphological tree, whereas the reduction is only 1.22 (4.56 to 3.33) for micromorphology, highlighting the weaker performance of the latter in recovering the internal merulinid phylogeny.

This result is unsurprising given that micromorphological traits show diagnostic differences mainly amongst major clades (*sensu* Fukami *et al*., 2008) but not within merulinid subclades (Budd & Stolarski, 2011). Most of our micromorphological characters are diagnostic of major groups, including the two with apomorphic states for Merulinidae – 'tooth tip orientation' (character 24) and 'granule shape' (character 29). The character 'more than six teeth per septum' (character 27) has below-average RI values on both the molecular and morphological trees (Table 1), but the loss of this character is a synapomorphy for the *Mycedium* + *Pectinia* clade. The worst-faring characters of all are 'tooth base outline' and 'tooth tip outline' (characters 22 and 23) that are invariant within the ingroup.

Macromorphological characters that consistently score highly in RI (Table 1) and are diagnostic of major groups include 'polymorphism' (character 3; present in *Mycedium* + *Pectinia*), 'monticules' (character 4; present in *Hydnophora*), and 'columella structure' (character 16; compact in *Cyphastrea* + *Orbicella*, *Goniastrea* + *Merulina* + *Scapophyllia*, and *Hydnophora*; lamellar in *Leptoria phrygia*, and spongy for the rest of Merulinidae).

Consistent with the analysis by Budd & Stolarski (2011), we find microstructural characters to have the highest level of congruence with both molecular and morphological trees. The three characters with states apomorphic for Merulinidae also display state changes internally amongst merulinids, such as strong costa centre clusters and septal intercluster distance of 0.3–0.5 mm in *Favites*. Several subclades can also be distinguished on the basis of the four informative characters relating to wall structure (excluding 'synapticulotheca'). For instance, subclade A (*sensu* Budd & Stolarski, 2011; *Goniastrea* + *Merulina* + *Scapophyllia*) has the unique signature of walls constructed mainly by strong abortive septa with partial septotheca.

Each of the 44 characters analysed here renders support for groups at varying phylogenetic scales. In our systematic account of the living taxa in Merulinidae, Montastraeidae, and Diploastraeidae, these characters constitute the main content for the diagnoses of Merulinidae and all the genera included in these families (Fig. 1).

DISCUSSION

The recovery of a monophyletic Merulinidae in molecular phylogenetic studies has been a challenge to explain (Huang *et al*., 2011; Arrigoni *et al*., 2012). Previous analyses have found few diagnostic characters for Merulinidae (Budd & Stolarski, 2011), and the clade was weakly supported when analysed under a morphological phylogenetic framework (Budd *et al*., 2012). We would not expect to find many synapomorphies associated with macromorphology given that there exist within Merulinidae four conventional families based on such features. Indeed, the five character states apomorphic for Merulinidae uncovered here are subcorallite in scale – two micromorphological and three microstructural. One of these, perpendicular or multiaxial tooth tip orientation, was also predicted to be a merulinid synapomorphy by Budd & Stolarski (2011). The character in question 'tooth tip orientation' (character 24) demonstrates no homoplasy (CI = 1.0, RI = 1.0), whereas most other synapomorphies show limited homoplasy (i.e. characters 29, 37, 38, and 41). Thus, the distinction of Merulinidae is apparent when observations are focused at the subcorallite level with a comprehensive sampling of the ingroup along with suitable state boundaries and parsimony model (i.e. ordering of states) for each character.

Several macromorphological traits, such as intracalicular budding (molecular tree, CI = 0.250, RI = 0.750; morphology tree, CI = 0.500, RI = 0.938) and corallite polymorphism (CI = 1.0, RI = 1.0), show limited or no homoplasy (Table 1). These are often synapomorphies for the least inclusive clade containing subclades A and B (i.e. distinguishing subclades C and I within Merulinidae), or for subclade E. For the latter case, these traits are diagnostic of Pectiniidae Vaughan & Wells, 1943, in which *Pectinia* and *Mycedium* were classified prior to revision by Budd *et al*. (2012). Our analysis shows that the efficacy of macromorphological characters is comparable to subcorallite morphology, suggesting that several of these traits should continue to serve alongside subcorallite ones as diagnostic characters for phylogenetically based taxa. Nevertheless, efforts should be focused toward discovering and testing more well-defined attributes in place of characteristics that tend to vary substantially within a genus and even species, such as calice width (character 8, CI ≤ 0.222, RI ≤ 0.611).

In spite of high homoplasy detected in micromorphology, most of these characters demonstrate high phylogenetic signal in the context of major subclades. For instance, perpendicular or multiaxial tooth tip orientation (character 24) is one of the synapomorphies of Merulinidae. Irregularity in granule shape (character 29) is a synapomorphy with changes occurring near the tree tips that reduce its RI value, yet these variations support the clades *Cyphastrea* and *Leptoria* + *Platygyra*. The performance of micromorphology in recovering the merulinid phylogeny is indeed somewhat variable, but the characters used in this study are nevertheless valuable as diagnostic traits, implying the need to supplement future analyses with more homologous micromorphological characters based on studies of skeletal growth.

Most subclades can be distinguished based on the dominance of different wall microstructural characteristics. Species are dominant in at least one type of wall morphology formed by different configurations of the rapid accretion deposits and fibres (see Budd & Stolarski, 2011), but may have secondary formation of another wall structure. For example, species in subclade B possess walls formed predominantly by dissepiments (paratheca), but may also have some elements of septal thickening (partial septotheca in *Dipsastraea*) and/or thickening perpendicular to the septa (partial trabeculotheca in *Coelastrea* and *Trachyphyllia*). Interestingly, although there is considerable signal associated with each of these characters, there are nonetheless instances of convergence at this level of morphology. Abortive septa have evolved three times independently (strong in *Goniastrea* + *Merulina* + *Scapophyllia*, weak in *Astrea* and *Echinopora*) and other characters also typically show increase or decrease in dominance of the respective wall structures in multiple parts of the tree. Our results indicate that although most morphological characters at both corallite and subcorallite scales are homoplastic, many described above are effective at distinguishing subclades and tracing their evolution.

The actual biomineralization processes associated with microstructural and micromorphological features are as yet 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 suggest that these characteristics may be taxonomically conserved (Stolarski, 2003). However, as these two ecological groups are not separate clades (Kitahara *et al*., 2010; Stolarski *et al*., 2011), phylogenetic signal could be limited for these traits. At a much finer scale, *Hydnophora exesa* appears to have a distinct chemical component present in the soluble organic matrix compared with *Hydnophora microconos*, *Hydnophora rigida*, and *Merulina scabricula*, and mineralization patterns are well varied amongst the four species (Dauphin, Cuif & Williams, 2008). Evidently, these features are useful in diagnosing individual species, but the evolutionary implications at the genus or subclade level appear to be more complicated (Budd *et al*., 2012).

The general concordance between molecular and morphological data in inferring merulinid evolution is encouraging for coral systematics, but there are variations within subclades worth mentioning, particularly with regards to intergeneric relationships. Within subclade A, *Goniastrea* (including *Astrea stelligera* Dana, 1846, but excluding species outside the subclade) is monophyletic on the morphology tree (Fig. 2B), but not on the molecular tree (Fig. 2A). This probably reflects the macromorphological contrast between the discrete-corallite *Goniastrea* and the uniserial *Scapophyllia* and *Merulina*. Support for this morphological hypothesis is not substantial however and is apparent only for two clades, *Scapophyllia* + *Merulina* and *Goniastrea edwardsi* + *Goniastrea favulus* + *Goniastrea pectinata*. The molecular topology appears well supported, but *Scapophyllia* and *Merulina* have only been analysed with one specimen per species, and there remains at least a third of the diversity in *Goniastrea* yet to be sampled. These factors need to be considered when making taxonomic decisions concerning the three genera. Nevertheless, *Astrea stelligera* Dana, 1846, is clearly sister to *Goniastrea retiformis*, the type species of *Goniastrea*. This relationship is not evident based on macromorphology, especially because of differences in wall fusion, but their subcorallite characteristics are identical and the possession of strong abortive septa firmly places them in subclade A. We thus propose the new combination *Goniastrea stelligera* (Dana, 1846).

The placement of *Goniastrea aspera* Verrill, 1866 and *Favia palauensis* Yabe & Sugiyama, 1936, in subclade B, grouping with *Dipsastraea* spp., is genetically well supported (Fig. 2A), which is not entirely surprising given that one of them was originally described under *Favia* (Yabe, Sugiyama & Eguchi, 1936). However, this relationship needs to be examined in the context of overwhelming macro- and subcorallite morphological differences between them. Their similarity with *Trachyphyllia*, also in subclade B, adds to the complication because this genus shares even fewer characters with *Dipsastraea*. Based on the long molecular branch length subtending *Trachyphyllia geoffroyi* (Huang *et al*., 2011; Arrigoni *et al*., 2012; but see Fukami *et al*., 2008), which may be symptomatic of a long-branch attraction problem even under a maximum likelihood framework (Gaut & Lewis, 1995; Huelsenbeck, 1995; Chang, 1996; Yang, 1997; Bergsten, 2005), we retain its generic status with the view that certain *Dipsastraea* species may also be more distinct (Arrigoni *et al*., 2012) and in due course afforded their own genus/genera. This interpretation is consequently extended to *Goniastrea aspera* and *Favia palauensis*, which are herein placed under *Coelastrea* Verrill, 1866 for their macromorphological similarities with *Coelastrea tenuis* Verrill, 1866. We further note that *Barabattoia* species are nested within *Dipsastraea* on both trees, although not affiliated to either *Coelastrea* or *Trachyphyllia* (Huang *et al*., 2011), and therefore propose to synonymize *Barabattoia* under *Dipsastraea*.

The relationships amongst *Caulastraea*, *Mycedium* + *Pectinia*, and *Oulophyllia* in subclade D/E are not consistent between data types (Fig. 2). This well-supported subclade is intriguing because of the diverse corallite forms ranging from discrete, uniserial to organically united, and having fused walls to being phaceloid. These dramatic evolutionary changes underlie the prior recognition of *Mycedium* and *Pectinia* in the family Pectiniidae (with *Echinophyllia* and *Oxypora*). Our analyses indicate that subcorallite characters unify this subclade, but also point to the need for more comprehensive sampling of the group, given the topological variations amongst several molecular reconstructions (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012). None of the characters examined here support the separation of *Mycedium* and *Pectinia*, corroborating the molecular hypothesis, but inadequate characters and species sampling cannot yet be ruled out as factors for the poor resolution.

The recovery of *Phymastrea valenciennesi* Milne Edwards & Haime, 1849b, *Montastraea magnistellata* Chevalier, 1971, and *Montastrea colemani* Veron, 2000 within the *Favites* clade (XVII-F) forms the basis for the synonymy of *Phymastrea* under *Favites*. Internal to the genus, these species remain clustered morphologically despite being dispersed on the molecular phylogeny (Fig. 2). Their limited coenosteum (with double wall) and nonconfluent costosepta inevitably contribute to this grouping, further evidenced by the sister species *Favites rotundata* that also has a double wall. This is just one example of many detailed in the systematic account below that illustrates the homoplastic nature of the trait 'coenosteum amount' (character 6, CI ≤ 0.174, RI ≤ 0.782; all below average). In particular, detailed analyses by Arrigoni *et al*. (2012) showed that whereas *Favites* is typically cerioid (with fused walls amongst adjacent corallites) and *Dipsastraea* plocoid (separate walls), many specimens have both wall types within the same colony, demonstrating that 'this character is not a phylogenetically informative one at either the genus or the species level' (Arrigoni *et al*., 2012: 190).

Our work has shown that there is much room to reduce homoplasy in several morphological characters used here. Quantitative approaches, including geometric morphometrics, offer a means to improve character definition and delimitation (Savriama & Klingenberg, 2011; Savriama *et al*., 2012), but such methods have so far been restricted to sets of closely related species (e.g. Budd, 1990, 1993; Budd, Johnson & Potts, 1994; Fukami *et al*., 2004b; Benzoni *et al*., 2010; Stefani *et al*., 2011; Schmidt-Roach *et al*., 2014). Recently developed procedures to dynamically apply landmark data using parsimony for tree optimization (Catalano, Goloboff & Giannini, 2010; Goloboff & Catalano, 2011; Catalano & Goloboff, 2012) present a possible solution for inferences at higher taxonomic levels where morphological convergence is rampant. More critically, a comprehensive understanding of scleractinian evolution is necessarily precluded without the integration of fossils in phylogenetic analyses and the current taxonomic classification. We may have eliminated the 'Bigmessidae' from extant coral taxa, but based on the number of genera (Wells, 1956), a bigger mess amongst extinct taxa awaits.

SYSTEMATIC ACCOUNT

Family Merulinidae Verrill, 1865: 146

Synonyms: Pectiniidae Vaughan & Wells, 1943: 196; Trachyphylliidae Verrill, 1901: 84.

Type genus
Merulina Ehrenberg, 1834: 328.

Diagnosis (apomorphies in italics)
Colonial, with intra- and/or extracalicular budding; attached or free-living. Corallites monomorphic or polymorphic; monticules may be present. Corallites discrete (1–3 mouths), uniserial or organically united. Walls fused, or with varying amount of coenosteum that may be costate or spinose. Calice of varying width (< 4 to > 15 mm) and relief (< 3 to > 6 mm). Costosepta may be confluent. Septa in varying number of cycles. Free septa may be present, regular or irregular. Septal spacing varies (< 6, 6–11, or > 11 septa per 5 mm). Costosepta may be equal or unequal in relative thickness. Columellae of varying sizes relative to calice width, and may be trabecular or lamellar; continuous or discontinuous amongst adjacent corallites. *Paliform (uniaxial) lobes may be weak/moderate or well developed*. Septal (multiaxial) lobes may be present. Epitheca and endotheca developments vary amongst species.

Tooth base at midcalice circular. Tooth tip at midcalice irregular; *tip orientation perpendicular to septum or multiaxial*. Tooth height low (< 0.3 mm) or medium (0.3–0.6 mm). Tooth spacing narrow (< 0.3 mm) or medium (0.3–1.0 mm). Number of teeth per septum varies amongst species. Granules aligned or scattered on septal face; *generally irregular in shape*. Interarea smooth, palisade, or with horizontal bands.

Synapticulotheca absent. Septotheca, abortive septa, trabeculotheca and paratheca developments vary amongst taxa. Thickening deposits fibrous without forming concentric rings. *Costa centre clusters generally weak*; *≤ 0.6 mm between clusters*; medial lines present. Septum centre clusters weak or not distinct; *≤ 0.5 mm between clusters*; medial lines present. Transverse crosses may be present. Columella centres clustered or aligned.

Genera included

1. *Merulina* Ehrenberg, 1834: 328.
2. *Astrea* Lamarck, 1801: 371.
3. *Australogyra* Veron & Pichon, 1982: 138.
4. *Boninastrea* Yabe & Sugiyama, 1935: 402.
5. *Caulastraea* Dana, 1846: 197.
6. *Coelastrea* Verrill, 1866: 32.
7. *Cyphastrea* Milne Edwards & Haime, 1848a, vol. 27: 494.
8. *Dipsastraea* de Blainville, 1830: 338.
9. *Echinopora* Lamarck, 1816: 252.
10. *Erythrastrea* Pichon, Scheer & Pillai in Scheer & Pillai, 1983: 104.
11. *Favites* Link, 1807: 162.
12. *Goniastrea* Milne Edwards & Haime, 1848a, vol. 27: 495.
13. *Hydnophora* Fischer von Waldheim, 1807: 295.
14. *Leptoria* Milne Edwards & Haime, 1848a, vol. 27: 493.
15. *Mycedium* Milne Edwards & Haime, 1851, vol. 15: 130.
16. *Orbicella* Dana, 1846: 205.
17. *Oulophyllia* Milne Edwards & Haime, 1848a, vol. 27: 492.
18. *Paraclavarina* Veron, 1985: 179.
19. *Paramontastraea* Huang & Budd gen. nov.
20. *Pectinia* de Blainville, 1825: 201.
21. *Physophyllia* Duncan, 1884: 118.
22. *Platygyra* Ehrenberg, 1834: 323.

23. *Scapophyllia* Milne Edwards & Haime, 1848a, vol. 27: 492.
24. *Trachyphyllia* Milne Edwards & Haime, 1848a, vol. 27: 492.

Taxonomic remarks

The clade Merulinidae was provisionally named 'Bigmessidae' (Budd, 2009) because of the profound confusion that surrounded the classification of four living families comprising it – Faviidae, Merulinidae, Pectiniidae, and Trachyphylliidae – prior to the comprehensive revision by Budd *et al*. (2012; see also Huang *et al*., 2011). Molecular phylogenetic analyses unequivocally showed that, other than the monotypic Trachyphylliidae, these families were not monophyletic (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012). For instance, *Trachyphyllia geoffroyi*, the only extant Trachyphylliidae species, was nested within Indo-Pacific *Favia* (now *Dipsastraea*), whereas species of Merulinidae belonged to two separate subclades within 'Bigmessidae'. Yet, most 'Bigmessidae' genera were monophyletic (the exceptions being *Favia*, *Favites*, *Goniastrea*, and *Montastraea*) (Fig. 2A; Huang *et al*., 2011), and well-defined genus-level subclades appeared to be supported by subcorallite morphological features (Budd & 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 & 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 synonymized (Budd *et al*., 2012). 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'; ICZN, 1999).

Members of Merulinidae have been closely associated in the past. Its type genus *Merulina* was initially placed in the family-level taxon Daedalina Ehrenberg, 1834: 315, along with other traditional Faviidae taxa such as *Favia* and *Platygyra* (Ehrenberg, 1834). It was only later that Verrill (1865) recognized the family-level morphological distinction between *Merulina* and the Faviidae taxa, concurred by Vaughan & 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* to either family was unclear (see Vaughan & Wells, 1943; Wells, 1956; Chevalier, 1975; Veron *et al*., 1977; Veron & Pichon, 1980; Wood, 1983; Veron, 1986, 2000). Furthermore, Trachyphylliinae Wells, 1956: F407, was a subfamily within Faviidae, and Pectiniidae was hypothesized to be very closely related (Vaughan & Wells, 1943). The historic links amongst these taxa are evidently extensive, and thus the incorporation of the entire 'Bigmessidae' clade under Merulinidae should hardly be surprising.

Several molecular studies have found *Catalaphyllia jardinei* (Saville Kent, 1893: 158, pl. 25: fig. 3, chromo pl. 4: fig. 7) to be nested within the merulinid clade (Romano & Cairns, 2000; Barbeitos *et al*., 2010; Huang, 2012; Huang & Roy, 2013). Its initial description of *Pectinia jardinei* Saville Kent, 1893: 158, suggests that it is possible to regard the monotypic *Catalaphyllia* Wells, 1971: 368, as a part of the present family. However, Saville Kent's (1893) placement of the species reflects the prevailing interpretation of his time, that *Pectinia* de Blainville, 1825, actually referred to morphotypes associated with *Meandrina* Lamarck, 1801: 372, and *Euphyllia* Dana, 1846: 157, rather than the merulinid species we know of today (Wells, 1971; note below the lack of subsequent descriptions of *Pectinia* in the 1800s). For this reason, and also because all the molecular studies have utilized the same single sample of *Catalaphyllia jardinei* from an unknown location (Romano & Palumbi, 1996), *Catalaphyllia* is herein transferred to *incertae sedis* pending further analyses.

Merulinidae is widely distributed on reefs of the Indo-Pacific, and absent in the eastern Pacific. Only one merulinid genus, *Orbicella*, inhabits the Atlantic Caribbean.

Morphological remarks

There are five synapomorphies defining Merulinidae (bootstrap support of 72 and decay index of 5): (1) perpendicular or multiaxial tooth tip orientation (likelihood of 0.99 based on the Mk1 model); (2) irregularly shaped granules (likelihood 0.90); (3) weak costa centre clusters (likelihood 0.97); with (4) ≤ 0.6 mm separating costa clusters (likelihood 0.98); and (5) ≤ 0.5 mm separating septum centre clusters (likelihood 0.96). These comprise two micromorphological and three microstructural features, respectively. Only three of these may be considered nonhomoplastic synapomorphies – perpendicular or multiaxial tooth tip orientation (two states), ≤ 0.6 mm separating costa clusters (two states), and ≤ 0.5 mm separating septum clusters (two states) – as changes occur farther away from the root of Merulinidae for all other characters. Weak to strong development of paliform lobes is also a synapomorphy according to the morphological phylogeny and one of the most parsimonious reconstructions on the molecular tree, but the likelihood based on the Mk1 model is low (0.28).

Aside from Merulinidae, paliform lobes are independently acquired in *Acanthastrea* and *Echinophyllia* of Lobophylliidae, and *Mycetophyllia* of Mussidae. The microstructural synapomorphies for Merulinidae are also present in outgroups. Weak costa centre clusters are present in Faviinae and some Lobophylliidae genera (*Cynarina*, *Echinophyllia*, *Oxypora*, and *Parascolymia*), and small separations between costa (≤ 0.6 mm) and septum (≤ 0.5 mm) clusters are found in Faviinae. Only irregular tooth tips that are multiaxial or perpendicular to the septum, and unevenly shaped granules, both micromorphological characters, are unique to Merulinidae.

GENUS *MERULINA* EHRENBERG, 1834: 328 (FIG. 3)

Synonym

Clavarina Verrill, 1864: 56 (type species: *Merulina scabricula* Dana, 1846: 275, pl. 16: figs 2, 2a, b; original designation, Verrill, 1864: 56).

Type species

Madrepora ampliata Ellis & Solander, 1786: 157, pl. 41: figs 1, 2; original designation, Ehrenberg, 1834: 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.' (Ehrenberg, 1834: 328).

Subsequent descriptions

Dana, 1846: 271, 272; Milne Edwards & Haime, 1851, vol. 15: 143; Milne Edwards & Haime, 1857, vol. 2:

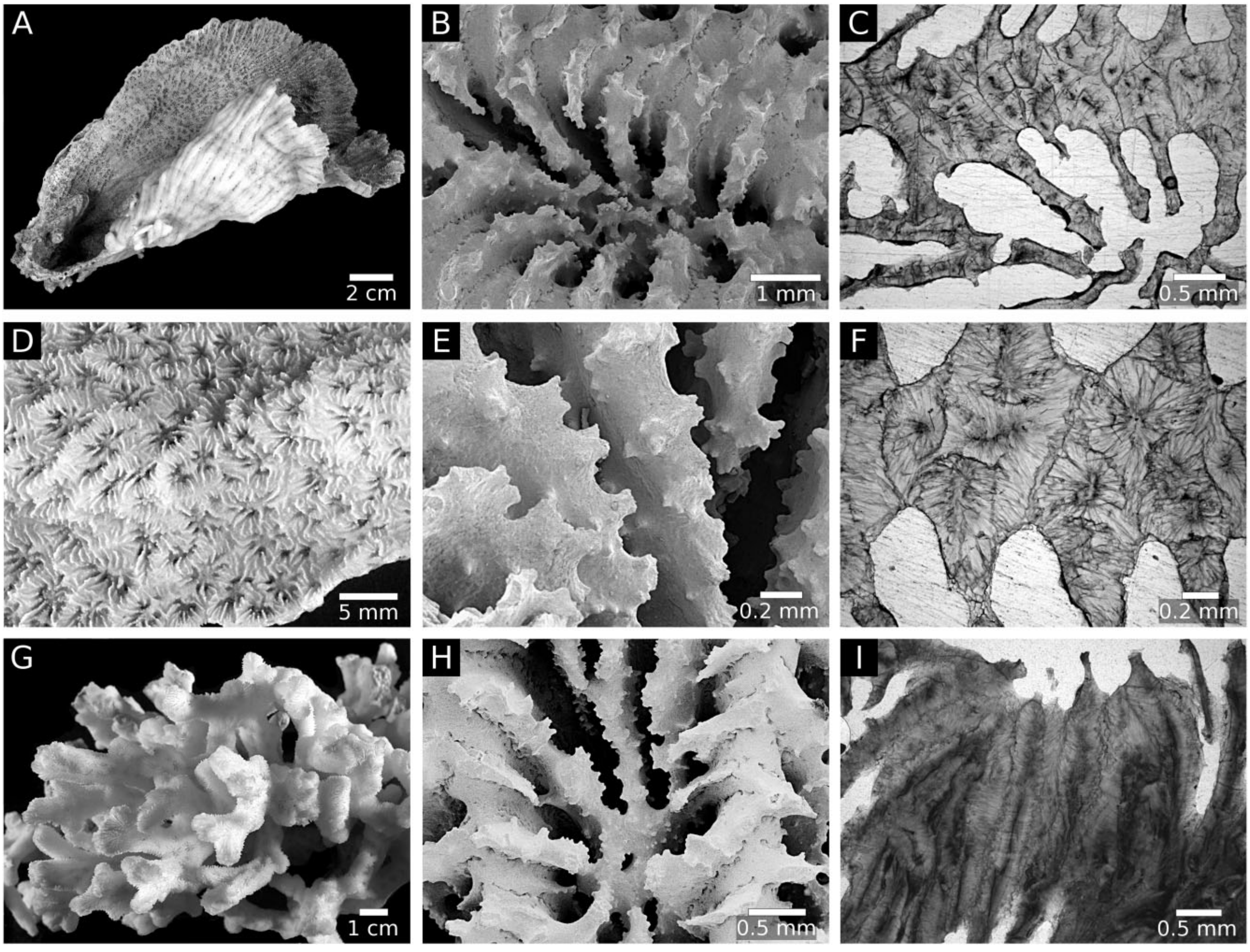


Figure 3. *Merulina* Ehrenberg, 1834, has uniserial corallites with few centres, fused walls, small (< 4 mm) and low-relief (< 3 mm) calices, septa in < three cycles (< 24 septa), compact columellae, well-developed paliform (uniaxial) lobes and no epitheca. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm). Walls formed by strong abortive septa and partial septotheca. A–F, *Merulina ampliata* (Ellis & Solander, 1786), type species of *Merulina*; macromorphology, holotype GLAHM 104015, unknown locality (A, D; photo by K. G. Johnson); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C, F), hypotype UF 2051 (FA1056), Palau. G–I, *Merulina scabricula* Dana, 1846; macromorphology (G), micromorphology (H), and microstructure (I), syntype USNM 165, Fiji.

628; Dana, 1859: 40; Verrill, 1864: 56; Quenstedt, 1881: 1031; Quelch, 1886: 109; Saville Kent, 1893: 168; Vaughan, 1918: 126; Hickson, 1924: 60, 61; Hoffmeister, 1925: 31; Faustino, 1927: 163, 164; Matthai, 1928: 125, 126; Yabe *et al*., 1936: 41; Vaughan & Wells, 1943: 190; Alloiteau, 1952: 632; Crossland, 1952: 151; Wells, 1956: F416; Nemenzo, 1959: 125; Chevalier, 1975: 208; Veron & Pichon, 1980: 216; Head, 1983: 419; Scheer & Pillai, 1983: 143, 144; Wood, 1983: 186, 187; Veron, 1986: 434; Chevalier & Beauvais, 1987: 720, 721; Veron & Hodgson, 1989: 268, 269; Sheppard, 1990: 14; Best & Suharsono, 1991: 334; Sheppard & Sheppard, 1991: 119; Veron, 2000, vol. 2: 376.

Diagnosis (apomorphies in italics)

Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; monticules absent. Walls fused. Calice width small (< 4 mm), with low relief (< 3 mm). Costosepta confluent. *Septa in < three cycles (< 24 septa)*. Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular but compact (one to three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes well developed. Epitheca absent and endotheca sparse (Fig. 3A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 3B, E, H).

Walls formed by strong abortive septa and partial septotheca; trabeculothecal elements may be present. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 3C, F, I).

Species included

1. *Merulina ampliata* (Ellis & Solander, 1786: 157, pl. 41: figs 1, 2); holotype: GLAHM 104015 (dry specimen; Fig. 3A, D); type locality: 'les mers de l'Inde' (Lamarck, 1816: 243); phylogenetic data: molecular and morphology.
2. *Merulina scabricula* Dana, 1846: 275, pl. 16: figs 2, 2a, b; syntypes: USNM 165, 167 (two dry specimens); syntypes: YPM IZ 1927A, B (two dry specimens; Fig. 3G–I); type locality: Fiji; phylogenetic data: molecular and morphology.
3. *Merulina scheeri* Head, 1983: 420, figs 1–6; holotype: NHMUK 1981.4.1.1 (dry specimen); paratypes: NHMUK 1981.4.1.2, 1981.4.1.3 (two dry specimens); type locality: West Harvey, Sudan, Red Sea, 23 m depth; phylogenetic data: none.

Taxonomic remarks

The genus was first described as part of the family Daedalina Ehrenberg, 1834: 315, and subsequently Astraeidae Dana, 1846: 154, which incorporated a diversity of genera including *Lobophyllia* de Blainville, 1830: 321, *Favia* Milne Edwards & Haime, 1857, vol. 2: 426, and *Mycedium* Milne Edwards & Haime, 1851, vol. 15: 130. The designation of *Merulina* as the type of Merulinidae Verrill, 1865, was unclear because the family name was only listed and not defined (Verrill, 1865: 146), but this had thereafter been assumed. Even as Daedalina's constituent genera were redistributed into newly erected families such as Mussidae Ortmann, 1890: 315, Faviidae Gregory, 1900: 29, Trachyphylliidae Verrill, 1901: 84, and Pectiniidae Vaughan & Wells, 1943: 196, the placement of *Merulina* remained ambiguous according to some authors (Vaughan, 1918; Hoffmeister, 1925), whereas Hickson (1924), Faustino (1927), and Matthai (1928) continued to recognize Dana's (1846) Astraeidae. The separation of *Merulina* from Faviidae Gregory, 1900, was only complete in the comprehensive treatise by Vaughan & Wells (1943).

Molecular data support *Merulina* as nested within the largest clade of *Goniastrea* but the latter is not monophyletic as it minimally excludes *G. aspera* and *G. palauensis* (Fukami *et al*., 2004a, 2008; Kitahara *et al*., 2010; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012). In contrast, the morphological tree supports *Merulina* as sister taxon to *Scapophyllia*, which together are sister group to the main clade of *Goniastrea* that includes *G. retiformis*, its type species.

Merulina is widely distributed on reefs of the Indo-Pacific, present as far east as the Austral Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

Only one synapomorphy has been found for *Merulina*: septa in < three cycles (< 24 septa; likelihood of 1.0 based on the Mk1 model). It shares all other analysed characters with *Scapophyllia*. The loss of epitheca and sparse endotheca occur at the base of the *Merulina* + *Scapophyllia* clade on the morphology tree (bootstrap support of 72), and all subcorallite character transitions occur at or before the most recent common ancestor of *Merulina*, *Scapophyllia*, and *Goniastrea*. They are therefore plesiomorphic with respect to *Merulina*.

Examination of the type material of *Merulina scheeri* at the Natural History Museum, London, suggests that this species shares all macromorphological characters with the other species in the genus, except for a thick thecal structure on the underside of the corallum.

Although the number of septa often exceeds 24, they clearly form two alternating cycles and the lower range is under 24. With its molecular phylogenetic affinity unknown, we hereby preserve its generic placement.

GENUS *ASTREA* LAMARCK, 1801: 371 (FIG. 4)

Type species
Madrepora rotulosa Ellis & Solander, 1786: 166, pl. 55: figs 1–3 (*non Astrea rotulosa* Lamarck, 1801: 371; see Article 70.3.1 of the Code); original designation, Lamarck, 1801: 371.

Original description
'Polypier pierreux, crustacé, en masse glomérulée ou en expansion lobée subfoliacée, ayant sa surface supérieure parsemée d'étoiles lamelleuses et sessiles.' (Lamarck, 1801: 371).

Subsequent descriptions
Lamarck, 1816: 257, 258; Lamouroux, 1821: 57; de Blainville, 1830: 332; Quoy & Gaimard, 1833: 199, 200; de Blainville, 1834: 366, 367; Ehrenberg, 1834: 319; Lamarck, 1836: 401–404; Dana, 1846: 200–205; Milne Edwards & Haime, 1848a, vol. 27: 494; Milne Edwards & Haime, 1849b, vol. 12: 97; d'Orbigny, 1851: 170; Milne

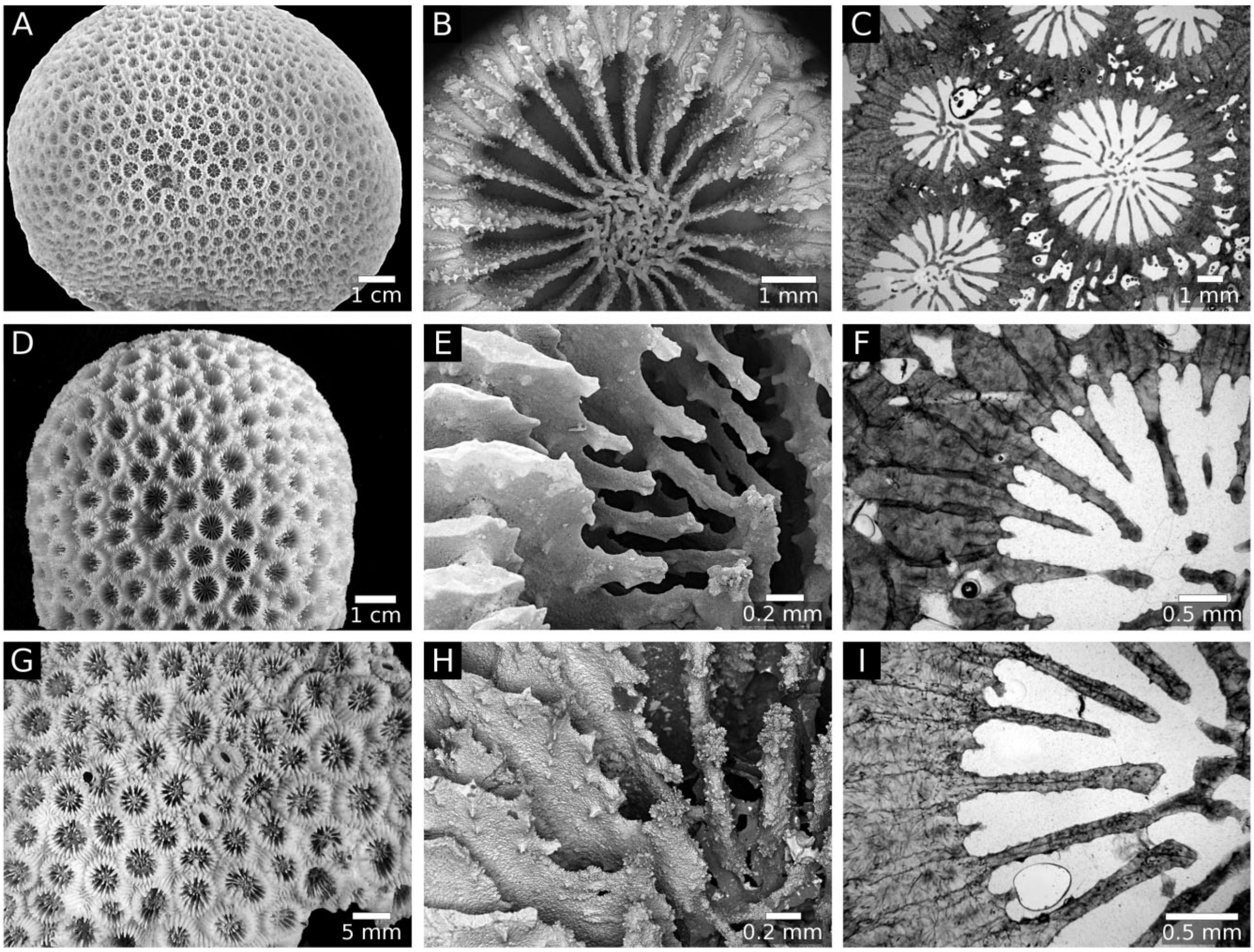


Figure 4. *Astrea* Lamarck, 1801, has discrete corallites that bud extracalicularly, medium-size (4–15 mm) and medium-relief (3–6 mm) calices, septa in three cycles (24–36 septa), well-developed paliform (uniaxial) lobes, and spongy columellae. Septal teeth with low–medium height (≤ 0.6 mm) and medium spacing (0.3–1 mm). Walls formed by dominant paratheca, partial septotheca, and weak abortive septa. A, *Astrea rotulosa* (Ellis & Solander, 1786), type species of *Astrea*; macromorphology, holotype GLAHM 104014, unknown locality (photo by KG Johnson). B–F, *Astrea curta* Dana, 1846; micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype MTQ G61882, Orpheus Island, Australia; macromorphology (D), micromorphology (E), and microstructure (F), syntype USNM 14, Fiji. G–I, *Astrea annuligera* Milne Edwards & Haime, 1849b; macromorphology, holotype MNHN IK-2010-699, Australia (G); micromorphology (H) and microstructure (I), hypotype RMNH 10718, Heron Island, Australia.

Edwards & Haime, 1857, vol. 2: 505; Dana, 1859: 22; Quenstedt, 1885: 1000; Quelch, 1886: 96; Gardiner, 1899: 747, 748.

Diagnosis (apomorphies in italics)
Colonial, with extracalicular budding; *no intracalicular budding*. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, moderate amount (< corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta not confluent. Septa in three cycles (24–36 septa). Free septa present, may be regular or irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width. Paliform (uniaxial) lobes well developed. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 4A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low to medium (≤ 0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 4B, E, H).

