



Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia)

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Molecular analyses are transforming our understanding of the evolution of scleractinian corals and conflict with traditional classification, which is based on skeletal morphology. A new classification system, which integrates molecular and morphological data, is essential for documenting patterns of biodiversity and establishing priorities for marine conservation, as well as providing the morphological characters needed for linking present-day corals with fossil species. The present monograph is the first in a series whose goal is to develop such an integrated system. It addresses the taxonomic relationships of 55 Recent zooxanthellate genera (one new) in seven families (one new), which were previously assigned to the suborder Faviina (eight genera are transferred to *incertae sedis*). The present monograph has two objectives. First, we introduce the higher-level classification system for the 46 genera whose relationships are clear. Second, we formally revise the taxonomy of those corals belonging to the newly discovered family-level clade (restricted today to the western Atlantic and Caribbean regions); this revised family Mussidae consists of ten genera (one of which is new) and 26 species that were previously assigned to the 'traditional' families Faviidae and Mussidae. To guide in discovering morphologic characters diagnostic of higher-level taxa, we mapped a total of 38 morphologic characters [19 macromorphology, eight micromorphology, 11 microstructure] onto a molecular tree consisting of 67 species [22 Indo-Pacific and seven Atlantic species in the traditional family Faviidae; 13 Indo-Pacific and ten Atlantic species in the traditional family Mussidae; 13 species in the traditional families Merulinidae (5), Pectiniidae (7), and Trachyphylliidae (1); two Atlantic species of traditional *Montastraea*], and trace character histories using parsimony. To evaluate the overall effectiveness of morphological data in phylogeny reconstruction, we performed morphology-based phylogenetic analyses using 27 (80 states) of the 38 characters, and compared morphological trees with molecular trees. The results of the ancestral state reconstructions revealed extensive homoplasy in almost all morphological characters. Family- and subfamily-level molecular clades [previously identified as XVII–XXI] are best distinguished on the basis of the shapes of septal teeth and corresponding microstructure. The newly revised family Mussidae (XXI) has septal teeth with regular pointed tips (a symplesiomorphy) and a stout blocky appearance. It has two subfamilies, Mussinae and Faviinae. The subfamily Mussinae is distinguished by spine-shaped teeth and widely spaced costoseptal clusters of calcification centres. The subfamily Faviinae is distinguished by blocky, pointed tricorne or paddle-shaped teeth with elliptical bases, transverse structures such as carinae that cross the septal plane, and well-developed aligned granules. Defining diagnostic characters for the broader data set is more challenging. In analyses of taxonomic subsets of the data set that were defined by clade, morphological phylogenetic analyses clearly distinguished the families Mussidae (XXI) and Lobophylliidae (XIX), as well as the two subfamilies of Mussidae (Mussinae, Faviinae), with one exception (*Homophyllia australis*). However, analyses of the entire 67-species data set distinguished the family Lobophylliidae (XIX), but not the Merulinidae (XVII) and not the newly defined Mussidae (XXI), although the subfamily Mussinae was recovered as monophyletic. Some lower-level relationships within the Merulinidae (XVII) agree with molecular results, but this particular family is especially

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problematic and requires additional molecular and morphological study. Future work including fossils will not only allow estimation of divergence times but also facilitate examination of the relationship between these divergences and changes in the environment and biogeography.

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INTRODUCTION

Molecular analyses are transforming our understanding of scleractinian systematics (Romano & Palumbi, 1996, 1997; Romano & Cairns, 2000; Cuif *et al.*, 2003; Fukami *et al.*, 2004, 2008; Kitahara *et al.*, 2010), and have shown that many traditional suborders, families, and genera within the order Scleractinia Bourne, 1900 are polyphyletic. At the level of suborder, initial molecular work by Romano & Palumbi (1996, 1997) suggested that instead of the traditional five to seven suborder subdivisions (Vaughan & Wells, 1943; Wells, 1956; Veron, 1995), the Scleractinia consist of two distinct and highly divergent lineages, the ‘complex’ and ‘robust’ corals, which diverged more than 240 million years ago. Even more remarkably, molecular analyses have indicated that more than half of the traditional suborders (Astrocoeniina Vaughan & Wells, 1943; Fungiina Verrill, 1865; Caryophylliina Vaughan & Wells, 1943; Dendrophylliina Vaughan & Wells, 1943; plus the Meandriina and Poritiina proposed by Veron, 1995) contain members that belong to both the complex and robust groups. The most recent studies suggest that the picture is even more complex, with the robust coral group being a lineage that is imbedded within the complex coral group (Fukami *et al.*, 2008; Kitahara *et al.*, 2010) and several genera of azooxanthellate corals being basal to both groups (Kitahara *et al.*, 2010). Thus, how to structure the Scleractinia at the suborder level remains unclear.

Here we do not address the suborder level, but instead focus on the family and genus levels. This contribution is the first in what will be a series of monographs revising the systematics of modern zooxanthellate corals that have traditionally been assigned to the suborder Faviina sensu Vaughan & Wells (1943) and Wells (1956), or the Faviina plus Meandriina sensu Veron (1995). This grouping includes eight extant families (Vaughan & Wells, 1943; Wells, 1956), all of which fall within the robust group. Initial phylogenetic analyses of mitochondrial [cytochrome *b* (cyt *b*), and cytochrome oxidase I (COI)] and nuclear (β -tubulin, ribosomal DNA) genes from six of these eight families (Fig. 1) indicated that all six are

polyphyletic; five of these six families consist of zooxanthellate corals [Faviidae Gregory, 1900 (including Trachyphylliidae Verrill, 1901); Mussidae Ortmann, 1890; Pectiniidae Vaughan & Wells, 1943; Merulinidae Verrill, 1865; Meandrinidae Gray, 1847], and one consists of primarily azooxanthellate corals (Oculinidae Gray, 1847). Subsequent molecular analyses (COI) of the two remaining families (Rhizangiidae d’Orbigny, 1851; Anthemiphylliidae Vaughan, 1907) that were not included in Fukami *et al.* (2004, 2008) have found the Rhizangiidae to be closely related to members of the Oculinidae, and the Anthemiphylliidae to be polyphyletic, basal to robust corals and the family Pocilloporidae, and distantly related to other members of the Faviina (Kitahara *et al.*, 2010). Molecular analyses have also revealed several previously unrecognized clades (e.g. clades XII, XIII, and XXI of Fukami *et al.*, 2008) whose restriction to the Atlantic (and adjacent basins) has important biogeographical implications for understanding the evolution of Atlantic reef corals. Finally, many traditional genera, including *Favia* Milne Edwards, 1857, *Montastraea* de Blainville, 1830, and *Scolymia* Haime, 1852 (Fukami *et al.*, 2004, 2008), have also been shown to be polyphyletic by these analyses.

In this first monograph in the series, we focus on Recent members of one of the new clades of Atlantic corals (clade XXI of Fukami *et al.*, 2008), which is composed of species traditionally assigned to the families Faviidae and Mussidae, two families that also occur in the Indo-Pacific based on traditional taxonomy. The molecular results indicate that apparent similarities between Indo-Pacific and Atlantic members of the Faviidae and Mussidae may be a result of morphological convergence. The most extreme examples are seen in genera once thought to be cosmopolitan. The Atlantic ‘faviid’ *Favia* and the Atlantic ‘mussid’ *Scolymia* (sensu Veron, 2000) are more closely related to each other than Atlantic *Favia* are related to Indo-Pacific *Favia* or Atlantic *Scolymia* to Indo-Pacific *Scolymia*. This new Atlantic clade is important because it contradicts long-held notions of: (1) Cenozoic diversification (especially at deep nodes) being concentrated in the tropical Indo-Pacific and (2)

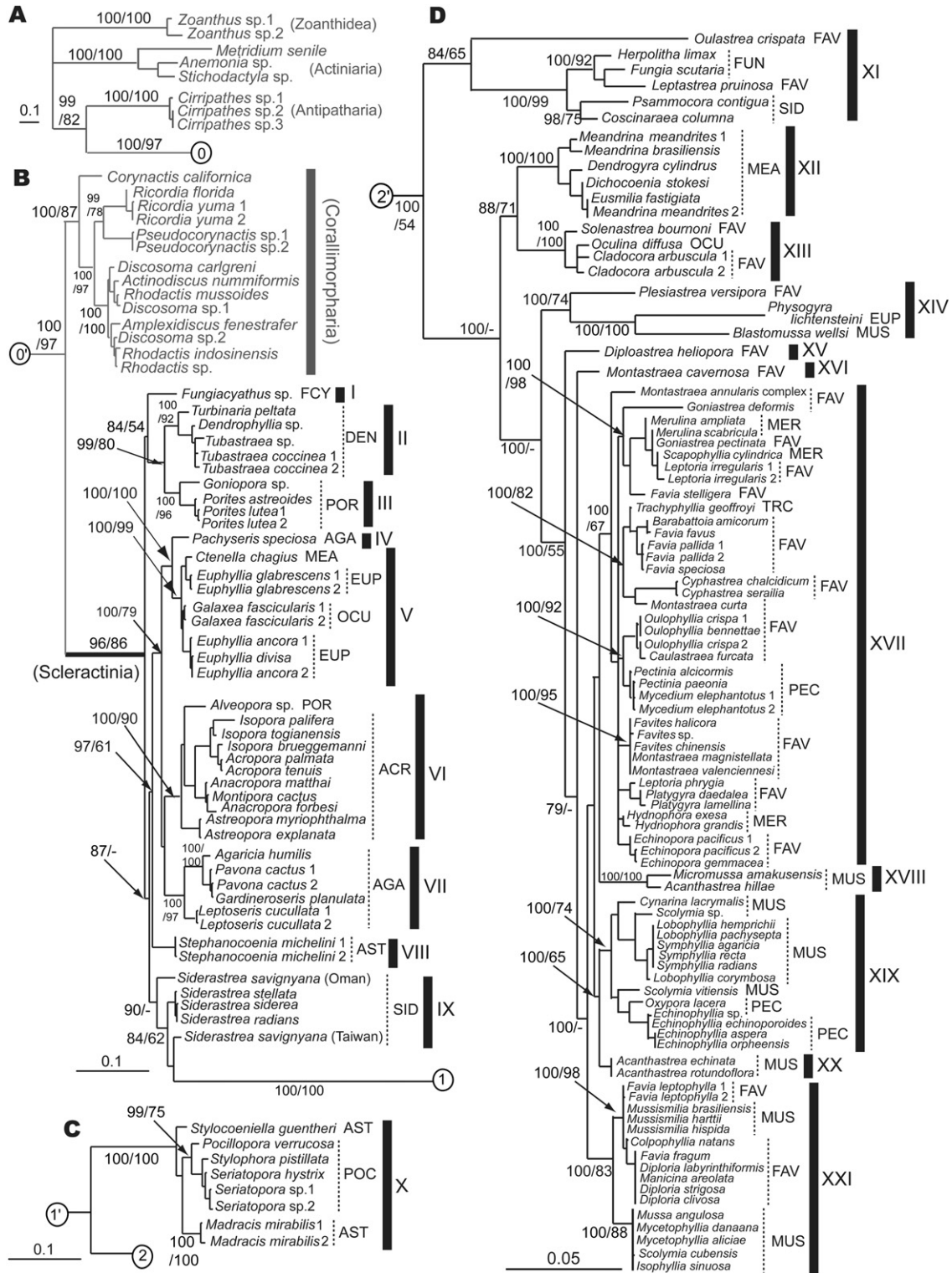


Figure 1. Phylogenetic relationships amongst scleractinian corals. Topology was inferred by Bayesian analysis, based on combined mitochondrial *cox1* and *cob* DNA sequences. Numbers on main branches show percentages of Bayesian probability (> 70%) and bootstrap values (> 50%) in maximum likelihood analysis. Three-letter codes correspond with traditional families; numbers in Roman numerals indicate clades interpreted from the tree. A, outgroups; B, complex corals and corallimorpharians; C, the family Pocilloporidae; D, robust corals. Connections among trees A–D are indicated by numbers in circles. After Fukami *et al.* (2008: 3).

Atlantic species bearing close evolutionary relationships with Indo-Pacific species (Veron, 1995, 2000; Paulay, 1997). The clade is therefore significant for understanding the timing and patterns of diversification associated with biogeography, in addition to morphological character evolution.

We also consider the broader taxonomic context of this new clade within the robust corals. We have formally revised scleractinian classification (Table 1) on the basis of molecular phylogenetic trees because of greater support for nodes at the genus-level and higher in the scleractinian taxonomic hierarchy. Diagnostic morphologic characters were determined by mapping morphologic character states onto a molecular tree, reconstructing ancestral states, and identifying synapomorphies for families and subfamilies (Figs 2–6). As a final step in the analyses of morphological data, we also performed preliminary morphological phylogenetic analyses (Figs 7–8). In future work, we will further explore morphology-based phylogenies by including fossil taxa, thereby increasing taxon sampling and facilitating estimation of divergence times.

Our treatment of morphology differs from that of what is herein termed ‘traditional taxonomy’ (Vaughan & Wells, 1943; Wells, 1956; Veron, 2000) in the greater emphasis on micromorphological and microstructural characters (Budd & Stolarski, 2009, 2011). The taxonomy of scleractinian corals has traditionally been based on examination of the coral skeleton at a macroscopic level using a binocular microscope (reviewed by Stolarski & Roniewicz, 2001). The development and coarse-scale structure of the septa and associated corallite architectural features (e.g. the columella, corallite wall, and coenosteum) have been used to distinguish suborders and families, whereas features related to the budding of new corallites and integration of corallites within colonies distinguish genera (Vaughan & Wells, 1943; Wells, 1956). Here we supplement these traditional macroscopic characters with recently discovered micromorphological and microstructural characters (Budd & Stolarski, 2009, 2011), which are based on up-to-date models of skeletal growth (Stolarski, 2003). Micromorphology involves the shapes of teeth and granules along the margins and faces of septa, and is observed using scanning electron microscopy. Microstructure involves the arrangement of calcification centres and fibres, and is observed using transverse thin sections.

Additionally, few earlier studies attempted to distinguish between plesiomorphic and apomorphic character states when making taxonomic decisions. Morphology-based phylogenetics is still in its infancy in scleractinian systematics, and only a handful of studies have been performed to date, all of which reveal extensive homoplasy (reviewed by Budd *et al.*, 2010). Preliminary phylogenetic comparisons between

molecular and morphological data sets show that the two data types generally yield congruent results and complement one another. Branch support in molecular trees tends to be greater in basal nodes, whereas branch support in morphological trees is higher near the tips of branches (Budd *et al.*, 2010). In the present monograph, we performed exploratory analyses of a morphological character matrix consisting of the 67 species in clades XV–XXI of Fukami *et al.* (2008) and including both traditional macromorphological (19 characters, 55 states) and new micromorphological and microstructural characters (19 characters, 56 states). Our aim was to develop a strategy for recovering the Recent members of the three major family-level clades (XVII, XIX, XXI), which can eventually be applied to the fossil record.

REVISED CLASSIFICATION

Here we formally revise the classification of scleractinian corals assigned to the traditional suborder Faviina Vaughan & Wells, 1943 (Table 1), following the molecular trees and the rationale presented in supplementary table 2 of Fukami *et al.* (2008). As indicated in Table 1, newly conceived families correspond directly with the molecular clades indicated by Roman numerals in Fukami *et al.* (2008), with three exceptions. These exceptions are clades (XIV, XVIII, and XX), whose relationships are unclear. Members of clade XIV (and also clades XI and XIII) are transferred to *incertae sedis*. Members of clades XVII and XX (*Acanthastrea*, *Micromussa*) are assigned to the new family Lobophylliidae until further molecular and morphological work can be carried out to assess their relationships. In determining formal taxonomic names for these newly conceived family groups, we have used the oldest previously published family name based on the genera (valid, not synonyms) that we include in that family. The only such family group for which there is no previously published name is clades XVIII–XX, to which we give the new family name Lobophylliidae. By the same token, we have used the oldest previously published genus name based on the species (valid, not synonyms) that we include in that genus. Only one new genus, *Pseudodiploria*, is described.

The main differences between our revised classification and the ‘traditional’ classifications of Wells (1956) and Veron (2000) at the family level are summarized as follows (Table 2):

- We have created one new family (Lobophylliidae = clades XVIII–XX), resurrected two previously published families (Montastreidae = clade XVI, Diploastreidae = clade XV), dissolved two previous families (Pectiniidae, Trachyphylliidae within clade

Table 1. Type species and citations for families, subfamilies, and genera treated in this monograph series

Family Mussidae, Ortmann, 1890; clade XXI

Subfamily Mussinae Ortmann, 1890

Genus *Mussa* Oken, 1815: 73 [type species: *Madrepora angulosa* Pallas, 1766 (SD: Vaughan, 1918)]

Genus *Isophyllia* Milne Edwards & Haime, 1851a: 87 [type species: *Oulophyllia? spinosa* Milne Edwards & Haime, 1849 (SD: Matthai, 1928) = *Madrepora sinuosa* Ellis & Solander, 1786] (= genus *Isophyllastrea* Matthai, 1928)

Genus *Mycetophyllia* Milne Edwards & Haime, 1848: 491 [type species: *Mycetophyllia lamarchiana* Milne Edwards & Haime, 1849 (SD: Milne Edwards & Haime, 1849)]

Genus *Scolymia* Haime, 1852: 279 [type species: *Madrepora lacera* Pallas, 1766 (SD: Vaughan, 1901)]

Subfamily Faviinae Gregory, 1900

*Genus *Favia* Milne Edwards, 1857 (2): 426 [type species: *Madrepora fragum* Esper, 1795 (SD: Verrill, 1901)]

Genus *Colpophyllia* Milne Edwards & Haime, 1848: 492 [type species: *Meandrina gyrosa* de Lamarck, 1816 (OD) = *Madrepora natans* Houttuyn, 1772]

Genus *Diploria* Milne Edwards & Haime, 1848: 493 [type species: *Meandrina cerebriformis* de Lamarck, 1816 (OD) = *Madrepora labyrinthiformis* Linnaeus, 1758]

Genus *Manicina* Ehrenberg, 1834: 325 [type species: *Madrepora areolata* Linnaeus, 1758 (SD: Milne Edwards & Haime, 1848)]

Genus *Mussismilia* Ortmann, 1890: 292 [type species: *Mussa harttii* Verrill, 1867 (OD)]

Genus *Pseudodiploria* Fukami, Budd, & Knowlton gen. nov. (type species: *Meandrina strigosa* Dana, 1846)

Family Diploastreidae Chevalier & Beauvais, 1987; clade XV

Genus *Diploastrea* Matthai, 1914: 72 [type species: *Astrea heliopora* de Lamarck, 1816 (OD)]

Family Montastraeidae Yabe & Sugiyama, 1941; clade XVI

Genus *Montastraea* de Blainville, 1830: 339 [type species: *Astrea guettardi* DeFrance, 1826, fossil (SD: Lang & Smith, 1935)] ('*Montastraea cavernosa*-like corals').

Family Merulinidae Verrill, 1865; clade XVII

Genus *Merulina* Ehrenberg, 1834: 328 [type species: *Madrepora ampliata* Ellis & Solander, 1786 (OD)]

?Genus *Australogyra* Veron & Pichon, 1982: 138 [type species: *Platygyra zelli* Veron *et al.*, 1977 (OD)]

Genus *Barabattoia* Yabe & Sugiyama, 1941: 72 [type species: *Barabattoia mirabilis* Yabe & Sugiyama, 1941 (OD)]

?Genus *Boninastrea* Yabe & Sugiyama, 1935: 402 [type species: *Boninastrea boninensis* Yabe & Sugiyama, 1935 (OD)]

Genus *Caulastraea* Dana, 1846: 197 [type species: *Caulastraea furcata* Dana, 1846 (SD: Matthai, 1928)]

Genus *Cyphastrea* Milne Edwards & Haime, 1848: 494 [type species: *Astrea microphthalma* de Lamarck, 1816 (OD)]

Genus *Dipsastraea* de Blainville, 1830: 338 [type species: *Madrepora favus* Forskål, 1775 (SD: Wells, 1936)] [includes the following species of *Favia* in Veron (2000): *stelligera*, *favus*, *pallida*, *danae*, *helianthoides*, *laxa*, *maritima*, *matthaii*, *rotumana*, *speciosa*, *veroni*, *albidus*, *lacuna*, *lizardensis*, *marshae*, *maxima*, *rosaria*, *rotundata*, *truncates*, *vietnamensis*]

Genus *Echinopora* de Lamarck, 1816: 252 [type species: *Echinopora rosularia* de Lamarck, 1816 (OD)]

?Genus *Erythraastrea* Scheer & Pillai, 1983: 104 [type species: *Erythraastrea flabellata* Scheer & Pillai, 1983 (OD)]

Genus *Favites* Link, 1807: 162 [type species: *Favites astrinus* Link, 1807 (SD: Vaughan, 1901) = *Madrepora abdita* Ellis & Solander, 1786]

Genus *Goniastrea* Milne Edwards & Haime, 1848: 495 [type species: *Astrea retiformis* de Lamarck, 1816 (OD)]

Genus *Hydnophora* Fischer & von Waldheim, 1807: 295 [type species: *Hydnophora demidovii* Fischer & von Waldheim, 1807 (OD) = *Madrepora exesa* Pallas, 1766]

Genus *Leptoria* Milne Edwards & Haime, 1848: 493 [type species: *Meandrina phrygia* de Lamarck, 1816 (OD)]

*Genus *Mycedium* Milne Edwards & Haime, 1851b: 130 [type species: *Madrepora elephantotus* Pallas, 1766 (SD: Verrill, 1901)]

Genus *Orbicella* Dana, 1846: 205 [type species: *Madrepora annularis* Ellis & Solander, 1786 (SD: Vaughan, 1918)] (*Montastraea* 'annularis' complex)

Genus *Oulophyllia* Milne Edwards & Haime, 1848: 492 [type species: *Meandrina crispa* de Lamarck, 1816 (OD)]

?Genus *Paraclavarina* Veron, 1985: 179 [type species: *Clavarina triangularis* Veron & Pichon, 1980 (OD)]

*Genus *Pectinia* Blainville, 1825: 201 [type species: *Madrepora lactuca* Pallas, 1766 (SD: Vaughan, 1901)]

Genus *Phymastrea* Milne Edwards & Haime, 1848: 494 [type species: *Phymastrea valenciennesii* Milne Edwards & Haime, 1849 (SD: Milne Edwards & Haime, 1849)] [includes the following species of *Montastraea* in Veron (2000): *curta*, *magnistellata*, *valenciennesi*, *serageldini*, *salebrosa*, *colemanni*, *annuligera*, *multipunctata*]

Genus *Platygyra* Ehrenberg, 1834: 323 [type species: *Platygyra labyrinthica* Ehrenberg, 1834 (SD: Brüggemann, 1879) = *Platygyra lamellina* Ehrenberg, 1834]

Genus *Scapophyllia* Milne Edwards & Haime, 1848: 498 [type species: *Scapophyllia cylindrica* Milne Edwards & Haime, 1849 (OD)]

Table 1. *Continued*

Genus *Trachyphyllia* Milne Edwards & Haime, 1849: 492 [type species: *Manicina amarantum* Dana, 1846 (OD) = *Turbinolia geoffroyi* Audouin, 1826]

Family Lobophylliidae Fukami, Budd, & Knowlton fam. nov.; clades XVIII–XX

Genus *Lobophyllia* de Blainville, 1830: 321 [type species: *Madrepora corymbosa* Forskål, 1775 (SD: Matthai, 1928)]

Genus *Acanthastrea* Milne Edwards & Haime, 1848: 495 [type species: *Acanthastrea spinosa* Milne Edwards & Haime, 1848 (OD) = *Astraea echinata* Dana, 1846]

?Genus *Australomussa* Veron, 1985: 171 [type species: *Australomussa rowleyensis* Veron, 1985 (OD)]

Genus *Cynarina* Bruggemann, 1877: 305 [type species: *Cynarina savignyi* Bruggemann, 1877 (OD) = *Caryophyllia lacrymalis* Milne Edwards & Haime, 1849]

?Genus *Echinomorpha* Veron, 2000 (2): 333 [type species: *Echinophyllia nishihrai* Veron, 1990 (OD)]

Genus *Echinophyllia* Klunzinger, 1879: 69 [type species: *Madrepora aspera* Ellis & Solander, 1786 (SD: Wells, 1936)]

Genus *Homophyllia* Bruggemann, 1877: 310 [type species: *Caryophyllia australis* Milne Edwards & Haime, 1849 (OD)]

Genus *Micromussa* Veron, 2000 (3): 8 [type species: *Acanthastrea amakusensis* Veron, 1990 (OD)]

Genus *Moseleya* Quelch, 1884: 292 [type species: *Moseleya latistellata* Quelch, 1884 (OD)]

Genus *Oxypora* Saville Kent, 1871: 283 [type species: *Trachypora lacera* Verrill, 1864 (SD: Wells, 1936)]

Genus *Parascolymia* Wells, 1964: 379 [type species: *Scolymia vitiensis* Bruggemann, 1877 (OD)]

Genus *Symphyllia* Milne Edwards & Haime, 1848: 491 [type species: *Meandrina sinuosa* Quoy & Gaimard, 1833 (OD)]

Family Meandrinidae Gray, 1847; clade XII

Genus *Meandrina* de Lamarck, 1801: 372 [type species: *Madrepora meandrites* Ellis & Solander, 1786 (OD)]

Genus *Dendrogyra* Ehrenberg, 1834: 324 [type species: *Maeandra (Dendrogyra) cylindrus* Ehrenberg, 1834 (OD) (= genus *Goreaugyra* Wells, 1974)]

Genus *Dichocoenia* Milne Edwards & Haime, 1848: 469 [type species: *Astrea porcata* de Lamarck, 1816 (OD) = *Dichocoenia stokesii* Milne Edwards & Haime, 1848]

Genus *Eusmilia* Milne Edwards & Haime, 1848: 467 [type species: *Madrepora fastigiata*, Pallas, 1766 (OD)]

Family Euphylliidae (Alloiteau, 1952); clade V (in part, traditional ‘meandrinids’ only)

Genus *Ctenella* Matthai, 1928: 171 [type species: *Ctenella chagius* Matthai, 1928 (OD)]

*Genus *Galaxea* Milne Edwards, 1857 (2): 223 [type species: *Madrepora fascicularis* Linnaeus, 1767 (SD: Vaughan, 1918)]

?Genus *Gyrosmlia* Milne Edwards & Haime, 1851a: 55 [type species: *Manicina interrupta* Ehrenberg, 1834 (OD)]

?Genus *Montigyra* Matthai, 1928: 255 [type species: *Montigyra kenti* Matthai, 1928 (OD)]

?Genus *Simplastrea* Umbgrove, 1939: 24 [type species: *Simplastrea vesicularis* Umbgrove, 1939 (OD)]

Family *incertae sedis*

Genus *Blastomussa* Wells, 1968: 276 [type species: *Bantamia merleti* Wells, 1961: 189 (OD); molecular clade XIV]

Genus *Cladocora* Ehrenberg, 1834: 309 [type species: *Madrepora caespitosa* Linnaeus, 1767 (SD: Milne Edwards & Haime, 1851a); molecular clade XIII]

**Genus *Indophyllia* Gerth, 1921: 405 [type species: *Indophyllia cylindrica* Gerth, 1921 (OD)], which is exclusively fossil

Genus *Leptastrea* Milne Edwards & Haime, 1848: 494 [type species: *Leptastrea roissyana* Milne Edwards & Haime, 1849 (SD: Milne Edwards & Haime, 1850); molecular clade XI]

Genus *Oulastrea* Milne Edwards & Haime, 1848: 495 [type species: *Astrea crispata* de Lamarck, 1816: 265 (OD); molecular clade XI]

Genus *Parasimplastrea* Sheppard, 1985: 5 [type species: *Parasimplastrea omanensis* Sheppard, 1985 (OD) = *Goniastrea simplicitexta* Umbgrove, 1942]

Genus *Plesiastrea* Milne Edwards & Haime, 1848: 494 [type species: *Astrea versipora* de Lamarck, 1816: 264 (OD); molecular clade XIV]

Genus *Solenastrea* Milne Edwards & Haime, 1848: 494 [type species: *Astrea turonensis* Michelin, 1847 (SD: Milne Edwards & Haime, 1851a), fossil; molecular clade XIII]

Genera indicated with question marks were not studied molecularly by Fukami *et al.* (2008).