Walls formed by dominant paratheca and partial septotheca; *abortive septa weak*. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 4C, F, I).

Species included

1. *Astrea rotulosa* (Ellis & Solander, 1786: 166, pl. 55: figs 1–3); holotype: GLAHM 104014 (dry specimen; Fig. 4A); type locality: unknown; phylogenetic data: none.
2. *Astrea annuligera* Milne Edwards & Haime, 1849b, vol. 12: 103; holotype: MNHN IK-2010-699 (dry specimen; Fig. 4G); type locality: Australia; phylogenetic data: morphology only.
3. *Astrea curta* Dana, 1846: 209, pl. 10: fig. 3a–c; syntypes: USNM 14 (Fig. 4D–F), 22 (two dry specimens); type locality: Fiji; phylogenetic data: molecular and morphology.
4. *Astrea devantieri* (Veron, 2000, vol. 3: 228, figs 1, 2) (see also Veron, 2002: 167, figs 303–305; ICZN, 2011: 165); lectotype (designated herein): MTQ G55847 (dry specimen); type locality: Hawlaf, Socotra, Gulf of Aden, 3–12 m depth; phylogenetic data: molecular and partial morphology.

Taxonomic remarks
Astrea Lamarck, 1801: 371, is the oldest genus in Merulinidae, and was first established as part of a class of animals possessing polyps, Polypes Lamarck, 1801: 357. Sixteen of the genera were in the subdivision described as 'Polypier solide, entièrement pierreux et calcaire' (Lamarck, 1801: 369) – having polyps that are solid, completely stony and calcareous – resulting in the redistribution of species of the only stony coral genus prior to 1801, *Madrepora* Linnaeus, 1758: 793 (see Vaughan & Wells, 1943: 2, 3). Subsequent works, including Lamarck (1816: 257), de Blainville (1830: 332), and Dana (1846: 200), attributed as many as 61 species to *Astrea* before the establishment of additional genera by Milne Edwards & Haime (1848a, vol. 27: 494–496). *Astrea* was then split into several genera, and also assigned *Astrea argus* Lamarck, 1816: 259 as the type species (Milne Edwards & Haime, 1848a, vol. 27: 494), instead of *Astrea rotulosa* (Ellis & Solander, 1786: 166). Curiously, '*Astrea rotulosa* et *ananas*, Lamarck' was ascribed to be the type of *Parastrea* Milne Edwards & Haime, 1848a, vol. 27: 495, which is a synonym of *Dichocoenia* Milne Edwards & Haime, 1848a, vol. 27: 469 (see Gregory, 1895: 270).

The genus was synonymized by Matthai (1914: 84, 115), as *Favia* after recognizing types of both *Madrepora rotulosa* Ellis & Solander, 1786: 166, and *Astrea rotulosa* Lamarck, 1801: 371, to be part of *Favia*. Matthai (1914: 115) also compared Ellis & Solander's (1786: 166) type of *Madrepora rotulosa* with *Orbicella annularis*, a Caribbean species. This specimen, not *Astrea rotulosa* Lamarck, 1801: 371, or *Favia rotulosa* Ehrenberg, 1834: 319, is clearly the original designated type of *Astrea*. However, this specimen bears the closest resemblance to *Plesiastrea devantieri* Veron, 2000, vol. 3: 228, especially given their well-developed paliform lobes that are absent amongst the *Orbicella* species defined in this study. We thus revive this genus to include *Madrepora rotulosa*, *Plesiastrea devantieri*, as well as species that have been found to be closely related genetically and morphologically.

Astrea is widely distributed on reefs of the Indo-Pacific, recorded throughout most of French Polynesia and the Pitcairn Islands in the Southern Hemisphere (Glynn *et al.*, 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks
Astrea rotulosa has not been placed on the molecular phylogeny, but it is most similar to *Astrea devantieri*. Each macromorphological character examined is the same state for both species, except for the more compact columellae in the type specimen of the former. Spongy columellae can however be found in *Favia rotulosa* specimens studied by Ehrenberg (1834: 319; ZMB Cni 739II), and Wijsman-Best (1974: 258, pl. 4, fig. 4; ZMA Coel. 8888), collected from the Red Sea and Indonesia, respectively. Consequently, we hypothesize that *Astrea devantieri*, thus far recorded only from Socotra (type

locality), Madagascar, and Mayotte (Veron, 2002; Benzoni *et al*., 2011), is a sister species to *Astrea rotulosa*. Although we have limited data to place all *Astrea* spp. on the tree concomitantly, we infer that *Astrea annuligera* Milne Edwards & Haime, 1849b, vol. 12: 103, and *Astrea curta* Dana, 1846: 209, are closely related based on morphology.

As this genus is represented only by *Astrea curta* on the molecular tree, no synapomorphies are diagnosed – absence of intracalicular budding and weak abortive septa are autapomorphies. On the morphological phylogeny, however, these features are synapomorphies.

Goniastrea australensis has been recovered as the sister taxon to *Astrea curta* + *Favites russelli* in one instance (Huang *et al*., 2011; but see Arrigoni *et al*., 2012). Morphologically, *Goniastrea australensis* is very distinct from *Astrea* as it lacks extracalicular budding, has uniserial corallites, fused walls, confluent costosepta, evenly thick costosepta, and narrow distance between septum centre clusters (< 0.3 mm). Most of these characters, except uniserial corallites and confluent costosepta, and many others, also separate the *Goniastrea* proper from this genus.

Favites russelli is the sister taxon to *Astrea* on the molecular tree, but it buds intracalicularly and does not have abortive septa. Therefore it cannot be considered in the latter genus.

GENUS *AUSTRALOGYRA* VERON & PICHON, 1982: 138 (FIG. 5)

Type species
Platygyra zelli Veron, Pichon & Wijsman-Best, 1977: 110, figs 214–222, 459; original designation, Veron & Pichon, 1982: 138.

Original description
'This species was described in Part II, p. 110 as *Platygyra zelli*, where it was noted that 'the ramose growth form of this species, combined with the normal lack of a columella, separates it from all other *Platygyra* and makes its generic affinities obscure . . . As this is a monospecific genus, its characters are those of *zelli*.

["Colonies are up to 25 cm high and have main branches 1.5–3 cm in diameter. Actively growing branch ends are composed of intricate arrays of thecae and elongated septa reminiscent of branch tips of

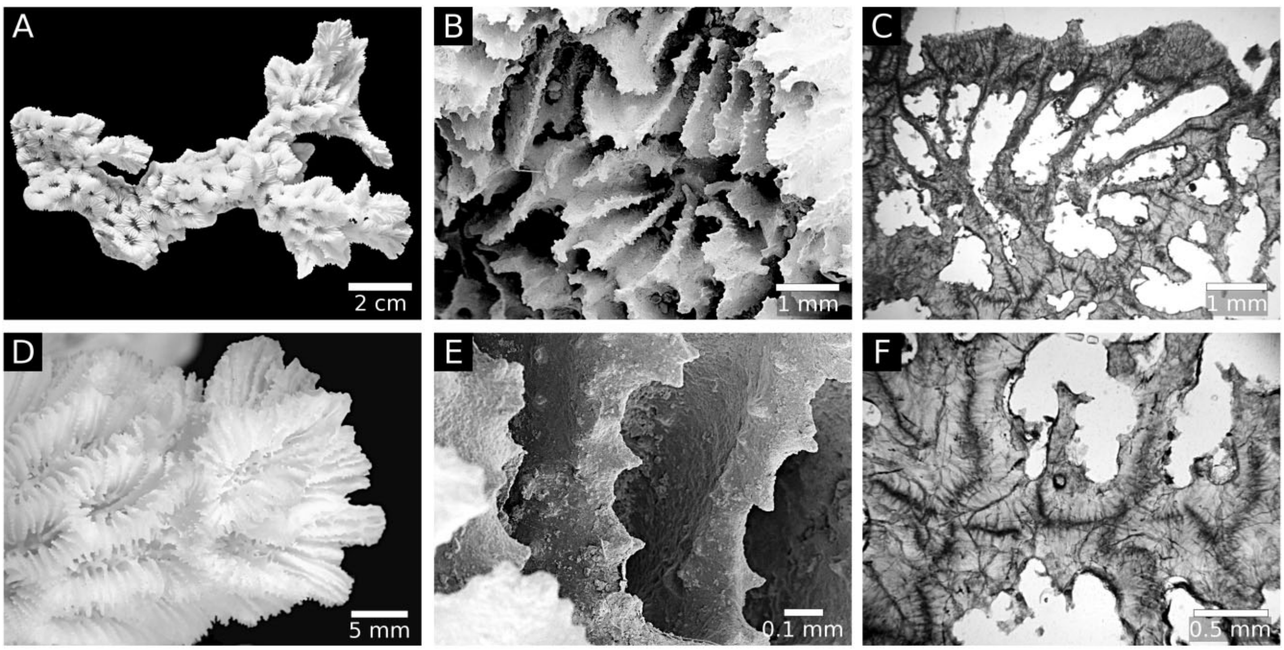


Figure 5. *Australogyra* Veron & Pichon, 1982, is ramose and has uniserial corallites with few centres, fused walls, septa in < three cycles (< 24 septa), equally thick costosepta and compact columellae. Septal teeth are low (< 0.3 mm) with medium spacing (0.3–1 mm); weak (rounded) granules aligned on septal face. Walls formed by dominant trabeculotheca and partial septotheca, with strong septal medial lines and aligned columella centres. A–F, *Australogyra zelli* (Veron, Pichon & Wijsman-Best, 1977), the type and only living species of *Australogyra*; macromorphology, holotype NHMUK 1977.1.1.4, Orpheus Island, Australia (A; photo by H. Taylor), and paratype MTQ G59708, Eclipse Island, Australia (D); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C, F), hypotype USNM 76312, the Philippines.

Hydnophora rigida on a larger scale. Dead skeleton forms the base of most colonies. The valleys are short and usually monocentric. The walls are thick (2–4 mm) especially towards the base of colonies where skeletal parts are heavily calcified. Valleys are usually shallow with smooth blister-like floors. There is usually no sign of a columella, although elongated, recurved septal dentations are occasionally found and occasionally these form a distinct columella. The septa are similar to those of *P. daedalea* and *P. lamellina*. They are dentate and have fine granulations on their sides. Some dentations are twisted to form tiny horizontal plates fringed with granulations, presumably sclerodermites." (Veron *et al*., 1977: 110)]' (Veron & Pichon, 1982: 138).

Subsequent descriptions
Veron, 1986: 494; Veron, 2000, vol. 3: 194.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic, uniserial, and ramose; monticules absent. Walls fused. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in < three cycles (< 24 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular but compact (one to three threads) or absent, < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 5A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules aligned on septal face, perpendicular to septal margin; weak (rounded). Interarea palisade (Fig. 5B, E).

Walls formed by dominant trabeculotheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines strong. Transverse crosses absent. Columella centres aligned (Fig. 5C, F).

Species included
Australogyra zelli (Veron, Pichon & Wijsman-Best, 1977: 110, figs 214–222, 459); holotype: NHMUK 1977.1.1.4 (dry specimen; Fig. 5A); paratype: MTQ G59708 (dry specimen; Fig. 5D); type locality: Pioneer Bay, Orpheus Island, Palm Islands, Australia, 3 m depth; phylogenetic data: morphology only.

Taxonomic remarks
Australogyra Veron & Pichon, 1982: 138, is a monotypic genus sister to *Platygyra* on the morphological phylogeny. This relationship is reflected in its taxonomic history, as *Australogyra zelli* was initially described as a *Platygyra* species, and only put in its own genus later.

Australogyra is only present in the Great Barrier Reef and Coral Sea of Australia, Papua New Guinea, and south Sulawesi (Hoeksema & van Ofwegen, 2004).

Morphological remarks
As suggested by the original description (Veron & Pichon, 1982: 138), it shares almost all characters with *Platygyra*, differing only in having a compact or no columella. Our character trace suggests that this state is plesiomorphic, and hence no apomorphies are yet present for the genus. The ramose growth form also distinguishes it from *Platygyra*. Molecular data would further clarify its phylogenetic placement.

GENUS *BONINASTREA* YABE & SUGIYAMA, 1935: 402 (FIG. 6)

Type species
Boninastrea boninensis Yabe & Sugiyama, 1935: 402, pl. 10: figs 1, 2; original designation, Yabe & Sugiyama, 1935: 402.

Original description
'Corallum compound, massive; calicular surface strongly convex. Epitheca indicated by fine ringlets of growth, thin, conspicuous, covering almost entirely underside. Calices numerous, subpolygonal, irregular in shape and arrangement oblique; usually one to three or more in number circumscribed in group by incomplete, oblique collines. Occasionally several of the groups are further bounded by prominent, incomplete, oblique ridges. In each group calices connected by trabecular bridges instead of toothed lamellae. Septa not numerous, up to three cycles, those of the first and some of the second cycles more stout and more prominent than others; their free ends strongly divided in irregular manner, to filiform processes. Surface of septa minutely granulated. Columella absent? Dissepiments numerous, vesicular. Growth by fission.' (Yabe & Sugiyama, 1935: 402).

Subsequent descriptions
Yabe *et al*., 1936: 45; Vaughan & Wells, 1943: 190; Wells, 1956: F416; Veron, 1986: 594; Chevalier & Beauvais, 1987: 721; Best & Suharsono, 1991: 339; Veron, 2000, vol. 2: 382.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; monticules absent. Walls fused. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in < three cycles (< 24 septa). Free septa present but irregular.

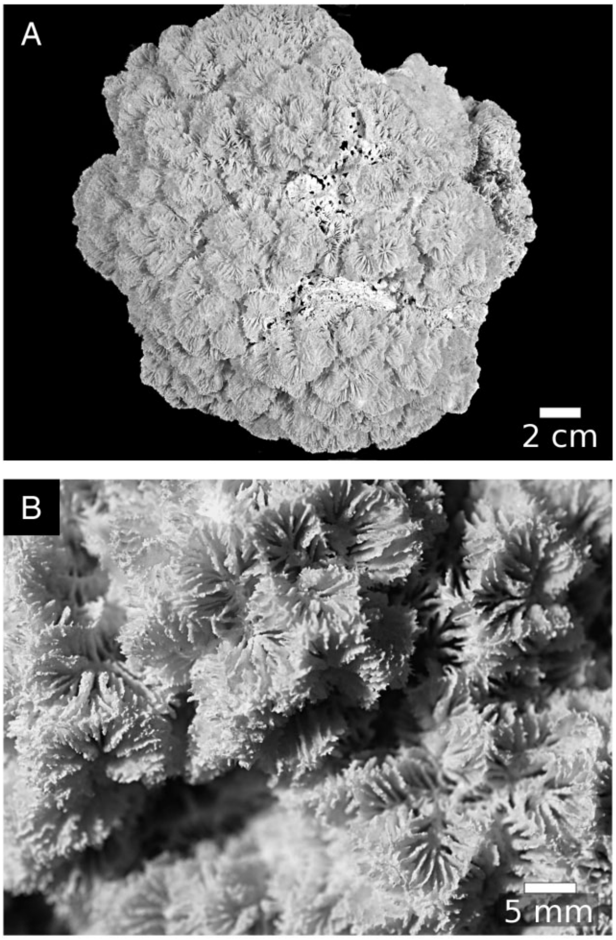


Figure 6. *Boninastrea* Yabe & Sugiyama, 1935, has uniserial corallites, fused walls, septa in < three cycles (< 24 septa), unequally thick costosepta, rudimentary columellae, and abundant (vesicular) endotheca. A, B, *Boninastrea boninensis* Yabe & Sugiyama, 1935, the type and only living species of *Boninastrea*; macromorphology, holotype TIU 44970, Ogasawara Islands, Japan.

Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular but compact (one to three threads) or absent, < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes weak or absent. Epitheca well developed and endotheca abundant (vesicular) (Fig. 6).

Species included
Boninastrea boninensis Yabe & Sugiyama, 1935: 402, pl. 10: figs 1, 2; holotype: TIU 44970 (dry specimen; Fig. 6); type locality: Futami-wan, Titi-zima, Ogasawara Islands, Japan; phylogenetic data: none.

Taxonomic remarks
Boninastrea Yabe & Sugiyama, 1935: 402, is a monotypic genus that has only been collected twice, once each in Japan (type locality) and Indonesia, and never for molecular analysis. We do not have sufficient data to place it on the tree, but note that it has been described as a 'mussoid [*sic*] coral, recalling *Symphyllia* and *Isophyllia* in general feature' (Yabe & Sugiyama, 1935: 402), but later placed in Merulinidae (prior to Budd *et al*., 2012) by Veron (1986: 594), Best & Suharsono (1991: 339), and Veron (2000, vol. 3: 382).

Boninastrea is known only from its type locality, the Ogasawara Islands of Japan, as well as Sumbawa (Best & Suharsono, 1991), Gulf of Tomini, Banda Sea, and the Moluccas of Indonesia.

Morphological remarks
In comparison with genera that were in Merulinidae before Budd *et al*. (2012), it does not appear to share the small calice width, low relief, equal costosepta thickness, well-developed paliform lobes, absence of epitheca, and sparse endotheca with *Merulina* and *Scapophyllia*. Its size and lack of lobes are akin to most *Hydnophora* spp., and the 'prominent, incomplete, oblique ridges' are analogous to monticules of *Hydnophora*, but homology cannot be ascertained without further sampling.

GENUS *CAULASTRAEA* DANA, 1846: 197 (FIG. 7)

Synonyms
Astraeosmilia Ortmann, 1892: 664 (type species: *Astraeosmilia connata* Ortmann, 1892: 664; original designation, Ortmann, 1892: 664); *Astreosmilia* Veron, 1986: 595 (misspelling); *Caulastrea* Vaughan & Wells, 1943: 165 (misspelling); *Dasyphyllia* Milne Edwards & Haime, 1848a, vol. 27: 492 (type species: *Dasyphyllia echinulata* Milne Edwards & Haime, 1849a, vol. 11: 265, vol. 10, pl. 8: fig. 5; subsequent designation, Milne Edwards & Haime, 1849a, vol. 11: 265).

Type species
Caulastraea furcata Dana, 1846: 198, pl. 9: figs 4, 4a–c; original designation, Dana, 1846: 198.

Original description
'Segregato-gemmate, cespitose, with the stems and calicles subcylindrical. Coralla fragile, exterior excavate; lamellae unequally exsert, subentire, very numerous.' (Dana, 1846: 197).

Subsequent descriptions
Milne Edwards & Haime, 1857, vol. 2: 188; Dana, 1859: 22; Duncan, 1884: 77; Quelch, 1886: 74; Saville Kent, 1893: 160; Delage & Hérouard, 1901: 617; Matthai, 1928: 272; Yabe *et al*., 1936: 19; Vaughan & Wells, 1943: 165; Alloiteau, 1952: 616; Crossland, 1952: 139; Wells, 1956: F401; Nemenzo, 1959: 83; Wijsman-Best, 1972: 54; Chevalier, 1975: 101; Veron *et al*., 1977: 11; Scheer &

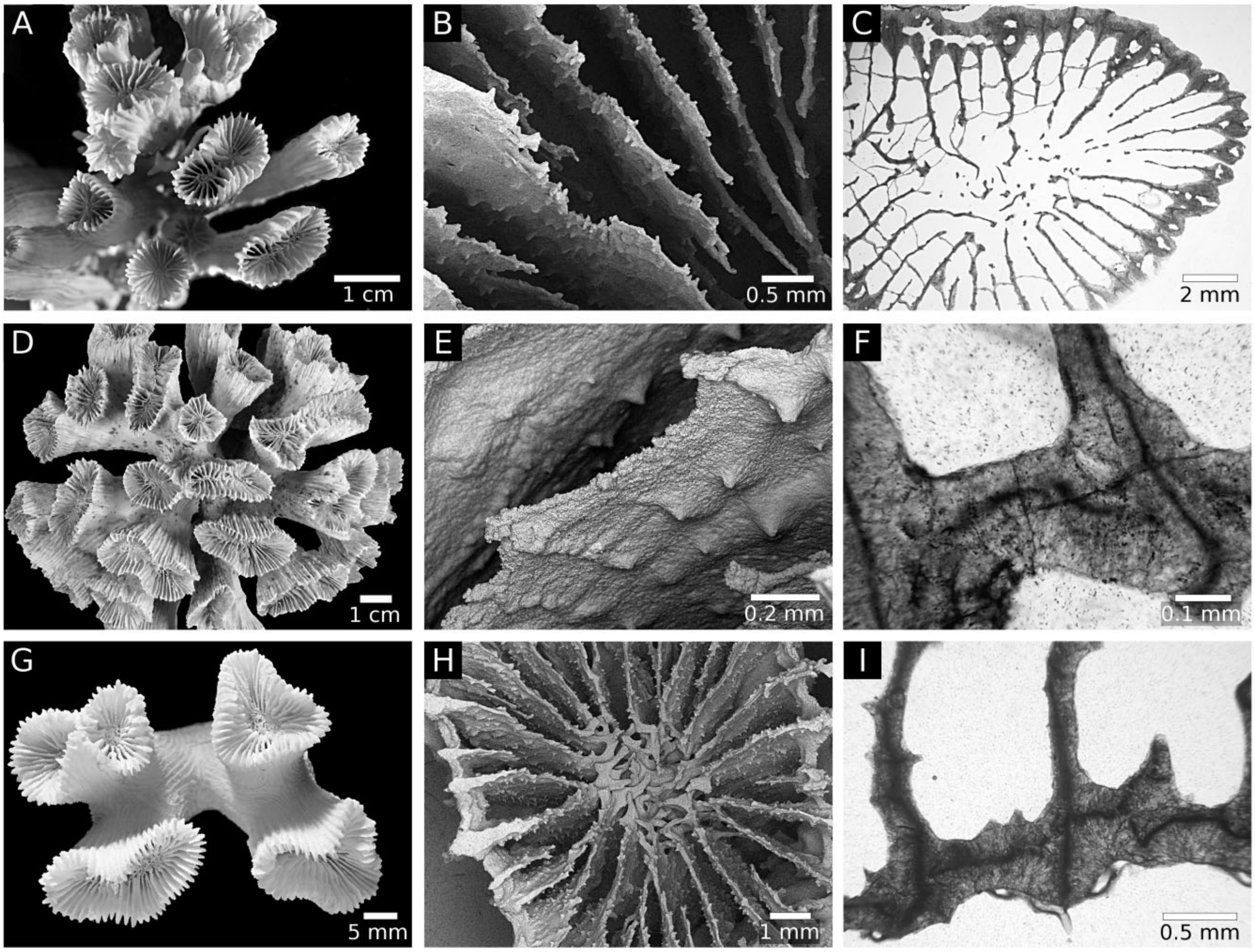


Figure 7. *Caulastraea* Dana, 1846, is phaceloid, with discrete corallites, equally thick costosepta spaced < six septa per 5 mm, weak/moderate paliform (uniaxial) and septal (multiaxial) lobes, and abundant (vesicular) endotheca. Septal teeth are low (< 0.3 mm) with medium spacing (0.3–1 mm). Walls formed by dominant paratheca, with strong costal and septal medial lines, and transverse septal crosses. A–C, *Caulastraea furcata* Dana, 1846, type species of *Caulastraea*; macromorphology, syntype USNM 80, Fiji (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 92394 (FA1035), Palau. D–F, *Caulastraea echinulata* (Milne Edwards & Haime, 1849a); macromorphology, holotype MNHN IK-2010-536, Singapore (D); micromorphology (E) and microstructure (F), hypotype RMNH 10752, Ambon, Indonesia. G–I, *Caulastraea tumida* Matthai, 1928; macromorphology, holotype NHMUK 1928.6.2.1, King's Sound, Australia (G; photo by H. Taylor); micromorphology (H) and microstructure (I), hypotype RMNH 21563, north of Komodo, Indonesia.

Pillai, 1983: 103; Wood, 1983: 142; Veron, 1986: 446; Chevalier & Beauvais, 1987: 718; Veron & Hodgson, 1989: 269; Sheppard & Sheppard, 1991: 120; Budd & Johnson, 1999: 38; Veron, 2000, vol. 3: 91.

Diagnosis (apomorphies in italics)
Colonial, with intracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. *Phaceloid.* Calice width medium (4–15 mm), with medium relief (3–6 mm). Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) and *septal (multiaxial) lobes weak or moderate.* Epitheca absent and endotheca abundant (vesicular) (Fig. 7A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. *Tooth height low (< 0.3 mm)* and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 7B, E, H).

Walls formed by dominant paratheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters not distinct; medial lines strong. Septum centre clusters not distinct; medial lines strong. Transverse crosses present. Columella centres clustered (Fig. 7C, F, I).

Species included

1. *Caulastraea furcata* Dana, 1846: 198, pl. 9: figs 4, 4a–c; syntype: USNM 80 (dry specimen; Fig. 7A); syntypes: YPM IZ 1986A, B, 4295 (three dry specimens); type locality: Fiji; phylogenetic data: molecular and morphology.
2. *Caulastraea connata* (Ortmann, 1892: 664); holotype: lost (not found in MZS, PMJ, and ZMB); type locality: Dar es Salaam, Tanzania; phylogenetic data: none.
3. *Caulastraea curvata* Wijsman-Best, 1972: 56, pl. 14: figs 3, 4; holotype: ZMA Coel. 5988 (dry specimen); paratypes: ZMA Coel. 5986, 5987, 5989 (three dry specimens); type locality: Baie de Prony, New Caledonia, 5 m depth; phylogenetic data: morphology only.
4. *Caulastraea echinulata* (Milne Edwards & Haime, 1849a, vol. 11: 265, vol. 10, pl. 8: fig. 5); holotype: MNHN IK-2010-536 (dry specimen; Fig. 7D); type locality: Singapore; phylogenetic data: molecular and morphology.
5. *Caulastraea tumida* Matthai, 1928: 275, pl. 72: figs 5, 6; holotype: NHMUK 1928.6.2.1 (dry specimen; Fig. 7G); type locality: King's Sound, Australia; phylogenetic data: molecular and morphology.

Taxonomic remarks

This genus was established by Dana (1846: 197) as part of the family Astraeidae Dana, 1846: 154 (see also Matthai, 1928: 272–273). He posited that *Caulastraea* is affiliated to *Caryophyllia* Lamarck, 1801: 370, and *Mussa* Oken, 1815: 73 (Dana, 1846: 198), placing it in a subdivision comprising corals that are massive ('glomerate') or 'calicularly branched' (Dana, 1846: 157). This united *Caulastraea* with a diverse group of genera, including *Tridacophyllia* de Blainville, 1830: 327 (= *Pectinia* de Blainville, 1825: 201), *Astrea* Lamarck, 1801: 371, and *Monticularia* Lamarck, 1816: 248 (= *Hydnophora* Fischer von Waldheim, 1807: 295), all of which are currently in Merulinidae. This association persisted for almost a century before Pectiniidae Vaughan & Wells, 1943: 196, was erected for *Pectinia* and *Mycedium*, amongst others, and *Caulastraea* transferred to Faviidae Gregory, 1900: 29.

This genus is relatively well sampled, with only *Caulastraea connata* yet to be placed on the phylogeny. It was only recently that Veron (2000, vol. 3: 91) synonymized *Astraeosmilia* Ortmann, 1892: 664, as *Caulastraea* Dana, 1846: 197, resulting in the genus change of *Astraeosmilia connata* Ortmann, 1892: 664.

Caulastraea is widely distributed on reefs of the Indo-Pacific, recorded as far east as the Pitcairn Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

Molecular and morphological data support *Caulastraea*, *Mycedium*, *Oulophyllia*, and *Pectinia* as a monophyletic group (subclade XVII-D/E; Huang *et al*., 2011; Arrigoni *et al*., 2012), even though they differ in almost one-third of all macromorphological characters examined. Subcorallite characters, including DNA sequences, are therefore the main source of synapomorphies for this clade.

Caulastraea is a well-defined and well-supported genus (bootstrap support of 89 and decay index of 3). The phaceloid colony form (likelihood of 1.0 based on the Mk1 model), weak or moderate septal lobes (likelihood 1.0), and low tooth height (likelihood 1.0) are identified as synapomorphies that clearly distinguish it from the above closely related genera. It is the only Merulinidae genus with phaceloid attached colonies and possesses septal lobes that are not as well developed as those in *Coelastrea*, *Goniastrea*, and *Trachyphyllia*.

GENUS *COELASTREA* VERRILL, 1866: 32 (FIG. 8)

Type species

Coelastrea tenuis Verrill, 1866: 33; original designation, Verrill, 1866: 33.

Original description

'Corallum massive, cellular, fasciculate, formed by prismatic coralites [*sic*] intimately united by their walls which are thin and simple. The exterior of the corallum is destitute of an epitheca, lobed and distinctly costate like that of *Metastrea*. The cells are polygonal, often closed below by the dissepiments, which, occuring [*sic*] at the same level, unite from all sides forming thus transverse septa. In a transverse section traces of a very rudimentary and loose columella are seen in some cells. Septa in three or four cycles, unequal, the inner edges prolonged into strong paliform teeth.

The polyps increase by fissiparity, and near the margin by disk-budding. This genus appears to bear the same relation to *Goniastrea* that *Metastrea* does to *Prionastrea*, differing from it in the absence of epitheca and the lobed and striated exterior, thinness of the walls, and rudimentary columella. From *Metastrea* it differs in the last character, and in its mode of increase as well as in the coincidence of the dissepiments and the strong pali.' (Verrill, 1866: 32).

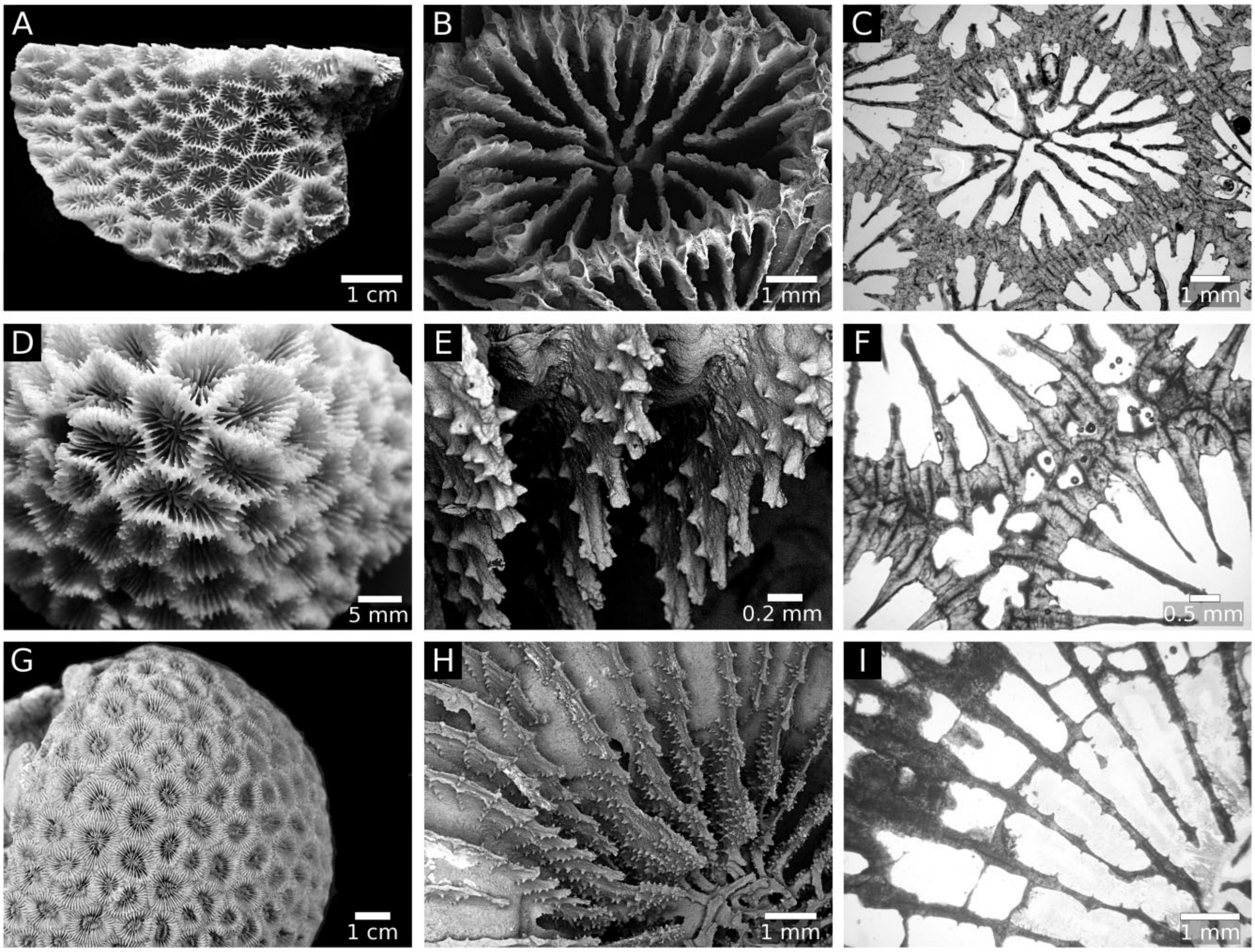


Figure 8. *Coelastrea* Verrill, 1866, has discrete corallites with double or fused walls, septa in ≥ four cycles (≥ 48 septa), regular free septa, and well-developed septal (multiaxial) lobes. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm). Walls formed by dominant paratheca and partial septotheca, with strong costal and septal medial lines. A, *Coelastrea tenuis* Verrill, 1866, type species of *Coelastrea*; macromorphology, holotype YPM IZ 476, unknown locality. B–F, *Coelastrea aspera* (Verrill, 1866); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), syntype USNM 402, Ryukyu Islands, Japan; macromorphology, syntype USNM 403, Ryukyu Islands, Japan (D); micromorphology (E) and microstructure (F), hypotype RMNH 13844, Gulf of Aqaba, Israel. G–I, *Coelastrea palauensis* (Yabe & Sugiyama, 1936); macromorphology, holotype TIU 56631, Palau (G); micromorphology (H) and microstructure (I), hypotype RMNH 14084, New Caledonia.

Subsequent descriptions
Leuckart, 1869: 214; Vaughan, 1907: 104; Vaughan & Wells, 1943: 168; Chevalier & Beauvais, 1987: 714.

Diagnosis (apomorphies in italics)
Colonial, with intracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, *limited amount (includes double wall) or fused walls*. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta not confluent. Septa in ≥ four cycles (≥ 48 septa). *Free septa regular.* Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Septal (multiaxial) lobes well developed. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 8A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 8B, E, H).

Walls formed by dominant paratheca and partial septotheca; trabeculothecal elements may be present;

abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines strong. Transverse crosses present. Columella centres clustered (Fig. 8C, F, I).

Species included

1. *Coelastrea tenuis* Verrill, 1866: 33; holotype: YPM IZ 476 (dry specimen; Fig. 8A); type locality: 'Sandwich Islands?' (Verrill, 1866: 33); phylogenetic data: none.
2. *Coelastrea aspera* (Verrill, 1866: 32); syntypes: USNM 402, 403 (two dry specimens; Fig. 8B–D); type locality: Ryukyu Islands, Japan; phylogenetic data: molecular and morphology.
3. *Coelastrea palauensis* (Yabe & Sugiyama in Yabe *et al*., 1936: 30, pl. 19: figs 5, 6); holotype: TIU 56631 (dry specimen; Fig. 8G); type locality: Palau; phylogenetic data: molecular and morphology.

Taxonomic remarks
Coelastrea was described by Verrill (1866: 33) based on the type specimen of *Coelastrea tenuis* collected by Dana during the US Exploring Expedition (1838–1842). The original museum label states 'Sandwich Islands?', referring tentatively to Hawai'i. The genus description was subsequently reproduced in Leuckart (1869: 214) and Vaughan (1907: 104, pl. 26: figs 2, 2a). The latter furthermore repeated Verrill's description of the species, which was listed by Studer (1901: 398) as one of several species from Hawai'i described by Verrill. An unidentified *Coelastrea* sp. from the locality was also figured in Bryan (1915, pl. 111: fig. 12).

Coelastrea was recognized as a distinct genus in Vaughan & Wells (1943: 168) with a note regarding its type locality being 'reputedly the Hawaiian Islands'. It was later synonymized by Wells (1956: F402) with *Goniastrea*. The status of the type species was not addressed, although it was presumably transferred into *Goniastrea*. More recently, Chevalier & Beauvais (1987: 714) listed *Coelastrea* as a valid genus and added Malaysia to its known range. However, there is much doubt that any living specimen has been collected since the initial description, certainly not in Hawai'i (D. Fenner, pers. comm.) where *Goniastrea* is not known to be present (Veron, 2000; Veron *et al*., 2009). Records of live *Coelastrea tenuis* being exported out of El Salvador in the eastern Pacific and an unspecified locality in the USA between 1996 and 1997 were reported by CITES (2001), but these were not substantiated by voucher collections and thus most likely misidentifications. Fossil corals from the Plio-Pleistocene of Nias, an island off western Sumatra, Indonesia, were attributed to this species as *Goniastrea tenuis* by Boekschoten *et al*. (1989: 118), along with *Goniastrea edwardsi* and *Goniastrea pectinata*.

We posit that *Coelastrea tenuis* may have been identified as *Goniastrea aspera* Verrill, 1866: 32, in more recent treatments, but without a more extensive investigation, we are unable to verify the species status of *Coelastrea tenuis*. On the bases that *Goniastrea aspera* and *Favia palauensis* Yabe & Sugiyama, 1936: 30, pl. 19: figs 5, 6, match *Coelastrea tenuis* in nearly all macromorphological characters (i.e. lack of spongy columellae in *Coelastrea tenuis*), and that they are distinct from the rest of the *Goniastrea* on both molecular and morphology trees, we resurrect the genus *Coelastrea* and transfer these species into it.

Coelastrea is widely distributed on reefs of the Indo-Pacific, and absent in the eastern Pacific. It is also not likely to be found in Hawai'i, as no living *Coelastrea tenuis* has been positively identified from Hawai'i and eastwards.

Morphological remarks
Coelastrea is a well-supported clade on the morphology tree, with bootstrap support of 86 and decay index of 2. Two synapomorphies have been identified for this genus: limited coenosteum or fused walls (likelihood of 0.60 based on the Mk1 model) and presence of regular free septa (likelihood 0.98). These apomorphies distinguish it from closely related genera, in particular *Dipsastraea* and *Trachyphyllia*, but they are also present in part amongst *Goniastrea*. Most *Goniastrea* spp. have fused walls, and regular free septa are present in *Goniastrea retiformis* and *Goniastrea stelligera*. Other characters, mostly subcorallite ones, are more useful for separating *Coelastrea* and *Goniastrea*, e.g. more septa (≥ four cycles), parathecal walls (no abortive septa), strong costa and septum medial lines, and transverse septal crosses in *Coelastrea*.

The present phylogenetic analysis is based on the clade *Coelastrea aspera* + *Coelastrea palauensis*. *Coelastrea tenuis*, if valid, most resembles *Coelastrea aspera*, differing only in the lack of spongy columellae, and in some corallites, having no columella at all. Its corallites are also more irregular in terms of size and shape (see Vaughan, 1907: 105).

GENUS *CYPHASTREA* MILNE EDWARDS & HAIME, 1848A: 494 (FIG. 9)

Type species
Astrea microphthalma Lamarck, 1816: 261; original designation, Milne Edwards & Haime, 1848a, vol. 27: 494.

Original description
'Diffère des trois genres précédents [*Astrea*, *Plesiastrea*, *Solenastrea*] par la compacité du coenenchyme et par

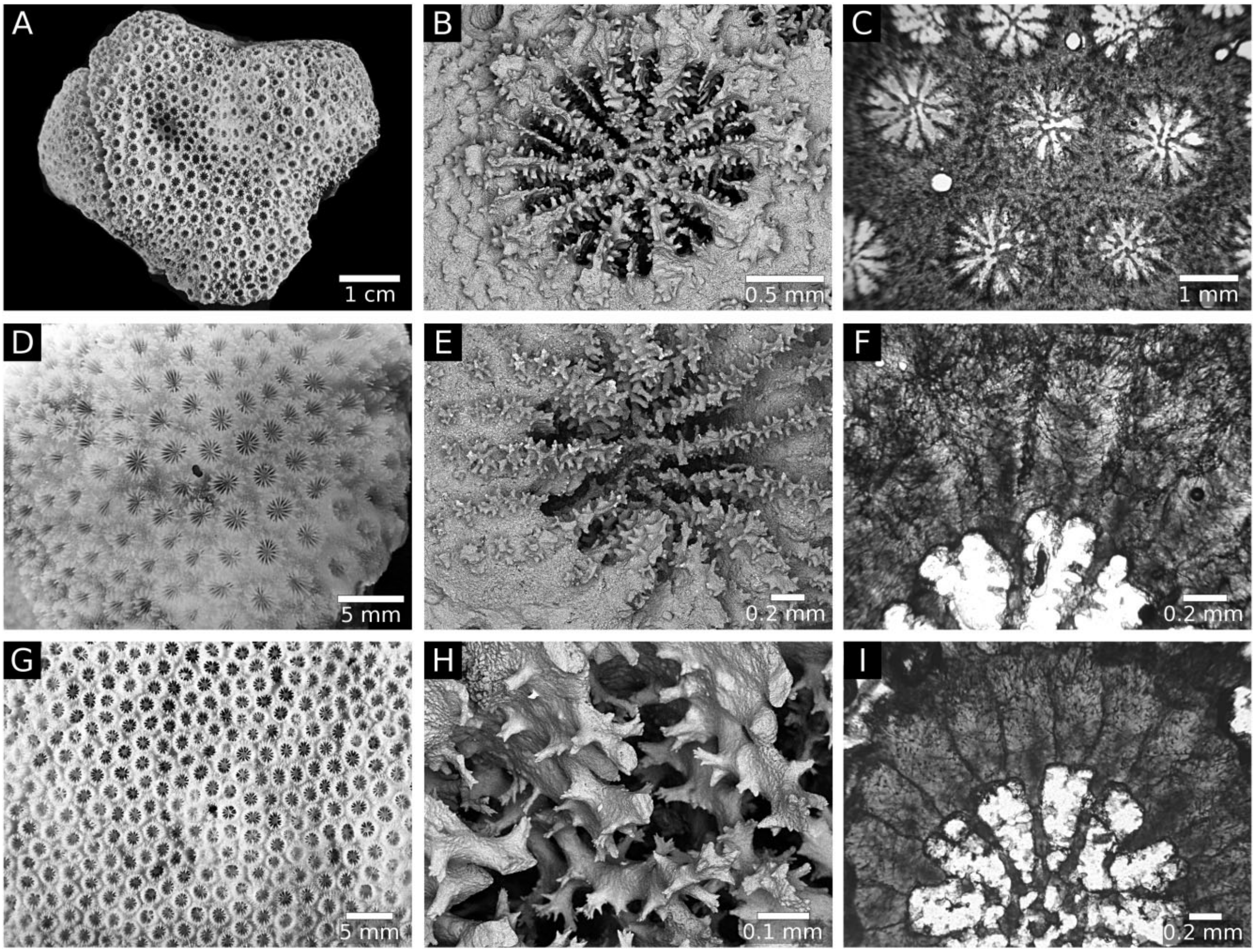


Figure 9. *Cyphastrea* Milne Edwards & Haime, 1848a has discrete corallites that bud extracalicularly, small (< 4 mm) and low-relief (< 3 mm) calices, regular free septa, and compact columellae. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm), with multiaxial tips; strong (pointed) granules scattered on septal face. Walls formed by dominant septotheca. A–C, *Cyphastrea microphthalma* (Lamarck, 1816), type species of *Cyphastrea*; macromorphology, holotype MNHN IK-2012–14002, unknown locality (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype RMNH 15111 (FA1035), southwest Sulawesi, Indonesia. D–F, *Cyphastrea chalcidicum* (Forskål, 1775); macromorphology, hypotype MTQ G61902, Orpheus Island, Australia (D); micromorphology (E) and microstructure (F), hypotype RMNH 12787, Gulf of Aqaba, Israel. G–I, *Cyphastrea serailia* (Forskål, 1775); macromorphology, syntype ZMUC ANT-000367, Red Sea (G; photo by M. A. Krag); micromorphology (H) and microstructure (I), hypotype RMNH 15106, southwest Sulawesi, Indonesia.

la structure poutrellaire de la partie interne des cloisons.' (Milne Edwards & Haime, 1848a, vol. 27: 494).

Subsequent descriptions

Milne Edwards & Haime, 1849b, vol. 12: 114; Milne Edwards & Haime, 1857, vol. 2: 484–485; Tenison-Woods, 1878: 322; Klunzinger, 1879: 50–51; Duncan, 1884: 107; Quelch, 1886: 106; Saville Kent, 1893: 27; Gardiner, 1899: 761; Delage & Hérouard, 1901: 630; Gardiner, 1904: 778; Matthai, 1914: 38–39; Vaughan, 1918: 87; Hoffmeister, 1925: 19; Faustino, 1927: 114–115; Yabe *et al.*, 1936: 23; Vaughan & Wells, 1943: 174; Alloiteau, 1952: 625; Crossland, 1952: 117; Wells, 1956: F406; Nemenzo, 1959: 112; Chevalier, 1975: 9; Veron *et al.*, 1977: 167; Wijsman-Best, 1980: 239; Scheer & Pillai, 1983: 133; Wood, 1983: 167, 170; Veron, 1986: 520; Chevalier & Beauvais, 1987: 716; Sheppard, 1990: 12; Sheppard & Sheppard, 1991: 139; Veron, 2000, vol. 3: 240.

Diagnosis (apomorphies in italics)

Colonial, with extracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum generally spinose (costate in *Cyphastrea agassizi* and apical corallites of *Cyphastrea decadia*), moderate amount (< corallite diameter; extensive in *Cyphastrea decadia*). Calice width small (< 4 mm), with low relief (< 3 mm). Costosepta not confluent. Septa in ≤ three cycles (≤ 36 septa). Free septa regular. Septa spaced > 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular but compact (one to three threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites. Paliform (uniaxial) lobes weak or moderate. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 9A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation multiaxial. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules scattered on septal face; *strong (pointed)*. Interarea smooth (Fig. 9B, E, H).

Walls formed by dominant septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 9C, F, I).

Species included

1. *Cyphastrea microphthalma* (Lamarck, 1816: 261); holotype: MNHN IK-2012–14002 (dry specimen; Fig. 9A); type locality: 'les mers de la Nouvelle-Hollande' (Lamarck, 1816: 261); phylogenetic data: molecular and morphology.
2. *Cyphastrea agassizi* (Vaughan, 1907: 101, pl. 25: figs 2, 2a, 3, 3a); syntypes: USNM 21633, 21634 (two dry specimens); type locality: O'ahu, Hawai'i; phylogenetic data: partial morphology.
3. *Cyphastrea chalcidicum* (Forskål, 1775: 136); holotype: lost (Matthai, 1914: 42); neotype: NHMUK 1978.1.1.4 (Wijsman-Best, 1980: 242), designated by Veron *et al*. (1977: 173), status unknown; type locality: southwest Swain Reefs, Australia, 5–14 m in depth; phylogenetic data: molecular and morphology.
4. *Cyphastrea decadia* Moll & Best, 1984: 56, figs 5, 6; holotype: RMNH 15271 (dry specimen); paratypes: RMNH 15272, 15273 (two dry specimens); type locality: 111 m offshore of north Pajenekang, Spermonde Archipelago, Indonesia, 8 m depth; phylogenetic data: partial morphology.
5. *Cyphastrea hexasepta* Veron, Turak & DeVantier, 2000 (Veron, 2000, vol. 3: 245, fig. 5; see also Veron, 2002: 171, figs 312–314; ICZN, 2011: 163); lectotype (designated herein): MTQ G55834 (dry specimen); type locality: northern Red Sea coast of Saudi Arabia, 10 m depth; phylogenetic data: none.
6. *Cyphastrea japonica* Yabe & Sugiyama, 1932: 161 (see also Yabe *et al*., 1936: 25, pl. 17: figs 4–6); holotype: TIU 40323 (dry specimen); type locality: Misaki, Shikoku, Japan; phylogenetic data: molecular only (Chen *et al*., 2004).
7. *Cyphastrea ocellina* (Dana, 1846: 218, plate 10: fig. 10); syntypes: YPM IZ 474, 4330 (two dry specimens); type locality: Hawai'i; phylogenetic data: molecular only (Romano & Palumbi, 1996).
8. *Cyphastrea serailia* (Forskål, 1775: 135); syntypes: ZMUC ANT-000367 (Fig. 9G) to ANT-000373, figured in Matthai (1914, pl. 11: figs 4–9; seven dry specimens); type locality: Red Sea; phylogenetic data: molecular and morphology.

Taxonomic remarks

Cyphastrea Milne Edwards & Haime, 1848a, vol. 27: 494, was established to accommodate species distinguished by their compact coenosteum – 'compacité du coenenchyme' (Milne Edwards & Haime, 1848a, vol. 27: 494). Following which, only one species – *Cyphastrea agassizi* – has ever been placed in another genus, implying limited confusion with its taxonomy.

Molecular data indicate that *Cyphastrea* is very dissimilar from other taxa as it is subtended by a long branch from its sister genus, *Orbicella*. Yet, the *Cyphastrea* + *Orbicella* clade (subclade C) is a well-supported relationship that has been recovered in several studies (Fukami *et al*., 2004a, 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012).

Cyphastrea is widely distributed on reefs of the Indo-Pacific, present in French Polynesia and the Pitcairn Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent in the eastern Pacific in the north.

Morphological remarks

Cyphastrea is a morphologically well-defined and moderately supported genus (bootstrap support of 69 and decay index of 2), but it is also exclusively associated with *Echinopora*, *Orbicella*, and *Paramontastraea*. *Cyphastrea* spp. share the plesiomorphic state of spinose coenosteum with *Echinopora* and *Paramontastraea*, amongst other characters with *Orbicella*, supporting them as a clade that is sister to the rest of Merulinidae.

Despite the recent emphasis that corals east and west of the Americas are genetically distinct from one another (Fukami *et al*., 2004a), and whilst *Cyphastrea* and *Orbicella* are found solely in the Indo-Pacific and Atlantic realms, respectively, synapomorphies are present for the clade comprising them, namely small calice width (likelihood of 0.69 based on the Mk1 model) and trabecular but compact columellae (likelihood 0.86). They also have walls formed predominantly by septotheca, a plesiomorphic state shared only with *Paramontastraea*.

On its own, *Cyphastrea* is defined by the synapomorphy of strong pointed granules on the septal face (likelihood 0.99). Because its closest relative does not overlap geographically, it is easily identified with the apomorphies shared with *Orbicella*. The multiaxial tooth tips, although also present amongst *Echinopora* and *Paramontastraea*, are much more conspicuous in *Cyphastrea* because of their small corallites.

To date, phylogenetic data are only available for about half of the members of *Cyphastrea* (see also Romano & Palumbi, 1996; Chen *et al*., 2004).

Genus *Dipsastraea* de Blainville, 1830: 338 (Fig. 10)

Synonyms
Barabattoia Yabe & Sugiyama, 1941: 72 (type species: *Barabattoia mirabilis* Yabe & Sugiyama, 1941: 72, pl. 61: figs 1, 1a–e; original designation, Yabe & Sugiyama, 1941: 72); *Bikiniastrea* Wells, 1954: 456 (type species: *Bikiniastr[e]a laddi* Wells 1954: 456, pl. 172; original designation, Wells, 1954: 456).

Type species
Madrepora favus Forskål, 1775: 132; subsequent designation, Wells, 1936: 109.

Original description
'Plus ou moins globuleuses, formées de loges profondes, infundibuliformes, subpolygonales, à parois communes, à bords élevés, multisillonnés et échinulés.' (de Blainville, 1830: 338).

Subsequent descriptions
de Blainville, 1834: 373; Wells, 1936: 109.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, moderate amount (< corallite diameter), limited (includes double wall) in some species. Generally, calice width medium (4–15 mm), with medium relief (3–6 mm); few species with wider and/or deeper calice. Costosepta not confluent. Septa in three cycles (24–36 septa). Free septa present but generally irregular (regular in *Dipsastraea helianthoides* and *Dipsastraea laxa*). Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes weak or moderate. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 10A, D, G, J).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 10B, E, H, K).

Walls formed by dominant paratheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters generally strong but highly variable; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak. Transverse crosses present. Columella centres clustered (Fig. 10C, F, I, L).

Species included

1. *Dipsastraea favus* (Forskål, 1775: 132); lectotype: ZMUC ANT-000466 (dry specimen; Fig. 10A); type locality: Red Sea; phylogenetic data: molecular and morphology.
2. *Dipsastraea albida* (Veron, 2000, vol. 3: 112, figs 1, 2) (see also Veron, 2002: 140, figs 257–259; ICZN, 2011: 164); lectotype (designated herein): MTQ G55788 (dry specimen); type locality: Ras Mohammed National Park, Sharm al-Sheikh, Sinai Peninsula, Egypt, 17 m depth; phylogenetic data: none.
3. *Dipsastraea amicorum* (Milne Edwards & Haime, 1849b, vol. 12: 171, vol. 10, pl. 9: fig. 9); holotype: MNHN IK-2010-470 (dry specimen; Fig. 10D); type locality: Tongatapu, Tonga; phylogenetic data: none.
4. *Dipsastraea camranensis* (Latypov, 2013: 223); holotype: FEBRAS 24193 (dry specimen); paratype: FEBRAS 24194 (dry specimen); type locality: Hon Nai Island, Cam Ranh Bay, Vietnam, 3 m depth; phylogenetic data: none.
5. *Dipsastraea danai* (Milne Edwards & Haime, 1857, vol. 2: 442); holotype: USNM 32 (dry specimen); paratype: USNM 31 (dry specimen); type locality: Tongatapu, Tonga; phylogenetic data: molecular and partial morphology.
6. *Dipsastraea helianthoides* (Wells, 1954: 458, pl. 174: figs 3–6); holotype: USNM 44980 (dry specimen); type locality: Bikini Island, Bikini Atoll, Marshall Islands; phylogenetic data: morphology only.
7. *Dipsastraea lacuna* (Veron, Turak & DeVantier, 2000, vol. 3: 111, fig. 6) (see also Veron, 2002: 139, figs 254–256; ICZN, 2011: 164); lectotype (designated herein): MTQ G55836 (dry specimen); type locality: northern Red Sea coast of Saudi Arabia; phylogenetic data: none.
8. *Dipsastraea laddi* (Wells, 1954: 456, pl. 172: figs 1–4); holotype: USNM 44942 (dry specimen; Fig. 10G–I); type locality: lagoon of Bikini Atoll, Marshall Islands, about 4 m depth; phylogenetic data: morphology only.
9. *Dipsastraea laxa* (Klunzinger, 1879: 49, plate 5, fig. 3, plate 10, figs 9a, b); holotype: ZMB Cni 2193 (dry specimen); type locality: Koseir, Egypt; phylogenetic data: morphology only.
10. *Dipsastraea lizardensis* (Veron, Pichon & Wijsman-Best, 1977: 45, figs 74–78, 428–430); holotype:

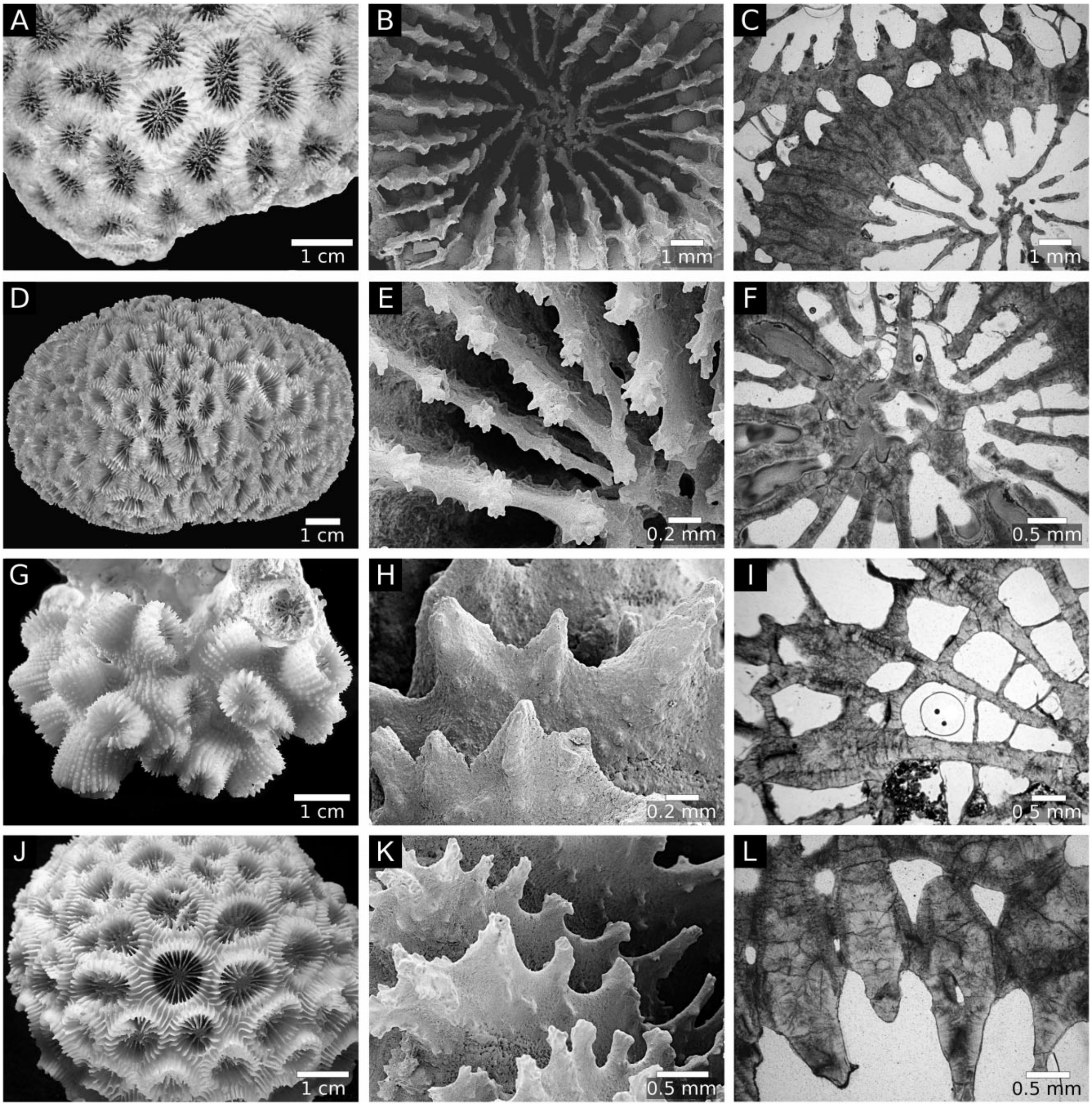


Figure 10. *Dipsastraea* de Blainville, 1830, has discrete corallites that bud intracalicularly, equally thick costosepta, and spongy columellae. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm). Walls formed by dominant paratheca and partial septotheca, with transverse septal crosses. A–C, *Dipsastraea favus* (Forskål, 1775), type species of *Dipsastraea*; macromorphology, lectotype ZMUC ANT-000466, Red Sea (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 93662, Madang, Papua New Guinea. D, *Dipsastraea amicorum* (Milne Edwards & Haime, 1849b); macromorphology, holotype MNHN IK-2010-470, Tongatapu, Tonga (photo by P. Lozouet). E, F, *Dipsastraea mirabilis* (Yabe & Sugiyama, 1941); micromorphology (E) and microstructure (F), hypotype USNM 93642, Madang, Papua New Guinea. G–I, *Dipsastraea laddi* (Wells, 1954); macromorphology (G), micromorphology (H), and microstructure (I), holotype USNM 44942, Bikini Atoll, Marshall Islands. J–L, *Dipsastraea pallida* (Dana, 1846); macromorphology, syntype USNM 30, Fiji (J); micromorphology (K) and microstructure (L), hypotype USNM 44952, Bikini Atoll, Marshall Islands.

NHMUK 1977.1.1.2 (dry specimen); paratype: MTQ G59707 (dry specimen); paratype: RMNH 10733 (dry specimen); type locality: McGillivray Reef, Lizard Island, Australia, 7 m depth; phylogenetic data: molecular and morphology.

11. *Dipsastraea maritima* (Nemenzo, 1971: 169, pl. 9: figs 1, 2); holotype: UP C-859 (dry specimen); type locality: Puerto Princesa Bay, Palawan, the Philippines; phylogenetic data: none.
12. *Dipsastraea marshae* (Veron, 2000, vol. 3: 122, figs 1, 2) (see also Veron, 2002: 145, figs 269, 270; ICZN, 2011: 164); lectotype (designated herein): WAM Z12910 (dry specimen); type locality: Ashmore Reef, northwest Australia, 9 m depth; phylogenetic data: none.
13. *Dipsastraea matthaii* (Vaughan, 1918: 109, pl. 39: figs 2, 2a, b); holotype: USNM 38381 (dry specimen); type locality: Seychelles, Aldabra Atoll, Assumption Island, or Glorioso Islands; phylogenetic data: molecular and morphology.
14. *Dipsastraea maxima* (Veron, Pichon & Wijsman-Best, 1977: 43, figs 67–73, 427, 445); holotype: NHMUK 1977.1.1.1 (dry specimen); paratype: MTQ G59706 (dry specimen); paratype: RMNH 10732 (dry specimen); type locality: Nara Inlet, Hook Island, Whitsunday Islands, Australia, 5 m depth; phylogenetic data: molecular and morphology.
15. *Dipsastraea mirabilis* (Yabe & Sugiyama, 1941: 72, pl. 61: figs 1, 1a–e); holotype: TIU 64330 (dry specimen); type locality: Yap Islands; phylogenetic data: molecular and morphology.
16. *Dipsastraea pallida* (Dana, 1846: 224, pl. 10: figs 13, 13a–e); syntype: USNM 30 (dry specimen; Fig. 10J); syntype: YPM IZ 4282 (dry specimen); type locality: Fiji; phylogenetic data: molecular and morphology.
17. *Dipsastraea rosaria* (Veron, 2000, vol. 3: 119, figs 3, 4) (see also Veron, 2002: 143, figs 264–268; ICZN, 2011: 164); lectotype (designated herein): MTQ G55822 (dry specimen); type locality: Milne Bay, Papua New Guinea, 10 m depth; phylogenetic data: molecular and morphology.
18. *Dipsastraea rotumana* (Gardiner, 1899: 750, pl. 47: fig. 3); holotype: lost (Wijsman-Best, 1972: 21); neotype: ZMA Coel. 5686, designated by Veron *et al*. (1977: 41) (dry specimen); type locality: New Caledonia; phylogenetic data: molecular and morphology.
19. *Dipsastraea speciosa* (Dana, 1846: 220, pl. 11: figs 1, 1a–d); syntype: USNM 37 (dry specimen); type locality: 'East Indies' (Dana, 1846: 220); phylogenetic data: molecular and morphology.
20. *Dipsastraea truncata* (Veron, 2000, vol. 3: 113, figs 3–6) (see also Veron, 2002: 142, figs 260–263; ICZN, 2011: 164); lectotype (designated herein): MTQ G55823 (dry specimen); type locality: Milne Bay, Papua New Guinea, 5 m depth; phylogenetic data: molecular and morphology.
21. *Dipsastraea veroni* (Moll & Best, 1984: 48, figs 1–3) (see also Veron *et al*., 1977: 49, fig. 81); holotype: RMNH 15209 (dry specimen); paratypes: RMNH 15210–15215 (six dry specimens); type locality: 100 m offshore of east Kudingareng Keke, Spermonde Archipelago, Indonesia, 2 m depth; phylogenetic data: none.
22. *Dipsastraea vietnamensis* (Veron, 2000, vol. 3: 127, figs 3–5) (see also Veron, 2002: 146, figs 271–273; ICZN, 2011: 164); lectotype (designated herein): MTQ G55859 (dry specimen); type locality: Nha Trang, Vietnam, 10 m depth; phylogenetic data: none.

Taxonomic remarks

This is a large genus that, prior to Budd *et al*. (2012), had all its species distributed amongst *Favia* Milne Edwards & Haime, 1857, vol. 2: 426, and *Barabattoia* Yabe & Sugiyama, 1941: 72. It was discovered through molecular phylogenetic analyses that *Favia* was actually comprised of at least two main lineages separated according to the geographical divisions of the Indo-Pacific and the Atlantic (Fukami *et al*., 2004a, 2008). As the type species of *Favia* is *Madrepora fragum* Esper, 1795: 79, an Atlantic species (see Hoeksema, Roos & Cadée, 2012), it followed that a taxonomic split of the genus will involve reassigning the Indo-Pacific species into the resurrected genus *Dipsastraea* de Blainville, 1830: 338.

Until the recent revision, *Dipsastraea* had never been applied since it was established. Wells (1936: 109) showed that all the species initially assigned to *Dipsastraea* had been placed in other genera, thus fixing *Madrepora favus* Forskål, 1775: 132, as the lectotype by elimination, following the transfer of *Madrepora favosa* Esper, 1795: 34 into *Favia* (Milne Edwards & Haime, 1857, vol. 2: 443). Matthai (1914: 79) subsequently moved *Madrepora favus* Forskål into *Favia* as well, effectively synonymizing *Dipsastraea* as *Favia*.

Here, we show that morphologically *Madrepora favus* Forskål falls well within the large clade of Indo-Pacific *Favia*, corroborating molecular results that show that these species are closely related (Fukami *et al*., 2004a, 2008; Huang *et al*., 2011; Kongjandtre *et al*., 2012). However, three major issues need to be addressed.

First, the synonymy of *Barabattoia mirabilis* Yabe & Sugiyama, 1941: 72, as *Barabattoia amicorum* by Veron *et al*., 1977: 32, is untenable, as these are clearly two distinct species. The specimen shown in Veron *et al*. (1977: fig. 37), is incorrectly referred to as the 'holotype of *Favia amicorum*'. We have verified that MNHN specimen IK-2010-470 is the holotype of *Barabattoia amicorum* (Fig. 10D), following the original description in Milne Edwards & Haime (1849b, vol. 12: 171) and illustration in Milne Edwards & Haime (1848b, vol. 10, pl. 9: fig. 9). All the molecular trees used here have essentially followed the taxonomy of Veron *et al*. (1977) when analysing *Barabattoia mirabilis*. We thus regard them both as valid species, and all molecular terminals identified as *Barabattoia amicorum* to be *Barabattoia mirabilis*, which has consistently been placed within the Indo-Pacific *Favia* clade (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012). Supported by recovery of two *Barabattoia* spp. (i.e. *Barabattoia laddi* and *Barabattoia mirabilis*) in the same clade on the morphological phylogeny, we consequently consider *Barabattoia* as a synonym of *Dipsastraea*.

Second, *Astrea* (*Orbicella*) *stelligera* Dana, 1846: 216, and *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977: 64, are more closely related to *Goniastrea* and *Favites*, respectively, than *Favia* (or *Dipsastraea*), and we give separate accounts below based on their phylogenetic affinities.

Third, our results show that *Trachyphyllia geoffroyi* (Audouin, 1826: 233), *Goniastrea aspera* Verrill, 1866: 32, and *Favia palauensis* Yabe & Sugiyama, 1936: 30, are morphologically distinct from *Dipsastraea*, but molecular data have often placed these species within the latter (Fukami *et al*., 2004a, 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012). On the basis of the morphological evidence and long molecular branch lengths leading to these species, we placed them in two other genera described here (i.e. *Trachyphyllia* Milne Edwards & Haime, 1848a, vol. 27: 492, and *Coelastrea* Verrill, 1866: 32).

Dipsastraea is widely distributed on reefs of the Indo-Pacific, present in French Polynesia and the Pitcairn Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

We find no apomorphies for *Dipsastraea* that are consistent across data types, mainly because the nesting of *Coelastrea* and *Trachyphyllia* on the molecular tree results in distinguishing features being optimized as plesiomorphic traits. Unequal costosepta is the only synapomorphy on the morphological phylogeny. In spite of this, *Dipsastraea* can be differentiated easily from the aforementioned close relatives by its moderate amount of coenosteum, three cycles of septa, and weak to moderate paliform lobes, rather than fused, limited walls or phaceloid colonies, four septal cycles, well-developed septal lobes. Thin sections also reveal that *Dipsastraea* has more distinct costa centre clusters but weaker costa and septum medial lines than *Coelastrea* and *Trachyphyllia*.

Being conventionally grouped with the Atlantic *Favia* spp. previously, the distinction between *Dipsastraea* and *Favia* is much clearer with the characters analysed here. Even with macromorphology, the differences are substantial, with *Dipsastraea* possessing larger and deeper corallites (after losing *Goniastrea stelligera*), fewer and less crowded septa, columellae that are smaller but denser, and paliform (single axis) instead of septal (fan-shaped) lobes. Of the 23 subcorallite characters used, 14 are distinct between them. Aside from the family-level synapomorphies associated with tooth shape, the walls of *Dipsastraea* are formed primarily by paratheca instead of septotheca as in *Favia*.

This genus is fairly well sampled, but most of the more recently described species of Veron (2000) are lacking data.

GENUS *ECHINOPORA* LAMARCK, 1816: 252 (FIG. 11)

Synonyms

Acanthelia Wells, 1937: 73 (type species: *Echinopora horrida* Dana, 1846: 282, pl. 17: figs 4, 4a–c; original designation, Wells, 1937: 73); *Acanthopora* Verrill, 1864: 54 (type species: *Echinopora horrida* Dana, 1846: 282, pl. 17: figs 4, 4a–c; original designation, Verrill, 1864: 54); *Echinastraea* de Blainville, 1830: 343 (type species: *Echinopora rosularia* Lamarck, 1816: 253 = *Madrepora lamellosa* Esper, 1795: 65, pl. 58: figs 1, 2; original designation, de Blainville, 1830: 344); *Heliastraea* Milne Edwards & Haime, 1857, vol. 2: 456 (type species: *Madrepora astroites* Forskål, 1775: 133 = *Astrea forskaliana* Milne Edwards & Haime, 1849b, vol. 12: 100; original designation, Milne Edwards & Haime, 1857, vol. 2: 457); *Stephanocora* Ehrenberg, 1834: 300 (type species: *Stephanocora hemprichii* Ehrenberg, 1834: 300 = *Explanaria gemmacea* Lamarck, 1816: 256; original designation, Ehrenberg, 1834: 300).

Type species

Echinopora rosularia Lamarck, 1816: 253 = *Madrepora lamellosa* Esper, 1795: 65, pl. 58: figs 1, 2 (see Matthai, 1914: 50); original designation, Lamarck, 1816: 253; holotype: MNHN IK-2010-635 (dry specimen; Fig. 11A); type locality: 'les mers de la Nouvelle-Hollande' (Lamarck, 1816: 254).

Original description

'Polypier pierreux, fixé, aplati et étendu en membrane libre, arrondie, foliiforme, finement striée des deux côtés. La surface supérieure chargée de petites papilles, et, en outre, d'orbicules rosacés, convexes, très-hérissés de papilles, percés d'un ou deux trous, recouvrant chacun une étoile lamelleuse.

Étoiles éparses, orbiculaires, couvertes; à lames inégales, presque confuses, saillantes des parois et du fond, et obstruant en partie la cavité.' (Lamarck, 1816: 252).

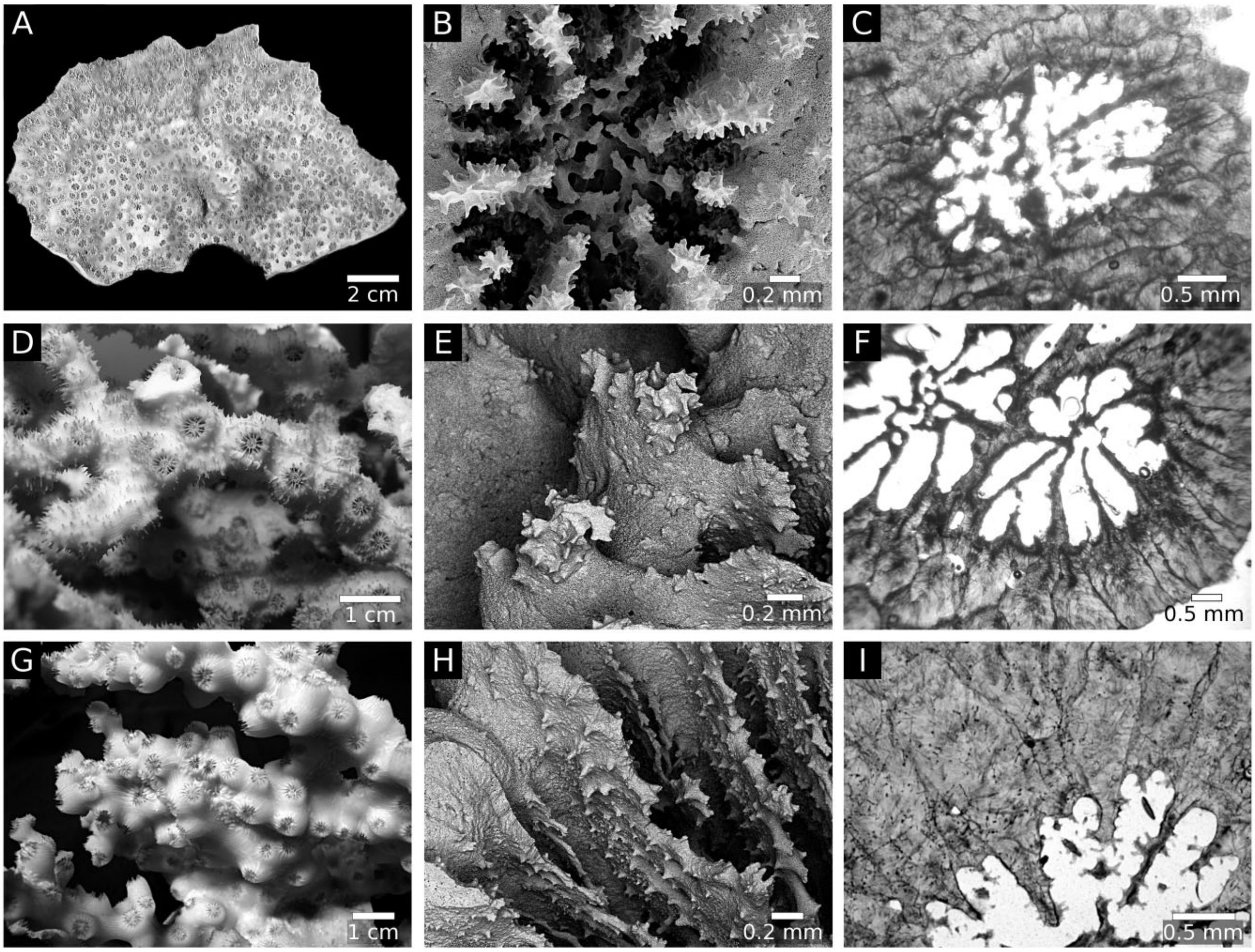


Figure 11. *Echinopora* Lamarck, 1816, has discrete corallites that bud extracalicularly, extensive coenosteum (≥ corallite diameter), medium-size (4–15 mm) and low-relief (< 3 mm) calices, large (≥ 1/4 of calice width) spongy columellae, and weak/moderate paliform (uniaxial) lobes. Septal teeth are low (< 0.3 mm) with medium spacing (0.3–1 mm) and multiaxial tips. Walls formed by partial septotheca and weak abortive septa. A–C, *Echinopora lamellosa* (Esper, 1795), type species of *Echinopora*; macromorphology, *Echinopora rosularia* Lamarck, 1816, holotype of *Echinopora* MNHN IK-2010-635, unknown locality (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 89851, Alofi, Niue. D–F, *Echinopora horrida* Dana, 1846; macromorphology, syntype USNM 162, Fiji (D); micromorphology (E) and microstructure (F), hypotype RMNH 33956, Kepulauan Seribu, Indonesia. G, *Echinopora mammiformis* (Nemenzo, 1959); macromorphology, holotype UP C-99, Puerto Galera, the Philippines. H, I, *Echinopora gemmacea* (Lamarck, 1816); micromorphology, hypotype RMNH 17270, Watamu, Kenya (H); microstructure, hypotype USNM 1113168, Red Sea (I).