OD, original designation, including monotypy; SD, subsequent designation.

See coralloosphere.org for additional nomenclatural details.

*Originally described by Oken (1815) but rejected by ICZN opinion 417 (ICZN Commission, 1956).

**The one previously reported Recent species (*Indophyllia macassarensis* Best & Hoeksema, 1987) belongs to *Cynarina* based on study of type material (NNM 22189) in Leiden, Netherlands. *Indophyllia macassarensis* has high, irregular lobate septal teeth, extensive thickening deposits, and unequal costoseptal cycles, features which are characteristic of *Cynarina* but not *Indophyllia*, and is transferred to *Cynarina*. *Indophyllia* is therefore an exclusively fossil genus.

Table 2. Comparison between two frequently cited classifications of Recent reef corals and the classification used in this study

Wells (1956)	Veron (2000)	This Study
<p>Family Mussidae</p> <p>Genus <i>Mussa</i> [=<i>Scolymia</i>]</p> <p>Genus <i>Isophyllia</i></p> <p>Genus <i>Isophyllastrea</i></p> <p>Genus <i>Mycetophyllia</i></p> <p>Genus <i>Mussismilia</i></p> <p>Genus <i>Lobophyllia</i></p> <p>Genus <i>Acanthastrea</i></p> <p>Genus <i>Symphyllia</i></p> <p>?Genus <i>Cynarina</i></p> <p>Genus <i>Homophyllia</i></p> <p>Genus <i>Parascolymia</i></p> <p>Genus <i>Blastomussa</i></p> <p>Family Faviidae</p> <p>Subfamily Faviinae</p> <p>Genus <i>Favia</i></p> <p>Genus <i>Colpophyllia</i></p> <p>Genus <i>Diploria</i></p> <p>Genus <i>Manicina</i></p> <p>Genus <i>Barabattoia</i></p> <p>Genus <i>Bikiniastrea</i></p> <p>Genus <i>Caulastrea</i></p> <p>Genus <i>Favites</i></p> <p>Genus <i>Goniastrea</i></p> <p>Genus <i>Leptoria</i></p> <p>Genus <i>Oulophyllia</i></p> <p>Genus <i>Platygyra</i></p> <p>Genus <i>Hydnophora</i></p> <p>Genus <i>Plesiastrea</i></p> <p>Subfamily Montastreinae</p> <p>Genus <i>Montastrea</i></p> <p>Genus <i>Diploastrea</i></p> <p>Genus <i>Cyphastrea</i></p> <p>Genus <i>Echinopora</i></p> <p>Genus <i>Cladocora</i></p> <p>Genus <i>Solenastrea</i></p> <p>Genus <i>Leptastrea</i></p> <p>?Genus <i>Oulastrea</i></p> <p>Subfamily Trachyphylliinae</p> <p>Genus <i>Indophyllia</i></p> <p>Genus <i>Trachyphyllia</i></p> <p>?Genus <i>Moseleya</i></p> <p>Family Pectiniidae</p> <p>Genus <i>Pectinia</i></p> <p>Genus <i>Mycedium</i></p> <p>Genus <i>Oxypora</i></p>	<p>Family Mussidae</p> <p>Genus <i>Mussa</i></p> <p>Genus <i>Isophyllia</i> [=<i>Isophyllastrea</i>]</p> <p>Genus <i>Mycetophyllia</i></p> <p>Genus <i>Mussismilia</i></p> <p>Genus <i>Lobophyllia</i></p> <p>Genus <i>Acanthastrea</i></p> <p>Genus <i>Symphyllia</i></p> <p>Genus <i>Australomussa</i></p> <p>Genus <i>Micromussa</i></p> <p>Genus <i>Cynarina</i></p> <p>Genus <i>Scolymia</i> [=<i>Homophyllia</i>, <i>Parascolymia</i>]</p> <p>Genus <i>Blastomussa</i></p> <p>Genus <i>Indophyllia</i></p> <p>Family Faviidae</p> <p>Genus <i>Favia</i></p> <p>Genus <i>Colpophyllia</i></p> <p>Genus <i>Diploria</i></p> <p>Genus <i>Manicina</i></p> <p>Genus <i>Barabattoia</i> [=<i>Bikiniastrea</i>]</p> <p>Genus <i>Caulastrea</i></p> <p>Genus <i>Favites</i></p> <p>Genus <i>Goniastrea</i></p> <p>Genus <i>Leptoria</i></p> <p>Genus <i>Oulophyllia</i></p> <p>Genus <i>Platygyra</i></p> <p>Genus <i>Australogyra</i></p> <p>Genus <i>Erythraestrea</i></p> <p>Genus <i>Montastrea</i></p> <p>Genus <i>Diploastrea</i></p> <p>Genus <i>Cyphastrea</i></p> <p>Genus <i>Echinopora</i></p> <p>Genus <i>Cladocora</i></p> <p>Genus <i>Solenastrea</i></p> <p>Genus <i>Leptastrea</i></p> <p>Genus <i>Oulastrea</i></p> <p>Genus <i>Plesiastrea</i></p> <p>Genus <i>Parasimplastrea</i></p> <p>Genus <i>Moseleya</i></p> <p>Family Trachyphylliidae</p> <p>Genus <i>Trachyphyllia</i></p> <p>Family Pectiniidae</p> <p>Genus <i>Pectinia</i></p>	<p>Family Mussidae (clade XXI)</p> <p>Subfamily Mussinae</p> <p>Genus <i>Mussa</i></p> <p>Genus <i>Isophyllia</i> [=<i>Isophyllastrea</i>]</p> <p>Genus <i>Mycetophyllia</i></p> <p>Genus <i>Scolymia</i> (Atlantic only)</p> <p>Subfamily Faviinae</p> <p>Genus <i>Favia</i> (Atlantic only)</p> <p>Genus <i>Colpophyllia</i></p> <p>Genus <i>Diploria</i></p> <p>Genus <i>Pseudodiploria</i>, new</p> <p>Genus <i>Manicina</i></p> <p>Genus <i>Mussismilia</i></p> <p>Family Lobophylliidae, new (clade XIX)</p> <p>Genus <i>Lobophyllia</i></p> <p>Genus <i>Acanthastrea</i></p> <p>Genus <i>Symphyllia</i></p> <p>?Genus <i>Australomussa</i></p> <p>Genus <i>Micromussa</i></p> <p>Genus <i>Cynarina</i></p> <p>Genus <i>Homophyllia</i> (part Indo-Pacific <i>Scolymia</i>)</p> <p>Genus <i>Parascolymia</i> (part Indo-Pacific <i>Scolymia</i>)</p> <p>Genus <i>Oxypora</i></p> <p>Genus <i>Echinophyllia</i></p> <p>?Genus <i>Echinomorpha</i></p> <p>Genus <i>Moseleya</i></p> <p>Family Montastreae (clade XVI)</p> <p>Genus <i>Montastrea</i> (<i>M. cavernosa</i> only)</p> <p>Family Diploastreidae (clade XV)</p> <p>Genus <i>Diploastrea</i></p> <p>Family Merulinidae (clade XVII)</p> <p>Genus <i>Merulina</i></p> <p>?Genus <i>Boninastrea</i></p> <p>?Genus <i>Paraclavarina</i></p> <p>Genus <i>Scapophyllia</i></p> <p>Genus <i>Hydnophora</i></p> <p>Genus <i>Barabattoia</i></p> <p>Genus <i>Caulastraea</i></p> <p>Genus <i>Favites</i></p> <p>Genus <i>Goniastrea</i></p> <p>Genus <i>Leptoria</i></p> <p>Genus <i>Oulophyllia</i></p> <p>Genus <i>Platygyra</i></p> <p>?Genus <i>Australogyra</i></p>

Table 2. *Continued*

<p>Genus <i>Echinophyllia</i></p> <p>Family Merulinidae</p> <p>Genus <i>Merulina</i></p> <p>Genus <i>Boninastraea</i></p> <p>Genus <i>Clavarina</i></p> <p>Genus <i>Scapophyllia</i></p> <p>Family Oculinidae</p> <p>Genus <i>Galaxea</i></p> <p>Genus <i>Simplastrea</i></p> <p>Family Meandrinidae</p> <p>Genus <i>Meandrina</i></p> <p>Genus <i>Dichocoenia</i></p> <p>Genus <i>Dendrogyra</i></p> <p>Genus <i>Ctenella</i></p> <p>*Family Caryophylliidae</p> <p>Genus <i>Eusmilia</i></p> <p>Genus <i>Gyrosmlia</i></p> <p>Genus <i>Montigyra</i></p>	<p>Genus <i>Mycedium</i></p> <p>Genus <i>Oxypora</i></p> <p>Genus <i>Echinophyllia</i></p> <p>Genus <i>Echinomorpha</i></p> <p>Family Merulinidae</p> <p>Genus <i>Merulina</i></p> <p>Genus <i>Boninastraea</i></p> <p>Genus <i>Paraclavarina</i></p> <p>Genus <i>Scapophyllia</i></p> <p>Genus <i>Hydnophora</i></p> <p>Family Oculinidae</p> <p>Genus <i>Oculina</i></p> <p>Genus <i>Schizoculina</i></p> <p>Genus <i>Galaxea</i></p> <p>Genus <i>Simplastrea</i></p> <p>Family Meandrinidae</p> <p>Genus <i>Meandrina</i> [=<i>Goreaugyra</i>]</p> <p>Genus <i>Dichocoenia</i></p> <p>Genus <i>Dendrogyra</i></p> <p>Genus <i>Ctenella</i></p> <p>Genus <i>Eusmilia</i></p> <p>Genus <i>Gyrosmlia</i></p> <p>Genus <i>Montigyra</i></p>	<p>?Genus <i>Erythrastraea</i></p> <p>Genus <i>Cyphastrea</i></p> <p>Genus <i>Echinopora</i></p> <p>Genus <i>Dipsastraea</i> (Indo-Pacific “<i>Favia</i>”)</p> <p>Genus <i>Phymastrea</i> (Indo-Pacific “<i>Montastraea</i>”)</p> <p>Genus <i>Orbicella</i> (“<i>Montastraea</i>” annularis complex)</p> <p>Genus <i>Trachyphyllia</i></p> <p>Genus <i>Pectinia</i></p> <p>Genus <i>Mycedium</i></p> <p>Family Meandrinidae (clade XII)</p> <p>Genus <i>Meandrina</i></p> <p>Genus <i>Dichocoenia</i></p> <p>Genus <i>Dendrogyra</i></p> <p>Genus <i>Eusmilia</i></p> <p>*Family Euphylliidae (clade V)</p> <p>Genus <i>Ctenella</i></p> <p>?Genus <i>Gyrosmlia</i></p> <p>?Genus <i>Montigyra</i></p> <p>Genus <i>Galaxea</i></p> <p>?Genus <i>Simplastrea</i></p> <p>*Family Incertae sedis</p> <p>Genus <i>Blastomussa</i> (clade XIV)</p> <p>Genus <i>Cladocora</i> (clade XIII)</p> <p>Genus <i>Leptastrea</i> (clade XI)</p> <p>Genus <i>Oulastrea</i> (clade XI)</p> <p>Genus <i>Parasimplastrea</i></p> <p>Genus <i>Plesiastrea</i> (clade XIV)</p> <p>Genus <i>Solenastrea</i> (clade XIII)</p>
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See Stolarski & Roniewicz (2001) for further comparisons with Alloiteau (1952) and Chevalier & Beauvais (1987).

Blocks of genera highlighted in different colours represent groups that were interpreted as closely related in all three classification systems and can be traced across the chart.

*indicates that the list includes only Recent genera that were previously assigned to the families Faviidae, Meandrinidae, Merulinidae, Mussidae, Oculinidae, Pectiniidae, or Trachyphylliidae.

- XVII), and lowered one previous family (Faviidae within clade XXI) to the rank of subfamily.
- The previous family Mussidae has been subdivided into Atlantic (Mussidae = clade XXI) vs. Indo-Pacific (Lobophylliidae = clades XVIII–XX) groups.
- The previous family Faviidae has been subdivided into Atlantic (Mussidae = clade XXI) vs. Indo-Pacific (Merulinidae = clade XVII) groups.
- The previous families Merulinidae and Trachyphylliidae have been merged with previous Indo-Pacific ‘faviids’, and named Merulinidae (clade XVII).

- The previous family Pectiniidae has been split into two groups: one merged with the family Lobophylliidae (clades XVIII–XX), and the other merged with the family Merulinidae (clade XVII).
- The genera *Montastraea* (clade XVI) and *Diploastrea* (clade XV) have been elevated to each become separate families.
- The newly conceived Atlantic Mussidae (clade XXI) has been split into two subfamilies (Mussinae, Faviinae).

Our revised classification has consequences for several genera, which are summarized as follows.

In addition to Fukami *et al.* (2008), rationale for these changes is provided in the formal systematic account.

- The genus *Mussismilia* has been transferred from Atlantic ‘mussids’ (Mussinae) to Atlantic ‘faviids’ (Faviinae).
- The previous genus *Diploria* has been split into two genera: (1) *Diploria*, which consists only of the species *Diploria labyrinthiformis*, and (2) a new genus, *Pseudodiploria*, which consists of the species *Pseudodiploria strigosa* and *Pseudodiploria clivosa*.
- The previous genus *Favia* has been split into two genera: (1) *Favia* in the Atlantic (assigned to family Mussidae = clade XXI) and (2) *Dipsastraea* in the Indo-Pacific (assigned to family Merulinidae = clade XVII).
- The previous genus *Montastraea* has been split into three genera: (1) *Montastraea* in the Atlantic (assigned to family Montastreidae = clade XVI), (2) *Orbicella* in the Atlantic (assigned to family Merulinidae = clade XVII), and (3) *Phymastrea* in the Indo-Pacific (assigned to family Merulinidae = clade XVII).
- The previous genus *Scolymia* has been split into three genera – *Scolymia* (assigned to family Mussidae = clade XXI), *Parascolymia* (assigned to family Lobophylliidae = clades XVIII–XX), and *Homophyllia* (assigned to family Lobophylliidae = clades XVIII–XX), following the previous usage of Wells (1964).
- The genus *Eusmilia* has been transferred to the family Meandrinidae (clade XII).
- The genera *Galaxea* and *Simplastrea* are transferred to the family Euphylliidae (clade V), *Simplastrea* being questionably transferred.
- The genera *Blastomussa*, *Cladocora*, *Indophyllia*, *Leptastrea*, *Oulastrea*, *Plesiastrea*, *Parasimplastrea*, and *Solenastrea* have been transferred to *incertae sedis* until further work on these genera is complete.

In addition, the species previously referred to as ‘*Favia leptophylla*’ has been transferred to the genus *Mussismilia*.

MATERIAL AND METHODS

TAXA STUDIED

Although the focus of the present monograph is on clade XXI (the revised family Mussidae) in the molecular tree of Fukami *et al.* (2008), we also analysed the morphology of clades XV to XX (Fig. 1) in an effort to identify synapomorphies and diagnostic characters for clade XXI. As in Fukami *et al.* (2008), we analysed the morphology of a total of 17 genetically characterized species within clade XXI, which include

representatives of previously described extant Atlantic genera traditionally assigned to the families Faviidae [*Colpophyllia* (one species, seven specimens), *Diploria* + *Pseudodiploria* (three species, ten specimens), Atlantic *Favia* (two species, nine specimens), *Manicina* (one species, seven specimens)] and Mussidae [*Isophyllia* (one species, five specimens), *Mussa* (one species, six specimens), *Mussismilia* (four species, including *Mussismilia leptophylla*, 11 specimens)], *Mycetophyllia* (two species, nine specimens), *Scolymia* (two species, 15 specimens)]. We also analysed the morphology of a total of 50 genetically characterized species in clades XV–XX, including:

- two original Atlantic species of *Montastraea*, *Montastraea cavernosa* (four specimens) and *Orbicella annularis* (three specimens), which are the only Atlantic ‘faviids’ not part of clade XXI;
- 22 Indo-Pacific species in 12 genera in the previous family Faviidae [*Barabattoia* (one species, two specimens), *Caulastraea* (one species, two specimens), *Cyphastrea* (two species, six specimens), *Diploastrea* (one species, three specimens), *Echinopora* (one species, three specimens), Indo-Pacific ‘*Favia*’ [= *Dipsastraea*] (four species, 18 specimens), *Favites* (two species, five specimens), *Goniastrea* (two species, four specimens), *Leptoria* (one species, six specimens), Indo-Pacific ‘*Montastraea*’ [= *Phymastrea*] (three species, six specimens), *Oulophyllia* (two species, eight specimens), *Platygyra* (two species, four specimens)];
- 13 Indo-Pacific species in five genera in the previous family Mussidae [*Acanthastrea* (three species, ten specimens), *Cynarina* (one species, four specimens), *Lobophyllia* (three species, 18 specimens), *Micromussa* (one species, two specimens), *Symphyllia* (three species, 12 specimens), Indo-Pacific ‘*Scolymia*’ (one species of *Homophyllia* + one species of *Parascolymia*, five specimens)];
- five species in the previous family Merulinidae [*Merulina* (two species, five specimens), *Scapophyllia* (one species, one specimen), *Hydnophora* (two species, six specimens)];
- seven species in the previous family Pectiniidae [*Pectinia* (two species, eight specimens), *Mycedium* (one species, three specimens), *Oxypora* (one species, three specimens), *Echinophyllia* (three species, ten specimens)];
- one species in the previous family Trachyphylliidae (*Trachyphyllia*, two specimens).

Wherever possible, we examined the same specimen as the one that was sequenced for the molecular analyses of Fukami *et al.* (2004, 2008).

In addition, as part of the formal systematic account, we examined the existing primary types of the type species of each Atlantic genus listed above

(30 total), and designated neotypes for species within each genus (11 total) that have unknown or poorly defined type localities. We also examined 20 primary types of selected species in clades XV–XX. A total of 295 specimens has been morphologically characterized (Appendix S1). As our sampling focused on representing genera within each clade, we have not attempted to revise definitions of species or quantitatively assess variation within species and, unless indicated otherwise, follow the species designations of Veron (2000, 2002).

MORPHOLOGICAL CHARACTERS

Following Budd & Stolarski (2009, 2011), our morphological examination involved three approaches: (1) macromorphology (using a stereoscope, at magnifications $< 50\times$), (2) micromorphology (using a scanning electron microscope, at magnifications ranging from 50–200 \times), and (3) microstructure (using transverse thin sections, at magnifications $< 100\times$). As described earlier, macromorphological features have primarily served as diagnostic characters in traditional classification (Vaughan & Wells, 1943; Wells, 1956), and as the basis for previous morphological phylogenetic analyses (recently reviewed by Budd *et al.*, 2010). Micromorphological features, especially septal structure, were also included in the traditional definition of families and higher taxonomic levels, but only in a cursory way that did not involve the use of electron microscopy. They have not usually played a major role in morphological phylogenetic analyses (but see Hoeksema, 1989). Although included in the previous classification systems of Alloiteau (1952) and Chevalier & Beauvais (1987), most microstructural features were not used in the traditional classification of Vaughan & Wells (1943) and Wells (1956), or in subsequent morphological phylogenetic analyses (with the exception of corallite wall structure). Micromorphological and microstructural analyses are therefore relatively new to morphological phylogenetic analysis, and have not been previously defined or delineated. A glossary of morphological terms is provided in Appendix S2. Illustrations of the 38 characters analysed in the present study are provided in Appendix S3.

Macromorphology

Macromorphology involves the study of many traditional diagnostic features that are architectural in nature, including colony form (corallite budding and integration, the length and shape of calical series); the size and shape of the calice; the structure and development of the septa (number, spacing, relative thickness and length), the columella (and associated internal lobes), the corallite wall, endo- and exotheca, and the coenosteum. They are features that are com-

monly used in ecological field work and environmental monitoring that require the identification of species (e.g. Edmunds & Elahi, 2007; Riegl & Dodge, 2008; Alvarez-Filip *et al.*, 2011), and in morphometric analyses examining patterns of variation within and amongst species (e.g. Budd, Johnson & Potts, 1994; Budd & Klaus, 2001; Pandolfi, Lovelock & Budd, 2002; Klaus & Budd, 2003; Budd & Pandolfi, 2004, 2010).

Vaughan & Wells (1943) and Wells (1956) used macromorphological characters to distinguish genera within the traditional families Faviidae and Mussidae. For example, these authors split the family Faviidae into three subfamilies based on intracalicular (Faviinae, Trachyphylliinae) vs. extracalicular (Montastraeinae) budding. The subfamily Trachyphylliinae was further diagnosed as having prominent internal lobes. Within the Faviinae, genera were distinguished primarily based on colony form, including *Caulastraea* (phaceloid), *Favia* (plocoid), *Favites* (cerioid, lacking internal lobes), *Goniastrea* (cerioid-submeandroid, having internal lobes), *Hydnophora* (hydriophoroid), *Diploria* (meandroid, having a trabecular columella and septothecal walls), *Oulophyllia* (cerio-meandroid, lacking internal lobes and having a trabecular columella and parathecal walls), *Colpophyllia* (meandroid, having a trabecular columella, small internal lobes, lamellar linkages between centres, and a distinctive double-wall), *Platygyra* (meandroid, having a trabecular columella and small internal lobes), *Manicina* (meandroid, having a trabecular columella, small internal lobes, and large valleys), and *Leptoria* (meandroid, having a lamellar columella). Within the Montastraeinae, genera were distinguished based on the structure of the coenosteum or peritheca, including *Montastraea* (costate coenosteum), *Cyphastrea* (spinose coenosteum with imperforate corallite walls), and *Echinopora* (spinose coenosteum with perforate corallite walls).

Genera in the family Mussidae were also traditionally distinguished based on colony form, including *Mussismilia* (phaceloid with irregular or lacerate teeth), *Mussa* (phaceloid with regular teeth and trabecular linkage), *Lobophyllia* (phaceloid with regular teeth and lamellar linkage), *Acanthastrea* (cerioid), *Symphyllia* (meandroid with long series and continuous collines), *Mycetophyllia* (meandroid with long series and discontinuous collines), and *Isophyllia* (meandroid with short series). Similar features were used to distinguish genera within the families Merulinidae and Pectiniidae, including colony form, colony shape, series continuity, and structure of the coenosteum and collines.