Subsequent descriptions
Lamouroux, 1821: 57; Lamarck, 1836: 395, 396; Dana, 1846: 277, 278; Milne Edwards & Haime, 1849b, vol. 12: 185; Milne Edwards & Haime, 1857, vol. 2: 621; Dana, 1859: 42; Klunzinger, 1879: 54, 55; Quenstedt, 1881: 1030–1031; Duncan, 1884: 117; Ortmann, 1890: 298, 299; Saville Kent, 1893: 170; Delage & Hérouard, 1901: 631; Gardiner, 1904: 782; Matthai, 1914: 48, 49; Hickson, 1924: 61; Faustino, 1927: 122; Yabe *et al.*, 1936: 48; Vaughan & Wells, 1943: 175; Alloiteau, 1952: 625; Crossland, 1952: 118; Wells, 1956: F406; Nemenzo, 1959: 117; Chevalier, 1975: 68, 69; Veron *et al.*, 1977: 182; Wijsman-Best, 1980: 239, 240; Scheer & Pillai, 1983: 135; Wood, 1983: 170; Veron, 1986: 526; Chevalier & Beauvais, 1987: 716; Sheppard, 1990: 16; Sheppard & Sheppard, 1991: 141; Veron, 2000, vol. 3: 252.

Diagnosis (apomorphies in italics)
Colonial, with extracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum generally spinose (costate in *Echinopora mammiformis*), *extensive amount*

(≥ corallite diameter). Generally, calice width medium (4–15 mm), with low relief (< 3 mm). Costosepta not confluent. Septa in three cycles (24–36 septa). Free septa regular. Septa spaced > 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), ≥ *1/4 of calice width*, and discontinuous amongst adjacent corallites. Paliform (uniaxial) lobes weak or moderate. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 11A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation multiaxial. Tooth height low (< 0.3 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea smooth (Fig. 11B, E, H).

Walls formed by partial septotheca; *abortive septa weak*. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 11C, F, I).

Species included

1. *Echinopora lamellosa* (Esper, 1795: 65, pl. 58: figs 1, 2); holotype: lost (Chevalier, 1975: 70; Scheer, 1990: 398); type locality: unknown; phylogenetic data: molecular and morphology.
2. *Echinopora ashmorensis* Veron, 1990: 152, figs 58–62, 87, 88; holotype: MTQ G32491 (dry specimen); type locality: Ashmore Reef, Western Australia, 2 m depth; phylogenetic data: none.
3. *Echinopora forskaliana* (Milne Edwards & Haime, 1849b, vol. 12: 100); holotype: MNHN IK-2010-406 (dry specimen); type locality: Red Sea; phylogenetic data: none.
4. *Echinopora fruticulosa* Klunzinger, 1879: 55 = *Stephanocora hemprichii* forma fruticulosa Ehrenberg, 1834: 301; holotype: ZMB Cni 749, see Matthai (1914: 56) (dry specimen); type locality: Red Sea; phylogenetic data: none.
5. *Echinopora gemmacea* (Lamarck, 1816: 256); holotype: MNHN IK-2010-529 (dry specimen); type locality: 'l'Océan indien?' (Lamarck, 1816: 256); phylogenetic data: molecular and morphology.
6. *Echinopora hirsutissima* Milne Edwards & Haime, 1849b, vol. 12: 187; holotype: MNHN IK-2010-491 (dry specimen); type locality: 'l'océan Indien' (Milne Edwards & Haime, 1849b, vol. 12: 187); phylogenetic data: morphology only.
7. *Echinopora horrida* Dana, 1846: 282, pl. 17: figs 4, 4a–c; syntype: USNM 162 (dry specimen; Fig. 11D); syntypes: YPM IZ 1980A, B, 4307 (three dry specimens); type locality: Fiji; phylogenetic data: molecular and morphology.
8. *Echinopora irregularis* Veron, Turak & DeVantier, 2000, vol. 3: 262, fig. 1 (see also Veron, 2002: 175, figs 318–321; ICZN, 2011: 163); lectotype (designated herein): MTQ G55835 (dry specimen); type locality: northern Red Sea coast of Saudi Arabia, 2 m depth; phylogenetic data: none.
9. *Echinopora mammiformis* (Nemenzo, 1959: 112, pl. 14: fig. 2); holotype: UP C-99 (dry specimen; Fig. 11G); type locality: Muelle, Puerto Galera, the Philippines; phylogenetic data: molecular and partial morphology.
10. *Echinopora pacificus* Veron, 1990: 150, figs 55–57, 86; holotype: MTQ G32490 (dry specimen); type locality: entrance to Kabira Bay, Ishigaki Island, Ryukyu Islands, Japan, 15 m depth; phylogenetic data: molecular and morphology.
11. *Echinopora robusta* Veron, 2000, vol. 3: 263, figs 2–4 (see also Veron, 2002: 176, figs 322–324; ICZN, 2011: 163); lectotype (designated herein): MTQ G55849 (dry specimen); type locality: southern Sri Lanka, 2 m depth; phylogenetic data: none.
12. *Echinopora taylorae* (Veron, 2000, vol. 2: 327, fig. 6) (see also Veron, 2002: 173, figs 315–317; ICZN, 2011: 163); lectotype (designated herein): UP MSI-3005-CO (dry specimen); type locality: Calamian Islands, Palawan, the Philippines, 12 m depth; phylogenetic data: none.
13. *Echinopora tiranensis* Veron, Turak & DeVantier, 2000, vol. 3: 265, figs 4, 5 (see also Veron, 2002: 178, figs 322–324; ICZN, 2011: 163); lectotype (designated herein): MTQ G55843 (dry specimen); type locality: Tiran Island, northern Red Sea coast of Saudi Arabia, 15 m depth; phylogenetic data: none.

Taxonomic remarks

Echinopora Lamarck, 1816: 252, is a relatively large genus, with four new species only recently described (Veron, 2000). It was first described as having an upper surface filled with small papillae – 'la surface supérieure chargée de petites papilles' (Lamarck, 1816: 252) – a plesiomorphic trait shared with *Cyphastrea*. Together with *Paramontastraea* and *Orbicella*, these taxa have been consistently recovered at the base of the tree, either as paraphyletic (Huang *et al*., 2011; Huang, 2012), or as a sister clade to the rest of Merulinidae (Arrigoni *et al*., 2012). The latter hypothesis appears to be more well supported with molecular data, and it also corresponds to the morphological tree topology obtained here.

It should be noted that the type species of *Echinopora* is *Echinopora rosularia* Lamarck, 1816: 253, which has been synonymized as *Echinopora lamellosa* (Esper, 1795: 65; Ranson, 1943: 118). The latter's holotype is lost (Chevalier, 1975: 70; Scheer, 1990: 398), but Lamarck's holotype of *Echinopora rosularia* (MNHN IK-2010-635; Fig. 11A) should still be considered the type for this genus.

Echinopora is widely distributed on reefs of the Indo-Pacific, present as far east as the Tuamotu Archipelago in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks
This genus is one of the most distinct and well-defined genera in Merulinidae, being supported by a high bootstrap value (93) and decay index (2) on the morphology tree. Synapomorphies inferred are large columellae (≥ 1/4 of calice width; likelihood of 0.86 based on the Mk1 model), extensive coenosteum (≥ corallite diameter; likelihood 0.77), and weak abortive septa (0.98). The latter two features distinguish *Echinopora* from the closely related genera of *Cyphastrea*, *Paramontastraea*, and *Orbicella*. Large columella is only shared with *Orbicella* amongst all Merulinidae taxa.

Data are available only for six of the 13 species; the genus requires substantial additional sampling, particularly for the recently described species. None of the species described in Veron (2000) have been placed on the phylogeny.

GENUS *ERYTHRASTREA* PICHON, SCHEER & PILLAI IN SCHEER & PILLAI, 1983: 104 (FIG. 12)

Type species
Erythrastrea flabellata Pichon, Scheer & Pillai in Scheer & Pillai, 1983: 104, pl. 26: figs 3, 4; original designation, Scheer & Pillai, 1983: 104.

Original description
'Phaceloid, branches flabellate, compressed, epithecate. Wall thin. Calices meandering, valleys short or long and sinuous, 5 to 10 mm wide, 4 to 5 mm deep. Columella centres distinct, formed of septal fusion, adjacent ones linked by indistinct lamellae. Septa exsert vertically, edges dentate. Costae very conspicuous, extend to the base of the flabellate branches, often linked by transverse ridges.' (Scheer & Pillai, 1983: 104).

Subsequent descriptions
Veron, 1986: 595; Sheppard & Sheppard, 1991: 122; Veron, 2000, vol. 3: 98.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; monticules absent. Phaceloid (flabello-meandroid). Calice width medium (4–15 mm), with medium relief (3–6 mm). Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) and septal (multiaxial) lobes may be present but weak. Epitheca reduced or absent and endotheca abundant (vesicular) (Fig. 12).

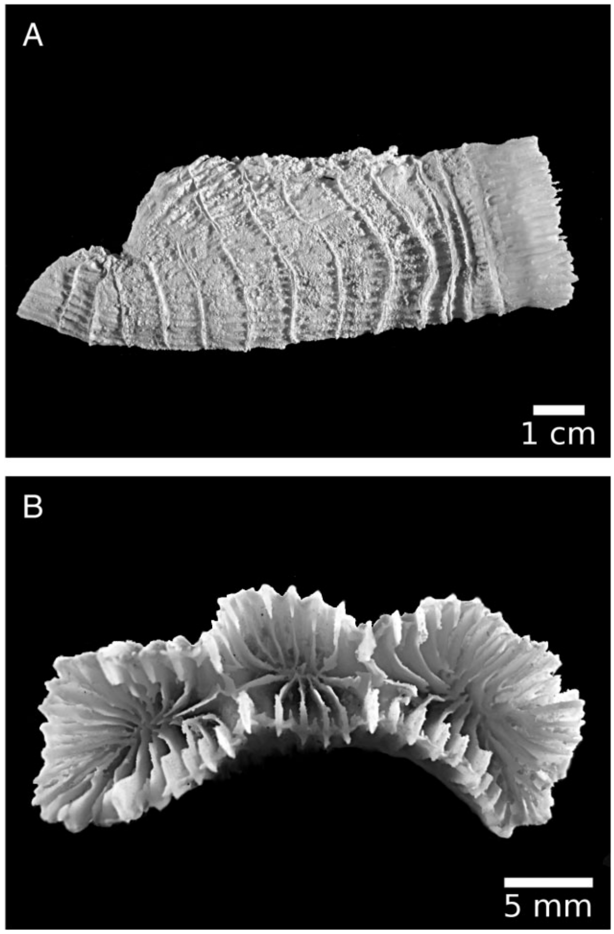


Figure 12. *Erythrastrea* Pichon, Scheer & Pillai in Scheer & Pillai, 1983, is phaceloid or flabello-meandroid, with equally thick costosepta spaced < six septa per 5 mm and abundant (vesicular) endotheca. A, B, *Erythrastrea flabellata* Pichon, Scheer & Pillai in Scheer & Pillai, 1983, the type and only living species of *Erythrastrea*; macromorphology, lectotype (designated herein) USNM 78094, Ghardaqa, Egypt.

Species included
Erythrastrea flabellata Pichon, Scheer & Pillai in Scheer & Pillai, 1983: 104, pl. 26: figs 3, 4 (see Cairns, 1991: 33); lectotype (designated herein): USNM 78094 (dry specimen; Fig. 12); paralectotypes (designated herein): ZMTAU NS 6062, 6063 (two dry specimens); type locality: Ghardaqa, Egypt; phylogenetic data: none.

Taxonomic remarks
Erythrastrea Pichon, Scheer & Pillai in Scheer & Pillai, 1983: 104 is a monotypic genus that is known only from

the Red Sea. In the original description of its species titled '*Erythrastrea flabellata* Pichon, Scheer and Pillai, in press', the authors list as paratypes USNM Wa 75a, b collected from Ghardaqa, Egypt, and NS 6062, 6063 from Tel Aviv, Israel, without any mention of a holotype. Cairns, 1991: 33, explains that the paper cited was never published, stating that 'Both the generic and species descriptions of Scheer & Pillai (1983) satisfy the requirements of the Code and therefore should be considered as the original descriptions'.

Furthermore, Cairns (1991) lists USNM 78094 as a 'paratype', in accordance with the original description. As, to our knowledge, no holotype has been specified, we consider USNM 78094, NS 6062 and NS 6063 to be a syntype series, from which we designate the USNM specimen that is the basis of our genus diagnosis as lectotype for *Erythrastrea flabellata*.

Erythrastrea has only been recorded in northern and central Red Sea, and the Gulf of Aden.

Morphological remarks: Erythrastrea has never been collected for molecular work or subcorallite morphology, and only macromorphological characters can be examined here.

Veron (1986: 595) described the genus as similar to *Caulastraea* based on 'skeletal structures', and it is also like *Trachyphyllia* (and *Nemenzophyllia*) because of the flabello-meandroid colony form.

Based on the holotype, we diagnosed *Erythrastrea* as matching in all but one character each with *Caulastraea* (discrete instead of uniserial) and *Oulophyllia* (fused walls instead of phaceloid), suggesting possible placement of the genus within subclade XVII-D/E (*Caulastraea* + *Oulophyllia* + *Pectinia* + *Mycedium*). It does not have the strong septal (multiaxial) lobes seen in *Trachyphyllia*, and its internal lobes are even weaker than in *Caulastraea* and *Oulophyllia*. A fine epitheca may be present – unlike in the latter genera – but the thin walls and phaceloid form are indicative of its close affinity to *Caulastraea*, as interpreted by Scheer & Pillai (1983: 104).

GENUS *FAVITES* LINK, 1807: 162 (FIG. 13)

Synonyms
Aphrastrea Milne Edwards & Haime, 1848a, vol. 27: 495 (type species: *Astrea deformis* Lamarck, 1816: 264 = *Madrepora pentagona* Esper, 1795: 23, pl. 39: figs 1, 2; original designation, Milne Edwards & Haime, 1848a, vol. 27: 495); *Astrophyllia* Ehrenberg, 1834: 322 (type species: not designated); *Phymastrea* Milne Edwards & Haime, 1848a, vol. 27: 494 (type species: *Phymastrea valenciennesii* Milne Edwards & Haime, 1849b, vol. 12: 124, vol. 10, pl. 9: figs 3, 3a; subsequent designation, Milne Edwards & Haime, 1849b, vol. 12: 124); *Prionastrea* Milne Edwards & Haime, 1848a, vol. 27: 495 (type species: *Astrea abdita* Lamarck, 1816: 265; original designation, Milne Edwards & Haime, 1848a, vol. 27: 495).

Type species
Favites astrinus Link, 1807: 162 = *Madrepora abdita* Ellis & Solander, 1786 (see Vaughan, 1901a: 21; Vaughan, 1918: 109); original designation, Link, 1807: 162.

Original description
'Wabenkoralle. Unförmige, kalkartige Massen, mit oberflæchlichen zerstreuten sternförmig blættrigen Öffnungen.' (Link, 1807: 162).

Subsequent descriptions
Verrill, 1901: 92; Vaughan, 1918: 109; Vaughan, 1919: 414; Hoffmeister, 1925: 24; Faustino, 1927: 134; Coryell & Ohlsen, 1929: 200; Yabe *et al*., 1936: 31; Vaughan & Wells, 1943: 167; Alloiteau, 1952: 616, 617; Wells, 1956: F402; Nemenzo, 1959: 93; Chevalier, 1971: 178; Wijsman-Best, 1972: 26; Veron *et al*., 1977: 50–53; Scheer & Pillai, 1983: 113; Wood, 1983: 147, 150; Veron, 1986: 468; Chevalier & Beauvais, 1987: 714; Veron & Hodgson, 1989: 271; Sheppard, 1990: 10; Sheppard & Sheppard, 1991: 126; Veron, 2000, vol. 3: 134, 135.

Diagnosis
Colonial, with intra- and extracalicular budding. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, limited amount (includes double wall) or fused walls. Calice width medium (4–15 mm), but may be larger (> 15 mm), with medium relief (3–6 mm). Costosepta may be confluent. Septa generally in ≥ four cycles (≥ 48 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes weak to well developed. Epitheca well developed and endotheca generally abundant (vesicular) (Fig. 13A, D, G, J).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 13B, E, H, K).

Walls formed by dominant paratheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters generally strong; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; 0.3–0.5 mm between clusters;

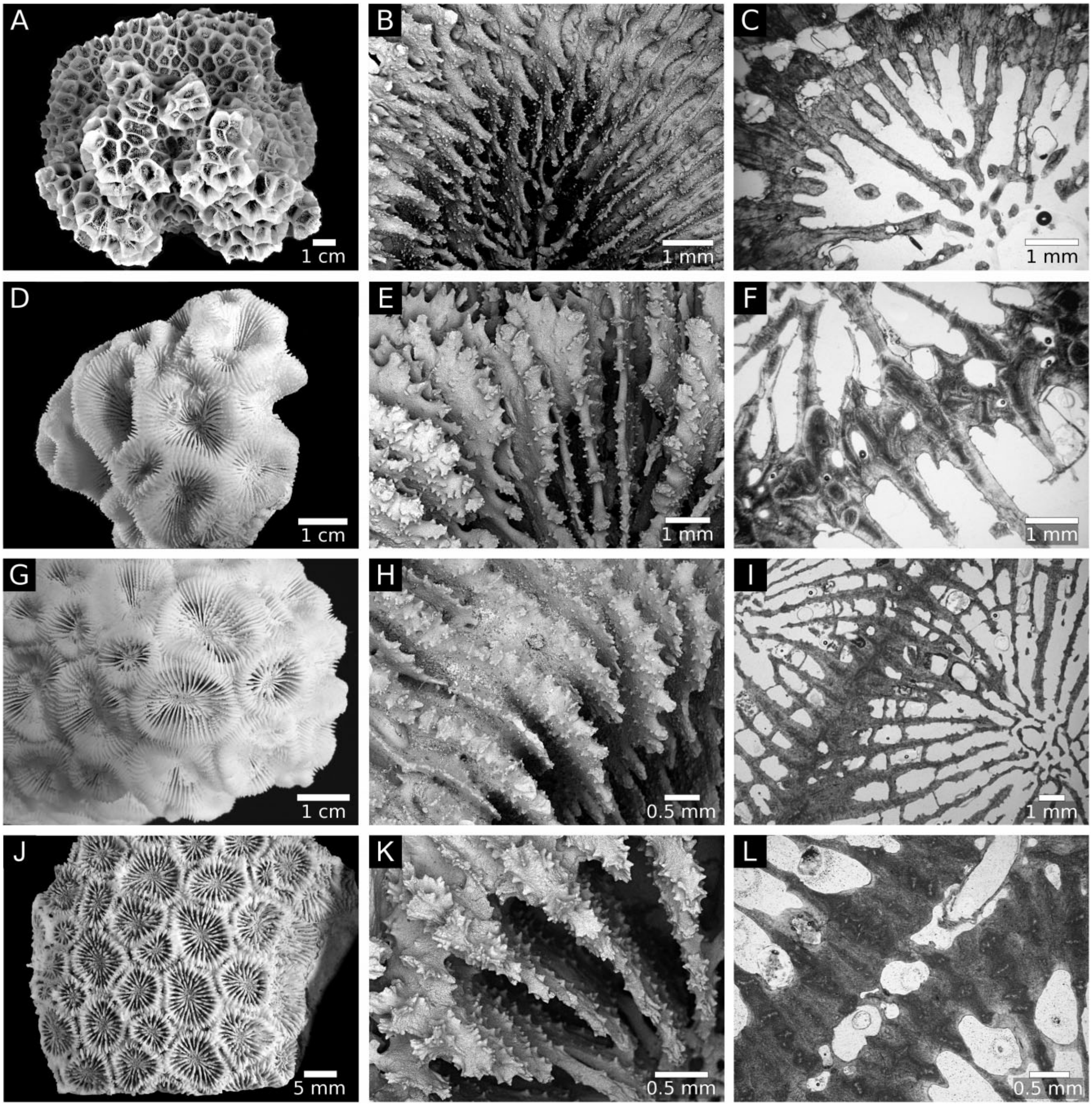


Figure 13. *Favites* Link, 1807, has discrete corallites with double or fused walls, septa generally in ≥ four cycles (≥ 48 septa), weak to well-developed paliform (uniaxial) lobes, and spongy columellae. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm). Walls formed by dominant paratheca and partial septotheca, with strong costa centre clusters and transverse septal crosses. A–C, *Favites abdita* (Ellis & Solander, 1786), type species of *Favites*; macromorphology, holotype GLAHM 104005, unknown locality (A; photo by K. G. Johnson); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype RMNH 10760, Pulau Air, Indonesia. D–F, *Favites flexuosa* (Dana, 1846); macromorphology, syntype USNM 27, Fiji (D); micromorphology (E) and microstructure (F), hypotype RMNH 14165, New Caledonia. G–I, *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977; macromorphology (G) and micromorphology (H; photo by N. Santodomingo), holotype NHMUK 1977.1.1.6, southwest Swain Reefs, Australia; microstructure, hypotype MTQ G61874, Pelorus Island, Australia (I). J–L, *Favites valenciennesi* (Milne Edwards & Haime, 1849b); macromorphology, holotype MNHN IK-2010-696, unknown locality (J); micromorphology (K) and microstructure (L), hypotype UP P1L02131, Batangas, the Philippines.

medial lines weak or strong. Transverse crosses generally present. Columella centres clustered (Fig. 13C, F, I, L).

Species included

1. *Favites abdita* (Ellis & Solander, 1786: 162, pl. 50: fig. 2); holotype: GLAHM 104005 (dry specimen; Fig. 13A); type locality: 'probablement les mers des Grandes-Indes' (Lamarck, 1816: 265); phylogenetic data: molecular and morphology.
2. *Favites acuticollis* (Ortmann, 1889: 528, pl. 16: fig. 11); holotype: ZMB Cni 4793 (dry specimen); type locality: Sri Lanka; phylogenetic data: none.
3. *Favites chinensis* (Verrill, 1866: 35); holotype: YPM IZ 1002 (dry specimen); type locality: Hong Kong; phylogenetic data: molecular and morphology.
4. *Favites colemani* (Veron, 2000, vol. 3: 219, figs 6–11) (see also Veron, 2002: 164, figs 301, 302; ICZN, 2011: 164); lectotype (designated herein): UP MSI-3008-CO (dry specimen); type locality: Calamian Islands, Palawan, the Philippines, 15 m depth; phylogenetic data: molecular and morphology.
5. *Favites complanata* (Ehrenberg, 1834: 317); holotype: ZMB Cni 695 (dry specimen); type locality: Red Sea; phylogenetic data: molecular and morphology.
6. *Favites flexuosa* (Dana, 1846: 227, pl. 11: figs 6, 6a–e); syntype: USNM 27 (dry specimen; Fig. 13D); type locality: Fiji; phylogenetic data: molecular and morphology.
7. *Favites halicora* (Ehrenberg, 1834: 321); holotype: ZMB Cni 733, lost (Chevalier, 1971: 197; not found in ZMB), figured in Klunzinger (1879, pl. 4: fig. 1); type locality: Red Sea; phylogenetic data: molecular and morphology.
8. *Favites magnistellata* (Chevalier, 1971: 293, pl. 9: fig. 3, pl. 34: fig. 2); holotype: H 78 m (Chevalier, 1971: 293), MNHN status unknown; type locality: fringing reef near southwest Hugon Island, New Caledonia; phylogenetic data: molecular and morphology.
9. *Favites melicerum* (Ehrenberg, 1834: 320) = *Favites bestae* Veron, 2000, vol. 3: 140, figs 1, 2 (see also Veron, 2002: 150, figs 277–279; ICZN, 2011: 164); holotype: ZMB Cni 734, lost (Wijsman-Best, 1972: 29; Veron, 2002: 150), figured in Matthai, 1914, pl. 36: fig. 4; neotype (designated herein): ZMA Coel. 5820 (dry specimen); type locality: southern New Caledonia, 5 m depth; phylogenetic data: none.
10. *Favites micropentagonus* Veron, 2000, vol. 3: 137, figs 6–9 (see also Veron, 2002: 148, figs 274–276; ICZN, 2011: 164); lectotype (designated herein): UP MSI-3006-CO (dry specimen); type locality: Calamian Islands, Palawan, the Philippines, 12 m depth; phylogenetic data: none.
11. *Favites monticularis* Mondal, Raghunathan & Venkataraman, 2013: 4510, figs 1, 2; holotype: ZSI/ANRC-7410 (dry specimen); type locality: off Shibpur, Diglipur, North Andaman, 14 m depth; phylogenetic data: none.
12. *Favites paraflexuosus* Veron, 2000, vol. 3: 155, figs 4–6 (see also Veron, 2002: 151, figs 280–282; ICZN, 2011: 164); lectotype (designated herein): WAM Z12911 (dry specimen); type locality: Houtman Abrolhos Islands, Western Australia, 15 m depth; phylogenetic data: molecular and morphology.
13. *Favites pentagona* (Esper, 1795: 23, pl. 39: figs 1, 2); holotype: lost (Chevalier, 1971: 216; Scheer, 1990: 390); type locality: 'probablement l'Océan indien' (Lamarck, 1816: 264); phylogenetic data: molecular and morphology.
14. *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977: 64, figs 110–117, 436–438; holotype: NHMUK 1977.1.1.6 (dry specimen; Fig. 13G, H); paratype: RMNH 10734 (dry specimen); type locality: southwest Swain Reefs, Australia, 5 m depth; phylogenetic data: molecular and morphology.
15. *Favites russelli* (Wells, 1954: 460, pl. 174: figs 7, 8); holotype: USNM 45004 (dry specimen); type locality: seaward slope of Bikini Atoll, Marshall Islands, 53–77 m depth; phylogenetic data: molecular and morphology.
16. *Favites solidocolumellae* Latypov, 2006: 149, figs 38: 7, 8 (= *Favites* sp. 1 Latypov, 1995: 48, pl. 8: fig. 1); holotype: FEBRAS 1/95118 (dry specimen); type locality: Nha Trang Bay, Chuong Island, Vietnam, 3 m depth; phylogenetic data: none.
17. *Favites spinosa* (Klunzinger, 1879: 39, pl. 4: fig. 7, pl. 10: fig. 5); holotype: ZMB 2154 (dry specimen); type locality: Red Sea; phylogenetic data: none.
18. *Favites stylifera* Yabe & Sugiyama, 1937: 426, fig. 1; holotype: NSMT (dry specimen); type locality: Yoronjima, Kagoshima, Japan; phylogenetic data: none.
19. *Favites valenciennesi* (Milne Edwards & Haime, 1849b, vol. 12: 124, vol. 10, pl. 9: figs 3, 3a; see Article 58.14 of the Code); holotype: MNHN IK-2010-696 (dry specimen; Fig. 13J); type locality: unknown; phylogenetic data: molecular and morphology.
20. *Favites vasta* (Klunzinger, 1879: 38, pl. 4: fig. 12, pl. 10: fig. 4a, b); holotype: ZMB Cni 2176 (dry specimen); type locality: 'Kossier' (specimen label), Egypt, Red Sea; phylogenetic data: none.

Taxonomic remarks
Favites Link, 1807: 162, has been a difficult genus to define. By convention, species tend to have 'cerioid, occasionally subplocoid' (Veron, 2000, vol. 3: 134) corallites. There is now little doubt that the clade with the

majority of *Favites* spp., including the type species *Favites abdita*, also contains species with fully plocoid corallites such as *Phymastrea valenciennesi* Milne Edwards & Haime, 1849b, vol. 12: 124, and *Montastrea colemani* Veron, 2000, vol. 3: 219 (Arrigoni *et al*., 2012), whereas *Montastraea magnistellata* Chevalier, 1971: 293, is sister to this clade (Huang *et al*., 2011; Huang, 2012). In this sense, *Favites* has been a paraphyletic group. The solution proposed here is thus to move the three species above into *Favites*.

On the one hand, recovery of *Favites pentagona*, *Favites russelli*, and *Favites peresi* (a *Goniastrea* sp. according to Veron, 2000, vol. 3: 166) separately in distant lineages renders the genus polyphyletic (Huang *et al*., 2011; Arrigoni *et al*., 2012). We resolve this partially by moving *Favites peresi* into the new genus *Paramontastraea* Huang & Budd. On the other hand, we find limited morphological basis for transferring *Favites pentagona* out of the genus because it is the sister group to the rest of *Favites* on the morphology tree. *Favites micropentagonus* 'looks like a diminutive form of the well know [*sic*] *Favites pentagona*' (Veron, 2002: 148) and is thus a likely sister species to *Favites pentagona*. For both species, further molecular sampling will clarify their affinities.

Favites bestae is a junior synonym of *Astraea melicerum* Ehrenberg, 1834: 320 described by Veron (2000, vol. 3: 140; see also Veron, 2002: 150), although the latter name is sometimes considered a synonym of *Favites pentagona* (Matthai, 1914: 95; Chevalier, 1971: 215; see also Wijsman-Best, 1972: 30). The reason given for establishing this species is that the holotype of the senior synonym had been lost, and thus the name *Favites melicerum* is 'unverifiable'. As Veron (2000, vol. 3: 140) deemed *Favites bestae* to be a separate species from *Favites pentagona*, by extension *Favites melicerum* is also regarded as distinct from *Favites pentagona*, a view held by Vaughan (1918: 112). The use of *Favites bestae* as a 'new name' or 'nomen novum' is considered unnecessary because it is neither a replacement for a preoccupied name (Article 60.3 of the Code; see Hoeksema, 1993) nor a substitute for an unavailable or invalid name (Article 23.3.5 of the Code). Nevertheless, a neotype needs to be designated for its senior synonym *Favites melicerum*, a task we have undertaken above.

Favites is widely distributed on reefs of the Indo-Pacific, present as far east as the Tuamotu Archipelago in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks
We find no apomorphies for *Favites* that are consistent across data types, primarily because of the recovery of *Favites russelli* and *Favites pentagona* in distant parts of the molecular phylogeny. Few characters separate them from other *Favites* spp., such as the number of septa and distinctiveness of costa centre clusters, and further studies are warranted to determine if they should be distinguished as separate genera.

For reasons unknown, *Favites rotundata* Veron, Pichon & Wijsman-Best, 1977: 64, was placed in *Favia* by Veron (2000, vol. 3: 124) although its 'coralla are subplocoid' (Veron *et al*., 1977: 64). Morphological and molecular analyses consistently recover this species within the *Favites* clade (Fig. 2; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012), supporting its original placement within *Favites*. *Favia marshae* Veron, 2000, vol. 3: 122, was described as a morphologically similar species (see also Huang, 2012), but without molecular data to justify this affinity, we preserve its membership within *Dipsastraea*.

The name *Montastraea valenciennesi* has been applied on two disparate plocoid species differing in the degree of separation between adjacent corallite walls (Fukami & Nomura, 2009). Presumably, the 'corallite-wall separate type' is a *Dipsastraea* species, whereas the 'corallite-wall fusion type' is the one recovered within the *Favites* clade (Huang *et al*., 2011). Based on thin section observations, we find no difference in wall separation between the two types. However, two synapomorphies of the most inclusive *Favites* clade omitting *Favites pentagona* – septa in four or more cycles and strong costa centre clusters – are clearly present in the specimen recovered within the *Favites* clade (UP P1L02131; Fig. 13L). The specimen also possesses unequal costosepta and well-developed paliform lobes that are found in Milne Edwards & Haime's holotype of *Phymastrea valenciennesi*. These traits are missing in the other type, which should therefore be considered as a cryptic *Dipsastraea* species.

GENUS *GONIASTREA* MILNE EDWARDS & HAIME, 1848A: 495 (FIG. 14)

Type species
Astrea retiformis Lamarck, 1816: 265; original designation, Milne Edwards & Haime, 1848a, vol. 27: 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.' (Milne Edwards & Haime, 1848a, vol. 27: 495).

Subsequent descriptions
Milne Edwards & Haime, 1849b, vol. 12: 160; d'Orbigny, 1851: 170; Milne Edwards & Haime, 1857, vol. 2: 444; Klunzinger, 1879: 32; Duncan, 1884: 102; Quelch, 1886: 99; Saville Kent, 1893: 163; Ogilvie, 1896: 146–153;

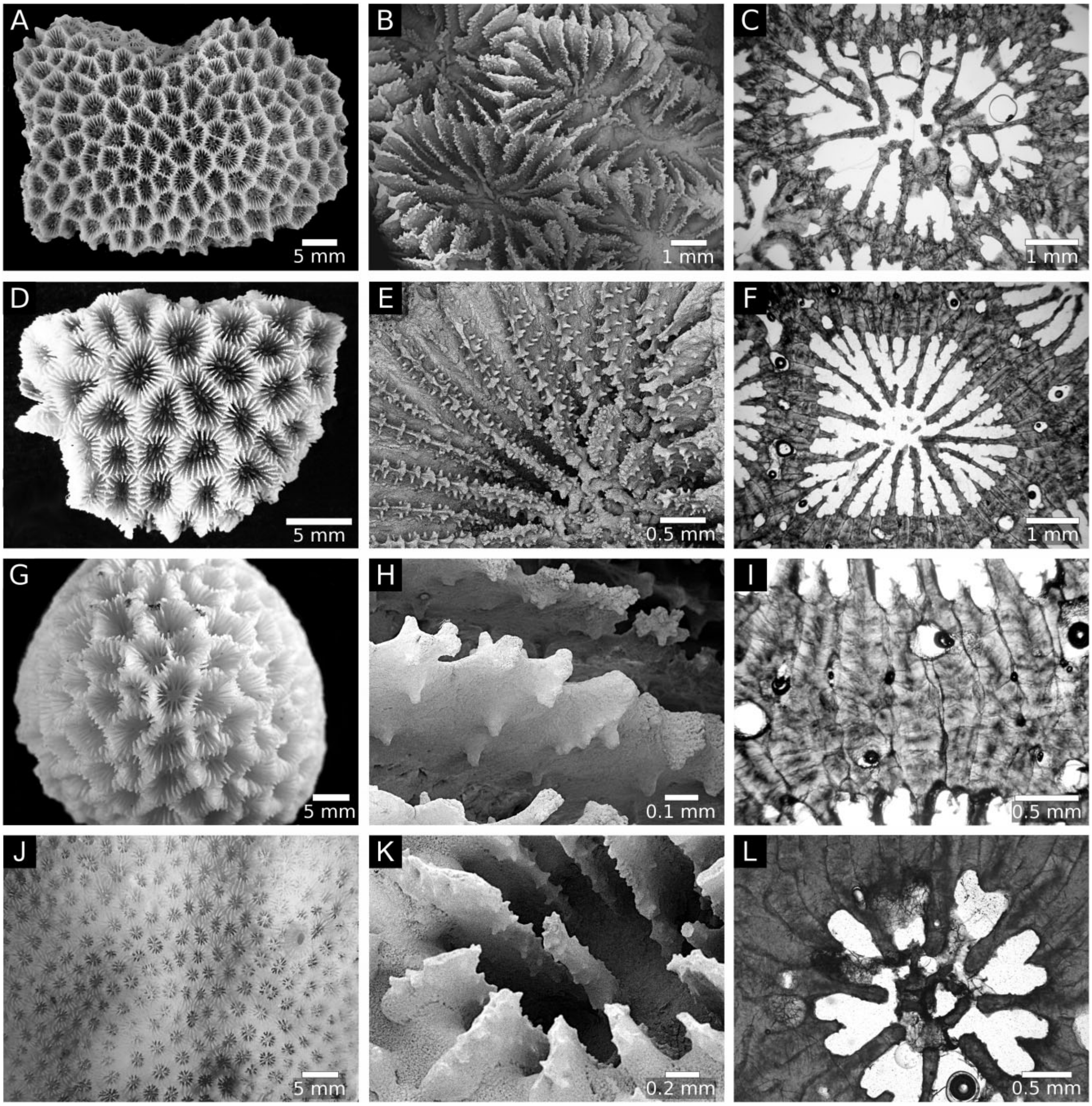


Figure 14. *Goniastrea* Milne Edwards & Haime, 1848a, generally has discrete corallites, small to medium (≤ 15 mm) calices, equally thick costosepta, and well-developed paliform (uniaxial) and/or septal (multiaxial) lobes. Septal teeth are often low (< 0.3 mm) and narrowly spaced (< 0.3 mm). Walls formed by strong abortive septa and partial septotheca; trabeculothecal elements may be present. A–C, *Goniastrea retiformis* (Lamarck, 1816), type species of *Goniastrea*; macromorphology, holotype MNHN IK-2010-693, unknown locality (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 1013047 (FA1030), Saipan, Mariana Islands. D–F, *Goniastrea edwardsi* Chevalier, 1971; macromorphology, holotype MNHN IK-2010-654, Seychelles (D); micromorphology (E) and microstructure (F), hypotype RMNH 11194, Lizard Island, Australia. G–I, *Goniastrea favulus* (Dana, 1846); macromorphology (G), micromorphology (H), and microstructure (I), syntype USNM 66, Fiji. J–L, *Goniastrea stelligera* (Dana, 1846); macromorphology (J), micromorphology (K), and microstructure (L), syntype USNM 55, Fiji.

Gardiner, 1899: 746; Delage & Hérouard, 1901: 629; Gardiner, 1904: 772; Matthai, 1914: 115, 116; Vaughan, 1918: 113, 114; Vaughan, 1919: 416; Hickson, 1924: 53, 54; Hoffmeister, 1925: 26; Faustino, 1927: 139; Coryell & Ohlsen, 1929: 201; Yabe *et al*., 1936: 33; Vaughan & Wells, 1943: 167, 168; Alloiteau, 1952: 617; Crossland, 1952: 132, 133; Wells, 1956: F402; Nemenzo, 1959: 97; Chevalier, 1971: 231; Wijsman-Best, 1972: 37; Veron *et al*., 1977: 79; Scheer & Pillai, 1983: 119; Wood, 1983: 150; Veron, 1986: 478; Chevalier & Beauvais, 1987: 714; Sheppard, 1990: 10; Sheppard & Sheppard, 1991: 130; Veron, 2000, vol. 3: 156, 157.

Diagnosis

Colonial, with intracalicular budding only. Corallites monomorphic and discrete (one to three centres) or uniserial; monticules absent. Walls generally fused, but moderate costate coenosteum (< corallite diameter) present in *Goniastrea stelligera*. Calice width small to medium (≤ 15 mm), with low to medium relief (≤ 6 mm). Costosepta generally not confluent. Septa in three cycles (24–36 septa). Free septa present, may be regular or irregular. Septa spaced ≥ six septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and generally compact (one to three threads), spongy (> three threads) in *Goniastrea australensis*, < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes well developed, and may be present as septal (multiaxial) lobes. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 14A, D, G, J).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low to medium (≤ 0.6 mm) and tooth spacing narrow to medium (≤ 1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 14B, E, H, K).

Walls formed by strong abortive septa and partial septotheca; trabeculothecal elements may be present; dominant paratheca in *Goniastrea australensis*. Thickening deposits fibrous. Costa centre clusters weak; ≤ 0.6 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 14C, F, I, L).

Species included

1. *Goniastrea retiformis* (Lamarck, 1816: 265); holotype: MNHN IK-2010-693 (dry specimen; Fig. 14A); type locality: 'les iles Seychelles' (Milne Edwards & Haime, 1849b, vol. 12: 161); phylogenetic data: molecular and morphology.
2. *Goniastrea australensis* (Milne Edwards & Haime, 1857, vol. 2: 520); holotype: MNHN IK-2010-409; type locality: Australia; phylogenetic data: molecular and morphology.
3. *Goniastrea columella* Crossland, 1948: 191, pls 8, 10a; holotype: NHMUK 1961.7.17.46 (dry specimen); type locality: Umpangazi, South Africa; phylogenetic data: none.
4. *Goniastrea deformis* Veron, 1990: 142, figs 48–50, 83; holotype: MTQ G32487 (dry specimen); type locality: Kushimoto, Japan, 4 m depth; molecular only (Fukami *et al*., 2008).
5. *Goniastrea edwardsi* Chevalier, 1971: 240, pl. 27: fig. 2, pl. 28: figs 6, 7, pl. 29: figs 5, 6; holotype: MNHN IK-2010-654, *Goniastrea solida* collected by Milne Edwards, and described by Milne Edwards & Haime (1849b, vol. 12: 160, vol. 10, pl. 9: figs 7, 7a; dry specimen; Fig. 14D); type locality: Seychelles; phylogenetic data: molecular and morphology.
6. *Goniastrea favulus* (Dana, 1846: 245, pl. 13: fig. 7); syntype: USNM 66 (dry specimen; Fig. 14G–I); syntype: YPM IZ 4323 (dry specimen); type locality: Fiji; phylogenetic data: molecular and morphology.
7. *Goniastrea minuta* Veron, 2000, vol. 3: 158, figs 1–5 (see also Veron, 2002: 153, figs 283–285; ICZN, 2011: 164); lectotype (designated herein): MTQ G55825 (dry specimen); hypotype: MTQ G60250, figured in Veron (2002: 154, fig. 285; dry specimen); type locality: Milne Bay, Papua New Guinea, 4 m depth; phylogenetic data: none.
8. *Goniastrea pectinata* (Ehrenberg, 1834: 320); holotype: ZMB Cni 726; type locality: Red Sea; phylogenetic data: molecular and morphology.
9. *Goniastrea ramosa* Veron, 2000, vol. 3: 160, figs 1, 2 (see also Veron, 2002: 155, figs 286–288; ICZN, 2011: 164); lectotype (designated herein): MTQ G55803 (dry specimen); type locality: Flores, Indonesia, 1 m depth; phylogenetic data: none.
10. *Goniastrea stelligera* (Dana, 1846: 216, pl. 10: fig. 9); syntype: USNM 55 (dry specimen; Fig. 14J–L); type locality: Fiji; phylogenetic data: molecular and morphology.
11. *Goniastrea thecata* Veron, DeVantier & Turak, 2000 (Veron, 2000, vol. 3: 169, fig. 5; see also Veron, 2002: 157, figs 289–291; ICZN, 2011: 164); lectotype (designated herein): MTQ G55837 (dry specimen); type locality: northern Red Sea coast of Saudi Arabia, 1 m depth; phylogenetic data: none.

Taxonomic remarks

Goniastrea Milne Edwards & Haime, 1848a, vol. 27: 495, accumulated new species gradually since the description of its type in the genus *Astrea* Lamarck, 1816, until as recently 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 and morphological phylogenies have consistently placed the majority of its species within a clade that also includes *Merulina* and/or *Scapophyllia* (Fig. 2; Huang *et al*., 2011; Arrigoni *et al*., 2012).

Both data types support the sister relationship between the type species of *Goniastrea*, *Goniastrea retiformis*, and *Astrea* (*Orbicella*) *stelligera* Dana, 1846: 216, the latter conventionally regarded as an Indo-Pacific *Favia* (Veron, 2000, vol. 3: 102). This lends further support to the reasoning that coenosteum amount, moderate in this species but absent in *Goniastrea*, is an extremely homoplastic character, experiencing multiple changes near the tips of the tree. *Astrea stelligera* is hereby synonymized as *Goniastrea stelligera*.

Goniastrea australensis and *Goniastrea deformis* are not nested within other *Goniastrea* spp. but have been recovered near the main *Goniastrea* clade to varying degrees (Fig. 2; Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012). Overall, the polyphyly of this genus ensures that the three remaining species – yet to be examined in a phylogenetic context – cannot be unequivocally placed (but see Huang, 2012). Despite forming at least two *Goniastrea* subclades that may not be sister groups, we consider it premature to make formal changes to these species until certainty of their positions increases appreciably.

On the contrary, *Goniastrea aspera* Verrill, 1866: 32, and *Favia palauensis* Yabe & Sugiyama, 1936: 30, clearly belong in a separate taxon with affinities to *Dipsastraea* (molecular; Huang *et al*., 2011; Arrigoni *et al*., 2012; Fig. 2A) and *Trachyphyllia* (morphology; Fig. 2B). Accordingly, we place them in *Coelastrea* Verrill, 1866: 32.

Goniastrea is widely distributed on reefs of the Indo-Pacific, recorded throughout most of French Polynesia and the Pitcairn Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

No apomorphies have been identified for *Goniastrea*, mainly because of the recovery of *Goniastrea australensis* outside of the *Goniastrea* clade.

Whereas the molecular trees generally show that *Merulina* and *Scapophyllia* are nested within the *Goniastrea* clade, morphological evidence indicates a sister relationship. It should be noted that they may not be as distinct as previously thought. In particular, the lack of apomorphies for *Goniastrea* amongst the suite of characters tested suggests that these genera share numerous traits, including all subcorallite characters analysed here. Nevertheless, *Goniastrea* differs from *Merulina* and *Scapophyllia* in having mostly discrete corallites, costosepta that are not confluent across walls, well-developed epitheca and low–moderate (tabular) endotheca.

Goniastrea is also commonly confused with *Favites* spp. that have fused walls, as they do share most macromorphological characters. However, the former do not generally possess confluent costosepta, and have fewer vesicular endotheca as well as internal lobes that are multiaxial (i.e. septal lobes). The more striking disparities are only observed via thin sections that show the presence of abortive septa and partial trabeculotheca only in *Goniastrea*, and by contrast, paratheca, strong costa centre clusters, and transverse crosses in *Favites*.

GENUS *HYDNOPHORA* FISCHER VON WALDHEIM, 1807: 295 (FIG. 15)

Synonyms

Hydnophorella Delage & Hérouard, 1901: 628, fig. 876 (type species: *Hydnophora contignatio* Klunzinger, 1879: 23, pl. 3: figs 2, 3, pl. 9: fig. 12a, b, c = *Madrepora exesa* Pallas, 1766: 290; original designation, Delage & Hérouard, 1901: 628); *Monticularia* Lamarck, 1816: 248 (type species: *Monticularia folium* Lamarck, 1816: 250 = *Madrepora exesa* Pallas, 1766: 290; original designation, Lamarck, 1816: 250); *Monticulina* Saville Kent, 1893: 169 (type species *Hydnophora rigida* Saville Kent, 1893: 168, chromo pl. 7: fig. 7; original designation, Saville Kent, 1893: 169).

Type species

Hydnophora demidovii Fischer von Waldheim, 1807: 295, pl. 4 = *Madrepora exesa* Pallas, 1766: 290 (see Milne Edwards & Haime, 1857, vol. 2: 420; Vaughan, 1918: 121; Matthai, 1928: 140; Chevalier, 1975: 175); original designation, Fischer von Waldheim, 1807: 295.

Original description

'Polypier pierreux, crustacé, en masse glomérulée ou en expansions lobées, subfoliacées, ayant sa surface supérieure parsemée d'étoiles lamelleuses, à centre solide, pyramidal, et plus ou moins élevé.' (Fischer von Waldheim, 1807: 295).

Subsequent descriptions

Milne Edwards & Haime, 1848a, vol. 27: 493; Milne Edwards & Haime, 1849a, vol. 11: 299, 300; d'Orbigny, 1851: 168; Milne Edwards & Haime, 1857, vol. 2: 418, 419; Klunzinger, 1879: 20; Quenstedt, 1881: 1013; Duncan, 1884: 97; Quelch, 1886: 95; Saville Kent, 1893: 168, 169; Gardiner, 1899: 744; Delage & Hérouard, 1901: 702; Gardiner, 1904: 764; Vaughan, 1918: 121; Hoffmeister, 1925: 29, 30; Faustino, 1927: 148, 149; Matthai, 1928: 136, 137; Coryell & Ohlsen, 1929: 202, 203; Yabe *et al*., 1936: 39; Vaughan & Wells, 1943: 169, 170; Alloiteau, 1952: 618; Wells, 1956: F402, F403; Nemenzo, 1959: 102; Wijsman-Best, 1972: 51; Chevalier, 1975: 167; Veron *et al*., 1977: 124; Scheer & Pillai, 1983: 127; Wood, 1983: 158; Veron, 1986: 428; Chevalier &

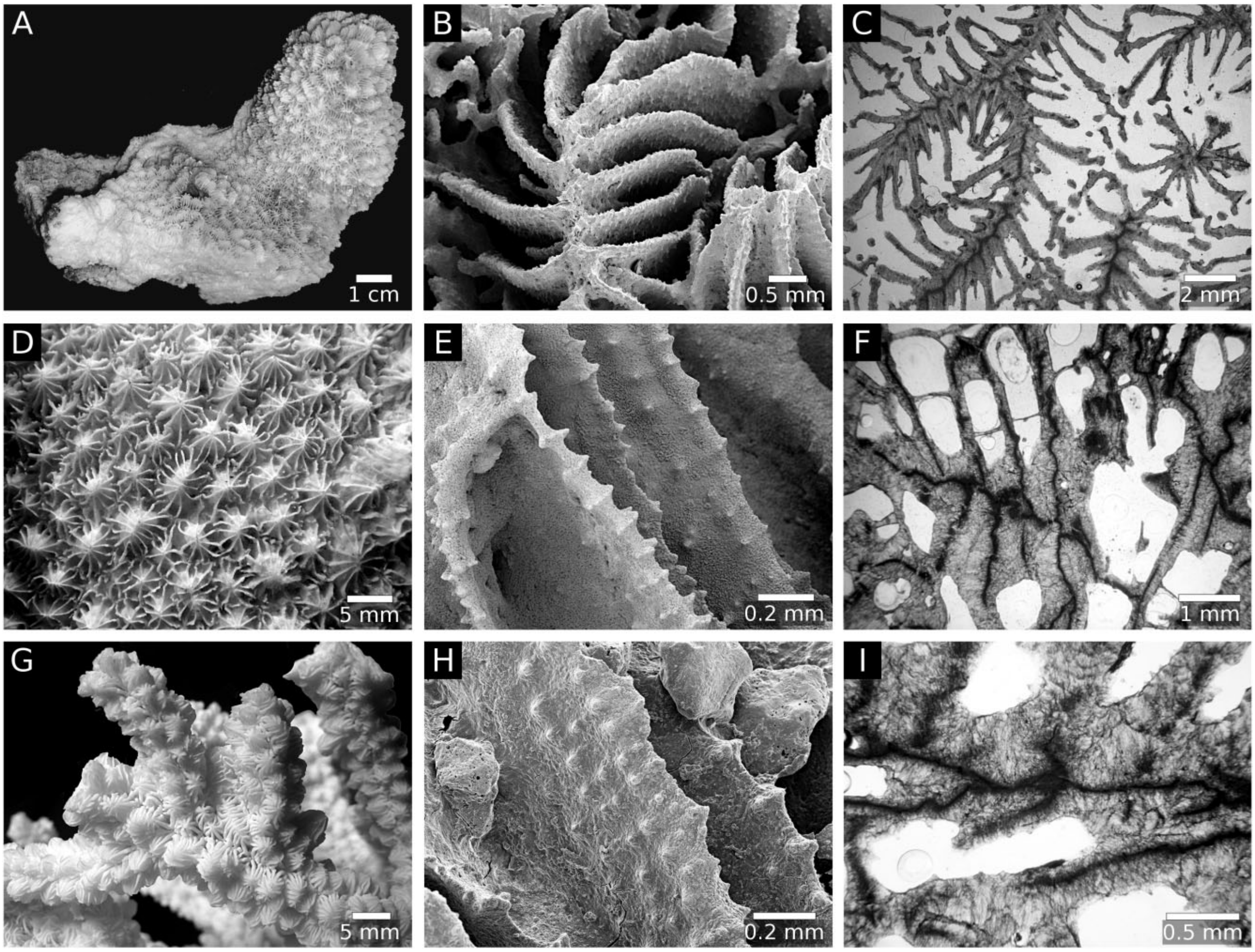


Figure 15. *Hydnophora* Fischer von Waldheim, 1807, has uniserial corallites, monticules and fused walls, septa in < three cycles (< 24 septa), no free septa, compact columellae, reduced epitheca, and generally sparse endotheca. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm); irregularly shaped granules aligned on septal face. Walls formed by dominant trabeculotheca and partial septotheca, with strong costal and septal medial lines, and aligned columella centres. A–C, *Hydnophora exesa* (Pallas, 1766: 290), type species of *Hydnophora*; macromorphology, neotype (designated herein) UP P1L02157, Batangas, the Philippines (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 91183, Lord Howe Island, Australia. D–F, *Hydnophora grandis* Gardiner, 1904; macromorphology, syntype NHMUK 1928.4.18.227, south Nilandu, Maldives (D); micromorphology (E) and microstructure (F), hypotype UF 2063 (FA1084), Palau. G–I, *Hydnophora rigida* (Dana, 1846); macromorphology (G) and microstructure (I), syntype USNM 148, Fiji; micromorphology, syntype of *Merulina laxa* Dana, 1846 USNM 4501, Sulu Sea (H).

Beauvais, 1987: 717; Veron & Hodgson, 1989: 268; Sheppard, 1990: 12; Best & Suharsono, 1991: 334; Sheppard & Sheppard, 1991: 117; Bosellini, 1999: 222; Veron, 2000, vol. 2: 364.

Diagnosis (apomorphies in italics)

Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; *monticules present*. Walls fused. Calice width small to medium (≤ 15 mm), with low to medium relief (≤ 6 mm). Costosepta not confluent. Septa in < three cycles (< 24 septa). *Free septa absent*. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular but compact (one to three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes absent. *Epitheca reduced and endotheca sparse* (Fig. 15A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules aligned on septal face, perpendicular to septal margin; irregular in shape. Interarea palisade (Fig. 15B, E, H).

Walls formed by dominant trabeculotheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; *medial lines strong*. Septum centre clusters weak; < 0.3 mm between clusters; medial lines strong. Transverse crosses absent. Columella centres aligned (Fig. 15C, F, I).

Species included

1. *Hydnophora exesa* (Pallas, 1766: 290); holotype: lost (Chevalier, 1975: 176); neotype (designated herein): UP P1L02157 (dry specimen; Fig. 15A); type locality: Talim Bay, Batangas, the Philippines, 2.5 m depth ('Oceanus Indicus'; Pallas, 1766: 291); phylogenetic data: molecular and morphology.
2. *Hydnophora bonsai* Veron, 1990: 139, figs 46, 47; holotype: MTQ G32486 (dry specimen); type locality: Kushimoto, Japan, 4 m depth; phylogenetic data: none.
3. *Hydnophora grandis* Gardiner, 1904: 764, pl. 60: fig. 11; syntypes: NHMUK 1928.4.18.227 (Fig. 15D), 1928.5.2.1 (two dry specimens); type locality: south Nilandu and Haddumati, Maldives (see also Matthai, 1928: 153); phylogenetic data: molecular (Fukami *et al*., 2008) and morphology.
4. *Hydnophora microconos* (Lamarck, 1816: 251); holotype: MNHN IK-2010-477 (dry specimen); type locality: 'lOcéan des Grandes-Indes' (Lamarck, 1836: 393); phylogenetic data: molecular and morphology.
5. *Hydnophora pilosa* Veron, 1985: 176, figs 26–28; holotype: WAM 174-84 (also WAM Z919; Griffith & Fromont, 1998: 235) (dry specimen); paratypes: WAM 175-84, 176-84 (also WAM Z920, Z921; Griffith & Fromont, 1998: 235) (two dry specimens); type locality: Elizabeth Reef, eastern Australia, 6 m depth; phylogenetic data: molecular and partial morphology.
6. *Hydnophora rigida* (Dana, 1846: 276, pl. 17: figs 1, 1a–c); syntype: USNM 148 (dry specimen; Fig. 15G, I); type locality: Fiji; phylogenetic data: morphology only.

Taxonomic remarks
Hydnophora Fischer von Waldheim, 1807: 295, is a distinct genus whose monophyly (subclade H) has been well supported by molecular data (Huang *et al*., 2011; Huang, 2012). Prior to Veron's (1986: 428, 2000, vol. 2: 364) placement of *Hydnophora* within Merulinidae, it was more often associated with Faviidae *sensu* Wells, 1956: F402 (see Vaughan & Wells, 1943: 169; Chevalier, 1975: 167; Veron *et al*., 1977: 124). Molecular phylogenies show that it is most closely related to *Favites*, *Leptoria*, and *Platygyra* (Huang *et al*., 2011), or *Astrea curta* and *Favites russelli* (Arrigoni *et al*., 2012), and relatively distinct from *Merulina* and *Scapophyllia*, the other Merulinidae taxa before the revision of Budd *et al*. (2012).

The genus is relatively well sampled. Only *Hydnophora bonsai*, a Japanese endemic (Veron, 1990: 141), has not been investigated in a phylogenetic context.

Hydnophora is widely distributed on reefs of the Indo-Pacific, present as far east as the Austral Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks
On the morphology tree, *Hydnophora* is supported by a high bootstrap value (95) and decay index (4), and is sister to the clade formed by *Australogyra*, *Leptoria*, and *Platygyra*. It is distinguished as the only scleractinian taxon to possess monticules. Other synapomorphies include the reduced epitheca (likelihood of 1.0 based on the Mk1 model), sparse endotheca (likelihood 1.0), and lack of free septa (likelihood 1.0), all of which make the genus easily separable from its close relatives. Note, however, that the type material of *Hydnophora grandis* has relatively vesicular endotheca, although other specimens examined possess the generic state.

GENUS *LEPTORIA* MILNE EDWARDS & HAIME, 1848A: 493 (FIG. 16)

Type species
Meandrina phrygia Lamarck, 1816: 248 = *Madrepora phrygia* Ellis & Solander, 1786: 162, pl. 48: fig. 2; original designation, Milne Edwards & Haime, 1848a, vol. 27: 493; holotype: MNHN IK-2012-14001 (dry specimen; Fig. 16A); type locality: 'l'Océan des Grandes-Indes et la mer Pacifique' (Lamarck, 1816: 248).

Original description
'Diffère des genres précédents [*Meandrina*, *Manicina*, *Diploria*] par sa columelle lamellaire. Les collines sont simples, minces ou vésiculeuses.' (Milne Edwards & Haime, 1848a, vol. 27: 493).

Subsequent descriptions
Milne Edwards & Haime, 1849a, vol. 11: 291; Milne Edwards & Haime, 1857, vol. 2: 405, 406; Klunzinger, 1879: 13; Duncan, 1884: 90; Gardiner, 1899: 739; Delage & Hérouard, 1901: 626; Gardiner, 1904: 764; Vaughan, 1918: 117; Vaughan, 1919: 421; Hoffmeister, 1925: 27; Faustino, 1927: 141; Matthai, 1928: 109, 110 (*non Platygyra* Ehrenberg); Coryell & Ohlsen, 1929: 205; Yabe *et al*., 1936: 38 (*non Platygyra* Ehrenberg); Vaughan & Wells, 1943: 169; Alloiteau, 1952: 617, 618; Crossland, 1952: 150; Wells, 1956: F402; Nemenzo, 1971: 166; Wijsman-Best, 1972: 50; Chevalier, 1975: 109; Veron *et al*., 1977: 114, 115; Scheer & Pillai, 1983: 126; Wood,

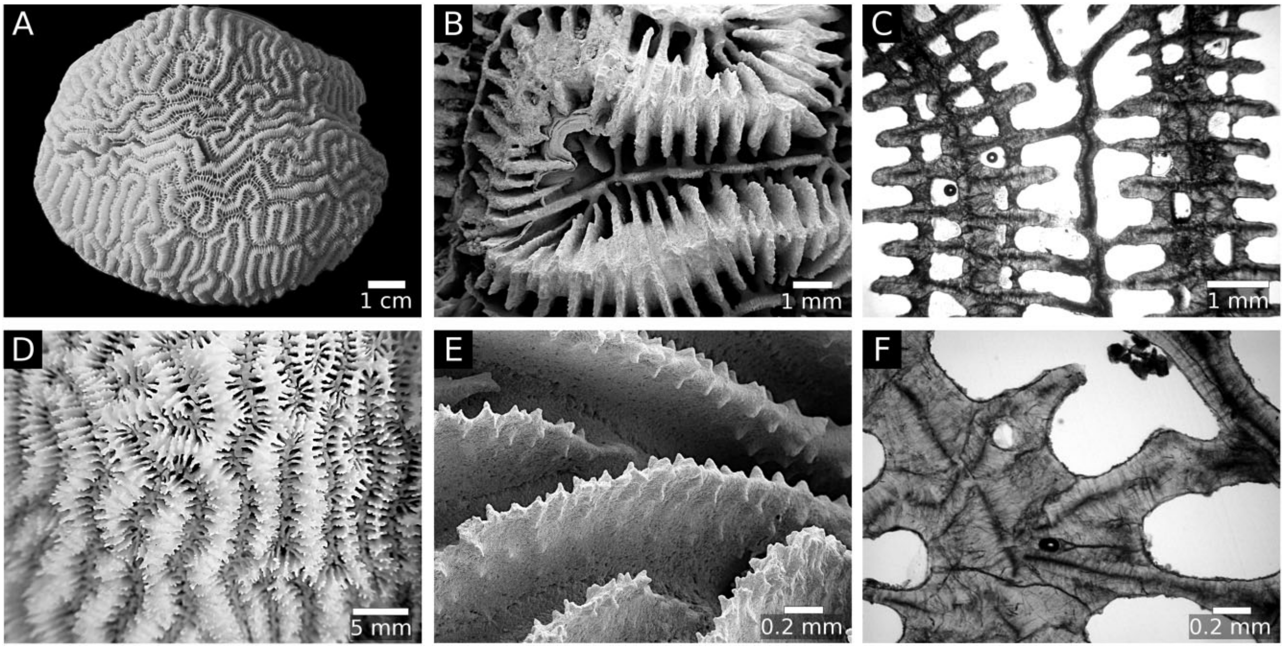


Figure 16. *Leptoria* Milne Edwards & Haime, 1848a, has uniserial corallites, fused walls, small (< 4 mm) and low-relief (< 3 mm) calices, septa in < three cycles (< 24 septa), and lamellar or spongy columellae. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm); weak (rounded) granules aligned on septal face. Walls formed by dominant trabeculotheca and partial septotheca, with strong septal medial lines and aligned columella centres. A–C, *Leptoria phrygia* (Ellis & Solander, 1786), type species of *Leptoria*; macromorphology, *Meandrina phrygia* Lamarck, 1816, holotype of *Leptoria* MNHN IK-2012–14001, unknown locality (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 38508, Murray Island, Australia. D, *Leptoria irregularis* Veron, 1990; macromorphology, holotype MTQ G32489, Ryukyu Islands, Japan. E, F, *Leptoria phrygia* (Ellis & Solander, 1786); micromorphology, hypotype USNM 89850, Mangata, Cook Island (E); microstructure, hypotype USNM 83200, Marshall Islands (F).

1983: 154; Veron, 1986: 496; Chevalier & Beauvais, 1987: 717; Sheppard, 1990: 14; Bosellini, 1999: 222; Veron, 2000, vol. 3: 202.

Diagnosis (apomorphies in italics)
Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; monticules absent. Walls fused. *Calice width small (< 4 mm), with low relief (< 3 mm).* Costosepta confluent. Septa in < three cycles (< 24 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae lamellar or spongy trabecular (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low-moderate (tabular) (Fig. 16A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules aligned on septal face, perpendicular to septal margin; weak (rounded). Interarea palisade (Fig. 16B, E).

Walls formed by dominant trabeculotheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines strong. Transverse crosses absent. Columella centres aligned (Fig. 16C, F).

Species included

1. *Leptoria phrygia* (Ellis & Solander, 1786: 162, pl. 48: fig. 2); holotype: GLAHM 104018 (dry specimen); type locality: 'Oceano pacifico' (Ellis & Solander, 1786: 162); phylogenetic data: molecular and morphology.
2. *Leptoria irregularis* Veron, 1990: 147, figs 53, 54, 95; holotype: MTQ G32489 (dry specimen; Fig. 16D); type locality: north side of Kayama Island, Sekisei Lagoon, Ryukyu Islands, Japan, 15 m depth; phylogenetic data: molecular and partial morphology.

Taxonomic remarks
Leptoria was established by Milne Edwards & Haime (1848a, vol. 27: 493) as a genus with lamellar columellae, and *Meandrina phrygia* Lamarck, 1816: 248, as the type. Two other living taxa, *Meandrina gracilis* Dana,

1846: 261, and *Meandrina tenuis* Dana, 1846: 262, were also included (Milne Edwards & Haime, 1857, vol. 2: 407) but later synonymized with the type species (Matthai, 1928: 112; Chevalier, 1975: 110; Veron *et al*., 1977: 115). All specimens used to describe them correspond to the original description in the possession of lamellar columellae.

The addition of *Leptoria irregularis* Veron, 1990: 147, necessitates the broadening of this description. Molecular phylogenies have placed this species at two distinct positions, sister to *Scapophyllia cylindrica* (Fukami *et al*., 2008) or *Leptoria phrygia* (Huang *et al*., 2011). Material for the former were collected from Okinawa, Japan, just 400 km north of the type locality, whereas the latter sample came from the Philippines. We have not been able to examine either of these types in detail, but assume the latter to be positively identified in order to preserve the taxonomic status quo. Nevertheless, the presence of 'irregularly fused trabeculae' (Veron, 1990: 148) suggests that lamellar columellae are only present in *Leptoria phrygia* and not the entire genus. Our character analysis shows that this trait is an autapomorphy.

Leptoria has been considered a synonym of *Platygyra* by several authors (Matthai, 1928: 110; Wells, 1936: 124; Ma, 1937: 97) because by elimination, the first three of five species listed by Ehrenberg (1834: 323) were deemed unsuitable as they were thought to refer to the Atlantic species *Madrepora labyrinthiformis* Linnaeus, 1758 (Matthai, 1928: 110). *Platygyra phrygia* (Lamarck, 1816: 248), fourth on the list, was therefore regarded as the type of *Platygyra*, with *Leptoria* becoming a synonym. This interpretation was short lived, as Vaughan & Wells (1943: 169) redesignated the first species on Ehrenberg's list, *Maeandra* (*Platygyra*) *labyrinthica* from the Red Sea, as type species of *Platygyra* (see also Vaughan, 1901a: 50), and also resurrected *Leptoria* immediately after (see remarks for *Platygyra* below).

Leptoria is widely distributed on reefs of the Indo-Pacific, present as far east as the Gambier Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

Leptoria is sister taxon to the clade comprising *Australogyra* and *Platygyra*, with small calice diameter (< 4 mm; likelihood of 1.0 based on the Mk1 model) and low relief (< 3 mm; likelihood 1.0) as synapomorphies. Along with the narrower spacing between teeth (< 0.3 mm; likelihood 1.0) in *Leptoria*, only these size-related features distinguish the genus from its closest relatives, subcorallite characters included.

Leptoria phrygia is the only species in Merulinidae to possess lamellar columellae, but this is lacking in its conspecific *Leptoria irregularis*, which may account for its association with the phylogenetically distant *Merulina ampliata* and *Scapophyllia cylindrica* (Veron, 2000, vol. 3: 202). However, subcorallite characters may separate them on the basis of *Leptoria*'s weak granule alignment and trabeculothecal walls without abortive septa. Only macromorphology has been characterized for *Leptoria irregularis*; detailed investigation on this species will clarify its status.

GENUS *MYCEDIUM* MILNE EDWARDS & HAIME, 1851: 130 (FIG. 17)

Synonym

Phyllastraea Dana, 1846: 269 (type species: *Phyllastraea tubifex* Dana, 1846: 270, pl. 16: figs 4, 4a, b = *Madrepora elephantotus* Pallas, 1766: 290; original designation, Dana, 1846: 270).

Type species

Madrepora elephantotus Pallas, 1766: 290; subsequent designation; Verrill, 1901: 133.

Original description

'Polypier en expansions frondiformes. Calices circonscrits, penchés, submamillaires, et disposés autour de l'individu parent qui reste plus développé que les autres. Plateau commun nu et costulé.' (Milne Edwards & Haime, 1851, vol. 15: 130).

Subsequent descriptions

Milne Edwards, 1860, vol. 3: 72, 73; Duncan, 1884: 158; Delage & Hérouard, 1901: 641; Verrill, 1901: 133; Wells, 1936: 121; Yabe *et al*., 1936: 49; Vaughan & Wells, 1943: 198; Wells, 1956: F419; Alloiteau, 1952: 632; Nemenzo, 1959: 120; Chevalier, 1975: 336, 337; Veron & Pichon, 1980: 319; Scheer & Pillai, 1983: 151; Wood, 1983: 199; Veron, 1986: 382; Chevalier & Beauvais, 1987: 725; Sheppard, 1990: 16; Sheppard & Sheppard, 1991: 109; Veron, 2000, vol. 2: 342.

Diagnosis

Colonial, with intracalicular budding only. Corallites polymorphic and organically united; monticules absent. Coenosteum costate, extensive amount (≥ corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites (lamellar linkage). Paliform (uniaxial) lobes weak or moderate. Epitheca absent and endotheca abundant (vesicular) (Fig. 17A, D).

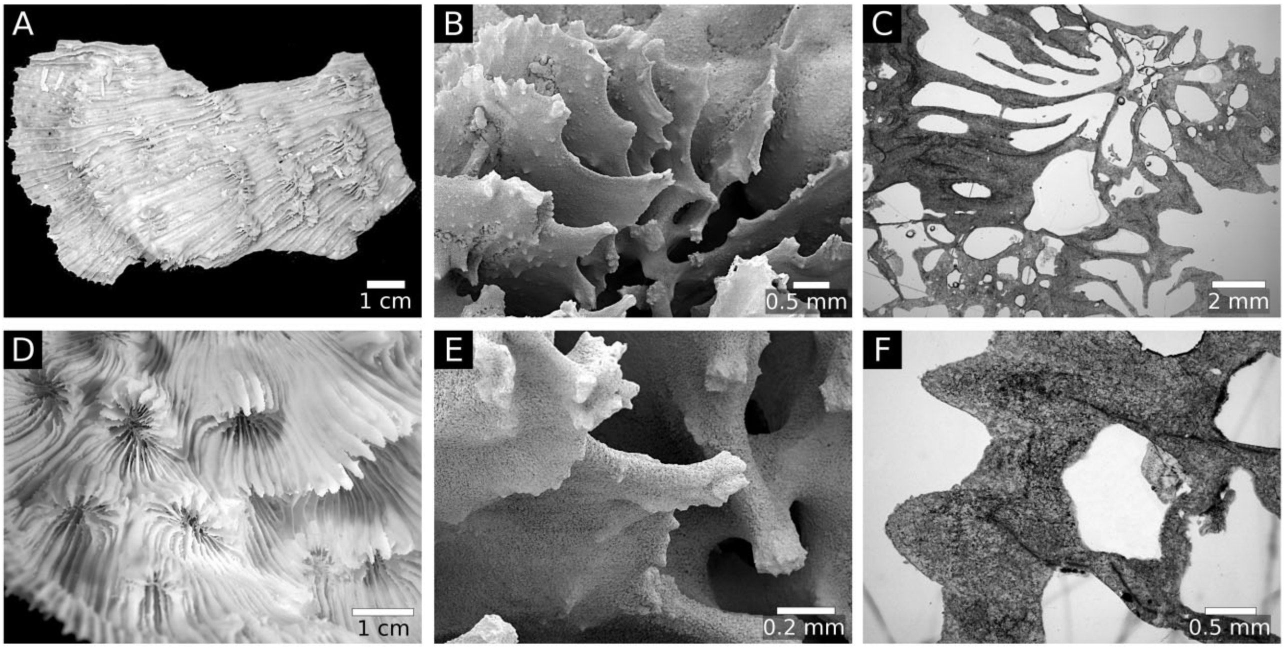


Figure 17. *Mycedium* Milne Edwards & Haime, 1851, has organically united corallites, extensive coenosteum (≥ corallite diameter), septa spaced < six septa per 5 mm and abundant (vesicular) endotheca. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm), no more than six teeth per septum and interarea formed by horizontal bands. Walls formed by dominant paratheca, with microfibrous deposits and strong costal and septal medial lines. A–C, *Mycedium elephantotus* (Pallas, 1766), type species of *Mycedium*; macromorphology, neotype (designated herein) RMBR ZRC.CNI.0916, Raffles Light, Singapore (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UF 2062 (FA1082), Palau. D, *Mycedium umbra* Veron, 2000; macromorphology, holotype MTQ G55783, Sharm al-Sheikh, Egypt. E, F, *Mycedium elephantotus* (Pallas, 1766); micromorphology (E) and microstructure (F), hypotype UF 2062 (FA1082), Palau.

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with no more than six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea formed by horizontal bands (Fig. 17B, E).

Walls formed by dominant paratheca; abortive septa absent. Thickening deposits microfibrous. Costa centre clusters not distinct; medial lines strong. Septum centre clusters not distinct; medial lines strong. Transverse crosses absent. Columella centres clustered (Fig. 17C, F).