In defining and coding phylogenetic characters for macromorphological features in the present study, we have modified the lists of characters and states pro-

posed by Beauvais *et al.* (1993) and Rosen & Darrell (2010), expanding upon previous phylogenetic analyses performed on fossil and living Caribbean brain corals by Johnson (1998) and on molecular clade XXI by Budd & Smith (2005). In particular, we focused on features used previously to distinguish genera, sub-families, and families in clades XV to XXI, and thus have not used characters such as 'A4. Attachment of skeleton', 'A5. Mode of attachment', or 'A1. Form of series' in Beauvais *et al.* (1993). A total of 19 macro-morphological characters (Table 3) was coded and analysed using the specimens listed in Appendix S1; 11 of the 19 characters were selected for use in morphological phylogenetic analyses. Character definitions and states are given in Table 3 and Appendices S2 and S3.

1. Corallite budding (increase) [characters 1, 2]
Character B1 (Budding or Increase – Budding) of Beauvais *et al.* (1993)

Corallite budding is the clonal addition of new corallites to form a 'colony'. It may occur within the calice of the parent (intracalicular) or outside of the calice of the parent (extracalicular), or it may involve a mixture of the two processes. Corals that lack corallite budding consist of a single 'solitary' corallite. Different colony shapes (branching, massive, platy) are a manifestation of different underlying patterns of budding (e.g. frequency, angle, direction), and are not included in the present analysis because of a lack of data on these measures and their correlation with budding pattern. Additional characters could be defined based on a rigorous analysis of colony shape.

Evaluation of budding in taxa with 'organically united' calices that lack corallite walls (the traditional family Pectiniidae) requires further examination; it is described by Wells (1956: F419) as 'intratentacular polystomodaal budding' and is coded herein as 'intracalicular budding'.

Note that we prefer the terms 'intracalicular'/'extracalicular' budding over the commonly used 'intratentacular'/'extratentacular' budding, because our observations are based on skeletal material. Intracalicular budding and extracalicular budding are treated as separate characters because some species have both [e.g. *Dipsastraea stelligera* (Dana, 1846)].

2. Circumoral budding and associated corallite polymorphism [character 3]
Character B4 (Budding or Increase – Polystomodaal budding) of Beauvais *et al.* (1993)

Circumoral budding is a special type of intracalicular budding, often associated with platy or explanate colony shapes, whereby concentric rows of corallites

(\geq three centres) surround a central parent corallite. The parent corallite may differ in size and shape from its surrounding offsets.

Circum-mural budding (hydnochoroid growth form) involves a row of corallites forming around a central wall structure ('monticule'), and is not analysed herein because it only occurs in *Hydnophora* (an autapomorphy).

3. Calical series (valleys) enclosed by corallite walls [character 4]
Character A11 (Corallum – Length of series) of Beauvais *et al.* (1993)

Intracalicular budding may involve the formation of corallite series, which may or may not be surrounded by corallite walls. If walls are present, they may enclose a single series or row of corallites (uniserial) or multiple series or rows of corallites (multiserial). The series may be short (fewer than four centres) or long (four or more centres). Colonies that lack distinct corallite walls are termed 'organically united' following Vaughan & Wells (1943).

This character corresponds with '3. Frequency of wall development' in Johnson (1998), and with '2. Number of centers per series' in Budd & Smith (2005). Johnson (1998) and Budd & Smith (2005) also included 'Meandroid series sinuosity' and 'Symmetry of bud geometry' in their phylogenetic analyses, but these characters are primarily effective at distinguishing free-living Neogene Caribbean corals and therefore not considered here.

4. Coenosteum (peritheca) [characters 5, 6]
Character E1 (Peritheca – Peritheca) of Beauvais *et al.* (1993)
Character E3 (Peritheca – Width of peritheca) of Beauvais *et al.* (1993)
Character A6 (Corallum – Arrangement of calices) of Beauvais *et al.* (1993)

Coenosteum is defined as skeletal material between corallites. It may be constructed primarily by radially arranged vertical partitions called costae (costate), by spines (spinose), or by dissepimental tissue (vesicular); or it may be solid. Dissepiments that form within the coenosteum are referred to as 'exotheca'. The amount of coenosteum varies from limited (including double wall), moderate (the distance between adjacent corallites \leq corallite diameter), to extensive (the distance between adjacent corallites \geq corallite diameter); or it may be absent altogether. Coenosteum is an important component of four terms commonly used to describe colony form:

Ceriod: corallite walls of adjacent corallites juxtaposed; coenosteum absent.

Plocoid: corallite walls of adjacent corallites separated by coenosteum.

Table 3. List of characters and states

Character ID no.	Type	Character	Number of states	State names	Model	Basal state	Character transitions	CI	RI	Included in phylogenetic analysis	Comments
1	Macro	Intracalicular budding	Two	0 = absent, 1 = present	Unordered	Absent	Three gains, six losses	0.111	0.273	No	Transition to 0 occurs early in group evolution; losses within clades XVII, XIX, and XXI; in XIX and XXI losses are associated with solitary forms
2	Macro	Extracalicular budding	Two	0 = absent, 1 = present	Unordered	Present	No gains, seven losses	0.143	0.667	Yes	Losses at clade XIX and XXI nodes; and 5 times near branch tips within clade XVII
3	Macro	Polymorphism	Two	0 = absent, 1 = present	Unordered	Absent	Three gains, no losses	0.333	0.714	Yes	Gains near branch tips within clades XVII, XIX, and XXI
4	Macro	Corallite integration	Three	0 = discrete (1–3 centres), 1 = uni- or multiserial, 2 = organically united	Ordered	Discrete	Eight gains for corallite series, two gains for no-walls, three losses	0.133	0.629	Yes	Gains occur near branch tips within clades XVII, XIX, XXI
5	Macro	Coenosteum structure	Four	0 = absent (fused walls or void), 1 = costate, 2 = spinose, 3 = vesicular or solid	Unordered	Costate	One gain for spinose, one gain for solid, nine losses	0.273	0.619	Yes	Transitions are near branch tips; gains are within clade XVII; losses are within clades XVII, XIX, and XXI
6	Macro	Coenosteum amount	Four	0 = absent, 1 = limited (includes double-wall), 2 = medium (< corallite diameter), 3 = extensive (> corallite diameter)	Ordered	Medium	Six gains, eight losses	0.137	0.627	No	Transition from 3 to 2 is early in group evolution; gains and losses occur within clades XVII, XIX, and XXI
7	Macro	Calice or valley width	Three	0 = small (< 4 mm), 1 = medium (4–15 mm), 2 = large (> 15 mm)	Ordered	Medium	Eight gains, nine losses	0.118	0.423	No	Transitions occur within all three major clades; gains and losses are within XVII, XIX, and XXI
8	Macro	Calice relief	Three	0 = low (< 3 mm), 1 = medium (3–6 mm), 2 = high (> 6 mm)	Ordered	Medium	Nine gains, 11 losses	0.100	0.561	Yes	Transitions occur within all three major clades; gains and losses are within XVII, XIX, and XXI; all Mussinae have high relief
9	Macro	Continuity of costosepta	Two	0 = mostly not confluent, 1 = mostly confluent	Ordered	Not confluent	Five gains, one loss	0.167	0.667	No	Gains and losses occur within clade XVII, only gains occur within XIX and XXI; confluency distinguishes subclades of traditional merulinids and pectinids
10	Macro	Number of septa	Three	0 = < 3 cycles (< 24), 1 = 3 cycles (24–36), 2 = > 4 cycles (> 36)	Ordered	Three cycles	Nine gains, 14 losses	0.087	0.400	No	With the exception of <i>M. caevrnosa</i> , transitions occur within clades; gains and losses occur within all three major clades
11	Macro	Free septa	Three	0 = absent, 1 = irregular, 2 = regular	Ordered	Irregular	Seven gains, six losses	0.154	0.154	No	Most taxa are irregular; gains and losses are in clades XVII and XXI; one loss is in XIX
12	Macro	Septa spacing (per 5 mm)	Three	0 = < 6, 1 = 6–12, 2 = > 12	Ordered	Six to 12	Nine gains, six losses	0.133	0.649	Yes	Loss at XIX node and Mussinae node; losses and gains within XVII and XXI, and gains within XIX
13	Macro	Relative costosepta thickness or height (c1 -vs- all others, or c1&c2 -vs- c3)	Three	0 = equal, 1 = slightly unequal, 2 = unequal	Ordered	Unequal	Eight gains, seven losses	0.133	0.519	No	Transition from 2 to 0 occurs early in group evolution; gains and losses within clade XVII, gains only within XIX and XXI

14	Macro	Corallite centre linkage	Three	0 = absent, 1 = continuous, 2 = discontinuous	Unordered	Absent	Two gains for discontinuous, four gains for continuous, four losses	0.200	0.680	Yes	Transition to discontinuous occurs below node XIX, transition to continuous occurs at node XVII; mixed results occur within clade XXI; both gains and losses occur within XVII
15	Macro	Columella structure	Three	0 = lamellar, 2 = trabecular, compact (1–3 threads); 2 = trabecular, spongy (>3 threads)	Unordered	Trabecular, spongy	Four gains, ten losses	0.133	0.458	No	Transitions occur within clades; both gains and losses are in XVII, only losses are in XIX and XXI; lamellar is an autapomorphy
16	Macro	Columella size (relative to calice width)	Two	0 = < 1/4, 1 = > 1/4	Ordered	> 1/4	Nine gains, one loss	0.100	0.526	Yes	One loss occurs early in group evolution, followed by gains within XVII, XIX, and XXI
18	Macro	Epitheca	Three	0 = absent, 1 = reduced, 2 = well developed	Ordered	Well developed	Three gains, seven losses	0.167	0.792	Yes	Transition to 1 at nodes XIX and/or XXI, then a gain within clade XXI and a loss within XIX; multiple losses within XVII
19	Macro	Endotheca	Three	0 = sparse, 1 = low-moderate/tabular, 2 = abundant/vesicular	Ordered	Low-moderate	Five gains, four losses	0.222	0.781	Yes	Transition to 2 at node XXI (and back to 1 in the <i>Favia</i> + <i>Diploria</i> + <i>Pseudodiploria</i> + Manicina subgroup) and also within clades XVII and XIX; transitions to 0 occur within XVII
21	Macro	Internal lobes	Four	0 = absent, 1 = weak paliform (one axis), 2 = well-developed paliform (one axis), 3 = septal (multiaxial fan)	Unordered	Absent	13 gains, two losses	0.158	0.529	Yes	Septal and paliform lobes arise at least five times each; gains occur within clades XVII, XIX, and XXI
35	Micro-m	Tooth base (mid-septum)	Three	0 = circular, 1 = elliptical-parallel, 2 = elliptical-perpendicular	Unordered	Elliptical-parallel	Two gains, three losses	0.400	0.864	Yes	Circular bases arise within clades XIX and XXI and at node XVII; transitions at nodes XIX and XXI are equivocal; elliptical-perpendicular bases arise at the Favinae node within XXI
38	Micro-m	Tooth tips (mid-septum)	Four	0 = regular pointed, 1 = irregular lobate, 2 = irregular jagged, 3 = irregular bulbous	Unordered	Regular pointed	Three gains, no losses	1.000	1.000	Yes	Transition to 1 at XIX node; transition to 2 at VII node; transition to 3 within clade XIX
39	Micro-m	Tooth height (S1) [Wells]	Three	0 = low (< 0.3 mm), 1 = medium (0.3–0.6 mm), 2 = high (> 0.6 mm)	Ordered	Medium	Seven gains, four losses	0.182	0.791	Yes	Transition to 2 at XIX node; no transitions at XVII and XXI nodes; gains and losses occur within all three major clades; low teeth distinguish the <i>Favia</i> + <i>Diploria</i> + <i>Pseudodiploria</i> + <i>Manicina</i> + <i>Colpophyllia</i> group within XXI
40	Micro-m	Tooth spacing (S1) [Wells]	Four	0 = narrow (< 0.3 mm), 1 = medium (0.3–1 mm), 2 = wide (1–2 mm), 3 = very wide (> 2 mm)	Ordered	Medium	Nine gains, seven losses	0.188	0.698	Yes	Transitions at nodes XVII and XIX are equivocal; no transitions at node XXI but transition to wide at the Mussinae node; gains and losses occur within all three major clades
43	Micro-m	Granule shape and distribution	Five	0 = strong, scattered; 1 = strong, aligned; 2 = weak, enveloped by thickening deposits; 3 = weak, aligned; 4 = irregular	Unordered	Strong, scattered	Seven gains, two losses	0.444	0.872	Yes	Transitions occur below nodes XVII and XIX and within clades XVII and XIX; transition at node XXI is equivocal; two subclades within XXI have different states

Table 3. *Continued*

Character ID no.	Type	Character	Number of states	State names	Model	Basal state	Character transitions	CI	RI	Included in phylogenetic analysis	Comments
44	Micro-m	Interarea	Three	0 = horizontal bands, 1 = smooth, 2 = vertical palisade	Ordered	Smooth	Six gains, four losses	0.200	0.784	Yes	Transition to 0 at node XXI and to 2 at node XIX; no transition at node XVII; reversals within clades XIX and XXI; both gains and losses with clade XVII
45	Micro-m	Cs3/es1 tooth shape	Two	0 = equal, 1 = unequal	Unordered	Equal	One gain, one loss	0.500	0.900	Yes	Gain at node XIX and loss within clade XIX
47	Micro-m	Wall/septum tooth size	Two	0 = equal, 1 = unequal	Unordered	Equal	One gain, two losses	0.333	0.714	Yes	Gain and losses occur within clade XIX
22	Micro-s	Synapiculotheca	Two	0 = absent, 1 = present	Unordered	Present	One loss	1.000	0.000	Yes	Present in <i>Diploastrea</i> but not in any other taxa, therefore uninformative
23	Micro-s	Septotheca	Three	0 = absent, 1 = partial, 2 = well developed (= septothecal)	Ordered	Partial	Six gains, one loss	0.200	0.765	Yes	Transition to 0 early in group evolution; followed gains within all three clades XVII, XIX, XXI
24	Micro-s	Abortive septa	Two	0 = absent, 1 = present	Unordered	Absent	Four gains, no losses	0.250	0.571	No	Gains at <i>M. cavernosa</i> node and within clade XVII
25	Micro-s	Trabeculotheca	Three	0 = absent, 1 = irregular, 2 = well developed (= trabeculothecal)	Ordered	Absent	13 gains, two losses	0.087	0.475	No	Gains and losses within clades XVII and XXI; no transitions in clade XIX; transitions at the two <i>Acanthastrea</i> nodes
26	Micro-s	Paratheca	Three	0 = absent, 1 = irregular, 2 = well developed (= parathecal)	Ordered	Absent	13 gains, two losses	0.105	0.679	Yes	Transitions to parathecal at XIX and XXI nodes and within XVII; loss at node for <i>Favia + Diploria + Manicina + Pseudodiploria</i> subgroup
28	Micro-s	Thickening deposits/structure	Three	0 = micro-fibrous, 1 = fibrous, 2 = extensive, forming concentric rings	Ordered	Fibrous	Three gains, one loss	0.500	0.846	Yes	Gains are associated with XIX and the two <i>Acanthastrea</i> clades; one loss is within XVII
29	Micro-s	Costoseptum centre clusters	Three	0 = not distinct, 1 = weak, 2 = strong	Ordered	Weak	Five gains, one loss	0.333	0.833	Yes	Gains occur within clades XIX and XXI; the loss is within XVII
30	Micro-s	Distance between costoseptum clusters	Three	0 = 0.6–1.2 mm, 1 = 0.6–1.2 mm, 2 > 1.2 mm	Ordered	0.6–1.2 mm	Four gains, three losses	0.286	0.865	Yes	Losses occur at the XVII, <i>M. cavernosa</i> , and Favinae nodes; gains are at the XIX node and within XXI
31	Micro-s	Costoseptum medial lines	Three	0 = absent or weak, 1 = moderate, 2 = strong	Ordered	Absent or weak	Eight gains, four losses	0.125	0.517	No	Transition at the XXI node; gains and losses within clades XVII and XIX, losses within XXI
33	Micro-s	Transverse crosses	Three	0 = absent, 1 = centre clusters, 2 = carinae	Ordered	Absent	Six gains, two losses	0.200	0.826	Yes	Transition at the XXI node; gains and losses within clade XXI; losses within clades XVII and XIX
34	Micro-s	Columella centres	Two	0 = clustered, 1 = aligned	Unordered	Absent	Nine gains, no losses	0.111	0.652	Yes	Gains occur within clades XXI, XIX, and XVII

CI, consistency index; RI, retention index.

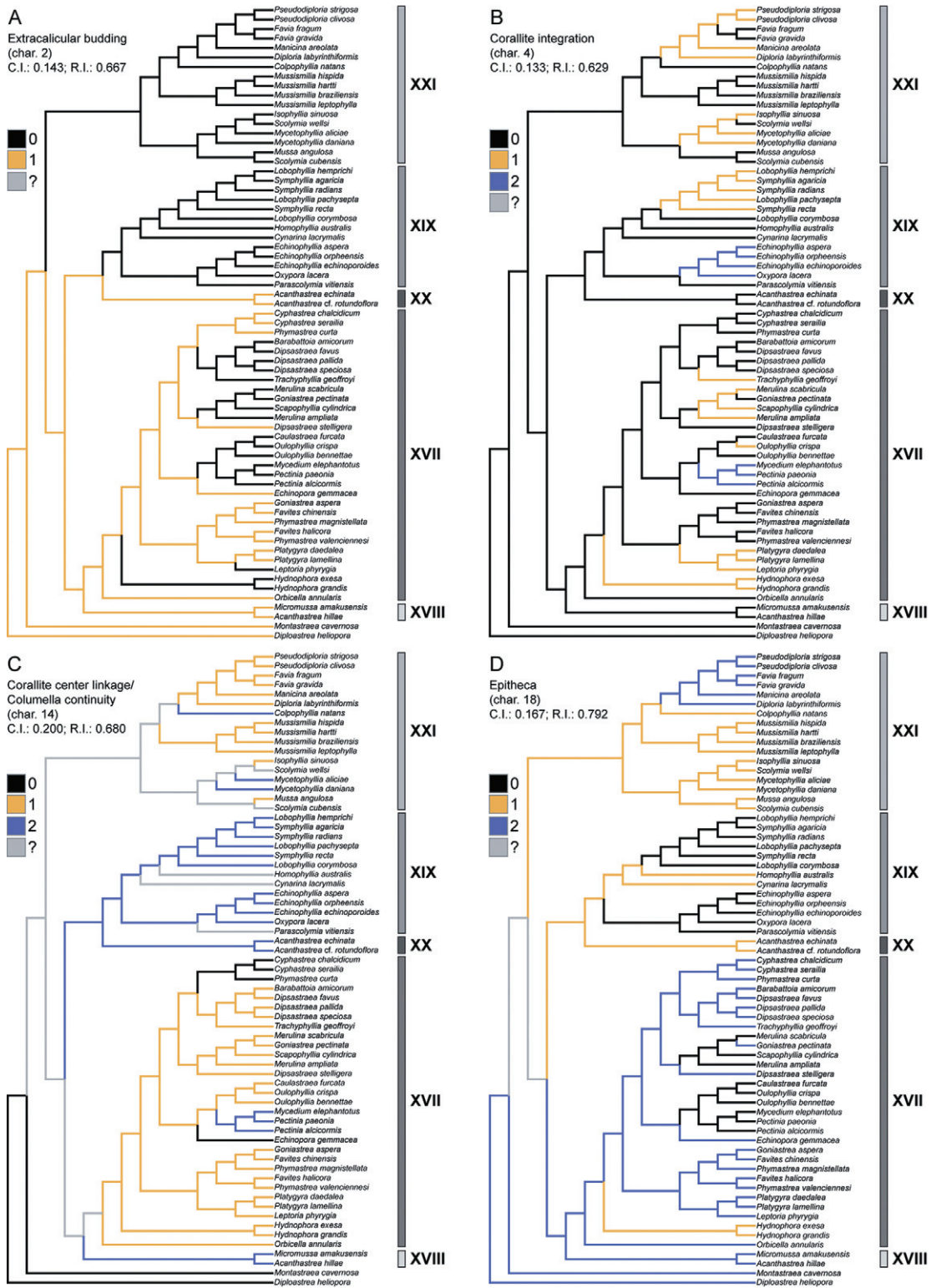


Figure 2. Phylogenetic character mapping of representative macromorphological characters on a subset (clades XV to XXI) of the molecular tree of Fukami *et al.* (2008). Clade XV is composed of *Diploastrea heliophora*, and clade XVI is composed of *Montastraea cavernosa*; clades XVII to XXI are indicated. Ancestral states have been reconstructed using parsimony and calculated using MESQUITE v. 2.72 (Maddison & Maddison, 2009); equivocal branches are in grey. Character states are given in Table 3. A, extracalicular budding; B, corallite integration; C, corallite centre linkage; D, epitheca. Additional macromorphological character maps are in Appendix S5.

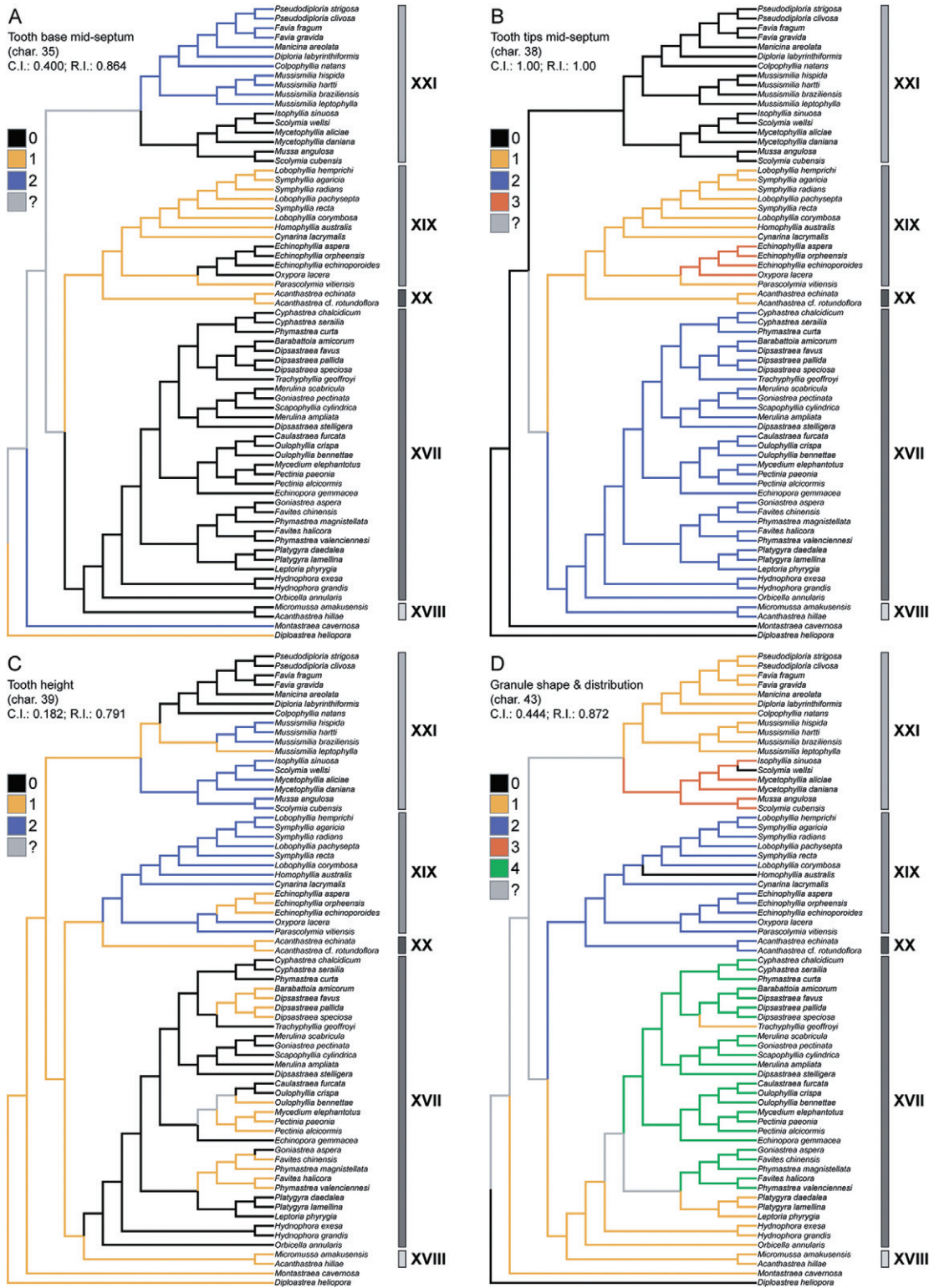


Figure 3. Phylogenetic character mapping of representative micromorphological characters on a subset (clades XV to XXI) of the molecular tree of Fukami *et al.* (2008). Clade XV is composed of *Diploastrea heliopora*, and clade XVI is composed of *Montastraea cavernosa*; clades XVII to XXI are indicated. Ancestral states have been reconstructed using parsimony and calculated using MESQUITE v. 2.72 (Maddison & Maddison, 2009); equivocal branches are indicated in grey. Character states are given in Table 3. A, tooth base; B, tooth tips; C, tooth height; D, granule shape and distribution. Additional micromorphological character maps are in Appendix S6.