Species included

1. *Mycedium elephantotus* (Pallas, 1766: 290); holotype: lost (Chevalier, 1975: 338); neotype (designated herein): RMBR ZRC.CNI.0916 (dry specimen; Fig. 17A); type locality: Raffles Light, Singapore, 8 m depth ('Oceanus Indicus'; Pallas, 1766: 290); phylogenetic data: molecular and morphology.
2. *Mycedium mancaoi* Nemenzo, 1979: 48, fig. 10; holotype: UP CCC-9 (dry specimen); type locality: Pinamungajan, Cebu, the Philippines; phylogenetic data: none.
3. *Mycedium robokaki* Moll & Best, 1984: 56, figs 10b, c, 11; holotype: RMNH 15270 (dry specimen); type locality: 150 m offshore of north Lumu Lumu, Spermonde Archipelago, Indonesia, 8 m depth; phylogenetic data: molecular and partial morphology.
4. *Mycedium spina* Ditlev, 2003: 204, figs 16, 17; holotype: BMRI 2533 (dry specimen); type locality: Bagahak, Darvel Bay, Sabah, 6 m depth; phylogenetic data: none.
5. *Mycedium steeni* Veron, 2000, vol. 2: 347, figs 4–6 (see also Veron, 2002: 120, figs 226–228; ICZN, 2011: 165); lectotype (designated herein): UP MSI-3011-CO (dry specimen); type locality: Calamian Islands, Palawan, the Philippines, 6 m depth; phylogenetic data: none.
6. *Mycedium umbra* Veron, 2000, vol. 2: 342, figs 1–3 (see also Veron, 2002: 118, figs 224, 225; ICZN, 2011: 165); lectotype (designated herein): MTQ G55783 (dry specimen; Fig. 17D); type locality: Ras Mohammed National Park, Sharm al-Sheikh, Sinai Peninsula, Egypt, 10 m depth; phylogenetic data: none.

Taxonomic remarks
Mycedium was originally described by Oken (1815: 68). According to ICZN Opinion 417 (ICZN, 1956), names proposed by Oken (1815) are rejected, so authority of this taxon is assigned to Milne Edwards & Haime (1851, vol. 15: 130), the second authors who used the name.

This genus has commonly been regarded to be similar to *Echinophyllia* (Lobophylliidae), because of its laminar growth form (Vaughan & Wells, 1943: 198; Wells, 1956: F419; Veron & Pichon, 1980: 319; Veron, 1986: 382; 2000, vol. 2: 342). The lack of distinct corallite walls, or corallites being 'organically united' (Vaughan & Wells, 1943: 196), is a distinguishing feature of Pectiniidae, the family in which *Mycedium* and *Echinophyllia* were placed prior to revision by Budd *et al*. (2012). It is now clear based on molecular phylogenetics that this genus is closest to and also nested within *Pectinia* de Blainville, 1825: 201 (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012; Huang, 2012). As only two of the six *Mycedium* spp. have been sampled for phylogenetic analysis, we maintain its genus-level status until more data are available.

Mycedium is widely distributed on reefs of the Indo-Pacific, present as far east as the Gambier Islands in the Southern Hemisphere (Glynn *et al*., 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks
Organically united corallites appear to have independently evolved twice, within Merulinidae in *Mycedium* + *Pectinia* (likelihood of 1.0 based on the Mk1 model), and within Lobophylliidae in *Echinophyllia* + *Oxypora* (Budd *et al*., 2012: fig. 2b). Other synapomorphies of the *Mycedium* + *Pectinia* clade are polymorphic corallites (likelihood 1.0), extensive coenosteum (≥ corallite diameter; likelihood 1.0), unequal costosepta thickness (likelihood 1.0), discontinuous columellae (lamellar linkage; likelihood 1.0), not more than six teeth per septum (likelihood 1.0), interarea made up of horizontal bands (likelihood 1.0), and microfibrous deposits (likelihood 1.0). Transverse crosses are also lost in this lineage (likelihood 1.0). The clade is highly supported, with a bootstrap of 100 and decay index of 9.

Mycedium and *Pectinia* share all morphological traits examined here, as opposed to the paraphyletic *Pectinia* recovered by molecular data. *Physophyllia* is also extremely similar on the basis of macromorphology. The lack of distinction amongst these three genera, and the paraphyly of *Pectinia*, may be grounds for regarding *Mycedium* as a synonym of *Pectinia* and/or *Physophyllia*, but as *Mycedium elephantotus* remains the only species placed on the morphology tree, no changes are proposed here.

Note that quantitative measurements were based on peripheral corallites as structures of the central corallite may be extremely large in comparison.

GENUS *ORBICELLA* DANA, 1846: 205 (FIG. 18)

Type species
Madrepora annularis Ellis & Solander, 1786: 169, pl. 53: figs 1, 2; subsequent designation, Vaughan, 1918: 85.

Original description
'Cells nearly circular, more or less prominent, not subdividing by growth, or rarely so; stars with distinct limits formed by the coalescence laterally of the lamellae, and therefore cells appearing tubular, and separated by interstices' (Dana, 1846: 205).

Subsequent descriptions
Dana, 1859: 23; Klunzinger, 1879: 47, 48; Quelch, 1886: 106; Gardiner, 1899: 751, 752; Delage & Hérouard, 1901: 629; Vaughan, 1901b: 300; Verrill, 1901: 93; Verrill, 1902: 77; Gardiner, 1904: 774; Vaughan, 1918: 85; Vaughan, 1919: 362; Hoffmeister, 1925: 19; Coryell & Ohlsen, 1929: 193, 194; Yabe *et al*., 1936: 22; Crossland, 1952: 123, 124.

Diagnosis (apomorphies in italics)
Colonial, with extracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, moderate amount (< corallite diameter). Calice width small (< 4 mm), with low relief (< 3 mm). Costosepta not confluent. Septa in three cycles (24–36 septa). Free septa regular. Septa spaced > 11 septa per 5 mm. *Costosepta equal in relative thickness.* Columellae trabecular but compact (one to three threads), ≥ *1/4 of calice width*, and discontinuous amongst adjacent corallites. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 18A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation multiaxial. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea smooth (Fig. 18B, E, H).

Walls formed by dominant septotheca and partial paratheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 18C, F, I).

Species included

1. *Orbicella annularis* (Ellis & Solander, 1786: 169, pl. 53: figs 1, 2); holotype: GLAHM 104008 (dry specimen; Fig. 18A); type locality: 'Antilles' (Weil & Knowlton, 1994: 155); phylogenetic data: molecular and morphology.

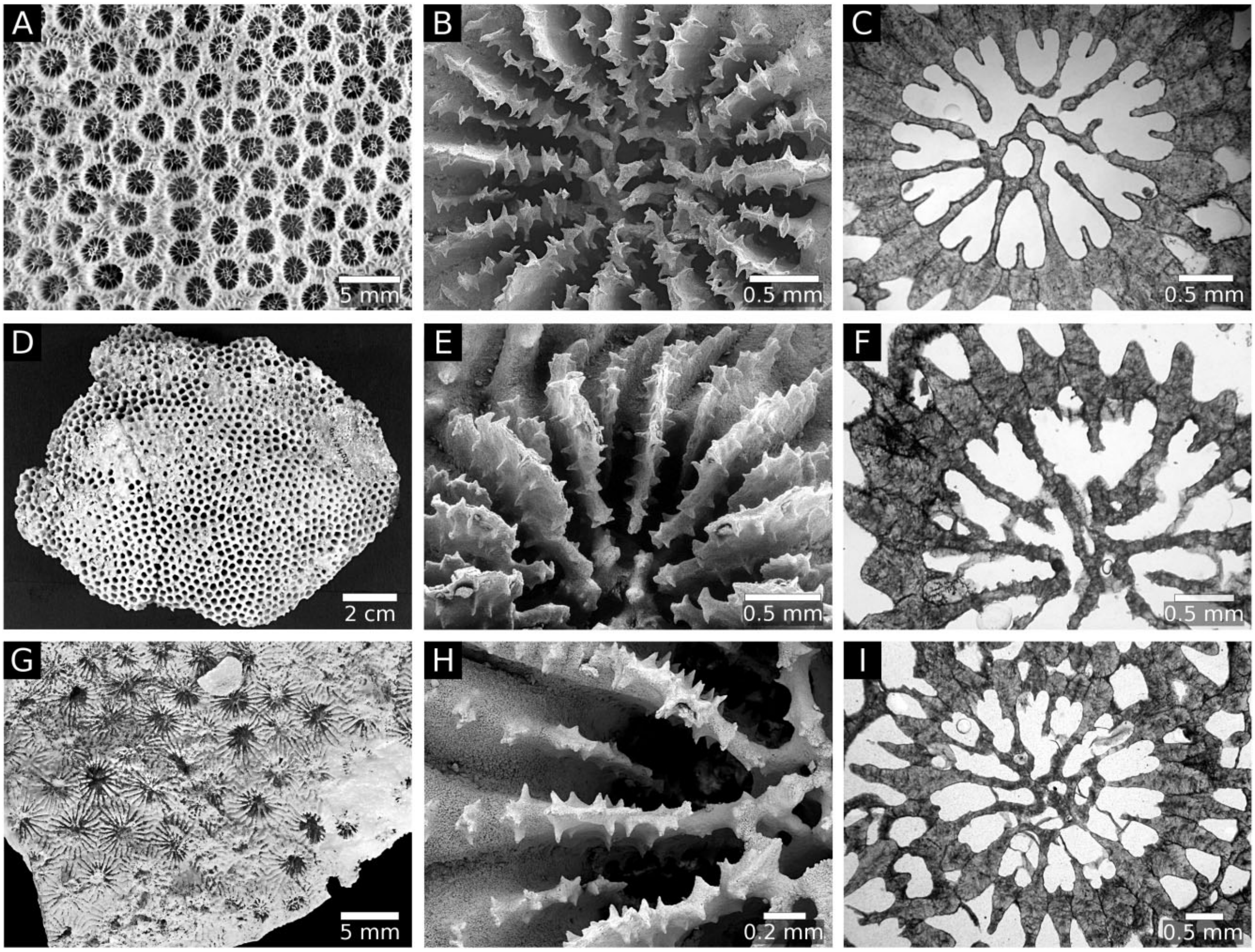


Figure 18. *Orbicella* Dana, 1846, has discrete corallites that bud extracalicularly, small (< 4 mm) and low-relief (< 3 mm) calices, regular free septa, equally thick costosepta, and large (≥ 1/4 of calice width) compact columellae. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm), with multiaxial tips. Walls formed by dominant septotheca and partial paratheca. A–C, *Orbicella annularis* (Ellis & Solander, 1786), type species of *Orbicella*; macromorphology, holotype GLAHM 104008, Antilles (A; photo by K. G. Johnson); micromorphology (scanning electron microscopy), hypotype SUI 95207, San Blas, Panama (B); microstructure (transverse thin section; C), hypotype SUI 122825 (FA1108), Anguilla. D–F, *Orbicella faveolata* (Ellis & Solander, 1786); macromorphology, holotype GLAHM 104009, probably Late Pleistocene, Antilles (D; photo by K. G. Johnson); micromorphology, hypotype SUI 95213, San Blas, Panama (E); microstructure, hypotype SUI 95215, San Blas, Panama (F). G–I, *Orbicella franksi* (Gregory, 1895); macromorphology, holotype NHMUK R2514, Pleistocene, Barbados (G; photo by H. Taylor); micromorphology, hypotype SUI 133923 (H); microstructure, hypotype SUI 133883 (I).

2. *Orbicella faveolata* (Ellis & Solander, 1786: 166, pl. 53: figs 5, 6); holotype: GLAHM 104009 (dry specimen; Fig. 18D); type locality: 'perhaps of Late Pleistocene age, collected in the Antilles' (Weil & Knowlton, 1994: 160); phylogenetic data: molecular (Fukami *et al*., 2004a, 2008) and morphology.
3. *Orbicella franksi* (Gregory, 1895: 274, pl. 11: figs 2a–c, 3); holotype: NHMUK R2514 (dry specimen; Fig. 18G); type locality: 'Pleistocene of Barbados' (Weil & Knowlton, 1994: 162); phylogenetic data: molecular (Fukami *et al*., 2004a, 2008) and morphology.

Taxonomic remarks

The three Caribbean members of this genus used to be known as the *Montastraea annularis* complex (Knowlton *et al*., 1992; Weil & Knowlton, 1994), and were the focus of extensive research aimed at describing morphological, genetic, reproductive, and physiological variation amongst them (Knowlton *et al*., 1992, 1997; van Veghel & Bak, 1993, 1994; van Veghel, 1994; van Veghel & Kahmann, 1994; Weil & Knowlton, 1994; van Veghel & Bosscher, 1995; van Veghel, Cleary & Bak, 1996; Lopez & Knowlton, 1997; Szmant *et al*., 1997;

Lopez *et al.*, 1999; Medina, Weil & Szmant, 1999; Manica & Carter, 2000; Knowlton & Budd, 2001; Levitan *et al.*, 2004, 2011; Fukami *et al.*, 2004b; Fukami & Knowlton, 2005).

Although currently restricted to the Caribbean showing no geographical overlap with any other living Merulinidae genus, the subgenus *Orbicella* described by Dana (1846: 205) within *Astrea* also included numerous Indo-Pacific species such as *Cyphastrea microphthalma*, *Astrea curta*, and *Oulastrea crispata* (*incertae sedis*). The subsequent designation of *Madrepora annularis* Ellis & Solander, 1786: 169, as type species by Vaughan (1918: 85) also did not constrain its geographical range, as *Plesiastrea versipora*, *Orbicella gravieri* (synonym of *Plesiastrea versipora*; Veron *et al.*, 1977: 150), and *Astrea curta* were retained. *Orbicella* was finally synonymized by Vaughan & Wells (1943: 173) as *Montastraea* de Blainville.

Molecular data have generally placed the *Orbicella* clade as sister to *Cyphastrea* with good support (Fukami *et al.*, 2004a; Huang *et al.*, 2011; Huang, 2012; Arrigoni *et al.*, 2012; but see Fukami *et al.*, 2008).

Morphological remarks

Our morphological analysis reveals that the present *Orbicella* members form a very well-supported clade (bootstrap support of 96 and decay index of 3), and a sister-clade relationship with *Cyphastrea* is recovered but not supported.

It is remarkable that these two genera are recovered as sister taxa on the morphology tree, particularly because they differ in up to four macromorphological characters, two of which are the only synapomorphies inferred for *Orbicella* – equal costosepta thickness (likelihood of 1.0 based on the Mk1 model) and large columellae (likelihood 1.0). Costate coenosteum and the lack of paliform lobes also distinguish *Orbicella* from *Cyphastrea*, which has spinose coenosteum and weak or moderate development of paliform lobes. However, their affinity to each other may be expected in the context of subcorallite characters, which show that they share all but two features of irregular granule shape and partial paratheca in *Orbicella*, rather than strong, pointed granules and no paratheca at all in *Cyphastrea*.

GENUS *OULOPHYLLIA* MILNE EDWARDS & HAIME, 1848A: 492 (FIG. 19)

Synonyms

Coelogyra Nemenzo, 1959: 109 (type species: *Coelogyra levis* Nemenzo, 1959: 109; pl. 8: fig. 2; original designation, Nemenzo, 1959: 109); *Ulophyllia* Milne Edwards & Haime, 1857, vol. 2: 377 (type species: *Meandrina crispa* Lamarck, 1816: 247; original designation, Milne Edwards & Haime, 1857, vol. 2: 378).

Type species

Meandrina crispa Lamarck, 1816: 247; original designation, Milne Edwards & Haime, 1848a, vol. 27: 492.

Original description

'Diffère du précédent [*Tridacophyllia* = *Pectinia*] par des murailles beaucoup moins élevées, par la présence d'une columelle spongieuse bien marquée, et par des cloisons très-granulées dont le bord est très-profondément divisé, surtout inférieurement.' (Milne Edwards & Haime, 1848a, vol. 27: 492).

Subsequent descriptions

Milne Edwards & Haime, 1849a, vol. 11: 268; d'Orbigny, 1851: 168; Milne Edwards & Haime, 1857, vol. 2: 377, 378; Quenstedt, 1881: 1010; Duncan, 1884: 94; Quelch, 1886: 88; Delage & Hérouard, 1901: 627; Matthai, 1928: 256; Yabe *et al.*, 1936: 42; Vaughan & Wells, 1943: 169; Alloiteau, 1952: 617; Crossland, 1952: 146, 147; Wells, 1956: F402; Wijsman-Best, 1972: 49; Chevalier, 1975: 160; Veron *et al.*, 1977: 117; Scheer & Pillai, 1983: 127; Wood, 1983: 155; Veron, 1986: 498; Chevalier & Beauvais, 1987: 716; Sheppard, 1990: 14; Sheppard & Sheppard, 1991: 134; Veron, 2000, vol. 3: 195.

Diagnosis (apomorphies in italics)

Colonial, with intracalicular budding only. Corallites monomorphic and discrete (one to three centres) or uniserial; monticules absent. *Walls fused*. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes weak or moderate. Epitheca absent and endotheca abundant (vesicular) (Fig. 19A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 19B, E, H).

Walls formed by dominant paratheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters not distinct; medial lines strong. Septum centre clusters not distinct; medial lines strong. Transverse crosses present. Columella centres clustered (Fig. 19C, F, I).

Species included

1. *Oulophyllia crispa* (Lamarck, 1816: 247); holotype: MNHN IK-2010-526 (dry specimen; Fig. 19A); type

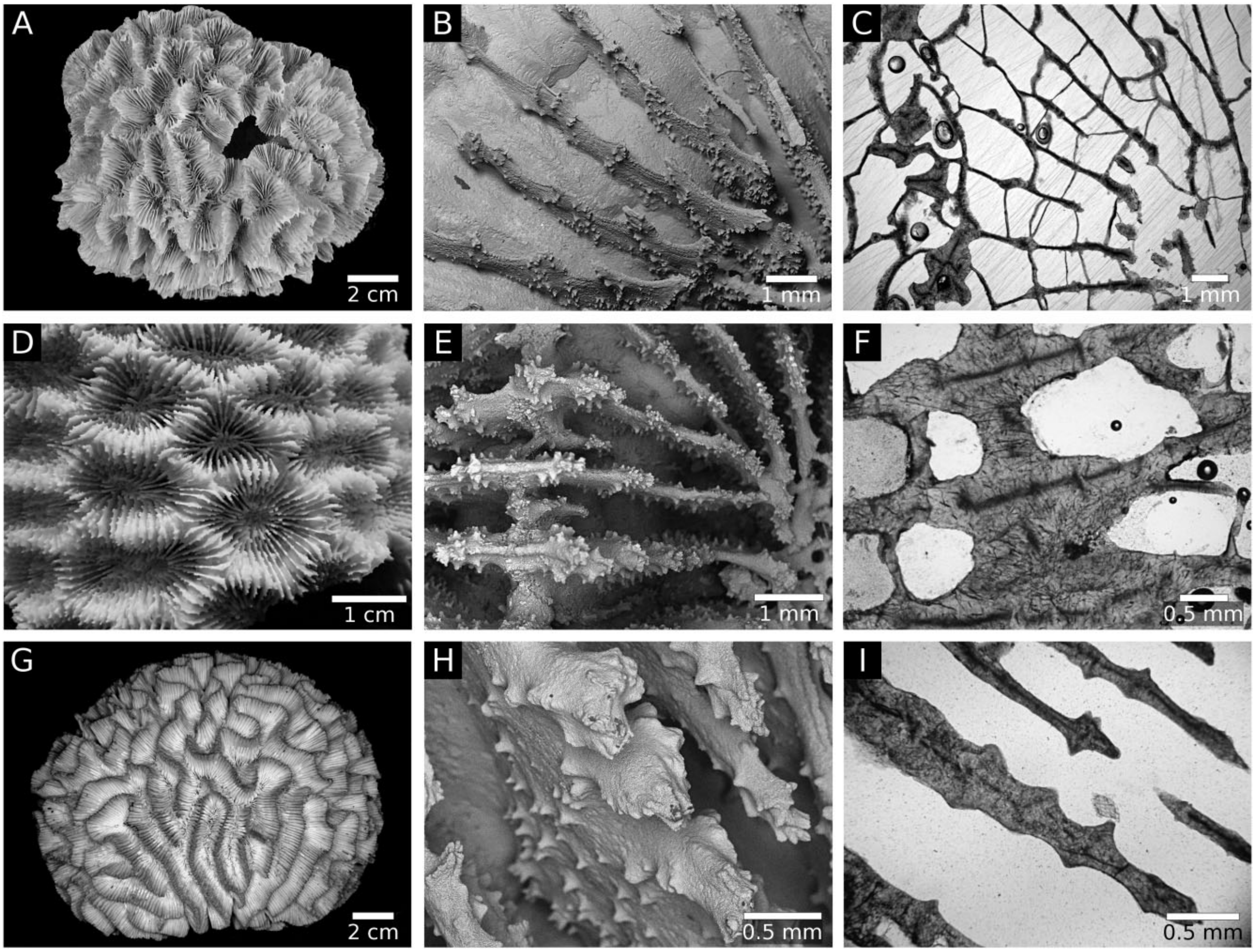


Figure 19. *Oulophyllia* Milne Edwards & Haime, 1848a, has fused walls, medium-size (4–15 mm) and medium-relief (3–6 mm) calices, septa spaced < six septa per 5 mm and abundant (vesicular) endotheca. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm). Walls formed by dominant paratheca, with strong costal and septal medial lines, and transverse septal crosses. A–C, *Oulophyllia crispa* (Lamarck, 1816), type species of *Oulophyllia*; macromorphology, holotype MNHN IK-2010-526, unknown locality (A); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UF 2104 (FA1070), Palau. D–F, *Oulophyllia bennettae* (Veron, Pichon & Wijsman-Best, 1977); macromorphology, holotype NHMUK 1977.1.1.3, Falcon Island, Australia (D); micromorphology (E) and microstructure (F), hypotype MTQ G61873, Pelorus Island, Australia. G, *Oulophyllia levis* (Nemenzo, 1959); macromorphology, holotype UP C-412, Cebu, the Philippines (photo by K. S. Luzon). H, I, *Oulophyllia bennettae* (Veron, Pichon & Wijsman-Best, 1977); micromorphology (H) and microstructure (I), hypotype RMNH 21743, Tukang Besi Islands, Indonesia.

locality: 'lOcéan indien?' (Lamarck, 1816: 247); phylogenetic data: molecular and morphology.

2. *Oulophyllia bennettae* (Veron, Pichon & Wijsman-Best, 1977: 73, figs 138–144, 445–448); holotype: NHMUK 1977.1.1.3 (dry specimen; Fig. 19D); paratype: MTQ G59712 (dry specimen); paratype: RMNH 10735 (dry specimen); type locality: Falcon Island, Palm Islands, Australia, 5–10 m depth; phylogenetic data: molecular and morphology.
3. *Oulophyllia levis* (Nemenzo, 1959: 109; pl. 8: fig. 2); holotype: UP C-412 (dry specimen; Fig. 19G); type locality: Pinamungajan, Cebu, the Philippines; phylogenetic data: none.

Taxonomic remarks

Oulophyllia Milne Edwards & Haime, 1848a, vol. 27: 492, is a small genus that has been recovered genetically as a well-supported clade (Fukami *et al*., 2004a; Huang *et al*., 2009, 2011; but see Fukami *et al*., 2008; Arrigoni *et al*., 2012). It was established for the type species *Oulophyllia crispa*, and compared with *Pectinia* it was found to have lower walls and more spongy columellae (Milne Edwards & Haime, 1848a, vol. 27: 492). The walls of *Pectinia* however refer to laminae that project upwards and may contain corallites formed by budding. Their corallites are organically united and thus the laminae may not be considered homologous to the walls of *Oulophyllia*, or other discrete or uniserial taxa. In spite of this, the two genera are indeed closely related, and together with *Caulastraea* and *Mycedium* form a well-supported molecular clade (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012).

Only *Oulophyllia crispa* and *Oulophyllia bennettae* have been studied phylogenetically. The third species, *Oulophyllia levis*, is very similar to the type in terms of macromorphology, differing only in having smaller valleys and less developed columellae (Veron, 2000, vol. 3: 198). In fact, it was originally described as having no columellae, with a 'loose mass of septal spines' in its place (Nemenzo, 1959: 109), thus expanding the morphological range specified by Milne Edwards & Haime (1848a, vol. 27: 492).

Oulophyllia is widely distributed on reefs of the Indo-Pacific, and absent eastwards from Hawai'i.

Morphological remarks
Oulophyllia is supported by a decay index of 2 on the morphological phylogeny, and the singular synapomorphy detected is wall fusion (likelihood of 0.98 based on the Mk1 model). The two-step change from moderate coenosteum to fused walls at its most recent common ancestor with *Caulastraea* accounts for the decay index of 2 despite having only one synapomorphy.

The genus is frequently associated with *Favites* and *Platygyra*, primarily because of their cerioid corallites (Vaughan & Wells, 1943: 169; Veron, 1986: 498, 2000, vol. 3: 195). The phylogeny based on both molecular and morphological evidence clearly shows this trait arising at least three times independently within Merulinidae, in the lineages represented by *Favites* + *Platygyra*, *Coelastrea*, and *Oulophyllia*. The initial placement of *Oulophyllia bennettae* in *Favites* also underscores the homoplastic nature of this character (see remarks for *Favites* above).

Another homoplastic character exemplified by this genus is corallite integration, which is polymorphic in this genus (uniserial in *Oulophyllia crispa* and *Oulophyllia levis*; discrete in *Oulophyllia bennettae*), *Goniastrea*, and *Platygyra*.

Amongst close relatives, these features may still be useful distinguishing characters, separating *Oulophyllia* from *Caulastraea* (phaceloid) and *Pectinia* + *Mycedium* (extensive coenosteum), as well as *Oulophyllia* and *Caulastraea* from *Pectinia* + *Mycedium* (organically united corallites). Few subcorallite characters are distinct for *Oulophyllia* within this clade, but a combination of medium tooth height (0.3–0.6 mm), more than six teeth per septum, palisade interarea, and transverse septal crosses would be diagnostic.

GENUS *PARACLAVARINA* VERON, 1985: 179 (FIG. 20)

Type species
Clavarina triangularis Veron & Pichon, 1980: 223, figs 375–384; original designation, Veron, 1985: 179.

Original description
'*Paraclavarina* is like *Merulina* except that it is ramose without any development of laminae. It is the only fully ramose genus in the Merulinidae.

The description of *Clavarina triangularis* by Veron & Pichon (1980) is repeated below.

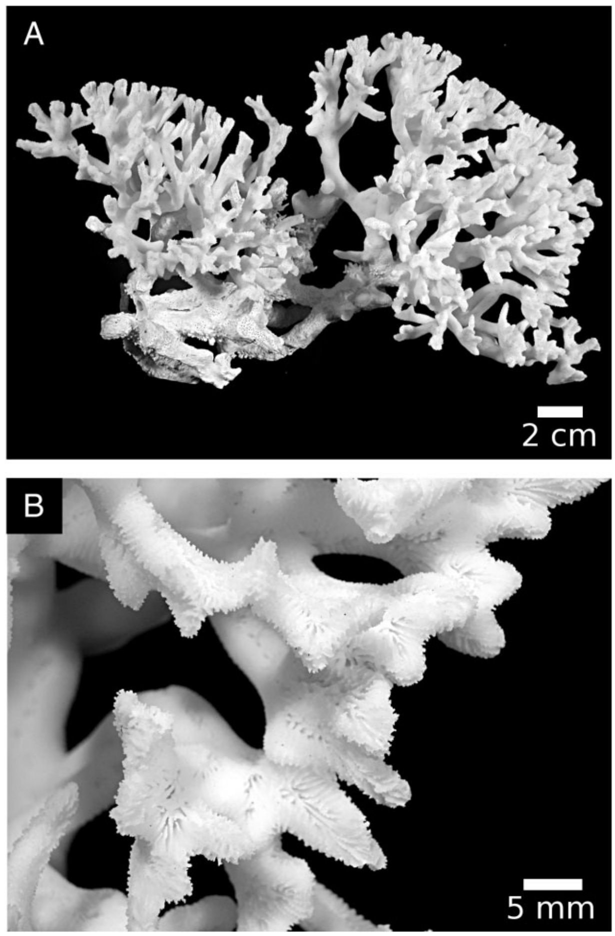


Figure 20. *Paraclavarina* Veron, 1985: 179, is ramose and has uniserial corallites with few centres, fused walls, small (< 4 mm) and low-relief (< 3 mm) calices, septa in < three cycles (< 24 septa), compact columellae, well-developed paliform (uniaxial) lobes, and no epitheca. A, B, *Paraclavarina triangularis* (Veron & Pichon, 1980), the type and only living species of *Paraclavarina*; macromorphology, holotype NHMUK 1983.9.27.2, Bushy Island-Redbill Reef, Australia.

“Colonies, which frequently exceed 1 m diameter, resemble those of *Hydnophora rigida* in consisting entirely of a network of anastomosing branches without any plate-like or foliaceous basal attachment. Some colonies have lax, open branching, while others are compact and bushy. Old branches may be up to 1.5 cm thick; most average 1 cm except towards the tips where they taper. All branches are basically triangular in section and have three series of centres, one on each side, with the angles being the common walls. On most branches the series of centres are straight and divide only when the branch divides. Thicker branches may have more irregular series with frequent divisions not associated with sub-branches and branch sections may be more circular than triangular. Branch tips are three-pointed star-shaped in section, with the centres lying along the valleys and the walls forming the points. Septa are in two alternating orders. First order septa are slightly exsert, either adjoined over the wall or, more usually, separated by a groove. They increase in thickness towards the “valley” axes and most curve towards the nearest centre. Their inner margins, which are mostly vertical, may have large dentations. However, most skeletal structures at the centres and along the valley axes are fused together so that the centres are star-shaped, consisting of 5–10 thick, radiating septa with fused inner margins and deep inter-septal loculi. Second order septa are short and usually thinner than those of the first order. All septa are dentate, those of the first order usually more so than those of the second. Centres are linked by a single, sometimes very thick, laminar plate, which itself is fused to adjacent septa. There are no clearly defined calices and valleys are often very superficial. Columellae may be trabecular or spongy, but are only distinguishable as such near branch tips. Individual centres and the perimeter of oral discs are clearly defined in living coralla. When polyps are expanded at night, fine, elongate tentacles usually occupy most of the space between the branches. Colonies are pale yellow or cream.” (Veron & Pichon, 1980: 225)’ (Veron, 1985: 179–180).

Subsequent descriptions
Veron, 1986: 438; Veron, 2000, vol. 2: 374.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic, uniserial, and ramose; monticules absent. Walls fused. Calice width small (< 4 mm), with low relief (< 3 mm). Costosepta confluent. Septa in < three cycles (< 24 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular but compact (one to three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes well developed. Epitheca absent and endotheca sparse (Fig. 20).

Species included
Paraclavarina triangularis (Veron & Pichon, 1980: 223, figs 375–384); holotype: NHMUK 1983.9.27.2 (dry specimen; Fig. 20); type locality: Bushy Island–Redbill Reef, Australia, 5 m depth; phylogenetic data: none.

Taxonomic remarks
Paraclavarina Veron, 1985: 179, was established as a monotypic genus with close affinity to *Merulina*. Its sole member was initially described as *Clavarina triangularis* Veron & Pichon, 1980: 223, for its similarity to *Merulina scabricula*, effectively resurrecting *Clavarina* Verrill, 1864: 56, for these two species (*Merulina scabricula* being the type), where Chevalier, 1975: 208, had previously synonymized it. Studying specimens from Phuket and the Mergui Archipelago, Veron (1985: 181) deemed *Clavarina triangularis* Veron & Pichon to be distinct from *Merulina ampliata* and *Merulina scabricula*, which were more similar to each other instead. No details on these new observations were offered. *Clavarina* effectively became synonymized as *Merulina* once again, and *Clavarina triangularis* was transferred into *Paraclavarina*.

It should be noted that two of the three syntypes of *Merulina scabricula* (USNM 165 and YPM IZ 1927A; see species included for *Merulina*) are ramose like *Clavarina triangularis*. Umbgrove (1940: 285) argued that Dana (1846: 275) based his description of this species only on part of a large colony that may have thin lamina at its base like *Merulina ampliata*. Evidently, neither he nor Veron (1985: 181), who referred to USNM 165 incorrectly as the holotype, saw the final syntype (YPM IZ 1927B), indeed a fragment of lamina. If this is indeed the pattern observed by Veron (1985: 181), then distinguishing the fully ramose *Clavarina triangularis* from *Merulina*, and by extension the establishment of *Paraclavarina* may be justified.

Evidently, the validity of *Paraclavarina* depends critically on its specific relationships with *Merulina ampliata* and *Merulina scabricula*. To date, *Paraclavarina triangularis* has never been collected for a phylogenetic study, and only three samples of each *Merulina* species have been analysed (Romano & Palumbi, 1996; Chen *et al*., 2002; Fukami *et al*., 2008; Huang *et al*., 2011).

Paraclavarina is known only from the Central Indo-Pacific region bounded by the Makassar Strait, Palau, Papua New Guinea, Vanuatu, and the Great Barrier Reef in Australia.

Morphological remarks
The holotype of *Paraclavarina triangularis* has been examined and found to share all analysed

macromorphological features with *Merulina*. It is however fully branching, lacking the encrusting and/or laminar base found in *Merulina*.

GENUS ***PARAMONTASTRAEA*** HUANG & BUDD **GEN. NOV.** (FIG. 21)

Type species
Plesiastrea salebrosa Nemenzo, 1959: 92, pl. 1: fig. 2; original designation.

Etymology
The name sets this taxon in contrast with other species present in both Indo-Pacific and Atlantic reefs that were classed according to superficial similarities in the genus *Montastrea* (*sensu* Veron, 1986: 502, 2000, vol. 3: 212). The latter is now restricted in modern scleractinians to the phylogenetically distinct Atlantic species, *Montastraea cavernosa*.

Diagnosis (apomorphies in italics)
Colonial, with mostly extracalicular budding (*Paramontastraea peresi* also has intracalicular budding). Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum may be spinose, moderate amount (< corallite diameter). Walls fused in *Paramontastraea peresi*. Calice width medium (4–15 mm), with low relief (< 3 mm) but slightly higher in *Paramontastraea peresi*. Costosepta not confluent. Septa in three cycles (24–36 septa); fourth cycle sometimes present in *Paramontastraea peresi*. Free septa regular. Septa spaced > 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites. *Paliform (uniaxial) lobes well developed.* Epitheca well developed and endotheca low–moderate (tabular) (Fig. 21A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation multiaxial. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea smooth (Fig. 21B, E).

Walls formed by dominant septotheca and partial paratheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines weak. Septum centre

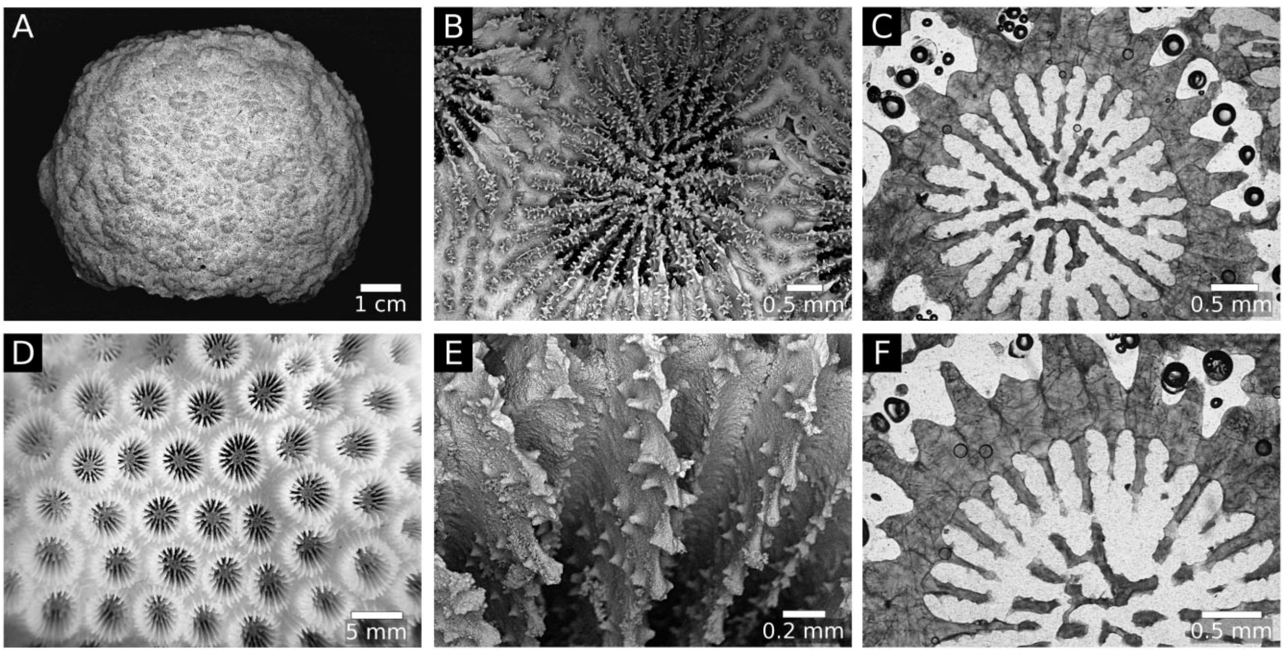


Figure 21. *Paramontastraea* Huang & Budd, this study, has corallites that mostly bud extracalicularly, regular free septa, septa spaced > 11 septa per 5 mm, and well-developed paliform (uniaxial) lobes. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm), with multiaxial tips. Walls formed by dominant septotheca and partial paratheca. A–C, *Paramontastraea salebrosa* (Nemenzo, 1959), type species of *Paramontastraea*; macromorphology, holotype UP C-192, Puerto Galera, the Philippines (A; photo by K. S. Luzon); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype UP P1L02158), Batangas, the Philippines. D, E, *Paramontastraea serageldini* (Veron, 2000); macromorphology, holotype MTQ G55844, Mahé, Seychelles (D); micromorphology, hypotype SIO Co2805, Mahé, Seychelles (E). F, *Paramontastraea salebrosa* (Nemenzo, 1959); microstructure, hypotype UP P1L02158, Batangas, the Philippines.

clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 21 C, F).