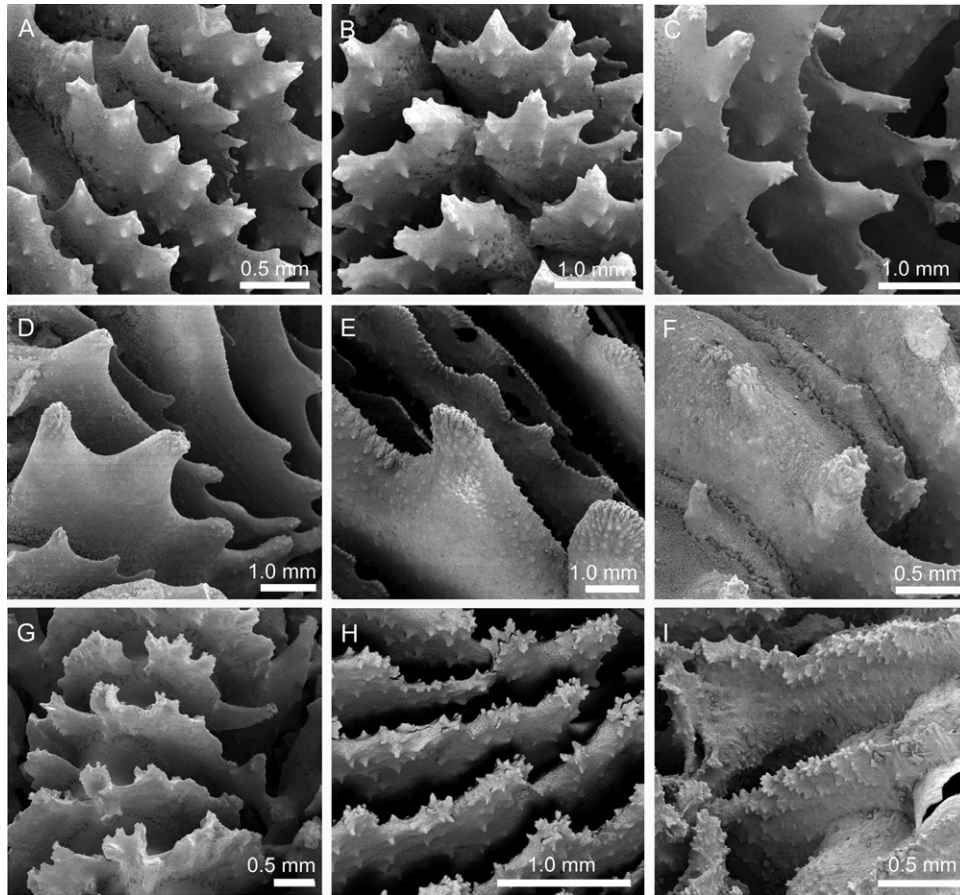


Figure 4. Micromorphological differences amongst the three major clades (XXI, XIX, XVII). The vertically oriented plates shown in each photo are septa. The projections along their upper margins are teeth, and those across their lateral faces are granules. Clade XXI (A–C) is distinguished by regular blocky teeth with pointed tips, and aligned granules. Clade XIX (D–F) is distinguished by irregular lobate or bulbous teeth with elliptical tooth bases, and rounded granules enveloped by extensive thickening deposits. Clade XVII (G–I) is distinguished by irregular multi-axial teeth with circular bases, and irregular scattered granules. A, XXI, *Pseudodiploria strigosa*, FA1062, SUI122813, Bocas del Toro, Panama, Atlantic. B, XXI, *Mussismilia braziliensis*, YPM9104, Abrolhos Archipelago, Brazil, Atlantic. C, XXI, *Isophyllia sinuosa*, FA1014, SUI102757, Bocas del Toro, Panama, Atlantic. D, XIX, *Lobophyllia pachysepta*, USNM45515, Murray Island, Australia, Indo-Pacific. E, XIX, *Parascolymia vitiensis*, USNM91254, Great Palm Island, Australia, Indo-Pacific. F, XIX, *Echinophyllia echinoporoides*, FA1023, UF2103, Palau, Indo-Pacific. G, XVII, *Merulina ampliata*, FA1033, USNM100519, Madagascar, Indo-Pacific. H, XVII, *Favites halicora*, USNM91305, Malaysia, Redang Island, Indo-Pacific. I, XVII, *Hydnophora exesa*, FA1068, UF2143, Palau, Indo-Pacific.

Phaceloid: corallites walls of adjacent corallites separated by void space; each corallite forms a branch.

Meandroid: corallites are arranged in series consisting of \geq three centres; series may or may not be separated by coenosteum.

These four terms are not used in the present analyses because they confound two different aspects of colony growth: coenosteum development and series length.

Characters corresponding with characters 5 and 6 are defined in Johnson (1998) as:

- ‘10. Coenosteum’ [states = absent; present with adjacent walls; present and narrow (less than meandroid valley width); present with medium width (equal to meandroid valley width); present and wide (greater than valley width)]
- ‘22. Double or single wall’ [states = single; double]

and in Budd & Smith (2005) as:

- ‘1. Corallite integration’ [states = solitary; phaceloid; flabelloid; meandroid (uniserial); meandroid (multiserial); meandroid (no walls)]

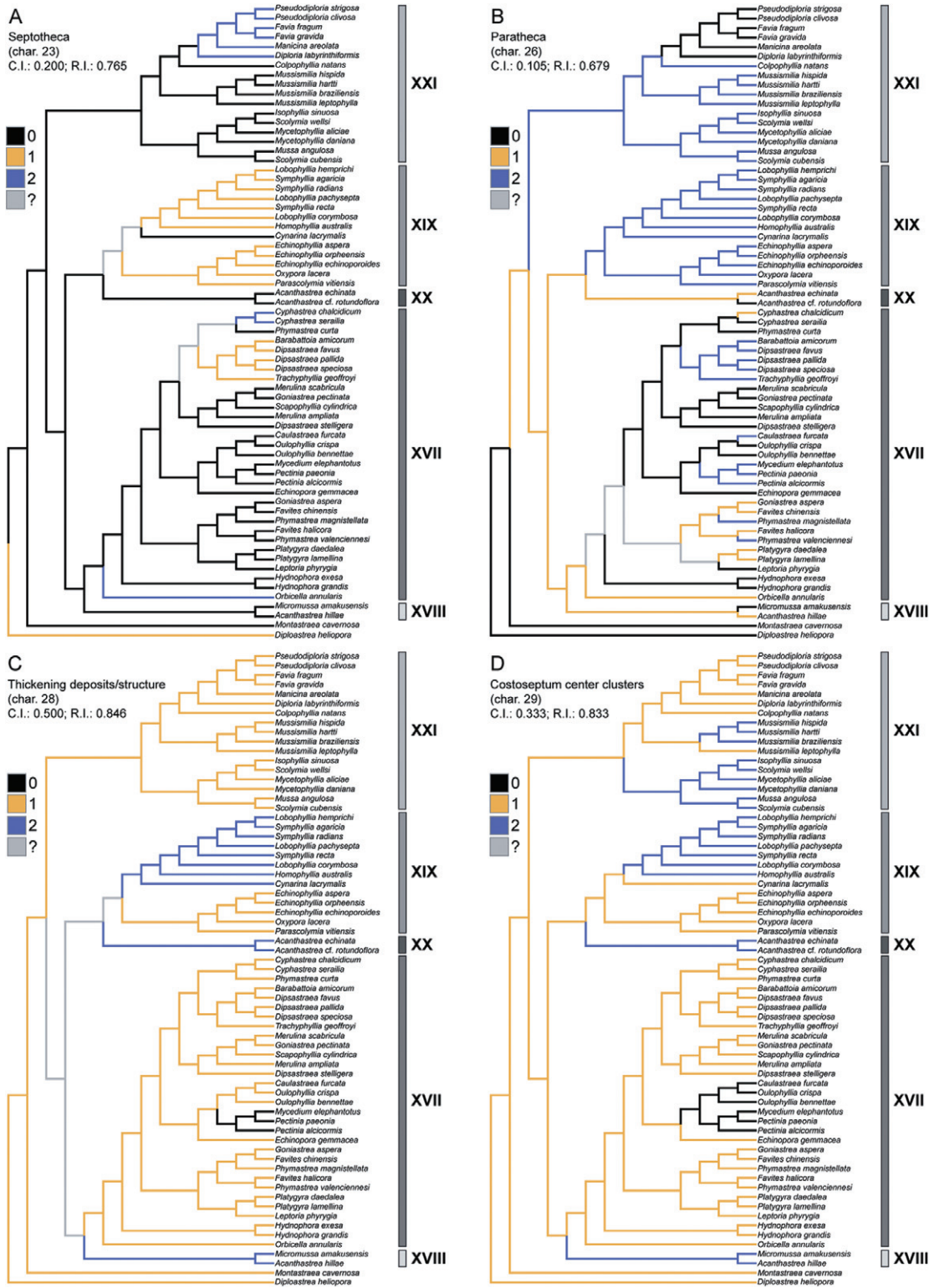


Figure 5. Phylogenetic character mapping of representative microstructural characters on a subset (clades XV to XXI) of the molecular tree of Fukami *et al.* (2008). Clade XV is composed of *Diploastrea heliopora*, and clade XVI is composed of *Montastraea cavernosa*; clades XVII to XXI are indicated. Ancestral states have been reconstructed using parsimony and calculated using MESQUITE v. 2.72 (Maddison & Maddison, 2009); equivocal branches are indicated in grey. Character states are given in Table 3. A, septotheca; B, paratheca; C, thickening deposits/structure; D, costoseptum centre clusters. Additional microstructural character maps are in Appendix S7.

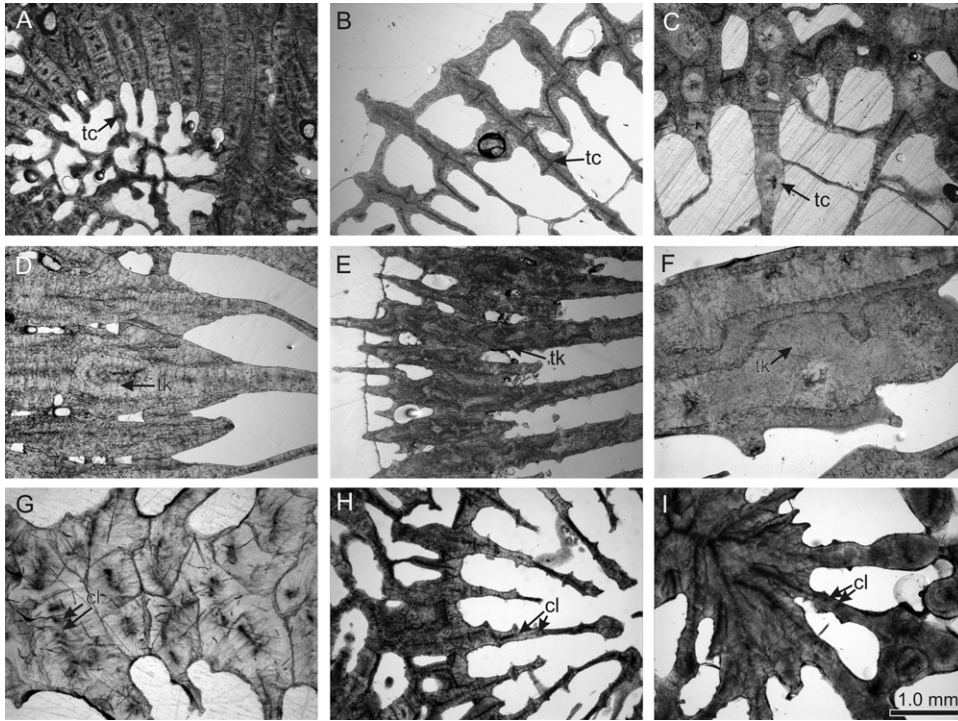


Figure 6. Microstructural differences amongst the three major clades (XXI, XIX, XVII). All photos are of transverse thin sections at the same scale. The radiating linear plates are costosepta, which are connected in different ways to form corallite walls. Clade XXI (A–C) has costoseptal medial lines that are crossed by transverse structures (tc) such as carinae or clusters of calcification centres; corallite walls are predominantly either septothecal (*Favia* + *Diploria* + *Pseudodiploria* + *Manicina* subgroup) or parathecal. Clade XIX (D–F) is distinguished by well-developed thickening deposits (tk) and parathecal corallite walls, and widely spaced clusters of calcification centres. Clade XVII (G–H) is distinguished by small, closely spaced clusters of calcification centres (cl); wall structures range the gamut, and appear to be diagnostic of genus-level subclades. A, XXI, *Favia fragum*, FA1065, SUI122816, Bocas del Toro, Panama, Atlantic. B, XXI, *Mussismilia hartti*, YPM4516, Maria Farinha, Brazil, Atlantic. C, XXI, *Isophyllia rigida*, FA1009, SUI102752, Bocas del Toro, Panama, Atlantic. D, XIX, *Lobophyllia pachysepta*, USNM45515, Murray Island, Australia, Indo-Pacific. E, XIX, *Homophyllia australis*, USNM85709, Blyth Island, Australia, Indo-Pacific. F, XIX, *Oxypora lacera*, USNM93809, Madang, Papua New Guinea, Indo-Pacific. G, XVII, *Merulina ampliata*, UF2051, Palau, Indo-Pacific. H, XVII, *Favites halicora*, USNM90627, Philippines, Indo-Pacific. I, XVII, *Hydnophora exesa*, USNM83232, Marshall Islands, Indo-Pacific.

- ‘5. Coenosteum development’ [states = void (phaceloid); fused walls (cerioid); narrow (< calice or valley width); wide (\geq calice or valley width)]
 - ‘21. Double or single wall’ [states = single; sometimes double; double]
5. Calice (or series) width and height [characters 7, 8, respectively]
 Character C8 (Calice – Calicular diameter) of Beauvais *et al.* (1993)
 Character C5 (Calice – Calicular platform) of Beauvais *et al.* (1993)
 Character A6 (Corallum – Colline height) of Beauvais *et al.* (1993)

Calice width is a linear measure extending laterally across the calice centre from the inner edge of the wall on one side of the calice, to the inner edge of the wall on the other. Calice height is a linear measure

extending vertically from the base of the calice to the uppermost septal margin, including the colline when present. Both characters are subdivided into three increments. These two characters are highly variable within species, and more specimens need to be characterized in order to assess properly the variation, especially within clade XVII.

Characters corresponding with characters 7 and 8 are defined as ‘6. Calice relief’ and ‘7. Calice or valley width’ in Johnson (1998); and as ‘8. Calice relief’ and ‘9. Calice or valley width’ in Budd & Smith (2005).

6. Septa: number, length, spacing [characters 10, 11, 12, respectively]
 Character F11 (Radial elements – Number of cycles of radial elements in adult calices) of Beauvais *et al.* (1993)

Character F13 (Radial elements – Density of radial elements in 10 mm) of Beauvais *et al.* (1993)

Character F16 (Radial elements – Relationship of radial elements to each other) of Beauvais *et al.* (1993)

Septa are the radially arranged vertical partitions (plates) within a calice. In scleractinians, they are typically arranged in cycles of six: six first cycle, six second cycle, 12 third cycle, 24 fourth cycle, and so on (abbreviated 6/6/12/24). Primary and secondary cycle septa that extend to the columella are considered to be ‘major’; higher septal cycles are ‘minor’. Septa whose outer margins do not fuse with the columella or other septa are termed ‘free’. Septal spacing is measured using the number of septa per 5 mm, and coded as $0 \leq 6$, $1 = 6-12$, $2 \geq 12$.

Characters 10, 11, and 12 correspond with ‘13. Number of septal cycles’ and ‘14. Septal spacing’ in Johnson (1998); and with ‘12. Number of septal cycles’, ‘13. Septal spacing (per 5 mm)’ and ‘14. Relative septa length’ in Budd & Smith (2005).

7. Relative development and confluence of costae [characters 9, 13, respectively]

Character F3 (Radial elements – Confluence of radial elements) of Beauvais *et al.* (1993)

Character D4 (External surface of the corallum – Costae arrangement) of Beauvais *et al.* (1993)

Costae are the radially arranged vertical partitions (plates) outside of the corallite wall, and are usually extensions of septa. They are arranged in cycles similar to septa. Major and minor cycle costae may or may not be equal in thickness and height. Costae may or may not continue from one corallite to another. Confluence of costae is not applicable (‘na’) in solitary and phaceloid forms.

Characters 9 and 13 correspond with ‘12. Continuity of costae’ and ‘9. Relative costae thickness’ in Johnson (1998); and with ‘11. Continuity of costae’ in Budd & Smith (2005). Johnson (1998) included characters for both relative costae and septa thickness whereas Budd & Smith (2005) only included a character for relative septa thickness. Here we use only relative costae thickness.

8. Columella size, structure, and centre linkage [characters 14, 15, 16, respectively]

Character G2 (Axial structure – Essential columella) of Beauvais *et al.* (1993)

Character G4 (Axial structure – Parietal or trabecular columella) of Beauvais *et al.* (1993)

The columella is the vertical axial structure within a corallite. In clades XV–XXI, it is either formed by interwoven threads (‘trabecular’) that extend from the major septa, or by a plate (‘lamellar’). Trabecular

columellae formed by a few threads are herein termed ‘compact’; those formed by > three threads, ‘spongy’. Centres of adjacent corallites within series may be continuous and linked by interwoven threads (‘trabecular linkage’), or discontinuous and linked by septal plates (‘lamellar linkage’).

Characters 14, 15, and 16 correspond with ‘Columella width’ and ‘Columella continuity’ in both Johnson (1998) and Budd & Smith (2005).

9. Development of epitheca and endotheca [characters 18, 19, respectively]

Character D1 (External surface of the corallum – Epitheca) of Beauvais *et al.* (1993)

Character H3 (Endotheca – Form of dissepiments) of Beauvais *et al.* (1993)

The endotheca is formed by dissepiments (horizontal plates) within the corallite, which support the base of the polyp. The dissepiments may be long and flat, extending across the whole corallite, termed ‘tabular’; or they may be short, curved, and overlapping, termed ‘vesicular’.

The epitheca, by contrast, is a thin, external sheath surrounding the lower part of the colony.

Characters 18 and 19 correspond with ‘Epitheca’ and ‘Endothecal dissepiments’ in Johnson (1998) and Budd & Smith (2005). Johnson (1998) also included a character for exothecal dissepiments, which is similar to our definition of coenosteum structure and therefore not included here.

10. Development of internal lobes [character 21]

Character F35 (Radial elements – Paliform teeth or lobes) of Beauvais *et al.* (1993)

Paliform lobes are enlarged septal teeth (single primary calcification axis) that form a ‘crown’ around the columella. They are not the result of septal substitution as is the case with ‘pali’. If present, they vary in height, thickness, and number.

Septal lobes occur along the distal edges of septa and are formed by an additional fan system of centres of rapid accretion (multiple primary calcification axes).

Paliform lobes and septal lobes are separate binary characters in Johnson (1998), and separate three-state characters in Budd & Smith (2005).

Characters excluded from the present study

Macromorphological characters that were analysed by Johnson (1998; 22 macromorphological + one microstructural = 23 characters, 62 macromorphological + two microstructural = 64 states) but were excluded in the present study are:

1. Attachment of skeleton (informative in analyses of free-living corals)

2. Meandroid series sinuosity (informative in analyses of meandroid corals)
4. Symmetry of bud geometry (informative in analyses of free-living corals)
11. Exothecal dissepiments (treated here as coenostem structure, character 5)
15. Equality of septal thickness (correlated with relative costoseptum thickness, character 13)
23. Size of colony (informative in analyses of free-living corals)

Macromorphological characters that were analysed by Budd & Smith (2005; 20 macromorphological + one microstructural + four micromorphological = 25 characters; 72 macromorphological + three microstructural + 11 micromorphological = 86 states) but were excluded in the present study are:

3. Symmetry of bud geometry (informative in analyses of free-living corals)
4. Meandroid series sinuosity (informative in analyses of meandroid corals)
6. Attachment of skeleton (informative in analyses of free-living corals)
10. Relative septa thickness (correlated with relative costoseptum thickness, character 13)

Micromorphology

Micromorphology focuses on the 3D geometry of teeth (dentation) along the upper margins of the costosepta and columella (the septal growing edge), as well as on granulation on septal faces and the sides of teeth. Teeth and granules are surficial projections that reflect the underlying calcification axes that build the internal structure and framework for the costoseptum. In the classification system of Vaughan & Wells (1943) and Wells (1956), families within the suborder Faviina are distinguished primarily on the basis of the size, shape, and internal structure of the septal teeth. The family Faviidae is characterized as having septa 'formed by 1 or 2 fan systems of simple (compound in some later forms) trabeculae, more or less regularly dentate marginally' (Wells, 1956: 400). The family Mussidae is characterized as having septa composed of 'several fan systems of large simple trabeculae, each fan system producing a lobulate dentation' (Wells, 1956: 416). The family Merulinidae is characterized as having 'septal teeth of one fan system of compound trabeculae, regularly dentate at first, later with scattered, spinose, ragged, very irregular dentations' (Wells, 1956: 416). The family Pectiniidae is characterized as having 'septal teeth irregularly dentate, formed by one fan system of compound trabeculae... or dentations may be almost completely reduced' (Wells, 1956: 419).

Wells' (1956) characterization of the structure of septal teeth assumes the 'trabecular organization' of

the septa (Ogilvie, 1897) and 'sperulitic crystallization' (Bryan & Hill, 1941). According to Wells (1956), a septum consists of a palisade of trabeculae, which he defined as being vertical spines, rods, or pillars composed of stacked series of calcification centres surrounded by radiating fibres. So-called 'simple' trabeculae consist of a single series of fibres; 'compound' trabeculae consist of multiple bundles of fibres. Both kinds of trabeculae are arranged in fan systems, one or more of which may form a septum. Owing to recent advances in microscopy, the concept of 'trabeculae' has recently been challenged by Cuif, Dauphin & Gautret (1998), Cuif & Dauphin (2005), Cuif & Perrin (1999), Cuif *et al.* (2003), and Stolarski (2003). These authors describe more complex biomineralization processes and features in their characterization of the septal teeth. Individual teeth are constructed by multiple calcification centres, which are variably arranged and supported by fibrous thickening deposits.

In view of these new findings, we have developed a new set of characters, based on the shape and orientation of septal teeth, the shape and distribution of granules on septal faces, and the structure of the interarea of teeth (Budd & Stolarski, 2009, 2011). We compared the size and shape of teeth in different septal cycles, and at different positions within the calice, including the columella. The following micromorphological features were coded as eight characters and analysed (Table 3):

1. Tooth shape at base and tip [characters 35, 38, respectively]
Character F29 (Radial elements – Distal margin – Shape of dentations or granules) of Beauvais *et al.* (1993)
Character F28 (Radial elements – Distal margin – Regularity of dentations or granules) of Beauvais *et al.* (1993)

Tooth shape was observed in the middle of a primary septum (the distal part), roughly half-way between the corallite wall and the columella. It consists of two characters, one involving the shape of the base of the tooth (Budd & Stolarski, 2009) and the other involving the shape of the tip of the tooth (Budd & Stolarski, 2011). The outline of the base of the tooth is either circular or elliptical, and orientated parallel or transverse to the septum. Teeth with circular bases are spine-like or conical in shape. Teeth with elliptical bases range from triangular to lobate when orientated parallel to the septum, and they range from tricornate or paddle-shaped (*sensu* Cuif & Perrin, 1999, and Cuif *et al.*, 2003) when orientated transverse to the septum. Tooth tips may be regular or irregular; and pointed, lobate, jagged, or bulbous. Irregular, jagged teeth have been termed 'lacerate' or even 'hirsute'.

In morphological phylogenetic analyses of the family Fungiidae, Hoeksema (1989) used binary characters similarly to distinguish simple, angular, lacerate, tapering, lobate, and club-shaped septal teeth. In morphological phylogenetic analyses of the genus *Acropora*, Wallace (1999) coded spinules on the upper surface of the coenosteum as absent, single-pointed, blunt or irregular, forked, elaborate, meandroid elaborate, papillae elaborate, or laterally flattened.

2. Tooth size [character 39]

Character F27 (Radial elements – Distal margin – Size of dentations or granules) of Beauvais *et al.* (1993)

One important diagnostic character in the Vaughan & Wells (1943) and Wells (1956) classification scheme is the size of the septal teeth. Traditional Faviidae have teeth that are intermediate in size and traditional Mussidae have large teeth. Tooth height was measured in the middle of a primary septum, roughly half-way between the corallite wall and the columella; and coded as low (< 0.3 mm), medium (0.3–0.6 mm), or high (> 0.6 mm).

3. Tooth distribution and interarea [characters 40, 44, respectively]

Not included in Beauvais *et al.* (1993)

Also important in the Vaughan & Wells (1943) and Wells (1956) classification scheme is the spacing between septal teeth; traditional Faviidae have narrow spacing and traditional Mussidae have wide spacing. Tooth spacing was measured in the middle of a primary septum, roughly half-way between the corallite wall and the columella, and coded as four states (Table 3).

In addition to spacing, we also characterized the structure of the area between teeth ('interarea'), which may be formed by horizontal bands or vertical palisades, or may lack distinctive layering ('smooth').

4. Granule size, shape and distribution [character 43]

Character F23 (Radial elements – Lateral faces – Size of ornamentation) of Beauvais *et al.* (1993)

Character F24 (Radial elements – Lateral faces – Density of ornamentation) of Beauvais *et al.* (1993)

Character F25 (Radial elements – Lateral faces – Arrangement of ornamentation) of Beauvais *et al.* (1993)

Granules are small projections on a septal face or a septal tooth, which are formed by secondary calcification axes. They vary in size and spacing, and their tips may be pointed or rounded. Granules may be evenly scattered across the surface or arranged in lines. Our observations involved five states (Table 3) and were from the middle of a primary septum, roughly half-way between the corallite wall and the

columella. We combined size, shape, and distribution into one character in order to facilitate recognition of synapomorphies.