Species included

1. *Paramontastraea salebrosa* (Nemenzo, 1959: 92, pl. 1: fig. 2); holotype: UP C-192 (dry specimen; Fig. 21A); type locality: Puerto Galera, the Philippines; phylogenetic data: molecular and morphology.
2. *Paramontastraea peresi* (Faure & Pichon, 1978: 107, pls. 1–3: figs 1–6); holotype: MNHN IK-2010-666 (dry specimen); type locality: Nosy Be, baie d'Ambavatoby, Madagascar, 15 m depth; phylogenetic data: molecular only (Arrigoni *et al*., 2012).
3. *Paramontastraea serageldini* (Veron, 2000 vol. 3: 213, figs 2–4) (see also Veron, 2002: 162, figs 298–300; ICZN, 2011: 164); lectotype (designated herein): MTQ G55844 (dry specimen; Fig. 21D); type locality: Mahé, Seychelles, 10 m depth; phylogenetic data: partial morphology.

Taxonomic remarks
Paramontastraea gen. nov. is hereby established based on a combination of molecular and morphological evidence from Huang *et al*. (2011), Arrigoni *et al*. (2012), and the present analysis. The three members of this genus have never been examined in the same context, but their positions on the Merulinidae phylogeny are well established.

The type species was first examined and shown to be sister to *Echinopora* by Huang *et al*. (2011) in subclade XVII-I with high statistical support. This association runs counter to conventional taxonomy at that time, and is supported by few unique morphological traits (e.g. spinose coenosteum).

Arrigoni *et al*. (2012) subsequently recovered a similar topology, but with *Echinopora mammiformis* more closely related to *Plesiastrea salebrosa* Nemenzo, 1959: 92, than to its congenerics. The tree also shows a striking association – that of *Favites peresi* Faure & Pichon, 1978: 107, as sister species to *Plesiastrea salebrosa*. Although this particular relationship is not well supported, the clade of *Echinopora* + *Plesiastrea salebrosa* + *Favites peresi* appears stable. As expressed by Arrigoni *et al*. (2012), *Favites peresi* has been placed in *Favites* and *Goniastrea* before, but their tree indicates that neither of these genera has close affinity. Our morphological phylogeny lends some support to this affiliation, as *Plesiastrea salebrosa* and *Montastrea serageldini* Veron, 2000 vol. 3: 213, are recovered as sister species within the clade of *Echinopora*, *Cyphastrea*, and *Orbicella*. By integrating across these diverse results, we infer that *Plesiastrea salebrosa*, *Favites peresi*, and *Montastrea serageldini* are close relatives and place them in the new genus *Paramontastraea*.

We also considered the alternative solution to synonymize them as *Echinopora* based on the molecular phylogeny, but they are morphologically more similar to *Cyphastrea* + *Orbicella*. Further investigation is necessary to validate the solution chosen here. *Paramontastraea* has a disjointed distribution amongst species – *Paramontastraea salebrosa* in the Central Indo-Pacific, and *Paramontastraea peresi* and *Paramontastraea serageldini* in the Indian Ocean region.

Morphological remarks
Paramontastraea is only supported by the presence of well-developed paliform lobes as a synapomorphy (likelihood of 1.0 based on the Mk1 model). Although genetically closest to *Echinopora*, this new genus can be distinguished based on its reduced coenosteum (< corallite diameter) and columellae (< 1/4 of calice width), strong paliform lobes, narrower tooth spacing (< 0.3 mm), as well as septotheca (dominant) and paratheca without abortive septa. It instead forms a clade with *Cyphastrea* and *Orbicella* on the morphology tree, but these have smaller corallites with less spongy columellae and do not develop strong paliform lobes.

GENUS *PECTINIA* DE BLAINVILLE, 1825: 201 (FIG. 22)

Synonyms
Parapectinia Nemenzo & Montecillo, 1981: 124 (type species: *Pectinia teres* Nemenzo & Montecillo, 1981: 124, fig. 3; original designation, Nemenzo & Montecillo, 1981: 124); *Tridacophyllia* de Blainville, 1830: 327 (type species: *Madrepora lactuca* Pallas, 1766: 289; original designation, de Blainville, 1830: 327).

Type species
Madrepora lactuca Pallas, 1766: 289; subsequent designation, Vaughan, 1901a: 15.

Original description
'Polypier formé de feuilles minces, plus ou moins roulées, avec des étoiles des deux côtés, et il y place à peu près les mêmes espèces.' (de Blainville, 1825: 201).

Subsequent descriptions
Vaughan, 1901a: 15, 16; Faustino, 1927: 159; Matthai, 1928: 158, 159; Wells, 1936: 122, 123; Vaughan & Wells, 1943: 198; Alloiteau, 1952: 632; Wells, 1956: F420; Nemenzo, 1959: 123; Chevalier, 1975: 390; Veron & Pichon, 1980: 325–330; Wood, 1983: 201, 202; Veron, 1986: 384; Chevalier & Beauvais, 1987: 726; Sheppard, 1990: 16; Veron, 2000, vol. 2: 348.

Diagnosis
Colonial, with intracalicular budding only. Corallites polymorphic and organically united; monticules absent.

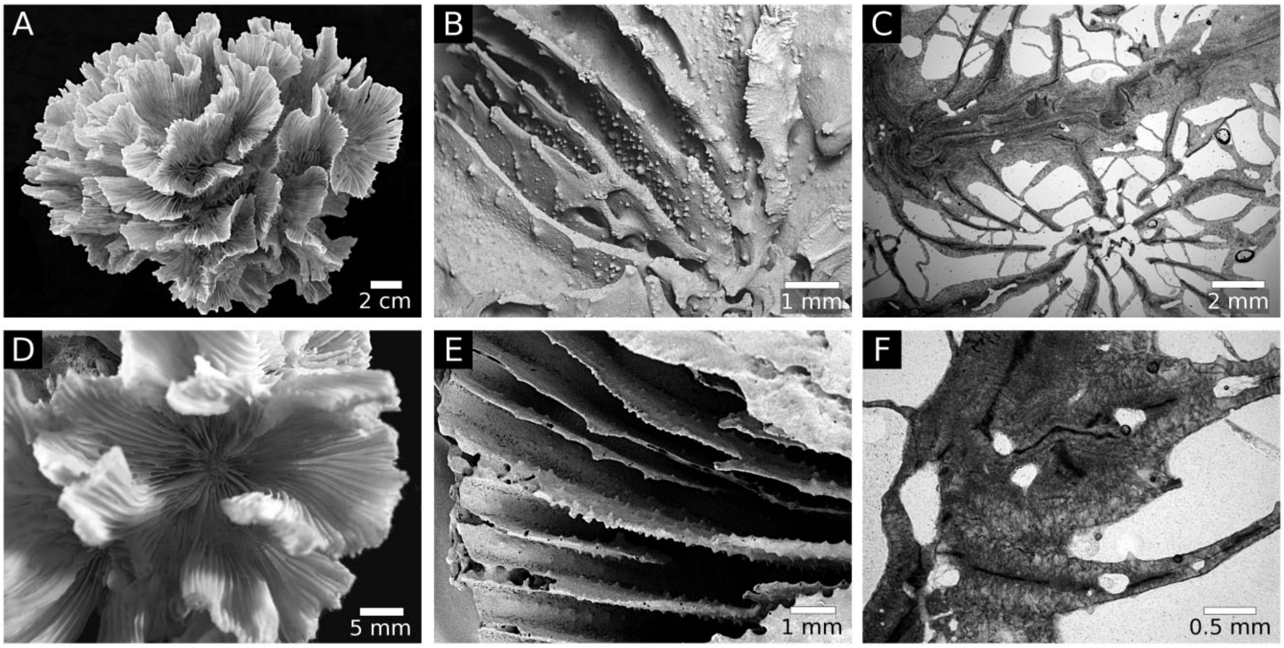


Figure 22. *Pectinia* de Blainville, 1825, has organically united corallites, extensive coenosteum (≥ corallite diameter), septa spaced < six septa per 5 mm and abundant (vesicular) endotheca. Septal teeth with medium height (0.3–0.6 mm) and spacing (0.3–1 mm), no more than six teeth per septum, and interarea formed by horizontal bands. Walls formed by dominant paratheca, with microfibrous deposits and strong costal and septal medial lines. A, *Pectinia lactuca* (Pallas, 1766: 289), type species of *Pectinia*; macromorphology, neotype (designated herein) NHMUK 1987.6.1.1, unknown locality. B, C, *Pectinia alcicornis* (Saville Kent, 1871); micromorphology (scanning electron microscopy), hypotype UF 2046 (FA1088), Palau (B); microstructure (transverse thin section), hypotype UF 2121 (FA1086), Palau (C). D–F, *Pectinia paeonia* (Dana, 1846); macromorphology (D), micromorphology (E), and microstructure (F), syntype USNM 132, Fiji.

Coenosteum costate, extensive amount (≥ corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites (lamellar linkage). Paliform (uniaxial) lobes weak or moderate. Epitheca absent and endotheca abundant (vesicular) (Fig. 22A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with no more than six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea formed by horizontal bands (Fig. 22B, E).

Walls formed by dominant paratheca; abortive septa absent. Thickening deposits microfibrous. Costa centre clusters not distinct; medial lines strong. Septum centre clusters not distinct; medial lines strong. Transverse crosses absent. Columella centres clustered (Fig. 22C, F).

Species included

1. *Pectinia lactuca* (Pallas, 1766: 289); holotype: lost (Cornelius & Wells, 1988: 85); neotype (designated herein): NHMUK 1987.6.1.1, figured in Ellis & Solander (1786: 158, pl. 44; see also Scheer, 1990: 387) (dry specimen; Fig. 22A); type locality: 'Mare Americanum?' (Pallas, 1766: 289), 'Samboanga Atoll, Philippines' (specimen label; probably incorrect); phylogenetic data: molecular and partial morphology.
2. *Pectinia africana* Veron, 2000, vol. 2: 353, figs 4–6 (see also Veron, 2002: 122, figs 229–231; ICZN, 2011: 165); lectotype (designated herein): MTQ G55856 (dry specimen); type locality: Chumbe Island, Zanzibar, Tanzania, 10 m depth; phylogenetic data: none.
3. *Pectinia alcicornis* (Saville Kent, 1871: 283, pl. 23: fig. 4); holotype: NHMUK 1855.12.7.156 (dry specimen); type locality: San Cristobal, Solomon Islands; phylogenetic data: molecular and morphology.
4. *Pectinia crassa* Ditlev, 2003: 204, figs 13–15 (= *Pectinia ayleni sensu* Veron, 2000, vol. 2: 352, figs 1–3); holotype: BMRI 3157 (dry specimen); paratype:

BMRI 860 (dry specimen); type locality: northeast Pulau Tabawan, Darvel Bay, Sabah; phylogenetic data: molecular (misidentified as *Pectinia ayleni* in Huang *et al*., 2011) and partial morphology.

5. *Pectinia elongata* (Rehberg, 1892: 18, pl. 2: fig. 4); holotype: unknown; type locality: Palau; phylogenetic data: none.
6. *Pectinia maxima* (Moll & Best, 1984: 55, figs 7, 8); holotype: RMNH 15267 (dry specimen); type locality: 480 m off west Langkai, Spermonde Archipelago, Indonesia, 9 m depth; phylogenetic data: none.
7. *Pectinia paeonia* (Dana, 1846: 196, pl. 9: figs 11, 11a); syntype: USNM 132 (dry specimen; Fig. 22D–F); type locality: Fiji; phylogenetic data: molecular and morphology.
8. *Pectinia pygmaea* Veron, 2000, vol. 2: 361, figs 4–6 (see also Veron, 2002: 123, figs 232–234; ICZN, 2011: 165); lectotype (designated herein): MTQ G55829 (dry specimen); type locality: Milne Bay, Papua New Guinea, 50 m depth; phylogenetic data: none.
9. *Pectinia teres* Nemenzo & Montecillo, 1981: 124, fig. 3; USC C-227 (dry specimen); type locality: Arangasa Island, Surigao del Sur, the Philippines; phylogenetic data: none.

Taxonomic remarks

Pectinia was originally described by Oken, 1815: 68. According to ICZN Opinion 417 (ICZN, 1956), names proposed by Oken (1815) are rejected, so authority of this taxon is assigned to de Blainville, 1825: 201, the next author to have used the name.

It is the type genus of Pectiniidae Vaughan & Wells (1943: 196), which also contains *Echinophyllia*, *Mycedium*, *Oxypora*, and *Physophyllia*, amongst the living scleractinians. Recent broad-scale molecular phylogenetic studies have placed the clade *Echinophyllia* + *Oxypora* within Lobophylliidae, whereas *Pectinia* and *Mycedium* form a monophyletic group in Merulinidae (Fukami *et al*., 2004a, 2008; Arrigoni *et al*., 2012). *Physophyllia* is expected to be a close relative of *Pectinia* based on macromorphology (see remarks for *Physophyllia* below).

Pectinia is often associated with *Oulophyllia* (e.g. Veron, 2000, vol. 2: 348), the latter being described as having comparatively lower walls and more spongy columellae (Milne Edwards & Haime, 1848a, vol. 27: 492). As noted above, laminae of the former are probably not homologous to the walls of *Oulophyllia*, but the two genera are indeed closely related, and together with *Caulastraea* and *Mycedium* form a well-supported molecular clade (Fukami *et al*., 2008; Huang *et al*., 2011; Arrigoni *et al*., 2012).

Pectinia is widely distributed on reefs of the Indo-Pacific, but distinctly absent in the northwestern Indian Ocean and the Red Sea, as well as east of Samoa in the central Pacific.

Morphological remarks

Pectinia and *Mycedium* share all morphological traits examined here, resulting in a polytomy on the phylogeny. *Physophyllia* also scored identically for macromorphology. There are thus no apomorphies yet for *Pectinia*, but its members generally have thin and acute laminae that project upward, lacking the large rounded vesicular ridges separating adjacent calices and inclined corallites as seen in *Physophyllia* and *Mycedium* respectively. Synapomorphies for the well-supported *Pectinia* + *Mycedium* clade (bootstrap support of 100 and decay index of 9) include organically united (likelihood of 1.0 based on the Mk1 model) and polymorphic corallites (likelihood 1.0), extensive coenosteum (≥ corallite diameter; likelihood 1.0), unequal costosepta thickness (likelihood 1.0), discontinuous columellae (lamellar linkage; likelihood 1.0), ≤ six teeth per septum (likelihood 1.0), interarea made up of horizontal bands (likelihood 1.0), and presence of microfibrous deposits (likelihood 1.0).

Note that quantitative measurements were performed on peripheral corallites; structures of the central corallite are not indicative of the main parts of the colony.

GENUS *PHYSOPHYLLIA* DUNCAN, 1884: 118 (FIG. 23)

Type species

Physophyllia ayleni Wells, 1935: 342, pl. 13, pl. 14: figs 1–3 (*non Pectinia ayleni sensu* Veron, 2000, vol. 2: 352, figs 1–3); subsequent designation, Wells, 1935: 340.

Original description

'Colony large, spreading, pedunculate, foliaceous, folia united and presenting faint broad ridges, which are crossed by septocostae. Corallites low, wide apart, arranged more or less in concentric circles. Calices distant, large, sunken, deep, elongate, forming series of 2 to 4, or circular. Fossa large and deep. Columella small, trabeculate. Septa large, exsert, spinulose, especially near the axis, unequal, wide apart; ending in septocostae which are confluent with those of the calices on either side, and some of which pass over broad ridges radially. Intercalicular surface large, gibbous or ridged, formed of convex vesicular endotheca; this endotheca fills up the interseptal loculi also, and is greatly developed. Calices on one side of the colony only. Common wall inferior, costulate to the base. Costae distinct, spinulose. No epitheca. Fissiparity occurs, and also gemmation.' (Duncan, 1884: 118).

Subsequent descriptions

Delage & Hérouard, 1901: 631, 632; Wells, 1935: 340; Yabe *et al*., 1936: 52; Vaughan & Wells, 1943: 198;

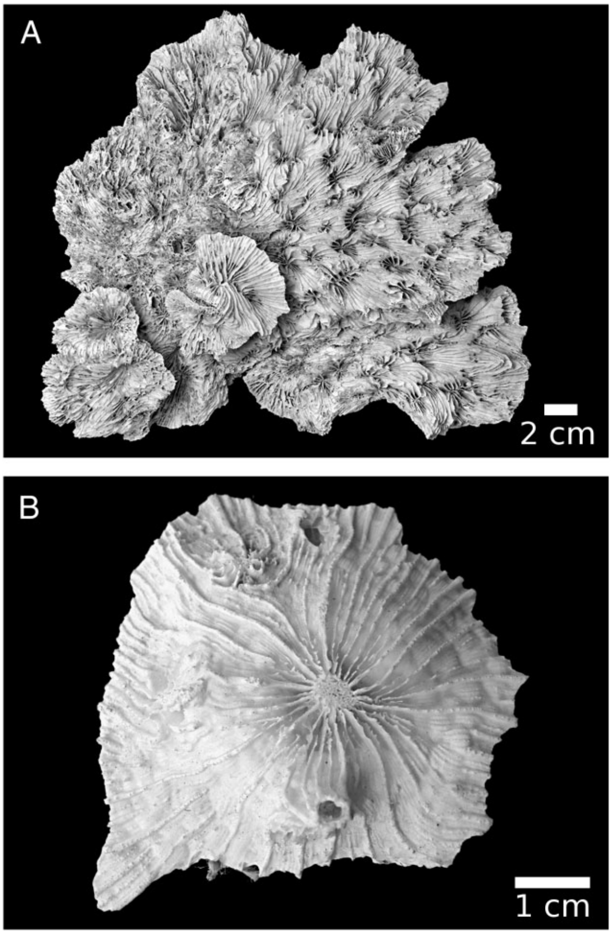


Figure 23. *Physophyllia* Duncan, 1884, has organically united and polymorphic corallites, extensive coenosteum (≥ corallite diameter), septa spaced < six septa per 5 mm, spongy columellae, and abundant (vesicular) endotheca. A, B, *Physophyllia ayleni* Wells, 1935, the type and only living species of *Physophyllia*; macromorphology, holotype NHMUK 1862.7.16.46, Japan (A; photo by H. Taylor), and paratype NHMUK 1893.9.1.188, Macclesfield Bank, South China Sea (B).

Alloiteau, 1952: 632; Wells, 1956: F419; Nemenzo, 1971: 176; Wood, 1983: 200,201; Veron, 1986: 592; Chevalier & Beauvais, 1987: 726.

Diagnosis
Colonial, with intracalicular budding only. Corallites polymorphic and organically united; monticules absent. Coenosteum costate, extensive amount (≥ corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and discontinuous amongst adjacent corallites (lamellar linkage). Paliform (uniaxial) lobes weak or moderate. Epitheca absent and endotheca abundant (vesicular) (Fig. 23).

Species included
Physophyllia ayleni Wells, 1935: 342, pl. 13, pl. 14: figs 1–3; holotype: NHMUK 1862.7.16.46 (dry specimen; Fig. 23A); paratypes: NHMUK 1892.10.17.97, 1893.9.1.185, 1893.9.1.186, 1893.9.1.187, 1893.9.1.188 (Fig. 23B), 1893.9.1.189, 1893.9.1.190 (seven dry specimens); type locality: Japan; phylogenetic data: none.

Taxonomic remarks
This is a monotypic genus with *Physophyllia ayleni* as its sole member. The species was placed in *Pectinia* by Veron (2000, vol. 2: 352) based on his collection, presumably shown in figs 1–3. These are however distinct from the type material studied by Wells (1935: 342) and thus have been described as *Pectinia crassa* Ditlev, 2003: 204, figs 13–15, with material from Sabah.

The distribution of *Physophyllia* remains as defined by the type material of *Physophyllia ayleni* – holotype from Japan and paratypes from Macclesfield Bank in the South China Sea. Subsequent studies appear to have expanded this range to the Maldives (Pillai & Scheer, 1976: 69, pl. 31: fig. 1; Scheer, 1984) and western Australia (Veron, 1993: 237), but only the former could be verified as a likely candidate for the species.

Morphological remarks
Based on an examination of the type material of *Physophyllia ayleni*, the genus shares all macromorphological characters studied here with *Pectinia* and *Mycedium.* Note that quantitative measurements were based on peripheral corallites as some structures of the central corallite, such as the columella, may be extremely large in comparison.

Although we recognize *Physophyllia* as distinct from *Pectinia* and *Mycedium*, subcorallite morphology and/or DNA sequence data will reveal the accuracy of this interpretation. The latter two genera are indistinguishable for all of the characters used for the present analysis, but they arguably span a wide range of morphologies not coded into phylogenetic data. The coenosteum of *Physophyllia* is made up of large ridges filled with vesicular endotheca, and does not form upwardly projecting laminae seen in most *Pectinia* species. Its corallites are also not distinctly inclined towards the periphery of the colony, a clear distinction from *Mycedium*. If *Physophyllia* is indeed separable from either of these genera based on the same molecular markers as employed here, it would probably be recovered outside of the *Pectinia* + *Mycedium* clade, and subcorallite disparities could be expected.

GENUS *PLATYGYRA* EHRENBERG, 1834: 323 (FIG. 24)

Synonyms

Astroria Milne Edwards & Haime, 1848a, vol. 27: 493 (type species: *Madrepora daedalea* Ellis & Solander, 1786: 163, pl. 46: fig. 1; subsequent designation, Milne Edwards & Haime, 1849a, vol. 11: 297); *Caeloria* Milne Edwards & Haime, 1848a, vol. 27: 493 (type species: *Meandrina daedalea* Lamarck, 1816: 246 = *Madrepora daedalea* Ellis & Solander, 1786: 163, pl. 46: fig. 1; original designation, Milne Edwards & Haime, 1848a, vol. 27: 493).

Type species

Maeandra (*Platygyra*) *labyrinthica* Ehrenberg, 1834: 323 (*non Madrepora labyrinthica* Ellis & Solander, 1786: 160, pl. 46: figs 3, 4) = *Maeandra* (*Platygyra*) *lamellina* Ehrenberg, 1834: 323; original designation, Ehrenberg, 1834: 323.

Original description

'Stolonibus in margine stirpis repentibus, in disco nullis.' (Ehrenberg, 1834: 323).

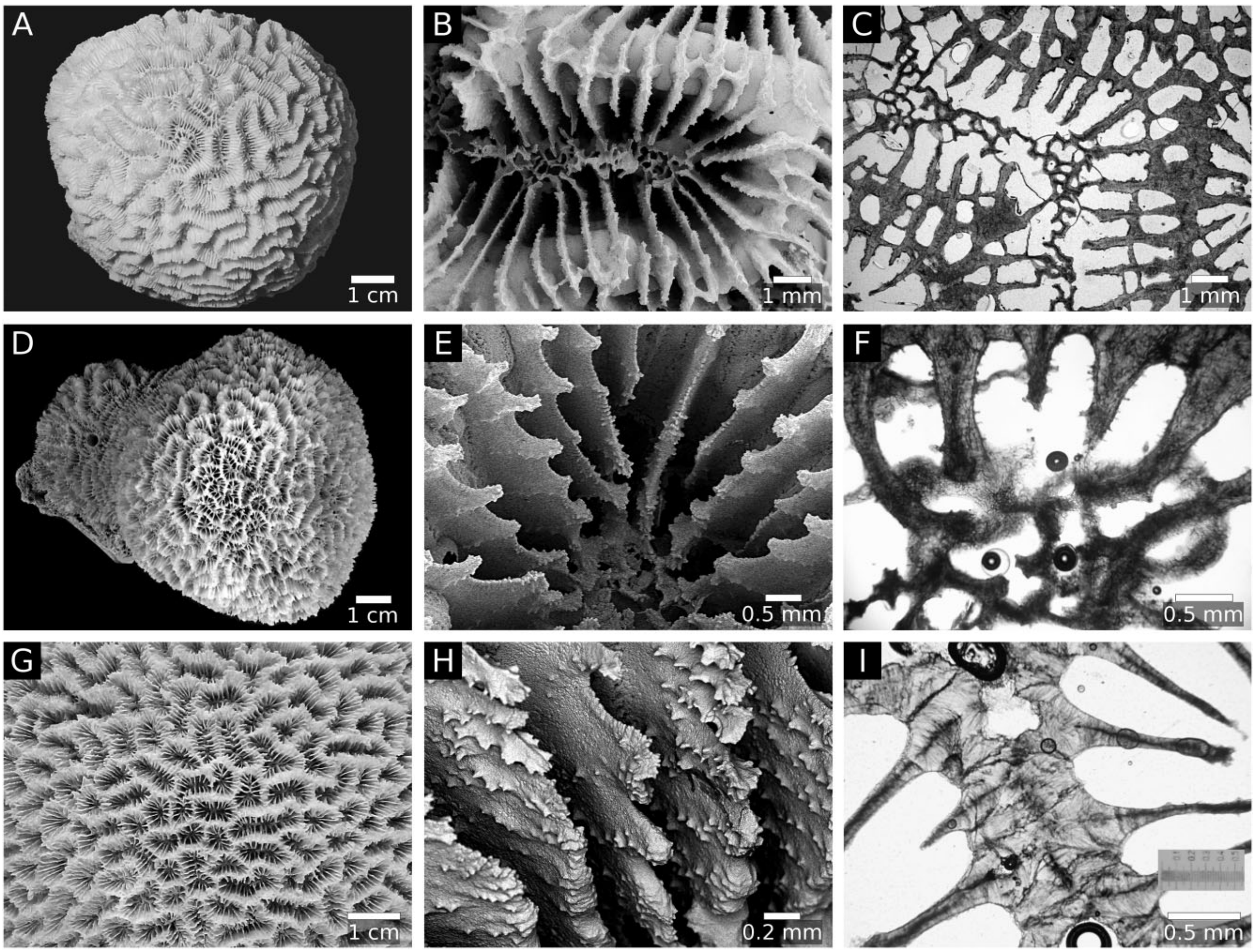


Figure 24. *Platygyra* Ehrenberg, 1834, has uniserial corallites, fused walls, septa in < three cycles (< 24 septa), equally thick costosepta, and spongy columellae. Septal teeth are low (< 0.3 mm) with medium spacing (0.3–1 mm); weak (rounded) granules aligned on septal face. Walls formed by dominant trabeculotheca and partial septotheca, with strong septal medial lines and aligned columella centres. A–C, *Platygyra lamellina* (Ehrenberg, 1834) = *Maeandra* (*Platygyra*) *labyrinthica* Ehrenberg, 1834, type species of *Platygyra*; macromorphology, syntype ZMB Cni 682, Red Sea (A; photo by K. Loch and W. Loch); micromorphology (scanning electron microscopy; B) and microstructure (transverse thin section; C), hypotype USNM 91127, Irian Jaya, Indonesia. D–F, *Platygyra daedalea* (Ellis & Solander, 1786); macromorphology, holotype GLAHM 104006 (D; photo by K. G. Johnson); micromorphology (E) and microstructure (F), hypotype SUI 122833 (FA1112), Lizard Island, Australia. G–I, *Platygyra sinensis* (Milne Edwards & Haime, 1849a); macromorphology, holotype MNHN IK-2010-417, unknown locality (G); micromorphology (H) and microstructure (I), hypotype RMNH 12162, Hope Island, Australia.

Subsequent descriptions
Vaughan, 1901b: 305; Wells, 1936: 124, 125; Vaughan & Wells, 1943: 169; Alloiteau, 1952: 618; Wells, 1956: F402; Nemenzo, 1959: 106; Wijsman-Best, 1972: 45; Chevalier, 1975: 122; Veron *et al*., 1977: 98; Scheer & Pillai, 1983: 122; Wood, 1983: 151; Veron, 1986: 488; Chevalier & Beauvais, 1987: 716; Sheppard, 1990: 14; Veron, 2000, vol. 3: 176, 177.

Diagnosis
Colonial, with intracalicular budding only. Corallites monomorphic and mostly uniserial, but may also be discrete (one to three centres); monticules absent. Walls fused. Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta confluent. Septa in < three cycles (< 24 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 24A, D, G).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules aligned on septal face, perpendicular to septal margin; weak (rounded). Interarea palisade (Fig. 24B, E, H).

Walls formed by dominant trabeculotheca and partial septotheca; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines strong. Transverse crosses absent. Columella centres aligned (Fig. 24C, F, I).

Species included

1. *Platygyra lamellina* (Ehrenberg, 1834: 323); syntype: ZMB Cni 682, figured in Matthai (1928, pl. 65: fig. 2) (dry specimen; Fig. 24A); syntypes: ZMB 669, 683, listed by Matthai (1928: 37, pl. 65: figs 1, 3) as types of *Maeandra* (*Platygyra*) *labyrinthica* var. *leptochila* and *Maeandra* (*Platygyra*) *labyrinthica*, respectively (not found); type locality: Red Sea; phylogenetic data: molecular and morphology.
2. *Platygyra acuta* Veron, 2000, vol. 3: 190, figs 1–4 (see also Veron, 2002: 161, figs 295–297; ICZN, 2011: 165); lectotype (designated herein): MTQ G55845 (dry specimen); type locality: Mahé, Seychelles, 15 m depth; phylogenetic data: molecular and partial morphology.
3. *Platygyra carnosa* Veron, 2000, vol. 3: 184, figs 1–3 (see also Veron, 2002: 159, figs 292–294; ICZN, 2011: 165); lectotype (designated herein): MTQ G55795 (dry specimen); type locality: Hong Kong, 5 m depth; phylogenetic data: none, but mitochondrial genome sequenced (Wang *et al*., 2013).
4. *Platygyra contorta* Veron, 1990: 145, figs 51, 52, 84; holotype: MTQ G32488 (dry specimen); type locality: Puerto Galera, the Philippines, 15 m depth; phylogenetic data: molecular and partial morphology.
5. *Platygyra crosslandi* (Matthai, 1928: 48, pl. 47: figs 1a, b, 2, pl. 56: fig. 8a, b); holotype: NHMUK 1928.3.1.7 (dry specimen); type locality: Red Sea; phylogenetic data: none.
6. *Platygyra daedalea* (Ellis & Solander, 1786: 163, pl. 46: fig. 1); holotype: GLAHM 104006 (dry specimen; Fig. 24D); type locality: 'Oceano Indiæ orientalis' (Ellis & Solander, 1786: 163); phylogenetic data: molecular and morphology.
7. *Platygyra pini* Chevalier, 1975: 155, pl. 9: figs 3, 6, pl. 12: figs 4–6, pl. 13: fig. 1; holotype: 'P 135e' (Chevalier, 1975: 155), MNHN status unknown; type locality: Baie de Gu, Ile des Pins, New Caledonia, 33 m depth; phylogenetic data: molecular and morphology.
8. *Platygyra ryukyuensis* (Yabe & Sugiyama, 1935: 394) (see also Yabe *et al*., 1936: 38, pl. 28: figs 3–5; holotype: TIU 48237 (dry specimen); type locality: Amami Ōshima, Ryukyu Islands, Japan; phylogenetic data: molecular and partial morphology.
9. *Platygyra sinensis* (Milne Edwards & Haime, 1849a, vol. 11: 298); holotype: MNHN IK-2010-417 (dry specimen; Fig. 24G); type locality: 'les mers de la Chine' (Milne Edwards & Haime, 1849a, vol. 11: 299); phylogenetic data: molecular and morphology.
10. *Platygyra verweyi* Wijsman-Best, 1976: 55, pl. 6: fig. 4; holotype: ZMA Coel. 9053a (dry specimen); paratypes: ZMA Coel. 8833, 9053b, 9054, 9984 (four dry specimens); type locality: Poeloe Dapoer, Thousand Islands, Indonesia; phylogenetic data: molecular only (Keshavmurthy *et al*., 2012).
11. *Platygyra yaeyamaensis* (Eguchi & Shirai in Shirai, 1977: 555); holotype: unknown; type locality: Yaeyama, Ryukyu Islands, Japan; phylogenetic data: none.

Taxonomic remarks
The taxonomic history of *Platygyra* Ehrenberg, 1834: 323, is extremely convoluted. It was described as a subgenus of *Maeandra* Oken, 1815: 68, with five species, the first of which being *Maeandra* (*Platygyra*) *labyrinthica* Ehrenberg, 1834: 323, to which he referenced as synonyms *Meandrina labyrinthica* (Lamarck, 1816: 246), *Madrepora labyrinthiformis* Linnaeus, 1758: 794, and *Madrepora labyrinthica* Ellis & Solander, 1786: 160, pl. 46: figs 3, 4. In order to clarify this, Brüggemann (1879: 571) fixed *Madrepora labyrinthica* (Ellis &

Solander, 1786: 160) as the type. This is problematic because the specimens described by Linnaeus (1758: 794) and Ellis & Solander (1786: 160) were derived from the Atlantic (Matthai, 1928: 110).

More recently, Chevalier (1975: 122) and Veron *et al.* (1977: 98) treated *Madrepora daedalea* Ellis & Solander, 1786: 163, pl. 46: fig. 1, as synonymous to Ehrenberg's definition of the type species. However, examination of one of Ehrenberg's syntypes of *Maeandra* (*Platygyra*) *labyrinthica* (ZMB Cni 682) strongly suggests that it is equivalent to the second (of five) species that he listed, *Maeandra* (*Platygyra*) *lamellina* Ehrenberg, 1834: 323. In accordance with Vaughan & Wells (1943: 169), Wells (1956: F402), and Wells (1986: 49), we regard *Platygyra lamellina* as the type species of *Platygyra*.

The genus has consistently been recovered as a well-supported clade in molecular phylogenies (Fukami *et al.*, 2004a, 2008; Huang *et al.*, 2009, 2011; Arrigoni *et al.*, 2012). There is a general lack of genetic variation amongst *Platygyra* spp. (Miller & Benzie, 1997; Lam & Morton, 2003), and where there is differentiation, morphotypes do not necessarily correspond with genotypes (Mangubhai *et al.*, 2007), partly caused by large phenotypic variation within species and high morphological overlap amongst species (Miller, 1992, 1994; Mangubhai *et al.*, 2007). *Platygyra*'s closest relative appears to be *Leptoria* (together as subclade G) but they are genetically distinguishable from each other. *Australogyra* has not been sampled for molecular phylogenetic work, but based on morphological similarities with *Platygyra* even at the subcorallite level, they are expected to be closely related.

Platygyra is widely distributed on reefs of the Indo-Pacific, present as far east as the Tuamotu Archipelago in the Southern Hemisphere (Glynn *et al.*, 2007), but absent eastwards from Hawai'i in the north.

Morphological remarks

Platygyra is supported by a decay index of 1 on the morphology tree, with the synapomorphy of spongy columellae (> three threads; likelihood of 1.0 based on the Mk1 model), distinguishing it from closely related *Australogyra* (compact; one to three threads) and *Leptoria phrygia* (lamellar). *Leptoria irregularis* has spongy columellae however, and so the character state is recovered as a plesiomorphy on the molecular tree, which samples this species. It is not easily confused with *Platygyra* because of its small (< 4 mm width) and shallow (< 3 mm depth) calices.

Platygyra and *Australogyra* share all other characters, although the latter's ramose growth form makes its colonies easily separable from those of *Platygyra*. Molecular data would further clarify the validity of *Australogyra* as a genus.

GENUS *SCAPOPHYLLIA* MILNE EDWARDS & HAIME, 1848A: 492 (FIG. 25)

Type species

Scapophyllia cylindrica Milne Edwards & Haime, 1849a, vol. 11: 278, vol. 10, pl. 8: figs 8, 8a; subsequent designation, Milne Edwards & Haime, 1849a, vol. 11: 278.

Original description

'Polypier cylindrique, dressé et composé de séries intimement unies par les murailles. Columelle tuberculeuse. Cloisons extrêmement épaisses et fortement granulées.' (Milne Edwards & Haime, 1848a, vol. 27: 492).

Subsequent descriptions

Milne Edwards & Haime, 1849a, vol. 11: 277, 278; Milne Edwards & Haime, 1857, vol. 2: 386; Quenstedt, 1881: 1011; Duncan, 1884: 95; Delage & Hérouard, 1901: 627; Matthai, 1928: 259; Yabe *et al.*, 1936: 42; Vaughan & Wells, 1943: 191; Alloiteau, 1952: 632; Wells, 1956: F416; Chevalier, 1975: 226; Veron & Pichon, 1980: 228, 229; Wood, 1983: 190, 191; Veron, 1986: 440; Chevalier & Beauvais, 1987: 721; Veron & Hodgson, 1989: 269; Sheppard, 1990: 14; Best & Suharsono, 1991: 334; Veron, 2000, vol. 2: 383.