In morphological phylogenetic analyses of the family Fungiidae, Hoeksema (1989) used binary characters to distinguish parallel, radiating, and irregular septal granulation.

5. Septal cycle differences [character 45]

Character F30 (Radial elements – Distal margin – Differentiation in different cycles) of Beauvais *et al.* (1993)

Differences in shape and size of teeth between primary and tertiary septa were assessed as equal or unequal.

6. Variation within individual septa [character 47]

Not included in Beauvais *et al.* (1993)

Differences in shape and size of teeth between the corallite wall and middle of a primary septum were assessed as equal or unequal.

Characters excluded from the present study

Micromorphological characters were not included in Johnson (1998). In Budd & Smith (2005), four micromorphological characters (11 states) were analysed: height of septal teeth (short, medium, tall); spacing of septal teeth (narrow, wide); shape of septal teeth (paddle, thick/blunt, spine); ornamentation (weak, medium, strong). In the present study, these characters have been further expanded into eight characters and 26 states (Table 3), following Budd & Stolarski (2009, 2011).

Microstructure

Microstructure involves the internal structure (i.e. the arrangement of centres of rapid accretion and fibres) within the wall, septa, and columella, and involves 2D observations made primarily using petrographic thin sections. Microstructure has been described and illustrated by numerous previous authors, including Alloiteau (1952) and Chevalier & Beauvais (1987), and recently reviewed by Stolarski & Roniewicz (2001). However, the classification system of Vaughan & Wells (1943) and Wells (1956) only incorporated one aspect of microstructure, wall structure, which was treated using a simplified approach distinguishing only septotheca, paratheca, and synapthotheca in clades XV–XXI of Fukami *et al.* (2008). Budd & Stolarski (2011) expanded these three wall types to also include trabeculotheca and abortive septa, as defined by Chevalier & Beauvais (1987).

Our characterization of microstructure focuses both on the corallite wall (the skeletal structure uniting the outer edges of septa in a corallite) using the wall types defined by Budd & Stolarski (2011), as well as

on the costosepta and columella. In the latter observations, we considered the degree to which calcification centres are clustered, the distinctiveness of costoseptum medial lines, and the presence of transverse lines or centre clusters crossing medial lines. We also examined thickening deposits to determine if they form distinct layers or concentric rings.

The following microstructural features were coded as 11 characters and analysed (Table 3):

1. Wall structure [characters 22–26, see below]

Character J2 (Wall – Wall structure) of Beauvais *et al.* (1993)

As the corals under consideration may have one or a combination of different corallite wall types, the five different wall types were analysed as separate characters, which are coded as well developed, partially developed, or absent.

Synapticulotheca: wall formed by synapticulae (rod- or bar-like structures extending between septal faces).

Septotheca: wall formed by the fusion of the outer edges of the septa.

Paratheca: wall formed by intercostal or epicostal dissepiments.

Trabeculotheca: wall formed by vertical plates (having distinct calcification centres) developed between costae.

Abortive septa: wall containing septal-like structures that do not protrude into the calicular space. These structures are long and slender, and form between normally developed septa. Abortive septa were considered a special type of septothecal wall structure by Beauvais *et al.* (1993).

2. Costoseptum thickening deposits [character 28]

Not included in Beauvais *et al.* (1993)

Thickening deposits are fibrous skeletal structures deposited outside of areas of rapid skeletal accretion where calcification centres are concentrated (Stolarski, 2003). They are characterized by having fewer organic components. These fibrous deposits have been referred to as ‘sclerenchyme’, ‘stereoplasm’, or ‘stereome’ (our preference being the latter). These deposits vary in amount, and in the size of the fibres themselves. They are coded as: microfibrinous, fibrous (forming layers), or extensive fibrous (forming concentric rings).

3. Distinctiveness and spacing of costoseptum calcification centres [characters 29, 30, respectively]

Not included in Beauvais *et al.* (1993)

Calcification centres may be clustered within areas of rapid accretion, which correspond with septal teeth on the calical surface (Stolarski, 2003). These clusters vary in degree of distinctiveness. Our two characters are each divided into three states (Table 3). One

aspect that is not considered is the degree of continuity (discreteness) from one cluster to the next, because of extensive variation.

In morphological phylogenetic analyses of the family Fungiidae, Hoeksema (1989) used binary characters to distinguish < 15 septal teeth per cm and < 30 septal teeth per cm.

4. Costoseptum medial lines [character 31]

Character K1 (Microstructure – Radial elements) of Beauvais *et al.* (1993)

Calcification centres may form lines that extend along the medial axis of the costoseptum (the medioseptal plane), and the medial lines may vary in degree of distinctiveness. We have coded them as three states: absent or weak, moderate, or strong.

5. Transverse structures crossing medial lines [character 33]

Not included in Beauvais *et al.* (1993)

Transverse structures (formed by secondary calcification axes) may cross costoseptum medial lines (Cuif & Perrin, 1999; Cuif *et al.*, 2003), and these structures may vary in distinctiveness from clusters of centres to carinae composed of lines of centres that may form ridges on lateral septal faces. These structures correspond with aligned granules or even continuous ridges on lateral septal faces.

6. Columella structure [character 34]

Not included in Beauvais *et al.* (1993)

Calcification centres in the columella may differ in arrangement from those forming costosepta. They may be either clustered or aligned.

Characters excluded from the present study

Only one microstructural character, wall structure, was analysed in Johnson (1998) and in Budd & Smith (2005). Johnson (1998) used two states, septothecal vs. parathecal, whereas Budd & Smith (2005) used three states, septothecal vs. parathecal vs. thickened by stereome. As different wall structure types occur in various combinations (Budd & Stolarski, 2011), we have created a separate character for each wall type, with states corresponding to development relative to other wall types.

ANALYSES

Molecular phylogenetic analysis

The phylogeny that serves as the basis for the revised classification and phylogenetic character mapping in the present study was constructed by Bayesian analysis of combined mitochondrial *cox1* (607 bp) and *cob* (776 bp) DNA sequences (Fukami *et al.*, 2008; Fig. 1). We focused on a subset of the phylogenetic tree of

Fukami *et al.* (2008), which consists of clades XV to XXI (67 species). These six clades contain the vast majority of the genera traditionally assigned to the family Faviidae, and all of the genera traditionally assigned to the family Mussidae. They also include genera traditionally assigned to the families Merulinidae, Pectiniidae, and Trachyphylliidae.

Morphological character evolution

To identify the characters that distinguish family-level clades and subclades defined in the molecular phylogenetic studies of Fukami *et al.* (2004, 2008), we mapped each of the morphological characters in Table 3 onto the phylogeny of Fukami *et al.* (2008) using maximum parsimony as implemented in MES-QUITE v.2.72 (Maddison & Maddison, 2009). Although fossils were excluded, this molecular 'scaffold' (sensu Murphy *et al.*, 2001) approach is useful for identifying potential character support for well-supported molecular clades that might not be recovered in an independent analysis of morphological characters. Character state transformations were evaluated under both ACCTRAN and DELTRAN optimizations. Levels of homoplasy for each character were assessed using consistency and retention indices (hereafter CI and RI). Our assessment of synapomorphies focused on exemplars of the three different classes of morphological characters (macromorphology, micromorphology, microstructure). Emphasis was also placed on those characters that distinguish clade XXI (herein termed 'Mussidae'), the two major subclades within clade XXI (herein termed 'Faviinae' and 'Mussinae'), and three smaller clades (*Mussismilia*; *Colpophyllia*; *Favia* + *Diploria* + *Pseudodiploria* + *Manicina*) within the Faviinae subclade.

Morphological phylogenetic analysis

We also explored the phylogenetic signal present in the morphological characters independent of the recent molecular phylogenetic 'scaffold' of Fukami *et al.* (2004, 2008). The primary questions that we sought to address were: (1) which groups are well supported in the morphological data set?; (2) which groups recovered in the morphological data set agree/conflict with the molecular phylogenies of Fukami *et al.* (2004, 2008)?; and (3) how does the taxonomic scope of the morphological analyses affect these first two issues? Our analysis sets the stage for future work employing different taxon sampling schemes, including fossils. The morphological data set consisted of 27 of the original 38 characters (Table 3). Eleven macromorphological characters were selected from the original 19, and eight microstructural characters from the original 11, based on CIs and RIs and ability to distinguish the three major clades (XXI, XIX, XVII) or subclades. All of the eight original micromorphological

characters were included. Of the 27 characters that were selected for analysis, seven are binary and 20 are multistate. Of the multistate characters, 15 were treated as ordered, as they represent potentially nested statements of primary homology.

Two separate phylogenetic analyses were performed (see Appendix S4 for character matrix). The first sampled only taxa within clades XIX, XX, and XXI, and rooted trees on members of clade XX, following Budd & Smith (2005) and Budd *et al.* (2010). The second analyses included all the taxa from the first analysis, as well as members of clades XVII and XVIII. These trees were rooted on *Diploastrea heliopora* and *Montastraea cavernosa* (clades XV and XVI, respectively), which were both recovered as relative outgroups to these taxa in the analyses of Fukami *et al.* (2008) and Kitahara *et al.* (2010). In some characters, the morphology present in a particular taxon or set of taxa could not be confidently hypothesized as homologous with any given character state. These taxa were coded as inapplicable (= '-') for those characters. In the context of a maximum parsimony analysis, this effectively treats these taxa as missing data (= '?') for those characters. Additionally, one character (character 20, 'Synapticulotheca') was invariant within the taxon sample of the smaller phylogenetic analysis, and was deleted before this analysis was performed.

Parsimony analyses of both data sets were performed in PAUP* 4.0b10 (Swofford, 2002). Heuristic searches were performed with 10 000 random addition sequence replicates to obtain the most parsimonious trees for each data set. Tree bisection and reconnection was utilized as the branch-swapping algorithm for searches. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions, following 'rule 1' of Coddington & Scharff (1994). Clade support was quantified by bootstrap analysis (Felsenstein, 1985). Heuristic searches were performed on 5000 pseudoreplicate data sets, with 20 random addition sequence replicates for each bootstrap search. The maximum number of trees saved for each random addition sequence replicate was set to 100 for the bootstrap analyses, to prevent searches from becoming stuck on large islands of most parsimonious trees (MPTs) during any particular random addition sequence replicate. This search strategy reduces the amount of tree space explored for any given random addition sequence replicate, while allowing for a much larger number of bootstrap replicates to be performed. Bremer support values were calculated for each node in the strict consensus of MPTs resulting from each analysis using TreeRot v.3 (Sorenson & Franzosa, 2007). The number of random addition sequence replicates performed for each constraint analysis was

changed to 2000 from the default setting of 20 generated in TreeRot v.3.

MUSEUM ABBREVIATIONS

BM(NH), The Natural History Museum, London, UK; MNHN, Muséum national d'Histoire naturelle de Paris, France; MTQ, Museum of Tropical Queensland, Australia; RMNH, Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands; STRI, Smithsonian Tropical Research Institute, Panama City, Panama; SUI, Paleontology Repository of the University of Iowa, Iowa City, IA, USA; UF, Florida Museum of Natural History, Gainesville, FL, USA; UP, Marine Science Institute, University of the Philippines, Manila, Philippines; USNM, The National Museum of Natural History, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZMA (Zoological Museum Amsterdam, Netherlands); ZMB, Berlin Museum, Berlin, Germany; ZMK, Zoologisk Museum, Copenhagen, Denmark.

RESULTS

MORPHOLOGICAL CHARACTER EVOLUTION

Macromorphology (Fig. 2; Table 3; Appendix S5)

All of the 19 macromorphological characters (Table 3, examples in Fig. 2) exhibit homoplasy, and no one character is diagnostic of any of the three major clades (XVII, XIX, XXI). CI values range from 0.087 [character (char.) 10] to 0.333 (char. 3), with an average of 0.158; RI values range from 0.154 (char. 11) to 0.792 (char. 18), with an average of 0.561. Polymorphism (char. 3), epitheca (char. 18), and endotheca (char. 19) have RI values > 0.7; whereas intracalicular budding (char. 1), calice size (char. 7), number of septal cycles (char. 10), development of minor (free) septa (char. 11), and columella structure (char. 15) all have RI values < 0.5. However, even in characters with relatively high RI values such as corallite integration (char. 4) and corallite centre linkage (char. 14) (Fig. 2B, C), character state transitions usually occur within major clades and near branch tips, rather than unequivocally at nodes where major clades diverge. With the possible exceptions of extracalicular budding (char. 2; Fig. 2A) and endotheca (char. 19, Appendix S6), no unequivocal transitions occur at the divergence of clade XXI (the subject of the present monograph), and few transitions distinguish subclades within clade XXI (but see epitheca char. 18, which distinguishes the *Favia + Diploria + Manicina + Pseudodiploria* subgroup; Fig. 2D).

Based on these results, we selected 11 characters with RI values > 0.5 for use in the morphological phylogenetic analyses (Table 3).

Micromorphology (Figs 3, 4; Table 3; Appendix S6)

Of all the morphological characters analysed, two micromorphological characters related to tooth shape (chars 35, 38) best match the molecular data (Fig. 3A, B, respectively). Moreover, all of the eight micromorphological characters possess high phylogenetic signal as evidenced by RI values > 0.7 (Table 3), including two characters (tooth height, char. 39, Fig. 3C, and spacing, char. 40, Appendix S6) used in the classification of Wells (1956) to distinguish families. Nevertheless, all but one of the micromorphological characters (Table 3, examples in Fig. 3) exhibit homoplasy. CI values range from 0.182 (char. 39) to 1.000 (char. 38), with an average of 0.406; RI values range from 0.698 (char. 40) to 1.000 (char. 38), with an average of 0.828. In addition to tooth tips (char. 38), RI values are high for tooth base (char. 35), granule shape and distribution (char. 43, Fig. 3D), and tooth comparisons amongst septal cycles (char. 45, Appendix S6), but are lower for the two Wells (1956) characters (chars 39, 40). Teeth and granules that are characteristic of the three major clades (XVII, XIX, XXI) are illustrated and described in Figure 4.

The one character that does not exhibit homoplasy is tooth tips (char. 38), which is diagnostic of the three major clades (XVII, XIX, XXI); however, clade XXI possesses a state (regular, pointed) that is plesiomorphic (Figs 3B, 4A–C). Regular pointed teeth (char. 38) subsequently transform to irregular lobes (clade XIX, Fig. 4D, E) and multiaxials (clade XVII, Fig. 4G–I). Irregular lobes further transform to bulbous tips within clade XIX (Fig. 4F). Clade XXI is therefore characterized by regular pointed, 'blocky' (=having stout, equidimensional supporting structures) teeth, which are orientated transverse (Faviinae; Fig. 4A, B) or parallel (Mussinae; Fig. 4C) to the septa (char. 35). The transverse orientations result in tricornate or paddle-shaped teeth, whereas the parallel orientations result in tall spine-shaped teeth. Tooth interareas are formed by horizontal bands in clade XXI, vertical palisades in clade XIX, and a mixture of the two states in clade XVII. Granules consist of aligned spikes in clade XXI (Fig. 4A–C), a state which is also plesiomorphic. They transform to rounded knobs at the divergence of clade XIX (Fig. 4D–F) and to irregular arrangements within clade XVII (Fig. 4G–I). Differentiation within costosepta and amongst septal cycles occurs only within clade XIX.

Based on these results, we used all eight micromorphological characters in the morphological phylogenetic analyses (Table 3).

Microstructure (Figs 5, 6; Table 3; Appendix S7)

All of the 11 microstructural characters except synapiculotheca (char. 22) (Table 3, Fig. 5) exhibit

homoplasy, but six characters have high phylogenetic signals as evidenced by RI values > 0.7 . CI values range from 0.087 (char. 25) to 1.000 (char. 22), with an average of 0.291; RI values range from 0.000 (char. 22) to 0.865 (char. 30), with an average of 0.639. *Synapticulotheca* (char. 22) occurs only in *Diploastrea* and is therefore uninformative. The highest RI values occur in the development of thickening deposits (char. 28; Fig. 5C), distinctiveness of clusters of calcification centres (char. 29; Fig. 5D), distance between clusters (char. 30; Appendix S7), and transverse crosses (char. 33; Appendix S7); however, with the possible exceptions of thickening deposits and cluster distances, none of these characters are diagnostic of major clades. Clade XXI is characterized by moderately developed costoseptal medial lines (char. 31) and the presence of transverse crosses (char. 33), but these features also arose within clades XVII and XIX. Transition to dominantly parathecal walls (char. 26; Fig. 5B) occurs at the divergence of clade XXI and of clade XIX. However, the *Favia* + *Diploria* + *Manicina* + *Pseudodiploria* subgroup within clade XXI experiences a reversal in parathecal walls (char. 26) when septothecal walls (char. 23; Fig. 5A) become

dominant. The Faviinae subclade within clade XXI is distinguished by narrow distances between clusters of calcification centres (char. 30) and by aligned columella calcification centres (char. 34; Appendix S7); however these features also arose within clades XVII and XIX.

Wall and costoseptal structures that are characteristic of each of the three major clades (XVII, XIX, XXI) are illustrated and described in Figure 6. Clade XXI (Fig. 6A–C) is characterized by transverse features that cross costoseptal medial lines, and septothecal (Fig. 6A) or parathecal (Fig. 6B, C) corallite walls. Clade XIX (Fig. 6D–F) is characterized by extensive thickening deposits. In clade XVII, small, closely spaced clusters of calcification centres form costoseptal medial lines (Fig. 6G–I).

Based on these results, we selected eight of the 11 microstructural characters with RI > 0.7 for use in the morphological phylogenetic analyses (Table 3).

Morphological phylogenetic analyses

Analysis 1 (Fig. 7)

The phylogenetic analysis focusing on clades XIX–XXI recovered four MPTs. Tree lengths were 93 steps,

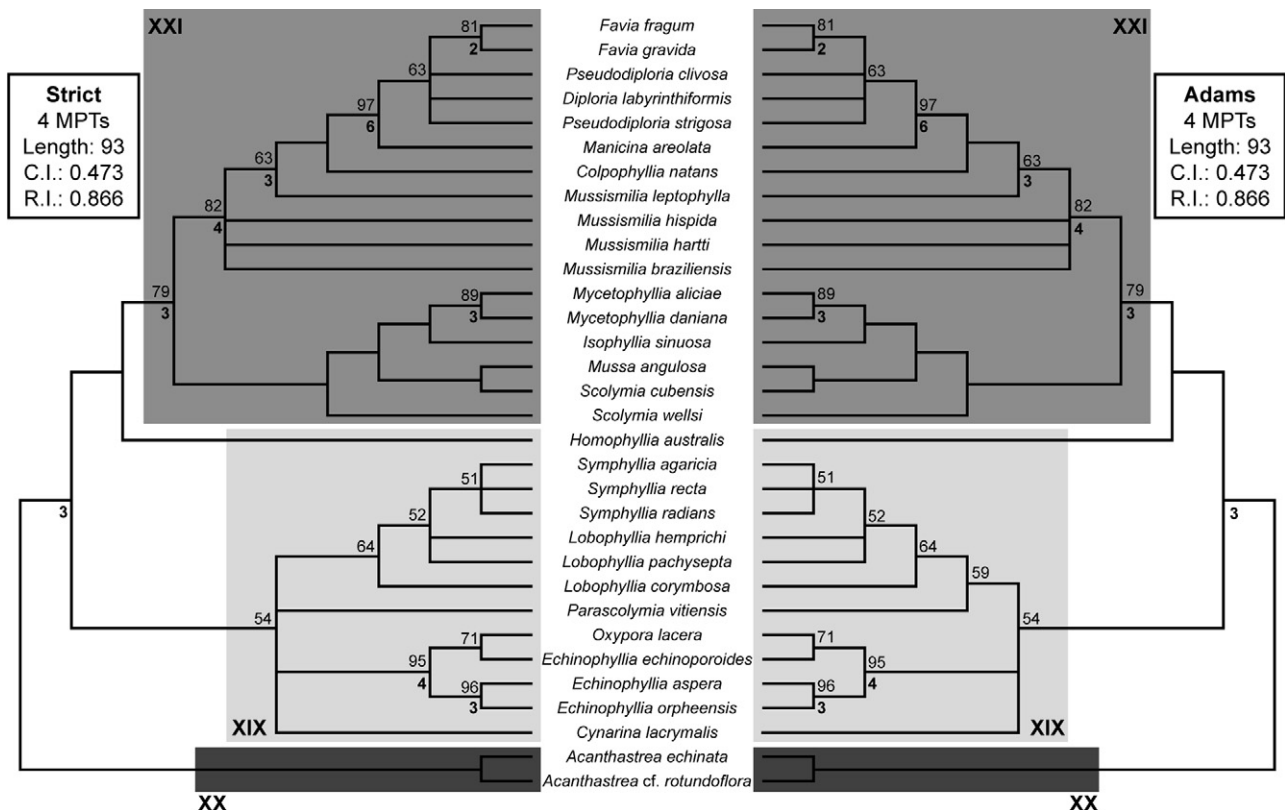


Figure 7. Strict and Adams consensus trees for the morphological phylogenetic analysis (maximum parsimony) focusing on clades XIX and XXI (analysis 1). Numbers above and below nodes are bootstrap values (> 50) and Bremer support values (> 1), respectively. C.I., consistency index; MPTs, most parsimonious trees; R.I., retention index.

with CIs of 0.473 and RIs of 0.866. Strict and Adams consensus trees of these MPTs are shown in Figure 7. Clade XXI was recovered as monophyletic with moderate support. Within clade XXI, a monophyletic group including *Favia fragum*, *Favia gravida*, *Diploria + Pseudodiploria* spp., and *Manicina areolata* was recovered, which was also found in previous morphological and molecular analyses (Fukami *et al.*, 2004, 2008; Budd & Smith, 2005; Nunes *et al.*, 2008), although the morphological support for this group (= clade 'A' of Budd & Smith, 2005: fig. 2) is much stronger in the present analysis. The present analysis is also similar to previous morphological and molecular analyses (Fukami *et al.*, 2004, 2008; Budd & Smith, 2005; Nunes *et al.*, 2008) in recovering a group that includes 'clade A', *Colpophyllia natans* and *Mussismilia* spp., including *Mussismilia leptophylla* (= clades 'A + B' of Budd & Smith, 2005: fig. 2). Morphological support for this group is much higher in the present analysis than that of Budd & Smith (2005), and the relative relationships between *Colpophyllia natans* and *Mussismilia* spp. (including *Mussismilia leptophylla*) differ between these two studies. Additionally, the present study recovered *Mussismilia hartti* as part of this group, which is supported by molecular data (Fukami *et al.*, 2004, 2008; Budd & Smith, 2005; Nunes *et al.*, 2008), but which the previous morphological analysis of Budd & Smith (2005) found as much more distantly related. A monophyletic group including *Mycetophyllia* spp., *Isophyllia sinuosa*, *Mussa angulosa*, *Scolymia cubensis*, and *Scolymia wellsi* (= clade 'C' of Budd & Smith, 2005: fig. 2) was recovered, which is strongly supported by molecular data (Fukami *et al.*, 2004, 2008; Budd & Smith, 2005), but was not recovered as monophyletic in a previous morphological phylogenetic analysis (Budd & Smith, 2005).

Clade XIX was recovered as paraphyletic in the present analysis, with *Homophyllia australis* weakly supported as the sister group to clade XXI. In the analysis of Fukami *et al.* (2008), this taxon was recovered as the sister group to a *Lobophyllia* spp. and *Symphyllia* spp. clade. The latter clade was also recovered in the present analysis, although *Lobophyllia* was found to be paraphyletic, which is also supported by molecular data (Fukami *et al.*, 2008). Similar to the analysis of Fukami *et al.* (2008), strong support was found for an *Oxypora lacera* and *Echinophyllia* spp. clade; however, the present analysis differs in recovering *Echinophyllia* as paraphyletic.

Analysis 2 (Fig. 8)

The more inclusive phylogenetic analysis focusing on clades XVII, XIX, and XXI (including XVIII and XX) recovered 243 MPTs. Tree lengths were 200 steps, with CIs of 0.265 and RIs of 0.811. Strict and Adams

consensus trees of these MPTs are shown in Figure 8. Node support for these MPTs is weak, and generally limited to lower phylogenetic levels.

Both clades XVII and XXI were recovered as polyphyletic and interspersed within each other in this larger analysis. The group including *Favia fragum*, *Favia gravida*, *Diploria + Pseudodiploria* spp., and *Manicina areolata* (= clade 'A' of Budd & Smith, 2005) was still recovered as monophyletic, as was the group including *Mycetophyllia* spp., *Isophyllia sinuosa*, *Mussa angulosa*, *Sc. cubensis*, and *Sc. wellsi* (= clade 'C' of Budd & Smith, 2005: fig. 2). However, the latter group was found to be the sister clade of a *Pectinia* spp. and *Mycedium elephantotus* clade (members of clade XVII). The remaining members of clade XXI were recovered in an unresolved polytomy outside of this group. Within clade XVII, some lower level relationships are congruent between the molecular analyses of Fukami *et al.* (2004, 2008) and the present analysis (e.g. the *Pectinia* spp. and *Mycedium elephantotus* clade; the *Oulophyllia* spp. and *Caulastraea furcata* clade; a monophyletic *Hydnophora*; a monophyletic *Platygyra*). However, most of the higher level relationships within clade XVII differ greatly between the results of Fukami *et al.* (2004, 2008) and the present analysis. For example, portions of the strongly supported grouping of *Dipsastraea stelligera*, *Merulina* spp., *Goniastrea pectinata*, *Scapophyllia cylindrica*, and *Leptoria phrygia* recovered by Fukami *et al.* (2008) were found to be polyphyletic in the present analysis.