Diagnosis

Colonial, with intracalicular budding only. Corallites monomorphic and uniserial; monticules absent. Walls fused. Calice width small (4 mm), with low relief (3 mm). Costosepta confluent. Septa in three cycles (24–36 septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta equal in relative thickness. Columellae trabecular but compact (one to three threads), 1/4 of calice width, and continuous amongst adjacent corallites. Paliform (uniaxial) lobes well developed. Epitheca absent and endotheca sparse (Fig. 25A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm), with > six teeth per septum. Granules scattered on septal face; irregular in shape. Interarea palisade (Fig. 25B, E).

Walls formed by strong abortive septa and partial septotheca; trabeculothecal elements may be present. Thickening deposits fibrous. Costa centre clusters weak; < 0.3 mm between clusters; medial lines weak. Septum centre clusters weak; < 0.3 mm between clusters; medial lines weak. Transverse crosses absent. Columella centres clustered (Fig. 25C, F).

Species included

Scapophyllia cylindrica Milne Edwards & Haime, 1849a, vol. 11: 278, vol. 10, pl. 8: figs 8, 8a; holotype: MNHN

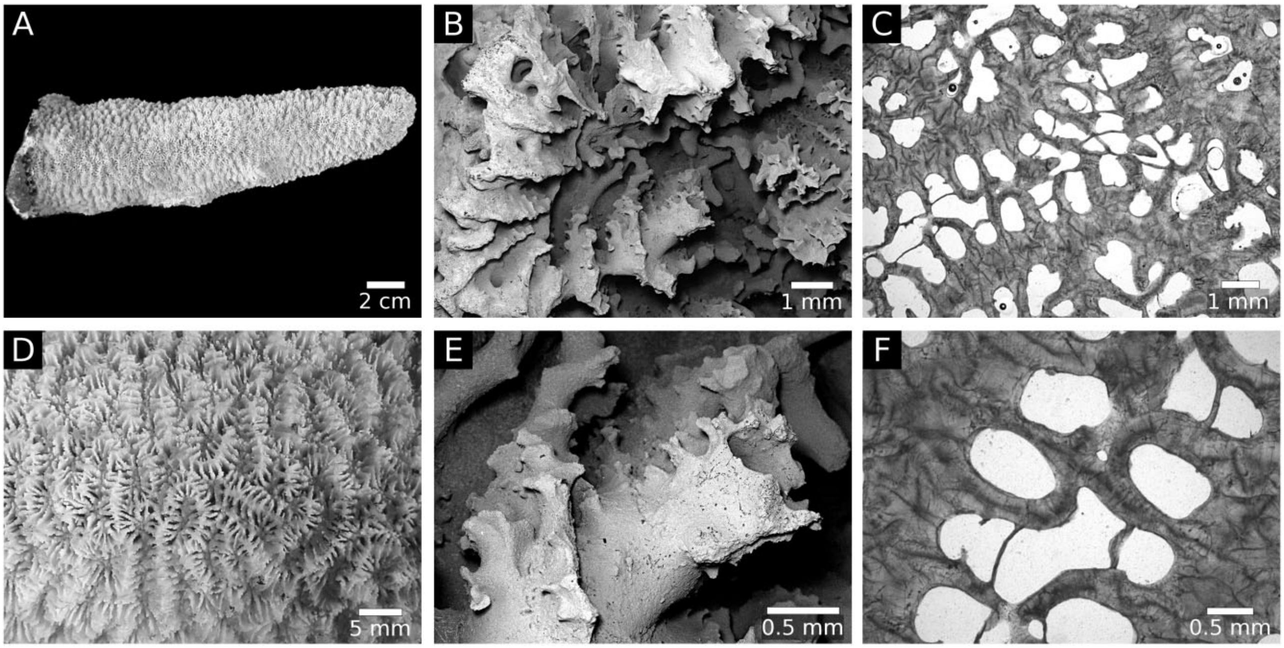


Figure 25. *Scapophyllia* Milne Edwards & Haime, 1848a, has uniserial corallites, fused walls, small (< 4 mm) and low-relief (< 3 mm) calices, compact columellae, well-developed paliform (uniaxial) lobes, and sparse endotheca. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm). Walls formed by strong abortive septa and partial septotheca. A–F, *Scapophyllia cylindrica* Milne Edwards & Haime, 1849a, the type and only living species of *Scapophyllia*; macromorphology, holotype MNHN IK-2010-715, unknown locality (A, D); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C, F), hypotype USNM 89934, Enewetak Atoll, Marshall Islands.

IK-2010-715 (dry specimen; Fig. 25A, D); type locality: 'les mers de la Chine?' (Milne Edwards & Haime, 1849a, vol. 11: 278); phylogenetic data: molecular and morphology.

Taxonomic remarks
Scapophyllia Milne Edwards & Haime, 1848a, vol. 27: 492, is a monotypic genus that is often regarded as a close relative of *Merulina*. Their taxonomic histories have overlapped substantially, being placed together in Merulinidae for the most part (e.g. Vaughan & Wells, 1943: 190; Wells, 1956: F416; Veron, 2000, vol. 2: 363). It has been described as another genus only once, not surprisingly as a *Merulina* – *Merulina studeri* Bedot, 1907: 214, pl. 31: figs 156, 160. Molecular phylogenies demonstrate this affiliation, with these two genera forming a well-supported clade (subclade A) along with some *Goniastrea* spp. (Fukami *et al*., 2008; Huang *et al*., 2011).

Scapophyllia is distributed on reefs of the Central Indo-Pacific, and along the coasts of India and Sri Lanka.

Morphological remarks
No apomorphies have been uncovered for *Scapophyllia* as yet. It shares all but one morphological character with *Merulina*, and they are distinguishable based on septal count – *Scapophyllia* with the plesiomorphy of septa in three cycles (24–36 septa), and fewer for *Merulina*. Loss of epitheca (likelihood of 0.66 based on the Mk1 model) and sparse endotheca (likelihood 0.67) occur at the base of the *Merulina* + *Scapophyllia* clade, setting *Goniastrea* apart from them. All subcorallite characters are shared with most of *Goniastrea*.

GENUS *TRACHYPHYLLIA* MILNE EDWARDS & HAIME, 1848A: 492 (FIG. 26)

Synonym
Wellsophyllia Pichon, 1980: 255 (type species: *Wellsophyllia radiata* Pichon, 1980: 257, figs 1–4 = *Callogyra formosa* Bedot, 1907: 176, pl. 15: figs 63–69, *non Callogyra formosa* Verrill, 1901: 86, pl. 24: figs 1, 2; see Best & Hoeksema, 1987; original designation, Pichon, 1980: 255).

Type species
Manicina amarantum Dana, 1846: 189, pl. 9: fig. 1 = *Turbinolia geoffroyi* Audouin, 1826: 233, pl. 4: figs 1.1, 1.2; subsequent designation, Milne Edwards & Haime, 1849a, vol. 11: 275.

Original description
'Diffère surtout du précédent [*Colpophyllia*] en ce que les séries restent libres par les côtés, que la columelle

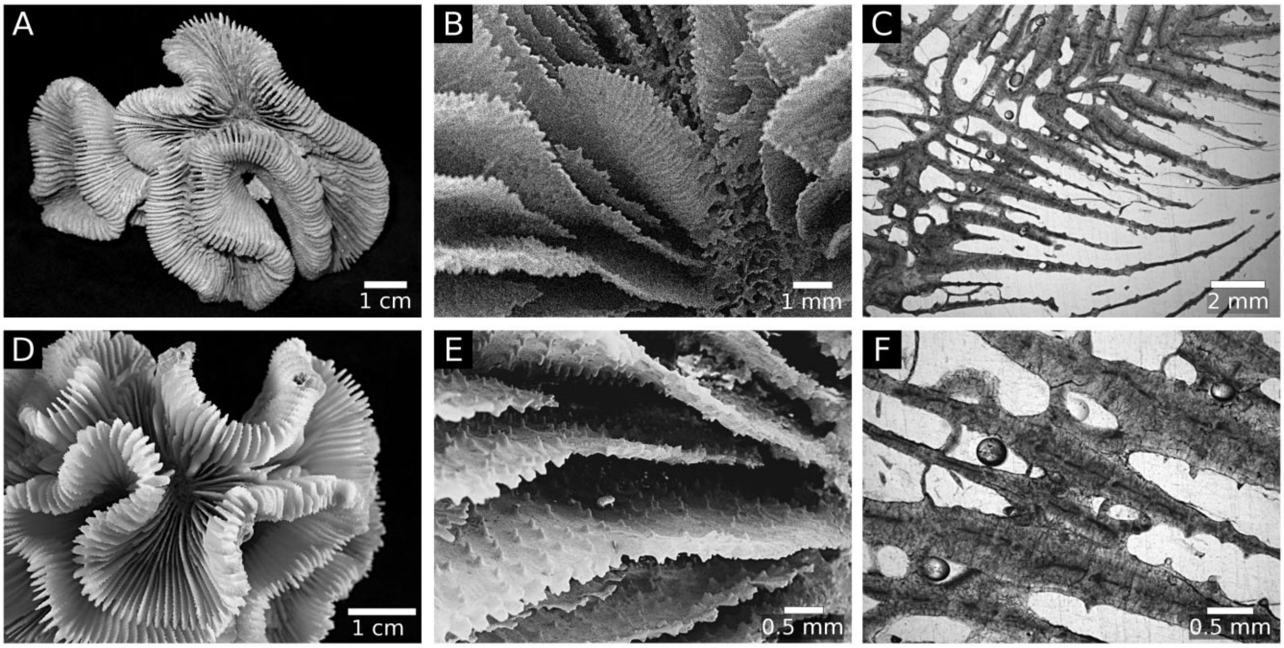


Figure 26. *Trachyphyllia* Milne Edwards & Haime, 1848a, is flabello-meandroid and free-living, with large (> 15 mm) and high-relief (> 6 mm) calices, septa in ≥ four cycles (≥ 48 septa) spaced < six septa per 5 mm, and well-developed septal (multiaxial) lobes. Septal teeth are low (< 0.3 mm) and narrowly spaced (< 0.3 mm); irregularly shaped granules aligned on septal face. Walls formed by dominant paratheca and partial septotheca, with strong costal and septal medial lines. A–F, *Trachyphyllia geoffroyi* (Audouin, 1826), the type and only living species of *Trachyphyllia*; macromorphology, syntype YPM 1974, unknown locality (A), and hypotype USNM 75192, the Philippines (D); micromorphology (scanning electron microscopy), hypotype USNM 91340, Negri Sembilan, western coast of Peninsula Malaysia (B, E); microstructure (transverse thin section), hypotype UF 1383 (FA1073), Palau (C, F).

est spongieuse et bien marquée et que les cloisons présentent un lobe paliforme bien distinct.' (Milne Edwards & Haime, 1848a, vol. 27: 492).

Subsequent descriptions

Milne Edwards & Haime, 1849a, vol. 11: 275; Milne Edwards & Haime, 1857, vol. 2: 340, 341; Quenstedt, 1881: 1006; Duncan, 1884: 82; Quelch, 1886: 77; Saville Kent, 1893: 161; Delage & Hérouard, 1901: 626; Faustino, 1927: 146, 147; Matthai, 1928: 95; Yabe *et al*., 1936: 21; Vaughan & Wells, 1943: 170, 171; Alloiteau, 1952: 618; Wells, 1956: F407; Nemenzo, 1959: 105; Chevalier, 1975: 201; Veron *et al*., 1977: 207; Scheer & Pillai, 1983: 139; Wood, 1983: 174; Veron, 1986: 538; Chevalier & Beauvais, 1987: 719; Veron, 2000, vol. 3: 272.

Diagnosis (apomorphies in italics)

Colonial and free-living, with intracalicular budding only. Corallites monomorphic and *uniserial*; monticules absent. *Phaceloid (flabello-meandroid). Calice width large (> 15 mm), with high relief (> 6 mm).* Septa in ≥ four cycles (≥ 48 septa). Free septa present but irregular. Septa spaced < six septa per 5 mm. *Costosepta unequal in relative thickness.* Columellae trabecular and spongy (> three threads), < 1/4 of calice width, and continuous amongst adjacent corallites. Septal (multiaxial) lobes well developed. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 26A, D).

Tooth base at midcalice circular. Tooth tip at midcalice irregular; tip orientation perpendicular to septum. *Tooth height low (< 0.3 mm) and tooth spacing narrow (< 0.3 mm)*, with > six teeth per septum. *Granules aligned on septal face, perpendicular to septal margin*; irregular in shape. Interarea palisade (Fig. 26B, E).

Walls formed by dominant paratheca and partial septotheca; trabeculothecal elements may be present; abortive septa absent. Thickening deposits fibrous. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines strong. Transverse crosses present. Columella centres clustered (Fig. 26C, F).

Species included

Trachyphyllia geoffroyi (Audouin, 1826: 233, pl. 4: figs 1.1, 1.2); syntypes of *Manicina amarantum*: USNM 85, YPM IZ 1974 (two dry specimens; Fig. 26A); type locality of *Manicina amarantum*: Singapore (Verrill, 1864: 48); phylogenetic data: molecular and morphology.

Taxonomic remarks
Trachyphyllia was established by Milne Edwards & Haime (1848a, vol. 27: 492) initially without a type, and compared with the genus *Colpophyllia*, a meandroid Atlantic genus. *Manicina amarantum* Dana, 1846: 189, pl. 9: fig. 1, was designated the type species shortly after, but this name had been used earlier on an Atlantic species *Colpophyllia amaranthus* (Houttuyn, 1772: 128) (Verrill, 1901: 81; Matthai, 1914: 97). The next available name that could be used was the second *Trachyphyllia* species studied by Milne Edwards & Haime (1849a, vol. 11: 276), *Trachyphyllia geoffroyi*. This incidentally was a young coral of Dana's species collected from the Red Sea, figured in Audouin (1826: 233, pl. 4: fig. 1.1).

Trachyphyllia remains a monotypic genus, phylogenetically recovered unexpectedly in a clade along with *Dipsastraea* and *Coelastrea*. It may be nested amongst these genera (Huang *et al*., 2011; Arrigoni *et al*., 2012), or as an outgroup to them (Fukami *et al*., 2008). Regardless, the long branch subtending it suggests that it is genetically very distinct, and we maintain its present generic status until more samples have been analysed.

Trachyphyllia is widely distributed on reefs of the Indo-Pacific, and absent east of Fiji.

Morphological remarks
Many apomorphies define *Trachyphyllia*, and even more so on the molecular tree simply because it is separated from *Coelastrea*, to which it is morphologically closest. Based on an integrated analysis of both data types, eight apomorphies of macro- and micromorphology are identified (see Diagnosis above), distinguishing this genus from *Coelastrea*, which in contrast has discrete corallites of medium width (4–15 mm) and relief (3–6 mm), limited or fused walls, evenly thick costosepta, medium tooth height (0.3–0.6 mm) and spacing (0.3–1 mm), and scattered granules.

Trachyphyllia is the only free-living coral in Merulinidae as defined here, noting that *Catalaphyllia*, possibly also a merulinid (see remarks for Merulinidae above; Romano & Cairns, 2000; Barbeitos *et al*., 2010; Huang, 2012; Huang & Roy, 2013), can also be free-living (Wells, 1971; Veron *et al*., 1977). This represents an autapomorphy that is not phylogenetically informative within the family, but which is *Trachyphyllia*'s most distinctive feature.

FAMILY MONTASTRAEIDAE YABE & SUGIYAMA, 1941: 72

Synonym
Montastreinae Vaughan & Wells, 1943: 171 (misspelling).

GENUS *MONTASTRAEA* DE BLAINVILLE, 1830: 339 (FIG. 27)

Synonym
Montastrea Vaughan & Wells, 1943: 173 (misspelling).

Type species
Astrea guettardi Defrance, 1826: 379, fossil (figured in Guettard, 1770, vol. 3, pl. 48: figs 2–4); subsequent designation, Lang & Smith, 1935: 554; holotype: lost; hypotype: MNHN R05933, figured in Michelin, 1842, pl. 12: fig. 3 (dry specimen; Fig. 27A); type locality: Miocene.

Original description
'En masses épaisses, composées de cellules tubuleuses assez serrées pour être polygonales, à bords non saillans, à cavité assez profonde, garnie de lamelles nombreuses, remontant le long d'une axe solide plus ou moins saillant.' (de Blainville, 1830: 339).

Subsequent descriptions
de Blainville, 1834: 374; Lang & Smith, 1935: 554; Wells, 1936: 120; Vaughan & Wells, 1943: 173; Smith, 1948: 90; Wells, 1954: 463; Wells, 1956: F404; Chevalier, 1971: 278; Veron *et al*., 1977: 136; Wijsman-Best, 1977: 84; Scheer & Pillai, 1983: 139; Wood, 1983: 49; Veron, 1986: 502; Chevalier & Beauvais, 1987: 714; Veron & Hodgson, 1989: 273; Sheppard, 1990: 24; Budd, 1991: 34; Sheppard & Sheppard, 1991: 135; Veron, 2000, vol. 3: 212.

Diagnosis
Colonial, with extracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, moderate amount (< corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta not confluent. Septa in ≥ four cycles (≥ 48 septa; including very short free septa). Free septa regular. Septa spaced > 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), ≥ 1/4 of calice width. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 27A, D).

Tooth base at midcalice elliptical–perpendicular. Tooth tip at midcalice regular (pointed). Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; weak (rounded). Interarea smooth (Fig. 27B, E).

Walls formed by partial septotheca; abortive septa weak. Thickening deposits fibrous. Costa centre clusters strong; 0.3–0.6 mm between clusters; medial lines absent. Septum centre clusters weak; 0.3–0.5 mm

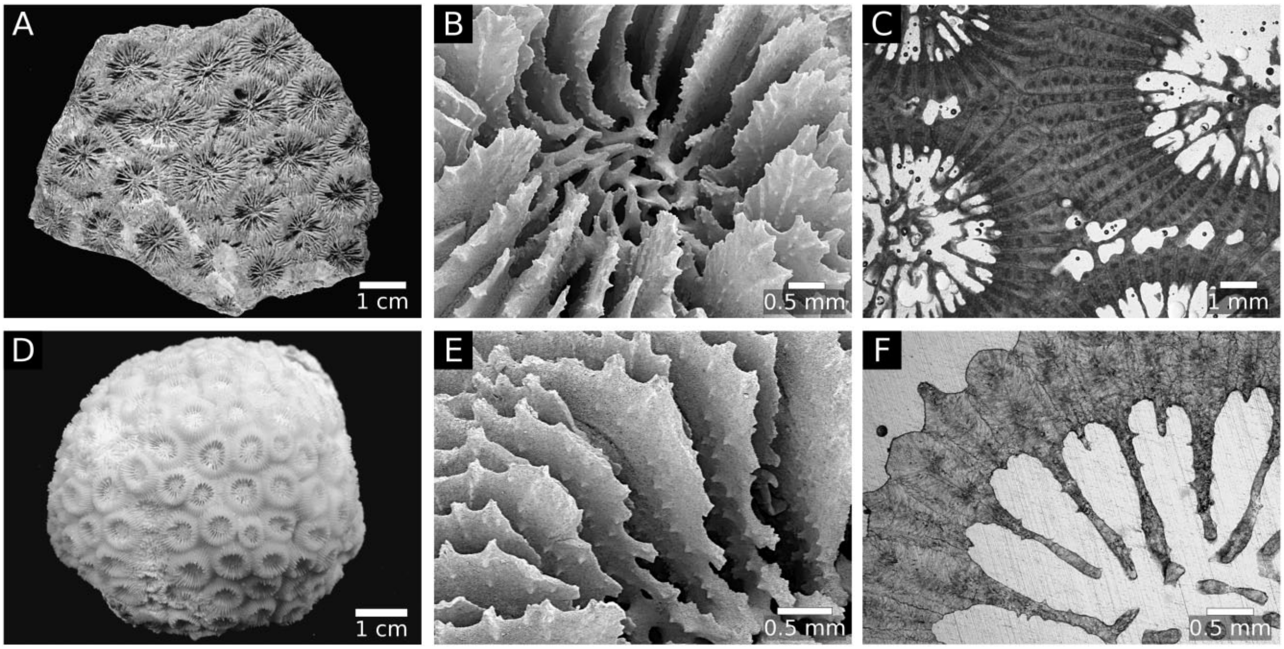


Figure 27. *Montastraea* de Blainville, 1830, has discrete corallites that bud extracalicularly, septa in ≥ four cycles (≥ 48 septa) spaced > 11 septa per 5 mm, regular free septa, and large (≥ 1/4 of calice width) spongy columellae. Septal teeth elliptical–perpendicular at base. Walls formed by partial septotheca and weak abortive septa, with strong costa centre clusters. A, *Astrea guettardi* Defrance, 1826, type species of *Montastraea*; macromorphology, hypotype MNHN R05933, Miocene, Turin, Italy. B–F, *Montastraea cavernosa* (Linnaeus, 1767), the only living species of *Montastraea*; macromorphology (D) and micromorphology (scanning electron microscopy; B, E), hypotype SUI 122829 (FA1109), Carrie Bow Cay, Belize; microstructure (transverse thin section), hypotype SUI 48763 (FA1110), Discovery Bay, Jamaica (C), and hypotype SUI 122828 (FA1093), Bocas del Toro, Panama (F).

between clusters; medial lines absent. Transverse crosses absent. Columella centres clustered (Fig. 27C, F).

Species included

Montastraea cavernosa (Linnaeus, 1767: 1276); holotype: unknown, figured in Seba (1758, pl. 112: fig. 19) (reproduced in Budd, 1991: 37, fig. 20); type locality: 'O. Americano' (Linnaeus, 1767: 1277); phylogenetic data: molecular and morphology.

Taxonomic remarks

Montastraea de Blainville, 1830: 339, was initially described as a subgenus of *Astrea* consisting solely of five fossil species. This name never caught on, partly because of its subgenus status, but also because of its association with the more commonly used name *Heliastraea* Milne Edwards & Haime, 1857, vol. 2: 456. Forty-five species of both modern and fossil corals were attributed to *Heliastraea*, including the type *Madrepora astroites* Forskål, 1775: 133 (= *Astrea forskaliana* Milne Edwards & Haime, 1849b, vol. 12: 100), as well as *Madrepora cavernosa* Esper, 1795: 18, pl. 37: figs 1, 2 (= *Madrepora cavernosa* Linnaeus, 1767: 1276).

Astrea guettardi Defrance, 1826: 379, is one of the species originally assigned to *Montastraea*, but it was only chosen as 'genolectotype' more than a century later by Lang & Smith (1935) and Wells (1936). The authors elevated this taxon to genus, and continued its restriction to fossil corals albeit spanning Cenozoic to Palaeozoic. Shortly after, Vaughan & Wells (1943: 173) redefined the genus and included as synonyms *Heliastraea* and *Orbicella* amongst several fossil genera, effectively incorporating the Recent Atlantic (*Madrepora cavernosa* and *Orbicella*) and Red Sea (*Astrea forskaliana*) within its range, although the latter was not explicitly stated. Note that an 'a' was omitted from the genus name in the process, a practice that has propagated until today (Veron, 2000, vol. 3: 212; but see Chevalier, 1971: 278; Budd *et al*., 2012). Wells (1956: F404) followed a similar treatment, but excluded *Heliastraea* as a synonym, thus restricting the living *Montastraea* to the Atlantic.

Subsequent workers expanded on the definition of this genus, characterizing it mainly with the trait of extracalicular budding, and consequently incorporated Indo-Pacific species such as *Astrea curta* Dana, 1846: 209, *Astrea annuligera* Milne Edwards & Haime, 1849b, vol. 12: 103, *Phymastrea valenciennesi* Milne Edwards & Haime, 1849b, vol. 12: 124, and *Montastraea magnistellata* Chevalier, 1971: 293 (Chevalier, 1971; Veron *et al*., 1977; Wijsman-Best, 1977; Veron, 1986, 2000). It is also clear that *Heliastraea* is a synonym of *Echinopora* instead of *Montastraea* because its type *Astrea forskaliana* (holotype: MNHN IK-2010-406) undoubtedly belongs in *Echinopora* (Wijsman-Best, 1980; Veron, 2000), even against the broader definition of *Montastraea*.

This genus is a challenge to define, and it has been argued that confusion with *Plesiastrea* Milne Edwards & Haime, 1848a, vol. 27: 494, is causing this taxonomic uncertainty (Veron *et al*., 1977). Recent molecular phylogenetic analyses have shown that the problem is far worse than previously thought. Fukami *et al*. (2008) and Kitahara *et al*. (2010) initially showed that *Montastrea* (*sensu* Veron, 2000) is polyphyletic and present in at least three separate clades, but more extensive samplings of the group placed it in up to six distinct lineages (Huang *et al*., 2011; Arrigoni *et al*., 2012). All species examined to date, with the exception of *Madrepora cavernosa* Linnaeus, 1767: 1276 (clade XVI), and *Montastrea multipunctata* Hodgson, 1985: 284 (clade XVIII, XIX or XX; Lobophylliidae), are nested within Merulinidae and have been dealt with above.

Montastraeidae is restricted to *Montastraea cavernosa* on the basis of molecular data that place it in one of the deepest branching lineages of clades XV to XXI (Budd *et al*., 2012), either sister to Merulinidae + Lobophylliidae + Mussidae (Fukami *et al*., 2008), or to Diploastraeidae (Huang *et al*., 2011; Arrigoni *et al*., 2012).

'*Montastrea' multipunctata* has been placed outside of the Merulinidae clade based on molecular and morphological data (Fig. 2; Huang *et al*., 2011; Arrigoni *et al*., 2014). It is in close alliance with Lobophylliidae species, although the precise relationship is unknown. There is however little evidence to suggest that it has any affinity to *Montastraea cavernosa*. Here, we place it in the family Lobophylliidae Dai & Horng, 2009: 59 that awaits detailed taxonomic revision.

Montastraea is distributed on reefs of the Atlantic, specifically in the Caribbean, Brazil, and West Africa.

Morphological remarks

Montastraea is an outgroup for the morphological phylogeny and thus no apomorphies were inferred. It can be distinguished from *Orbicella*, which co-occur in the Caribbean, in having larger (4–15 mm) and deeper (3–6 mm) calices, more septa (≥ 48), spongy columellae, larger and more widely spaced septal teeth (0.3–0.6 mm high, 0.3–1 mm apart) with elliptical–perpendicular bases and regular (pointed) tips, weak (rounded) granules, presence of weak abortive septa, strong costa centre clusters, and absence of medial lines.

FAMILY DIPLOASTRAEIDAE CHEVALIER & BEAUVAIS, 1987: 721

Synonym

Diploastreidae Budd *et al*., 2012: 469 (misspelling).

GENUS *DIPLOASTREA* MATTHAI, 1914: 72 (FIG. 28)

Type species

Orbicella minikoiensis Gardiner, 1904: 774, pl. 63: fig. 35 = *Astrea heliopora* Lamarck, 1816: 265; original designation, Matthai, 1914: 72; syntypes: NHMUK 1927.5.4.152, 1927.5.4.153 (Fig. 28A), 1927.5.12.8 (three dry specimens); type locality: Minicoy, Lakshadweep, India.

Original description

'Corallum. Incrusting or massive. Corallites circular not projecting. Walls fused and perforate, hence peritheca almost absent. Calices shallow. Septa in not less than two orders, the first two entocoelic, each consisting of twelve septa, exsert, much thickened towards their outer ends. Columella formed of twisted trabeculæ from septal margins. Calicular dissepiments oblique.

Polyps. Close together with narrow edge-zones, no coenosarc. Mesenteries in not less than two cycles, each of twelve couples, usually directly continuous from polyp to polyp, primaries meeting stomodæum; all with filaments. Mesoglæa thick. Tentacles corresponding in number and position with entocoeles and exocoeles. Stomodæum short, laterally compressed with two directive grooves. Multiplication by budding.' (Matthai, 1914: 72).

Subsequent descriptions

Vaughan, 1918: 142; Vaughan, 1919: 469; Hoffmeister, 1925: 47; Coryell & Ohlsen, 1929: 216, 217; Yabe *et al*., 1936: 54; Vaughan & Wells, 1943: 137; Alloiteau, 1952: 676; Wells, 1956: F405; Chevalier, 1975: 60; Veron *et al*., 1977: 153; Wijsman-Best, 1980: 240; Scheer & Pillai, 1983: 129; Wood, 1983: 163; Veron, 1986: 512; Chevalier & Beauvais, 1987: 721; Sheppard, 1990: 12; Sheppard & Sheppard, 1991: 137; Veron, 2000, vol. 3: 230.

Diagnosis

Colonial, with extracalicular budding only. Corallites monomorphic and discrete (one to three centres); monticules absent. Coenosteum costate, moderate amount (< corallite diameter). Calice width medium (4–15 mm), with medium relief (3–6 mm). Costosepta not confluent. Septa in ≥ four cycles (≥ 48 septa; including very short free septa). Free septa present but irregular. Septa spaced six to 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> three threads), ≥ 1/4 of calice

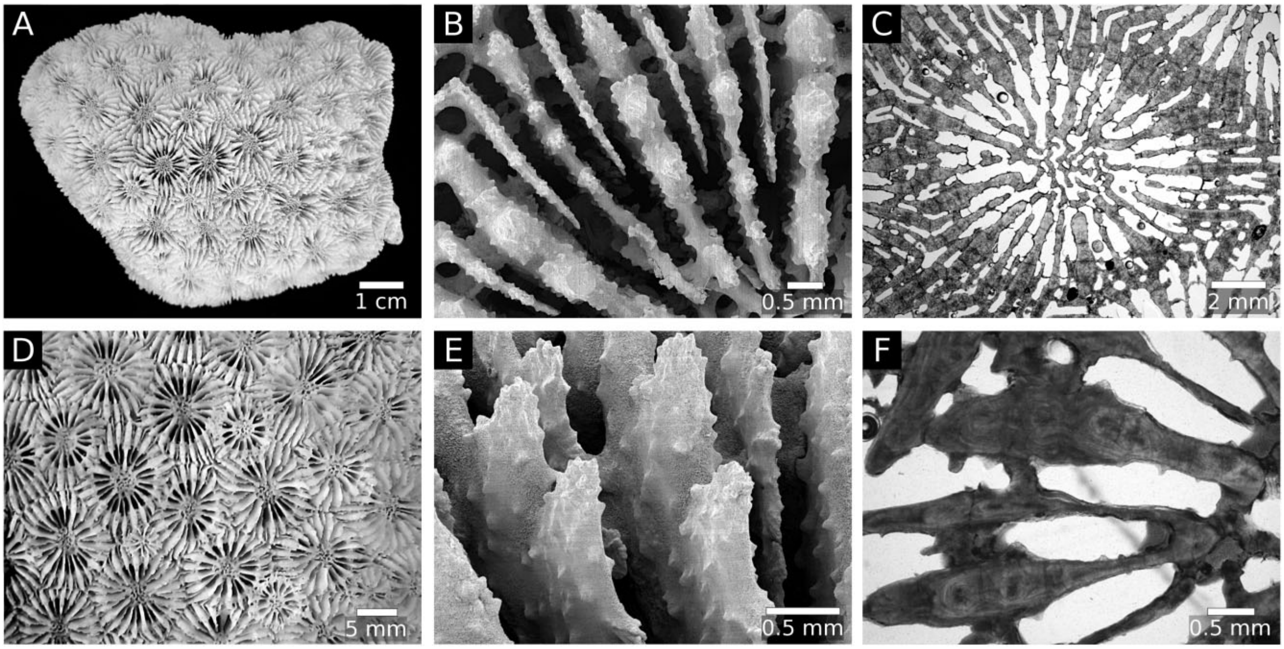


Figure 28. *Diploastrea* Matthai, 1914, has discrete corallites that bud extracalicularly, septa in ≥ four cycles (≥ 48 septa), and large (≥ 1/4 of calice width) spongy columellae. Septal teeth elliptical–parallel at base; weak (rounded) granules scattered on septal face. Walls formed by synapticulotheca and partial septotheca; thickening deposits in concentric rings with extensive stereome. A–F, *Diploastrea heliopora* (Lamarck, 1816), the only living species of *Diploastrea*; macromorphology, *Orbicella minikoiensis* Gardiner, 1904, syntype of *Diploastrea* NHMUK 1927.5.4.153, Minicoy, Lakshadweep, India (A; photo by N. Santodomingo); micromorphology (scanning electron microscopy; B, E) and microstructure (transverse thin section; C), hypotype USNM 93732, Madang, Papua New Guinea; macromorphology, holotype MNHN IK-2010-551, unknown locality (D); microstructure, hypotype USNM 48046, Redang Island, eastern coast of Peninsula Malaysia (F).

width. Paliform (uniaxial) lobes absent. Epitheca well developed and endotheca low–moderate (tabular) (Fig. 28A, D).

Tooth base at midcalice elliptical–parallel. Tooth tip at midcalice regular (pointed). Tooth height medium (0.3–0.6 mm) and tooth spacing medium (0.3–1 mm), with > six teeth per septum. Granules scattered on septal face; weak (rounded). Interarea smooth (Fig. 28B, E).

Walls formed by synapticulotheca and partial septotheca; abortive septa absent. Thickening deposits in concentric rings with extensive stereome. Costa centre clusters strong; > 0.6 mm between clusters; medial lines absent. Septum centre clusters strong; > 0.5 mm between clusters; medial lines absent. Transverse crosses absent. Columella centres clustered (Fig. 28C, F).

Species included
Diploastrea heliopora (Lamarck, 1816: 265); holotype: MNHN IK-2010-551 (dry specimen; Fig. 28D); type locality: 'les mers Australes' (Lamarck, 1816: 265); phylogenetic data: molecular and morphology.

Taxonomic remarks
Matthai (1914: 72) explicitly stated that *Diploastrea* was established based on *Orbicella minikoiensis* Gardiner, 1904: 774, pl. 63: fig. 35, which therefore is the type species. This species was shown to be the same as *Astrea heliopora* Lamarck, 1816: 265 (Matthai, 1914), commonly mistaken as the type of *Diploastrea* (Vaughan, 1918: 142, 1919: 469; Vaughan & Wells, 1943: 137; Wells, 1956: F405; Veron *et al*., 1977: 153; Veron, 1986: 512; Budd *et al*., 2012; but see Chevalier, 1975: 60; Chevalier & Beauvais, 1987: 721), but the genus description is clearly based on three specimens collected by Gardiner at Minicoy, Lakshadweep, India (i.e. type locality of *Diploastrea*).

Although *Diploastrea* is a monotypic genus for living corals, at least 11 fossil species have been assigned to it – e.g. *Diploastrea crassolamellata* (Duncan, 1863: 413, pl. 13: fig. 1a–c) by Coryell & Ohlsen (1929: 216, pl. 39: fig. 2); *Diploastrea harrisi* Wells, 1932: 248, pl. 30: fig. 9, pl. 37: fig. 6, pl. 38: figs 5, 6; and *Diploastrea aequalis* Budd in Budd, Stemann & Stewart (1992: 589, fig. 9.6) – extending its stratigraphical range to the Lower Cretaceous (Wells, 1956). The phylogenetic placement of *Diploastrea heliopora* as the deepest branching species of clades XV to XXI (Budd *et al*., 2012) appears consistent with these fossil assignments, but a detailed morphological analysis is necessary. A recent age estimate based on a time-calibrated relaxed molecular clock suggests that the lineage extends only up to ~70 Mya (Huang & Roy, 2013), but this needs to be verified with more data given its disparity with fossil collections.

Diploastrea heliopora is the only living species to have been assigned to the genus throughout its taxonomic history (Wijsman-Best, 1980), a testament to its phylogenetic uniqueness. Indeed, no other living taxon has been placed in the family Diploastraeidae, as proposed by Chevalier & Beauvais (1987: 721). This scheme was however not accepted by Veron (2000), whose use of Faviidae from Wells (1956) dominated conventional taxonomy until Budd *et al*. (2012) recently revived Diploastraeidae to reflect the unequivocal support for *Diploastrea heliopora* as a distinct lineage (clade XV) amongst living species, either sister to *Montastraea cavernosa* (Huang *et al*., 2011; Arrigoni *et al*., 2012), or to Montastraeidae + Merulinidae + Lobophylliidae + Mussidae (Fukami *et al*., 2008).

Diploastrea is widely distributed on reefs of the Indo-Pacific, and absent eastwards from Hawai'i.

Morphological remarks

Diploastrea is an outgroup for the morphological phylogeny and thus no apomorphies were inferred. However, the genus is easily distinguished from all of Montastraeidae, Merulinidae, Lobophylliidae, and Mussidae by its synapticulotheca, presumably an autapomorphy. Examination of the microstructure of clade XIV would enable this hypothesis to be tested.

In contrast to the other genera of Faviidae *sensu* Veron (2000), and Merulinidae in general, *Diploastrea* is differentiated on the basis of septal teeth that have elliptical–parallel bases and regular (pointed) tips, synapticulotheca, thickening deposits showing concentric rings with extensive stereome, costa and septum centre clusters that are spaced far apart (> 0.6 and > 0.5 mm, respectively), and absence of medial lines. Across its range, *Diploastrea* is easily recognizable and shows very limited variation (Crossland, 1952; Veron *et al*., 1977; Wijsman-Best, 1980; Wood, 1983; Veron, 1986, 2000).

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SUPPORTING INFORMATION

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

Appendix S1. List of specimens examined and morphological data.

Appendix S2. Nexus data file containing the character data matrix and molecular tree used in this study, as well as eight equally most parsimonious trees obtained from the morphological phylogenetic analysis.