Clade XIX was recovered as monophyletic in this larger analysis, and ingroup relationships are generally similar to those recovered in the less inclusive analysis (Fig. 7). Clade XX was recovered as the sister group of clade XIX, which is also supported by previous molecular analyses (Fukami *et al.*, 2004, 2008). Clade XVIII (*Acanthastrea hillae* and *Micromussa amakusensis*) was recovered as the paraphyletic sister group to clades XIX and XX, which contrasts with its recovery as the monophyletic sister group of clade XVII in the Fukami *et al.* (2004, 2008) analyses.

DISCUSSION

Morphology has provided the basis for classification of the order Scleractinia, but the use of morphologic characters is complex and fraught with many difficulties. These difficulties include: (1) extensive homoplasy (few if any unambiguous synapomorphies), (2) questionable character homology (limited understanding of how the skeleton is formed, and how colonies grow), (3) paucity of characters (simple morphology), and (4) widespread phenotypic plasticity ('noise'). Following Cuif *et al.* (2003), our approach in the present monograph has been to compare and

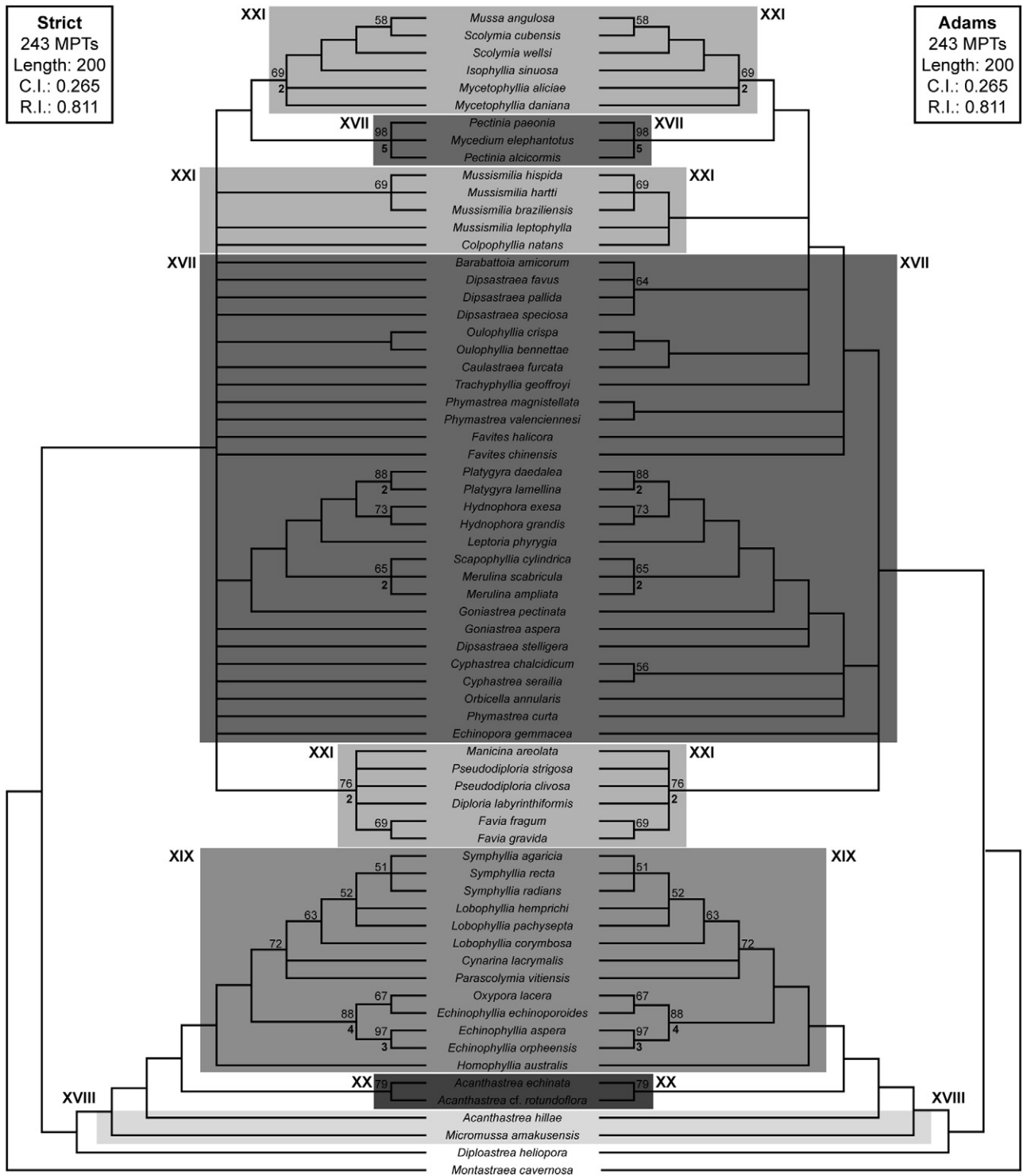


Figure 8. Strict and Adams consensus trees for the more inclusive morphological phylogenetic analysis (maximum parsimony) involving clades XVII, XIX, and XXI (analysis 2). Numbers above and below nodes are bootstrap values (> 50) and Bremer support values (> 1), respectively. C.I., consistency index; MPTs, most parsimonious trees; R.I., retention index.

integrate morphological and molecular data bringing multiple data types (including newly recognized micromorphological and microstructural characters of Budd & Stolarski, 2009, 2011) to bear on the problem. In view of the higher support previously found for basal nodes in the scleractinian molecular trees in comparison to morphologic trees (Budd *et al.*, 2010), following Cuif *et al.* (2003), we began our analysis by mapping individual morphological characters onto a molecular tree and determining ancestral state reconstructions. Homoplasy (both gains and losses) was found in all but two characters (chars 22, 38). One of the two nonhomoplastic characters (char. 22) was present only in the outgroup and therefore uninformative; the other character (char. 38) was plesiomorphic for the clade targeted in the present monograph (clade XXI). The high degree of observed homoplasy contrasts with the interpretations of synapomorphies in Cuif *et al.* (2003), who analysed 40 species from across the scleractinian tree, as opposed to 67 species from a narrower subsection of the tree as performed here. The increased number of species within clades in the present study has revealed increased variability and homoplasy within clades.

Nevertheless, despite the lack of synapomorphies, various combinations of morphological characters distinguish the three major clades (XVII, XIX, XXI) and two subclades (Mussinae, Faviinae) within clade XXI. For example, clade XXI is distinguished by abundant endotheca (char. 19) (macromorphology); regular blocky teeth with pointed tips (chars 35, 38), with horizontal bands between teeth and aligned granules (char. 44) (micromorphology; Fig. 4); costoseptal medial lines crossed by transverse features (char. 33) (microstructure; Fig. 6). Clade XIX is distinguished by lamellar columella linkage (chars 14, 15) and lack of epitheca (char. 18) (macromorphology); irregular lobate or bulbous teeth (char. 38) with elliptical tooth bases (char. 35) and rounded granules (char. 43) enveloped by extensive thickening deposits, with vertical palisade-like structures between teeth (char. 44) and differences in size/shape of teeth amongst septal cycles (char. 45) (micromorphology); dominantly parathecal walls (char. 26) (partially septothecal), and widely spaced clusters of calcification centres (char. 30) (microstructure). Clade XVII is distinguished by trabecular columella linkage (chars 14, 15) (except traditional pectiniids) (macromorphology), well-developed epitheca (char. 18) [except traditional pectiniids (+*Oulophyllia*) and traditional merulinids] (macromorphology); irregular multidirectional teeth (char. 38) with circular bases (char. 35) (micromorphology); and closely spaced clusters of calcification centres (char. 30) (microstructure).

Within clade XXI, the Faviinae subclade is distinguished by elliptical tooth bases (char. 35) orientated

transverse to the septa, strong and aligned granules (char. 43) (micromorphology); narrowly spaced clusters of calcification centres (char. 30), transverse structures crossing costoseptal medial lines (char. 33), and clustered columella calcification centres (char. 34) (microstructure). The Mussinae subclade is distinguished by circular tooth bases (char. 35) that are widely spaced (char. 40) (micromorphology); moderately to widely spaced clusters of calcification centres (char. 30) (microstructure), and aligned columella calcification centres (char. 34) (microstructure).

Of all the characters analysed, micromorphological characters related to the septal growing edge, especially the shape of septal teeth and granulation, are the most effective at distinguishing the three family-level clades. Although these characters were treated in a cursory manner by Vaughan & Wells (1943) and Wells (1956) and developed more fully in recently published glossaries (e.g. Beauvais *et al.*, 1993), they have rarely been mentioned in taxon descriptions and phylogenetic analyses of living scleractinians. Exceptions include Hoeksema (1989) and Gittenberger, Reijnen & Hoeksema (2011) for Fungiidae; Wallace (1999) for Acroporidae, Benzoni *et al.* (2007, 2011, 2012) for *Psammocora*, *Cycloseris*, and *Plesiastrea*; Huang *et al.* (2011) for Merulinidae as defined herein; as well as Cuif *et al.* (2003) and Budd & Smith (2005). For example, in accordance with molecular data, Benzoni *et al.* (2007) found tooth shapes in *Psammocora* that grouped this genus with the family Fungiidae instead of with the family Siderastreidae as in traditional classification, and Gittenberger, Reijnen & Hoeksema (2011) found different granulation patterns associated with different molecularly distinct genera of Fungiidae. Nevertheless, when micromorphological characters are mentioned, a different set of descriptive terms is used in each study, further complicating comparisons and understanding of these features. Most importantly, it is unclear whether the 'teeth' and 'spines' of different studies are formed by similar or different processes related to the interplay between centres of rapid accretion, calcification axes (primary, secondary, etc.), and thickening deposits.

Moreover, the relationship between 3D micromorphological characters on the skeletal surface and 2D microstructural characters in the skeletal interior is poorly understood. As explained by Cuif *et al.* (2003) and Stolarski (2003), teeth on the growing edge of the septa correspond with centres of rapid accretion (i.e. clusters of calcification centres), which vary in distinctiveness, spacing, and degree of connectivity. Transverse structures (secondary calcification axes) crossing the medioseptal plane in 2D correspond with paddle-shaped septa and aligned granules/carinae in 3D. However, micromorphological and microstruc-

tural characters in the present study show patterns that are uncorrelated, indicating that their correspondence is more complicated than previously appreciated and requires further investigation. Computer simulations would help to more accurately characterize micromorphology and microstructure.

Using the results of ancestral state reconstructions, we deleted excessively homoplastic characters (with low CIs and RIs, not diagnostic of branches near the base of the tree) from the data set and performed morphological phylogenetic analyses. Phenotypic plasticity is rampant in the clades under investigation (e.g. Foster, 1979; Tomascik, 1990; Van Veghel & Bak, 1993; Todd *et al.*, 2004; Todd, 2008; Pinzón & Weil, 2011; Hoeksema, 2012); therefore, deleting characters that reveal little or no congruence with molecular results was an important step in reducing noise. The results show that when clades XIX and XXI alone are compared, the morphological tree agrees well with the molecular tree. The two major clades (XIX and XXI) are distinct, as are the two subclades of XXI. The main exception is *Homophyllia australis*, and to a lesser extent, *Parascolymia vitiensis* and *Cynarina lacrymalis*, all three of which are solitary. However, when clade XVII is added to the analysis, clade XIX remains intact but the resolution of clades XVII and XXI breaks down. The Mussinae subclade within clade XXI remains intact, as does the *Favia* + *Diploria* + *Manicina* + *Pseudodiploria* subgroup within clade XXI; however, the relationships amongst many clade XVII taxa are unresolved, in part because of the low numbers of characters relative to numbers of taxa. These results indicate that because of the highly homoplastic nature of scleractinian morphology, data sets may need to be partitioned into taxonomic subsets (consisting of 30–40 species) when performing morphologic phylogenetic analyses. These issues will be treated further in a subsequent monograph in this series, which focuses on clade XVII (the family Merulinidae).

The convergence associated with clades XVII (Indo-Pacific) and XXI (Atlantic) suggests a complex pattern of evolutionary divergence as well as similar selective regimes in the two biogeographical regions after the two clades diverged. Although phylogenetic character mapping indicates that some of the observed similarities are plesiomorphic (e.g. char. 4, Fig. 2; char. 39, Fig. 3), most similarities appear to be related to evolutionary changes (gains and losses) that occurred closer to branch tips. Analyses of the quantitative genetics of incipient speciation associated with *Favia fragum* (Carlon *et al.*, 2011) suggest that selection, genetic drift, and constraints all play a role in the morphological evolution of these corals. Future studies that target genes responsible for calcification and the formation of the skeleton would help to

understand better these processes, as well as the resulting high degree of homoplasy.

In order to resolve many of the ambiguities in character evolution found in the present study, the current characters need to be further analysed, variation within species needs to be rigorously assessed, additional new characters need to be discovered, and more taxa need to be characterized. Quantitative approaches would improve character definition, delimitation, and ordering. Both additional living species belonging to the genera in clade XVII and fossil species will need to be added to morphological phylogenetic analyses. The addition of fossils will not only allow estimation of divergence times but also facilitate the examination of the relationship between these divergences and changes in the environment and biogeography.

SYSTEMATIC ACCOUNT

Family Mussidae Ortmann, 1890

Subfamily Mussinae Ortmann, 1890

Genus *Mussa* Oken, 1815

Genus *Isophyllia* Milne Edwards & Haime, 1851a

Genus *Mycetophyllia* Milne Edwards & Haime, 1848

Genus *Scolymia* Haime, 1852

Subfamily Faviinae Gregory, 1900

Genus *Favia* Milne Edwards, 1857

Genus *Colpophyllia* Milne Edwards & Haime, 1848

Genus *Diploria* Milne Edwards & Haime, 1848

Genus *Manicina* Ehrenberg, 1834

Genus *Mussismilia* Ortmann, 1890

Genus *Pseudodiploria* Fukami, Budd & Knowlton
gen. nov.

Remarks: Matthai (1928) comprehensively monographed meandroid members of the traditional families Faviidae and Mussidae, rigorously describing their morphology and reviewing their taxonomic history up until 1928. In this monograph, he located and illustrated type specimens for many of the species in the present account, presented extensive synonymies, and cleared up prior nomenclatural uncertainty. Unless otherwise indicated, we have accepted genus-level synonyms and nomenclatural decisions in Vaughan & Wells (1943) and Wells (1956), and thoroughly reviewed the taxonomic literature and searched for type specimens beginning with Matthai (1928) as a starting point.

FAMILY MUSSIDAE ORTMANN, 1890: 315

Type genus: *Mussa* Oken, 1815

[all taxa in Oken, 1815 rejected by ICZN opinion 417 (September 1956; ICZN Commission, 1956); but

Mussa Oken, 1815 conserved by ICZN opinion 2061 (March 2004; ICZN Commission, 2004)]

Diagnosis: Macromorphology: solitary or colonial. Budding, exclusively intracalicular, never extracalicular. Corallites discrete or arranged in series. Coenosteum costate, if present. Trabecular columella, with trabecular or lamellar linkage. Epithecium present (Fig. 2).

Micromorphology: septal teeth regular and pointed, often blocky, orientated either transverse to the plane of the septum or multidirectional. Septal granulation consisting of aligned spikes. Teeth usually equal in size and shape in different septal cycles (Figs 3, 4), except *Scolymia lacera*.

Microstructure: septothecal or parathecal corallite walls, sometimes partially trabeculothecal, never having abortive septa or thickened extensively by stereome. Costoseptal centres of calcification distinct, sometimes concentrated, and connected by moderately developed medial lines (Figs 5, 6).

Subfamilies included:

Faviinae Gregory, 1900
Mussinae Ortmann, 1890

Remarks: The family corresponds to the new Atlantic clade (clade XXI) first recognized by Fukami *et al.* (2004) using molecular data, and later confirmed by Fukami *et al.* (2008). It consists of Atlantic taxa that have traditionally been assigned to the families Faviidae and Mussidae (Vaughan & Wells, 1943; Wells, 1956; Veron, 2000), with the exception of species of traditional *Montastraea* (*Montastraea cavernosa* and the *Orbicella annularis* complex).

This family is distinguished from clades XVII to XX principally by the shape of their septal teeth (Figs 3, 4). These have regular pointed tips (a symplesiomorphy) and a stout blocky appearance. In contrast, teeth in clades XVII to XX are highly irregular, and consist of lobes, bulbs, or twisted multidirectional threads.

Unlike those in many traditional Indo-Pacific 'faviids' (clade XVII), corallite walls in the family never contain abortive septa (Figs 5, 6). They are also never thickened by stereome, which is diagnostic of traditional Indo-Pacific 'mussids' (clades XVII to XX). Centres of calcification in the corallite wall are either connected by medial lines or discrete. Transverse features such as carinae cross the septal plane. Septal granulation is aligned and 'spiky' (= having a sharp point), and differs in particular from Indo-Pacific 'mussids' (clade XIX), which consist of scattered rounded knobs. Unlike Indo-Pacific 'mussids' (clade XIX), with the exception of *Scolymia lacera*, teeth on different septal cycles are equal in size and shape.

Following the molecular results of Fukami *et al.* (2004, 2008), we restrict the definition of the family to

include only Atlantic taxa. The family, therefore, does not include the following Indo-Pacific genera, which have previously been assigned to the family Faviidae (Veron, 2000) and are hereby transferred to the family Merulinidae (Tables 1, 2):

Australogyra Veron & Pichon, 1982: 138

Barabattoia Yabe & Sugiyama, 1941: 72

Caulastraea Dana, 1846: 198

Cyphastrea Milne Edwards & Haime, 1848: 494

Echinopora de Lamarck, 1816: 252

Erythraea Scheer & Pillai, 1983: 104

Favites Link, 1807: 162

Goniastrea Milne Edwards & Haime, 1848: 495

Leptoria Milne Edwards & Haime, 1848: 493

Oulophyllia Milne Edwards & Haime, 1848: 492

Platygyra Ehrenberg, 1834: 323.

The family also does not include the following Indo-Pacific genus, previously assigned to the monotypic family Trachyphylliidae but sometimes considered a subfamily of the Faviidae (e.g. Wells, 1956) and hereby transferred to the family Merulinidae (Tables 1, 2): *Trachyphyllia* Milne Edwards & Haime, 1848: 492.

The family also does not include the following Indo-Pacific genera, which have traditionally been assigned to the family Mussidae (Veron, 2000) and are hereby transferred to the family Lobophylliidae (Tables 1, 2):

Acanthastrea Milne Edwards & Haime, 1848: 495

Australomussa Veron, 1985: 171

Cynarina Brüggemann, 1877: 305

Lobophyllia de Blainville, 1830: 321

Micromussa Veron, 2000 (3): 8

Moseleya Quelch, 1884: 292

Symphyllia Milne Edwards & Haime, 1848: 491.

The following genera, previously assigned to either the family Faviidae or Mussidae, are hereby designated as *incertae sedis* (Tables 1, 2) pending future analysis:

Blastomussa Wells, 1968: 276

Cladocora Ehrenberg, 1834: 309

Indophyllia Gerth, 1921: 405

Leptastrea Milne Edwards & Haime, 1848: 494

Parasimplastrea Sheppard, 1985: 5

Plesiastrea Milne Edwards & Haime, 1848: 494

Oulastrea Milne Edwards & Haime, 1848: 495

Solenastrea Milne Edwards & Haime, 1848: 494.

The genus *Diploastrea* Matthai, 1914: 72, traditionally assigned to the family Faviidae, belongs to its own separate family.

Following the molecular results of Fukami *et al.* (2004, 2008), three genera included in Veron (2000) are polyphyletic: *Favia*, *Montastraea*, *Scolymia*. We separate modern species of the traditional genus *Favia* into two genera: *Favia* Milne Edwards, 1857 (Atlantic) and *Dipsastraea* de Blainville, 1830 (Indo-

Pacific). *Favia* as previously defined was distinguished by having intracalicular budding, a costate coenosteum, a trabecular columella (compact or spongy), and well-developed epitheca (Vaughan & Wells, 1943; Wells, 1956). The two genera distinguished herein differ in morphology: *Favia* has paddle-shaped septal teeth (elliptical-perpendicular bases with regular pointed secondary calcification axes, as first recognized by Cuif *et al.*, (2003) and a septothecal wall, whereas *Dipsastraea* has irregular, multidirectional teeth (circular bases), and either a parathecal wall (*Dipsastraea favus*, *Dipsastraea pallida*, *Dipsastraea speciosa*) or septothecal wall with abortive septa (*Dipsastraea stelligera*) (Budd & Stolarski, 2011). The differences in wall structure suggest that the species currently assigned to *Dipsastraea* most likely belong to more than one genus, and require further investigation.

We separate modern species of the previous genus *Montastraea* into three genera: *Montastraea* de Blainville, 1830 (Atlantic *Montastraea cavernosa*), *Orbicella* Dana, 1846 (Atlantic *Orbicella annularis* complex), and *Phymastrea* Milne Edwards & Haime, 1848 (Indo-Pacific). The traditional genus is distinguished by having extracalicular budding, plocoid colony form, a costate coenosteum, a trabecular columella (compact or spongy), and well-developed epitheca (Vaughan & Wells, 1943; Wells, 1956). The three genera distinguished herein differ as follows: *Montastraea* has four or more septal cycles and its corallite wall is septothecal with abortive septa; *Orbicella* has three septal cycles and its corallite wall is septothecal (no abortive septa); and *Phymastrea* has three or more septal cycles and paliform lobes, and its corallite wall is either parathecal (*Phymastrea valenciennesi*, *Phymastrea magnistellata*) or septothecal with abortive septa (*Phymastrea curta*). In addition, *Montastraea* has paddle-shaped teeth (elliptical-perpendicular bases with regular pointed secondary calcification axes), and *Orbicella* and *Phymastrea* have irregular multidirectional teeth (circular bases). The differences in wall structure suggest that the species currently assigned to *Phymastrea* most likely belong to more than one genus and require further investigation.

The revised genus *Montastraea* de Blainville, 1830: 339, traditionally assigned to the family Faviidae, belongs to its own separate family. Members of traditional *Montastraea* (*Montastraea cavernosa* and the *Orbicella annularis* complex) are the only traditional Atlantic members of the family Faviidae that do not belong to the newly revised family Mussidae.

Veron (2000) synonymized three solitary zooxanthellate genera with well-developed septal teeth and four or more cycles of septa: *Homophyllia* Brügge-mann, 1877 (Indo-Pacific *Homophyllia australis*),

Parascolymia Wells, 1964 (Indo-Pacific *Parascolymia vitiensis*), and *Scolymia* Haime, 1852 (Atlantic). Following Wells (1964), we resurrect these three genera. Although all three genera have predominantly parathecal corallite walls, *Scolymia* has regular spine-shaped teeth (circular bases) and partially trabeculothecal walls, and *Homophyllia* and *Parascolymia* have irregular lobate teeth (elliptical-parallel bases) and partially septothecal walls. Septal granules are aligned in *Scolymia*, and evenly scattered in *Homophyllia* and *Parascolymia*. In *Homophyllia*, granules are especially well developed, and as noted by Wells (1964), teeth are relatively narrowly spaced (10–12 per cm) and calices are small (< 4 cm). In *Parascolymia*, epitheca is absent.

Distribution: Atlantic only.

SUBFAMILY MUSSINAE ORTMANN, 1890: 315

Type genus: *Mussa* Oken, 1815

Original description: ‘Von der Basis der Koralle erhebt sich keine Ringfalte, die eine echte Mauer abscheidet . . . Die Septen verbinden sich durch seitliche Verschmelzung zu einer falschen Mauer. . . Koloniebildung durch Theilung. Vorwiegend acrogenes Wachstum mit reichlicher Traversenbildung.’ (Ortmann, 1890: 314–315).

Diagnosis: Macromorphology: solitary or colonial; corallites discrete, or arranged in uniserial or multiserial valleys formed by circumoral budding (includes meandroid and phaceloid forms); coenosteum usually absent (except *Isophyllia*); medium to large calices with high relief (> 6 mm); widely spaced septa (< six per 5 mm); relatively small trabecular columella, with either lamellar or trabecular centre linkage; reduced epitheca; well-developed endotheca (Fig. 2).

Micromorphology: regular, tall (> 0.6 mm), widely spaced (1–2 mm), spine-shaped septal teeth, with circular bases; interarea of teeth consisting of horizontal bands; weak, aligned septal granules consisting of diffuse spikes (Figs 3, 4).

Microstructure: mostly parathecal corallite walls, containing trabeculothecal elements; clusters of centres of calcification within the costosepta and columella well developed, widely separated (> 0.6 mm), and connected by medial lines (Figs 5, 6).

Genera included:

Mussa Oken, 1815

Isophyllia Milne Edwards & Haime, 1851a

Mycetophyllia Milne Edwards & Haime, 1848

Scolymia Haime, 1852

Remarks: As explained by Vaughan & Wells (1943: 191), 'the most marked feature of the group is the large, multi-trabecular septal dentations marking the most complex type of faviid septum'. Both traditional Atlantic and Indo-Pacific 'mussids' have spine-shaped or triangular teeth. However, the teeth of traditional Indo-Pacific 'mussids' are orientated parallel to the septal plane, whereas the teeth of traditional Atlantic 'mussids' are transverse, sometimes forming carinae. Moreover, the septal granulation of traditional Indo-Pacific 'mussids' consists of rounded knobs, whereas the granules of traditional Atlantic 'mussids' consist of spikes. The walls of traditional Indo-Pacific 'mussids' are thickened extensively by stereome (see description in Budd & Stolarski, 2009).

The subfamily Mussinae is monophyletic (Fig. 7) and distinguished from the subfamily Faviinae on the basis of: greater distances (> 0.6 mm) between costoseptal clusters of calcification centres in the Mussinae, teeth with circular bases and weak granules in the Mussinae, and circumoral budding with wide septal spacing (< six septa per cm) in the Mussinae.

Distribution: Atlantic only.

GENUS *MUSSA* OKEN, 1815: 73 (FIGS 9A, B, 12A, B, 18A–C, 22A–C)

[all taxa in Oken, 1815 rejected by ICZN opinion 417 (September 1956; ICZN Commission, 1956); but *Mussa* Oken, 1815 conserved by ICZN opinion 2061 (March 2004; ICZN Commission, 2004)].

Synonyms: *Lithodendron* Schweigger, 1819, tab. vi [type species: *Madrepora angulosa* Pallas, 1766: 299–300, as listed by Schweigger, 1820: 415–416 (see Wells, 1936: 116).]

Type species: *Madrepora angulosa* Pallas, 1766: 299–300; by subsequent designation, Vaughan, 1918: 122. Holotype is lost (Matthai, 1928). We herein designate specimen YPM9035 (Fig. 9A, B) collected by J. C. Lang at Lime Cay off Port Royal, Jamaica as the neotype of *Mussa angulosa* (Pallas).

Original type species locality: 'Mare Americanum' (Pallas, 1766: 300) [Recent].

Early descriptions:

1. 'Sterne vertieft am End, meist gedrückt, weiter als Stamm, einzel oder wenige.' (Oken, 1815: 73).
2. 'Large *Astraeidae*, segregate, also explanatoglomerate; tentacles numerous, unequal, the inner tumid. Coralla calicularly branched or explanato-

glomerate; calicles very stout, subturbinate, with orbiculate or lobed cells, sometimes very broadly compressed with the cells long meandering; exterior stoutly lamello-striate and echinato-dentate; lamellae coarsely dentate or gashed-toothed, unequally exsert.' (Dana, 1846: 173).

3. 'Le polprier est composé, élevé, plus ou moins cespiteux; les polypières sont libres entre eux ou unis en séries toujours simples et toujours libres latéralement. Les murailles sont nues ou ne présentent qu'une épithèque rudimentaire; elles sont striées longitudinalement et garnies d'épines plus ou moins nombreuses. Les calices sont plus ou moins déformés; ils ont une fossette bien distincte et même assez profonde; la columelle est spongieuse et plus ou moins développée. Les systèmes cloisonnaires sont en général inégaux et irréguliers, mais on reconnaît ordinairement dans l'appareil septal des traces manifestes du type hexaméral. On trouve toujours des cloisons nombreuses, débordantes, très-peu granulées et fortement dentées; leurs dents sont longues, mais inégales, les extérieures étant beaucoup plus fortes que les autres et spiniformes. Les loges interseptales sont médiocrement profondes; le tissu endothécial est bien développé.' (Milne Edwards, 1857: 328–329).

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai (1928: 202–208); Wells (1936: 120–121; 1956); Vaughan & Wells (1943: 192, 195; F418); Walton Smith (1971: 92); Zlatarski & Estalella (1982: 165–177); Veron (2000: vol. 3: 64–65).

Diagnosis: Macromorphology: colonial; intracalicular budding. Phaceloid, with short series (usually one to three centres per series, but occasionally up to five); large calices (2.5–4.5 cm) with high relief (> 6 mm), four septal cycles, slightly unequal; thin, curved septa, with wide septal spacing; continuous, spongy (> three threads) columella with trabecular linkage; reduced epitheca; no septal or paliform lobes; abundant endotheca (Figs 9A, B, 12A, B).

Micromorphology: high (> 0.6 mm), widely spaced (1–2 mm), spine-shaped, pointed teeth, regularly arranged; layered (banded) interarea of septal teeth; teeth in major and minor septal cycles similar in size; spongy columella, with columellar teeth differing in size and shape from septal teeth; spiky, aligned granules (Fig. 18A–C).

Microstructure: parathecal wall with trabeculothecal elements. Widely separated (> 1.2 mm), well-developed clusters of calcification centres that cross medial lines; reduced thickening deposits (Fig. 22A–C).

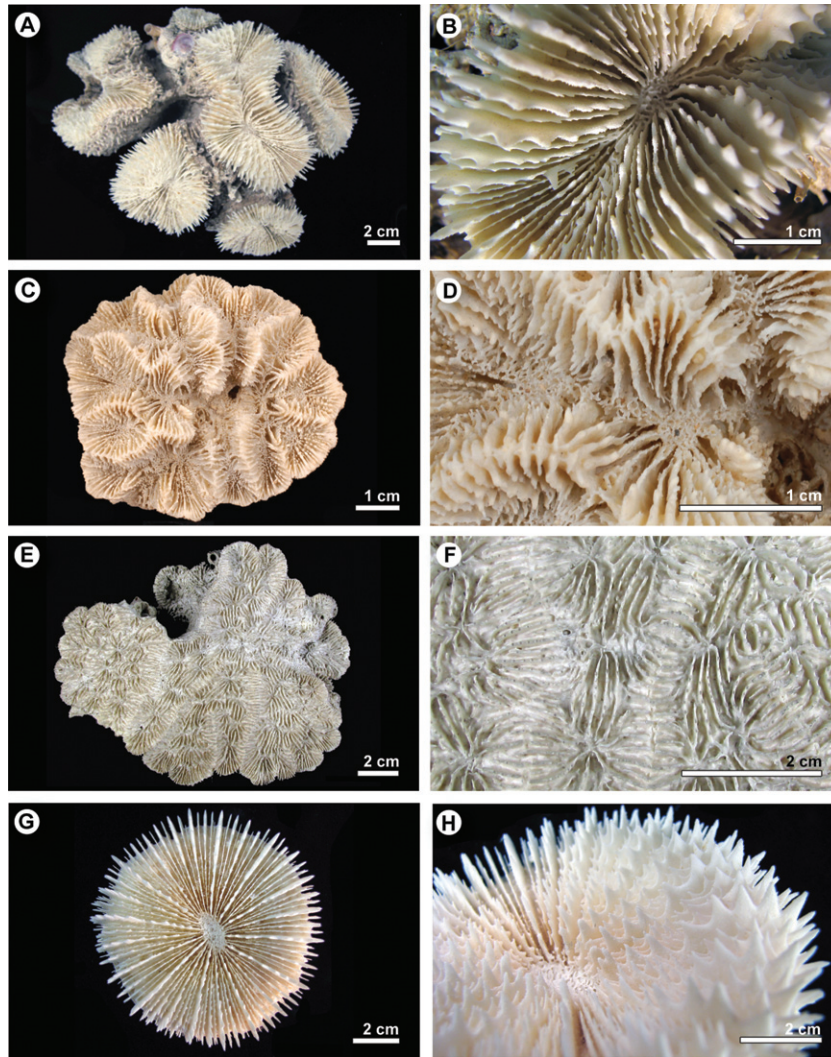


Figure 9. Type specimens of type species of genera in the subfamily Mussinae. A, B, genus *Mussa* Oken, 1815; *Madrepora angulosa* Pallas, 1766; neotype (designated herein) = YPM9035, Lime Cay, Port Royal, Jamaica. C, D, genus *Isophyllia* Milne Edwards & Haime, 1851a; *Oulophyllia?* *spinosa* Milne Edwards & Haime, 1849 [= *Isophyllia sinuosa* (Ellis & Solander)]; holotype = MNHN-scle866, unknown locality. E, F, genus *Mycetophyllia* Milne Edwards & Haime, 1848; *Mycetophyllia lamarchiana* Milne Edwards & Haime, 1849; holotype = MNHN-scle910, unknown locality. G, H, genus *Scolymia* Haime, 1852; *Madrepora lacera* Pallas, 1766; neotype (designated herein) = YPM9036, Rio Bueno, Jamaica.

Included species [monotypic genus]: *Mussa angulosa* (Pallas, 1766: 299). [Holotype is from 'Mare Americanum' and is lost; neotype (herein designated) = YPM9035, Fig. 9A, B, Port Royal, Jamaica.]

Remarks: Concepts of the genus have progressively narrowed through time. In Vaughan & Wells (1943) and Wells (1956), the genus was broadly defined to include solitary forms [e.g. *Scolymia* (= *Lithophyllia*)] in addition to the phaceloid colonial form *Mussa angulosa*. Later Wells (1964), followed by Walton

Smith (1971), separated solitary *Scolymia* from colonial *Mussa*.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Mussa* is distinguished by having a phaceloid colony form, regular septal dentation, and corallite centres with trabecular linkage (Vaughan & Wells, 1943: 192, 195). Our observations show further that, like other members of the subfamily Mussinae, it has a predominantly parathecal corallite wall; centres of calcification within the costosepta and columella that form a

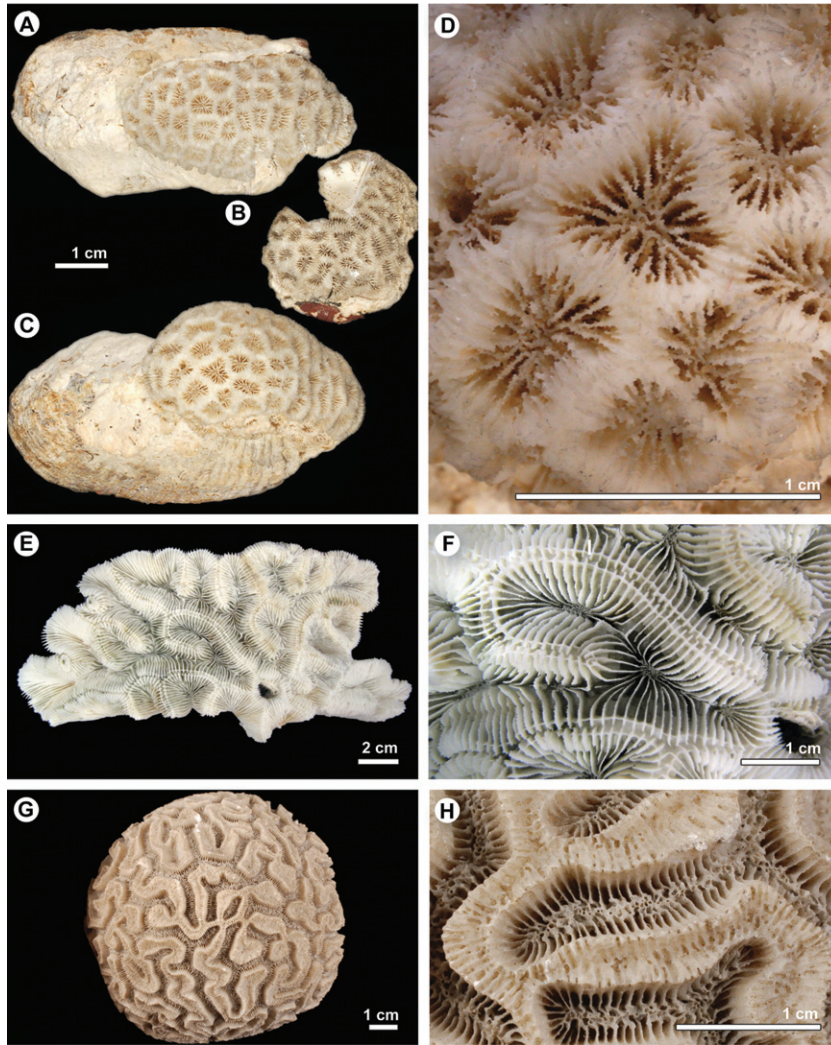


Figure 10. Type specimens of type species of genera in the subfamily Faviinae. A–D, genus *Favia* Milne Edwards & Haime, 1857; *Madrepora fragum* Esper, 1795; neotype (C, D, designated herein) = MNHN-scle560, Haiti. E, F, genus *Colpophyllia* Milne Edwards & Haime, 1848; *Meandrina gyrosa* de Lamarck, 1816 [= *Madrepora natans* Houttuyn, 1772]; neotype (designated herein) = SUI130588 (Carlson #828), Crawl Cay, Bocas del Toro, Panama. G, H, genus *Diploria* Milne Edwards & Haime, 1848; *Meandrina cerebriformis* de Lamarck, 1816; holotype = MNHN-scle102, unknown locality.

medial line crossed by well-developed clusters of centres; spine-shaped septal teeth; and septal granules consisting of aligned spikes. In addition to colony form, this genus differs from the meandroid members of the subfamily Mussinae by having four septal cycles and a spongy columella. Atlantic *Mussa* is superficially similar in growth form to Indo-Pacific *Lobophyllia*, but differs by having trabecular linkage (not lamellar) between corallite centres, better developed septal granules, and limited thickening deposits (e.g. thin septa).

The genus *Mussa* is recognized as monotypic by Walton Smith (1971); Zlatarski & Estalella (1982); Cairns, Hoeksema & Land (1999); and Veron (2000).

GENUS *ISOPHYLLIA* MILNE EDWARDS & HAIME, 1851A: 87 (FIGS 9C, D, 13A–F, 19A–F, 23A–F)

Synonyms: *Isophyllastrea* Matthai, 1928: 262 [type species: *Astraea rigida* Dana, 1846: 237; pl. 12, fig. 8a–d (by original designation).]

Type species: *Oulophyllia?* *spinosa* Milne Edwards & Haime, 1849: 269, holotype = MNHN-Scle866 (Fig. 9C, D) [= *Madrepora sinuosa* Ellis & Solander, 1786: 160]; by original designation.

Type species locality: ‘Patrie inconnue’ (Milne Edwards & Haime, 1849: 269) [Recent].

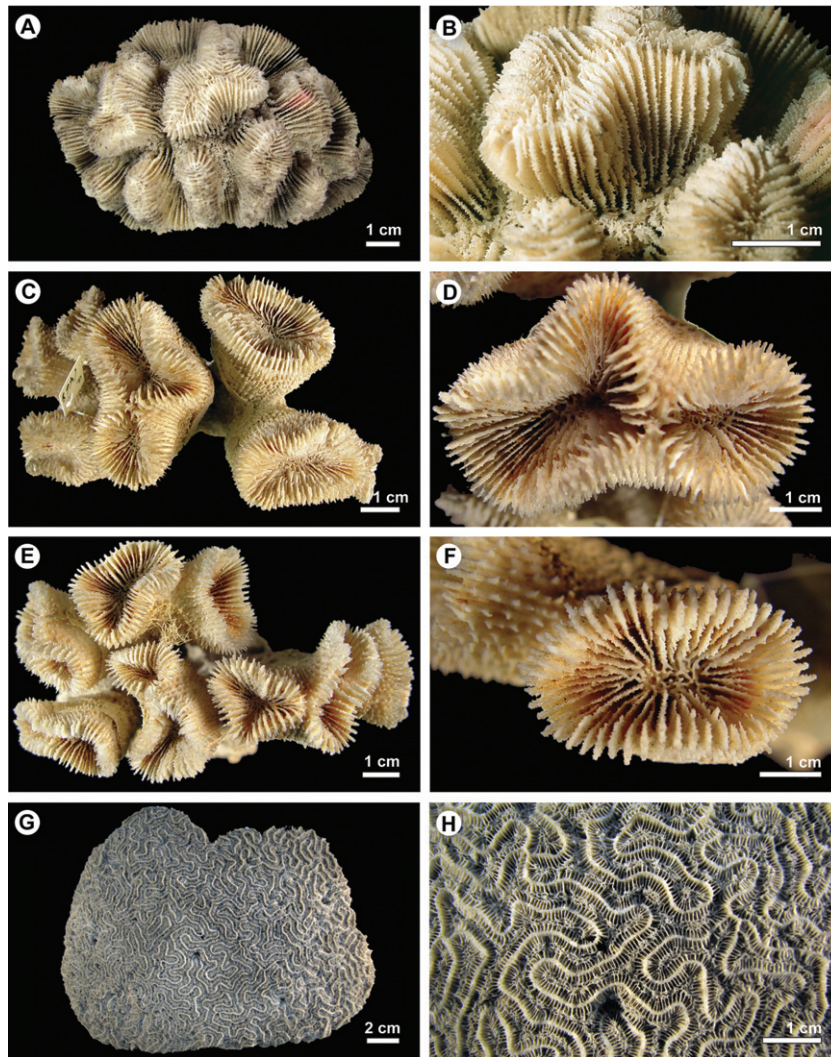


Figure 11. Type specimens of type species of genera in the subfamily Faviinae. A, B, genus *Manicina* Ehrenberg, 1834; *Madrepora areolata* Linnaeus, 1758; neotype (designated herein) = ZMB-Cni673, St. Thomas, US Virgin Islands. C–F, genus *Mussismilia* Ortmann, 1890; *Mussa harttii* Verrill, 1868; lectotype in two pieces (designated herein) = YPM1468a, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil. G, H, genus *Pseudodiploria* Fukami, Budd & Knowlton, new genus; *Meandrina strigosa* Dana, 1846; holotype = USNM00005, West Indies.

Early descriptions:

1. 'Polypier massif; multiplication par fissiparité; polypiérites à centres distincts, restant confondus en séries courtes qui sont soudées entre elles latéralement; cloisons fortement dentées, et dont les dents sont subégales; columelle rudimentaire; endothèque très-abondante; épithèque distincte.' (Milne Edwards & Haime, 1851a: 87).
2. Original description, *Isophyllastrea*: 'Corallum. Massive. Corallites mostly with mono- and di-stomodaeal polyps, those with monostomodaeal ones 10–12 mm in diameter. Colline somewhat thick, faintly grooved above or ridged. Septa thick-

ening towards wall, comparatively narrow, slightly sloping or almost vertical. Septal margins with teeth more or less resembling those in *Isophyllia*, sides of septa rough or spinulose. Septa meeting in groove on colline or continuous over ridged colline, exert ends toothed. Columella feebly developed, consisting of loosely interlocking septal trabeculae.' (Matthai, 1928: 262).

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai (1928: 235–248, 262–268); Vaughan & Wells (1943: 192–193, 195–196); Wells (1956: F418, F419); Walton Smith (1971: 92–94);

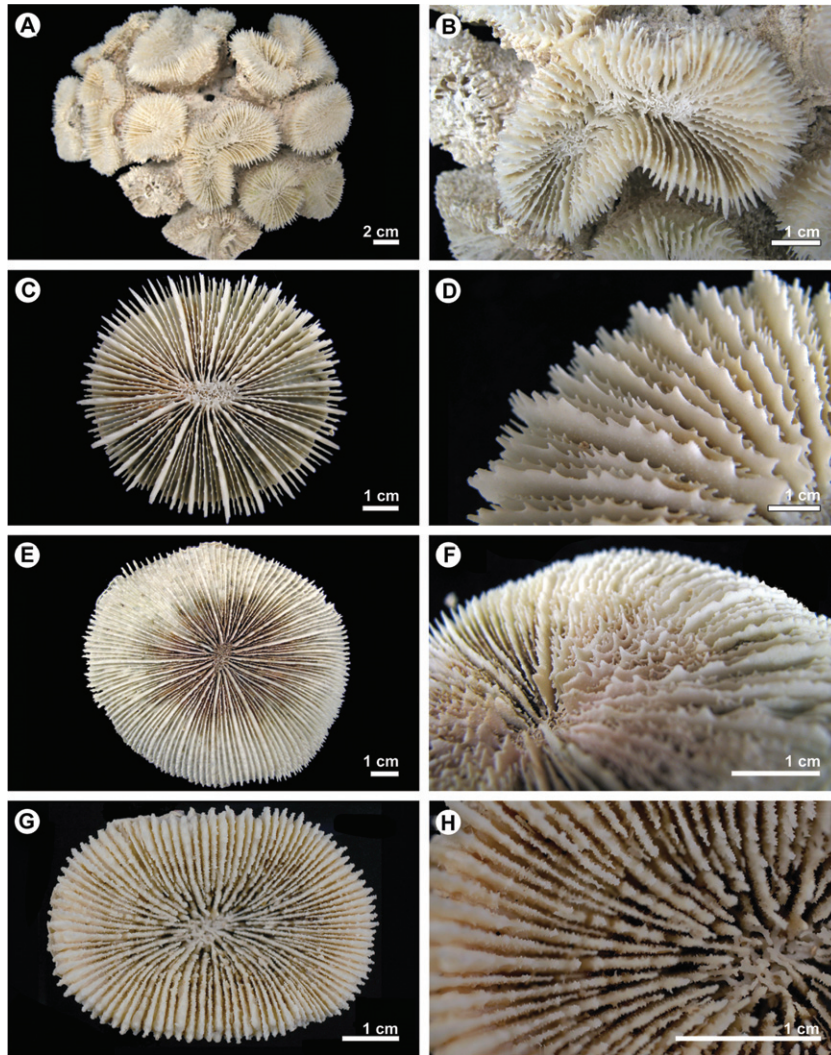


Figure 12. *Mussa* and *Scolymia* macromorphology. *Mussa* and *Scolymia* have large discrete calices (> 4 cm), and a trabecular columella; however *Mussa* is colonial (phaceloid) and *Scolymia* is solitary. *Mussa* has four complete septal cycles, whereas *Scolymia* has five. A, B, *Mussa angulosa* (Pallas, 1766); figured specimen = SUI102763 (FA1135), Key Largo, Florida, USA. C, *Scolymia lacera* (Pallas, 1766); figured specimen = YPM7567, Runaway Bay, Jamaica. D, *Scolymia lacera* (Pallas, 1766); figured specimen = YPM7568, Runaway Bay, Jamaica. E, F, *Scolymia cubensis* (Milne Edwards & Haime, 1849); neotype (designated herein) = YPM7569, Runaway Bay, Jamaica. G, H, *Scolymia wellsi* (Laborel, 1967); holotype = MNHN-scle20175, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil.

Zlatarski & Estalella (1982: 177–182); Veron (2000: vol. 3: 36–37).

Diagnosis: Macromorphology: colonial. Intracalicular budding; initially circumoral. Meandroid (uniserial), usually short series (< five centres per series); medium calices (2.5–5 cm) with high relief (> 6 mm); three or more septal cycles, equal; thin, costate coenosteum; costae not confluent; weak continuous columella with trabecular linkage; reduced epitheca; no septal or paliform lobes; abundant endothea (Figs 9C, D, 13A–F).

Microstructure: parathecal wall with trabeculothecal elements. Well-developed clusters of calcification centres encircled by concentric rings of fibrous thickening deposits; clusters cross medial lines; reduced thickening deposits (Fig. 23A–F).

Micromorphology: high (> 0.6 mm), widely spaced (1–2 mm), spine-shaped, pointed teeth, regularly arranged; layered (banded) interarea of septal teeth; teeth in major and minor septal cycles similar in size; compact columella, with columellar teeth differing in size and shape from septal teeth; spiky, aligned granules (Fig. 19A–F).

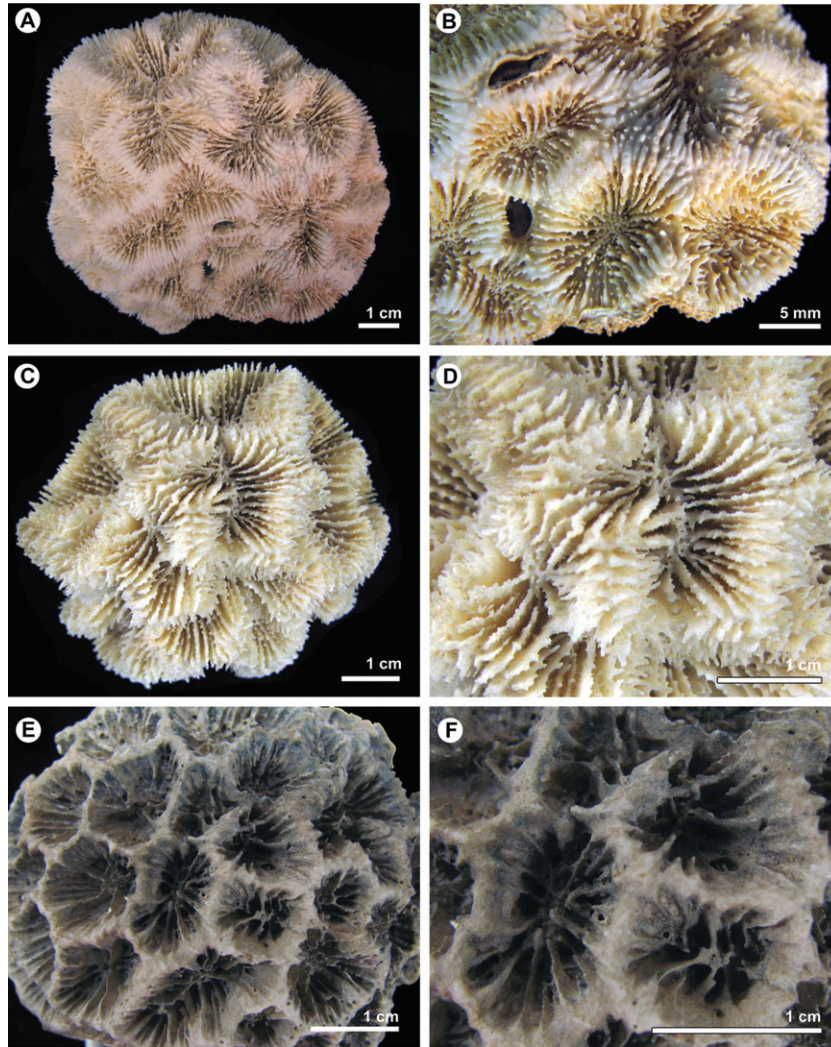


Figure 13. *Isophyllia* macromorphology. *Isophyllia* is distinguished by short, uniserial valleys; coenosteum; and trabecular linkage between centres. The three species differ in number of centres per series, calice width, and number of septa per cm. A, B, *Isophyllia sinuosa* (Ellis & Solander, 1786); neotype (designated herein) = SUI102759 (FA1134), Key Largo, Florida, USA. C, D, *Isophyllia multiflora* (Verrill, 1901); holotype = YPM4009, Bermuda. E, F, *Isophyllia rigida* (Dana, 1846); holotype = YPM4297, West Indies.

Included species: Isophyllia sinuosa (Ellis & Solander, 1786: 160) [holotype is from ‘Oceano Indie occidentalis’, and is lost; neotype (herein designated) = SUI102759 (FA1134), Fig. 13A, B, Key Largo, Florida].

Isophyllia multiflora (Verrill, 1901: 125) [holotype = YPM4009, Fig. 13C, D, Bermuda].

Isophyllastrea rigida (Dana, 1846: 237, pl. 12, fig. 8a–d) [holotype = YPM4297, Fig. 13E, F, West Indies].

Remarks: Milne Edwards & Haime (1849) originally designated *Oulophyllia? spinosa* as the type species of *Isophyllia* based on a specimen in their collection

(MNHN-Scle866). As indicated in Matthai (1928: 237), this species has subsequently been synonymized with *Isophyllia sinuosa* (Ellis & Solander), the type specimen of which is lost. A neotype (SUI102759, collected in Key Largo, Florida) has been therefore designated for *Isophyllia sinuosa*.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Isophyllia* is distinguished by having a meandroid colony form, and centres with trabecular linkage; colonies form initially by circumoral budding (Vaughan & Wells, 1943: 192). These authors point out that *Isophyllia* differs from *Symphyllia* (its superficially similar Indo-Pacific counterpart), in that *Symphyllia* has longer series and

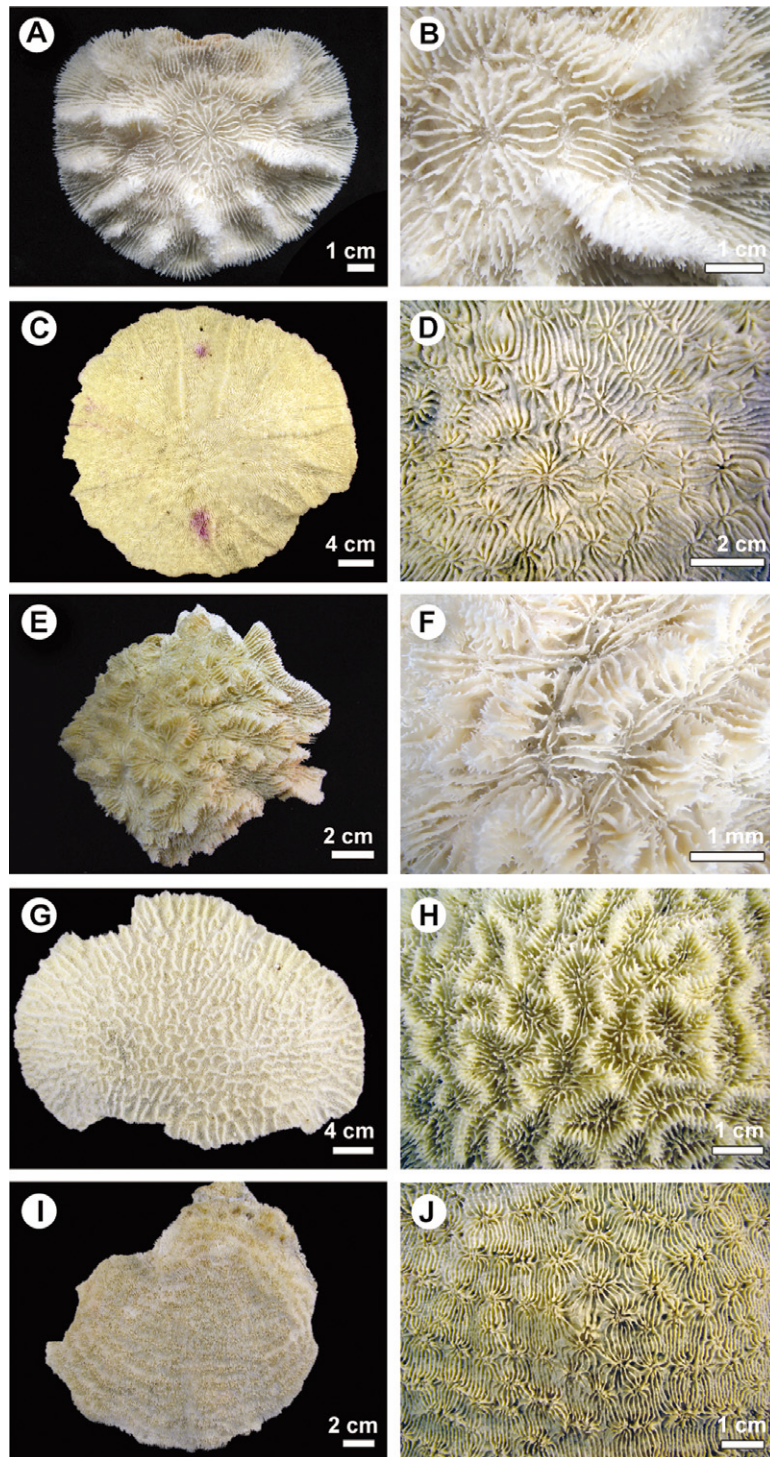


Figure 14. *Mycetophyllia* macromorphology. *Mycetophyllia* is distinguished by long, uniserial or multiserial valleys (absent in *Mycetophyllia reesi*); confluent septa; no coenosteum; and lamellar linkage between centres. The five species differ in colony form, especially the structure of valleys and collines. A, B, *Mycetophyllia lamarckiana* (Milne Edwards & Haime, 1849); figured specimen = SUI102774 (FA1138), Red Buoy, Discovery Bay, Jamaica. C, D, *Mycetophyllia aliciae* Wells, 1973; holotype = USNM53496, The Bull, Discovery Bay, Jamaica. E, F, *Mycetophyllia danaana* (Milne Edwards & Haime, 1849); neotype (designated herein) = SUI102772 (FA1003), Bocas del Toro, Panama. G, H, *Mycetophyllia ferox* Wells, 1973; holotype = USNM53494, Eaton Hall, Jamaica. I, J, *Mycetophyllia reesi* Wells, 1973; holotype = USNM53493, West Bull, Jamaica.

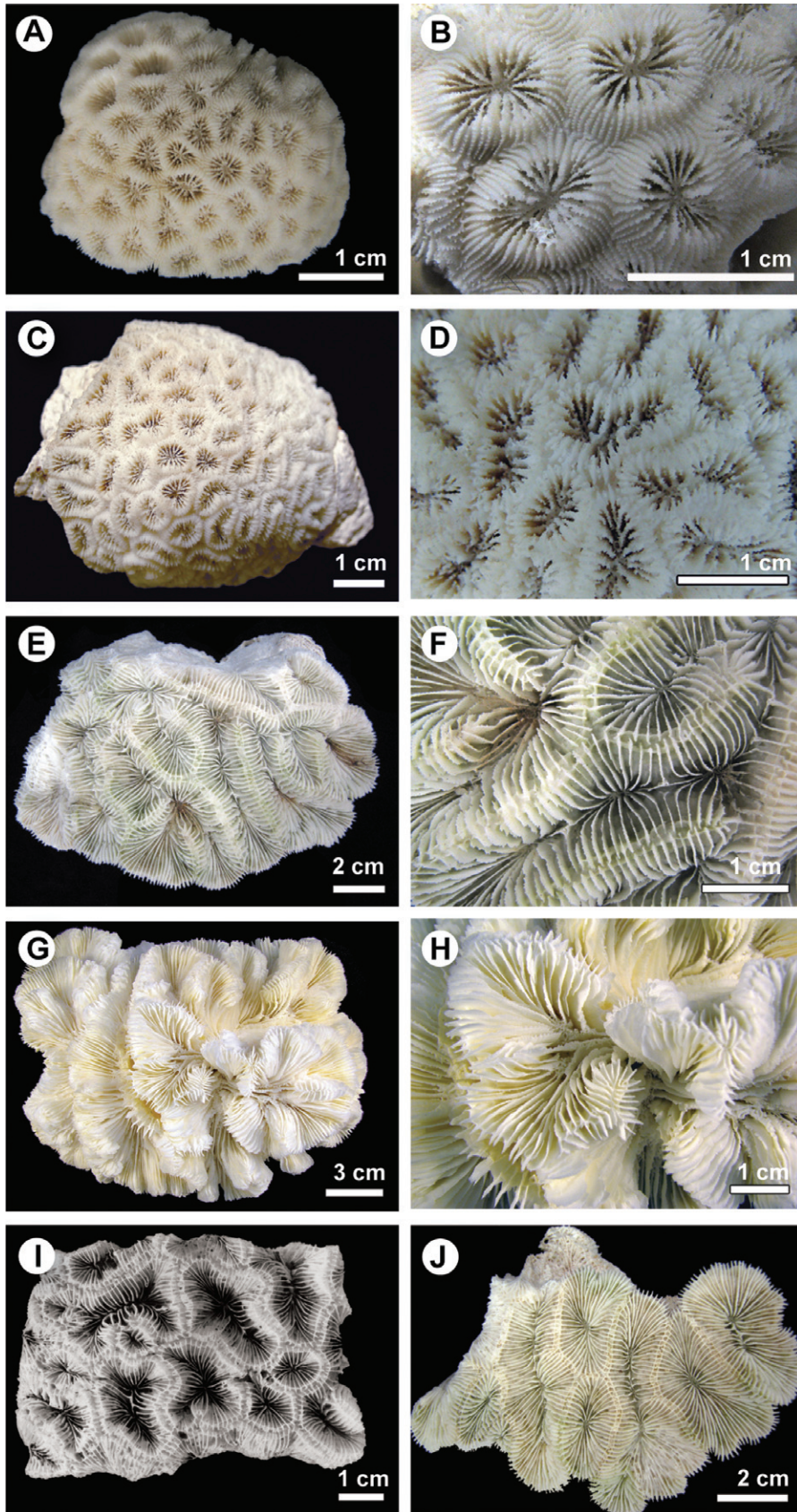


Figure 15. *Favia* and *Colpophyllia* macromorphology. *Favia* is plocoid (one to three centres) with a continuous compact trabecular columella, whereas *Colpophyllia* is meandroid with a discontinuous columella and lamellar linkage between centres. Both have small septal lobes and reduced coenosteum, which forms a distinctive double wall in *Colpophyllia*. Species of *Favia* differ in calical elevation and numbers of septa; species of *Colpophyllia* differ in valley length. A, *Favia fragum* (Esper, 1795); figured specimen = SUI131966 (Carlson #640), STRI Point, Bocas del Toro, Panama. B, *Favia fragum* (Esper, 1795); figured specimen SUI131967 (Carlson #644), STRI Point, Bocas del Toro, Panama. C, D, *Favia gravida* (Verrill, 1868); holotype = YPM1465, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil. E, F, *Colpophyllia natans* (Houttuyn, 1772); figured specimen = SUI130590 (Carlson #825), Crawl Cay, Bocas del Toro, Panama. G, H, *Colpophyllia amaranthus* (Houttuyn, 1772); neotype (designated herein) = USNM100498, Venezuela. I, *Colpophyllia breviserialis* (Milne Edwards & Haime, 1849); holotype = BM(NH)18.40.5.29. 6, unknown locality (figured by Matthai, 1928: pl. 71, fig. 9). J, *Colpophyllia breviserialis* (Milne Edwards & Haime, 1849); figured specimen = SUI130587 (Carlson #842), STRI Point, Bocas del Toro, Panama.

centres with lamellar linkage. Our observations show *Isophyllia* differs from *Mycetophyllia*, in that *Mycetophyllia* lacks coenosteum and has confluent costosepta, centres with lamellar linkage, and paliform lobes. *Isophyllia* differs from Indo-Pacific *Symphyllia* in *Isophyllia*'s possession of an epitheca, the shape of their septal teeth and granules, and the fact that teeth in major and minor septal cycles in *Symphyllia* differ in size and shape.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the monotypic genus *Isophyllastrea* is similar to *Isophyllia* in having similarly shaped, large teeth (regular, pointed with circular bases); colonies that form initially by circumoral budding; and short series with trabecular linkage. It is distinguished by having a cerioid colony form and feeble columella (Vaughan & Wells, 1943: 193, 195–196). However, our observations show that *Isophyllastrea* is not truly cerioid because it has coenosteum, like *Isophyllia*, and columellae in the two taxa are equally developed (Fig. 23A, B, D, E). Moreover, molecular data (cyt *b* and COI) show that *Isophyllia sinuosa* and *Isophyllastrea rigida* are identical (H. Fukami, unpubl. data). Nevertheless *Isophyllastrea rigida* is distinguished from *Isophyllia sinuosa* on the basis of microstructure (well-developed concentric rings associated with septal teeth, Fig. 23D–F), and micromorphology (smooth interarea of teeth, Fig. 19D–F). We feel that the similarities outweigh the differences, and synonymize the genus *Isophyllastrea* with *Isophyllia*, as in Zlatarski & Estalella (1982) and Veron (2000) but not Walton Smith (1971) and not Cairns, Hoeksema & Land (1999). We consider the two species to be distinct.

Following Matthai (1928), Walton Smith (1971) recognized three species of *Isophyllia* + *Isophyllastrea* (*Isophyllia sinuosa*, *Isophyllia multiflora*, *Isophyllastrea rigida*); whereas Zlatarski & Estalella (1982) recognized only one species (*Isophyllia sinuosa*), and Cairns, Hoeksema & Land (1999) recognized two species (*Isophyllia sinuosa*, *Isophyllastrea rigida*). Veron (2000) recognized *Isophyllia sinuosa* and *Isophyllastrea rigida*.

The three possible species of *Isophyllia* recognized herein (*I. sinuosa*, *I. multiflora*, *I. rigida*) are distinguished on the basis of number of centres per series, calice width, and number of septa per cm (Fig. 13). *Isophyllia sinuosa* and *I. multiflora* form series (valleys with two or more centres), whereas *I. rigida* is usually monocentric. Valley widths in *I. sinuosa* average 20–25 mm, in *I. multiflora* 12–15 mm, and in *I. rigida* 10–12 mm. Number of septa per cm range from seven to nine in *I. sinuosa*, and 11–12 in *I. multiflora*. *I. rigida* has 25–30 septa per corallite (more than three septal cycles).

GENUS *MYCETOPHYLLIA* MILNE EDWARDS & HAIME, 1848: 491–492 (FIGS 9E, F, 14A–J, 19G–O, 23G–O)

Synonyms: None.

Type species: *Mycetophyllia lamarchiana* Milne Edwards & Haime, 1849: 258, holotype = MNHN-Scle910 (Fig. 9E, F); by subsequent designation, Milne Edwards & Haime, 1849: 258.

Type species locality: 'Patrie inconnue' (Milne Edwards & Haime, 1849: 258) [Recent].

Original description: 'Très-voisin des Symphyllies, mais n'offrant pas de columelle et ayant les calices très-peu profonds. Murailles peu marqués, et cloisons en petit nombre.' (Milne Edwards & Haime, 1848: 491).

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai, 1928: 249–255; Vaughan & Wells (1943: 193, 196); Wells (1956: F419); Wells (1973: 34–43); Walton Smith (1971: 93–94); Zlatarski & Estalella (1982: 182–224); Veron (2000: vol. 3: 72–79).

Diagnosis: Macromorphology: colonial. Intracalicular and/or circumoral budding. Meandroid (uniserial and multiserial), with and without collines; centres spaced 5–15 mm apart; < three septal cycles, equal; limited

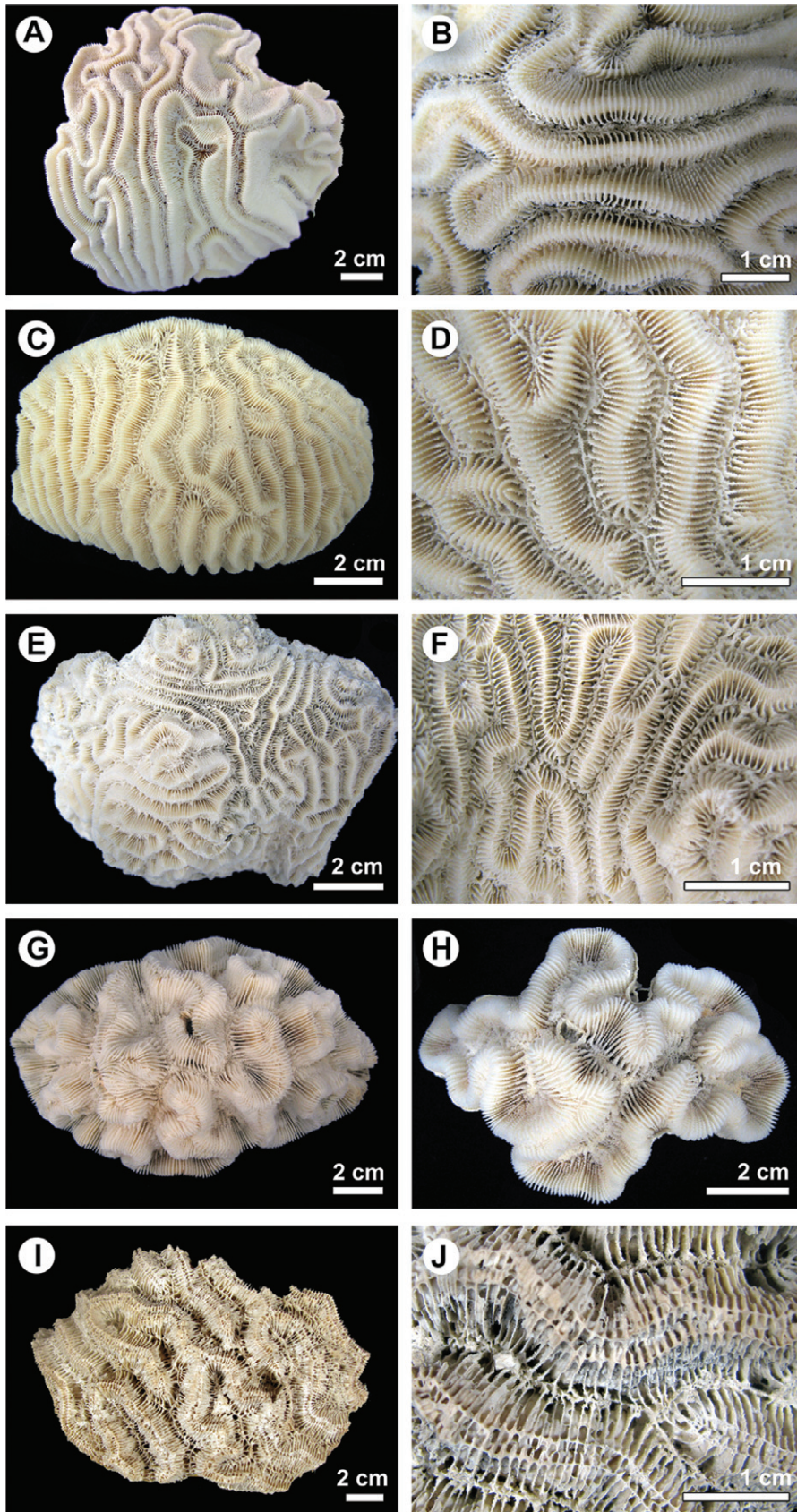


Figure 16. *Diploria*, *Pseudodiploria*, and *Manicina* macromorphology. *Diploria*, *Pseudodiploria*, and *Manicina* all have meandroid colony forms, with continuous trabecular columellae and septal lobes. *Diploria* is distinguished by medium valleys (4–8 mm), separated by a well-developed coenosteum and a grooved ambulacrum. *Pseudodiploria* has small to medium valleys (3.5–9 mm) containing distinct centres, which are separated by little or no coenosteum. *Manicina* has wider valleys (12–15 mm) with high relief (> 6 mm), limited coenosteum, and especially well-developed septal lobes. A, B, *Diploria labyrinthiformis* (Linnaeus, 1758); figured specimen = SUI122808 (FA1075), Bocas del Toro, Panama. C, D, *Pseudodiploria strigosa* (Dana, 1846); figured specimen = SUI122814 (FA1078), Bocas del Toro, Panama. E, F, *Pseudodiploria clivosa* (Ellis & Solander, 1786); neotype (designated herein) = SUI122811 (FA1076), Bocas del Toro, Panama. G, *Manicina areolata* (Linnaeus, 1758); figured specimen = SUI80507 (KJ-370), locality KJ-88P3, Punta Ventura, Panama. H, *Manicina areolata* (Linnaeus, 1758); figured specimen = SUI80495 (KJ-B316), locality KJ-88B3, Blue Ground Range, Belize. I, J, *Manicina mayori* (Wells, 1936); holotype = ZMB-Cni2859, unknown locality.

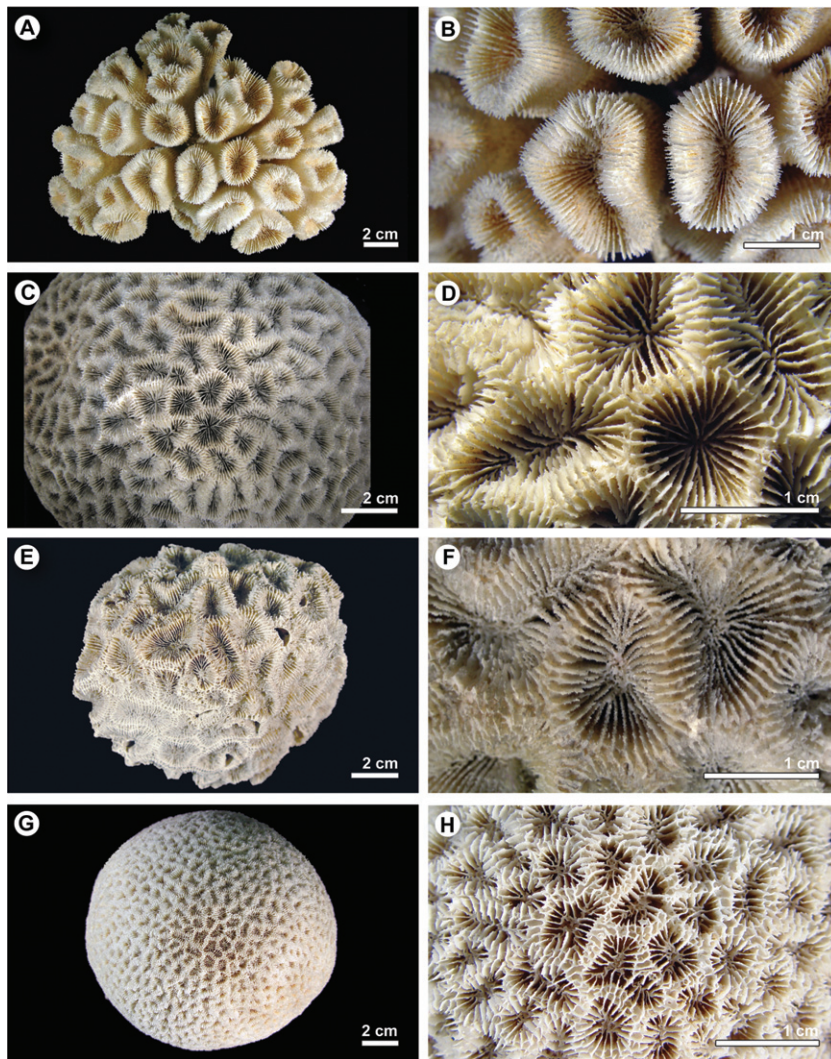


Figure 17. *Mussismilia* macromorphology. *Mussismilia* is phaceloid or subplocoid (one to three centres), with a distinctive double wall when coenosteum is present. The columella is continuous with trabecular linkage between centres. Species of *Mussismilia* differ in colony form and calice size. A, B, *Mussismilia hartti* (Verrill, 1868); figured specimen = YPM4516, Maria Farinha, Pernambuco, Brazil. C, D, *Mussismilia braziliensis* (Verrill, 1868); holotype = YPM1467, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil. E, F, *Mussismilia hispida* (Verrill, 1901); holotype = YPM4287, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil. G, H, *Mussismilia leptophylla* (Verrill, 1868); holotype = YPM1517A, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil.

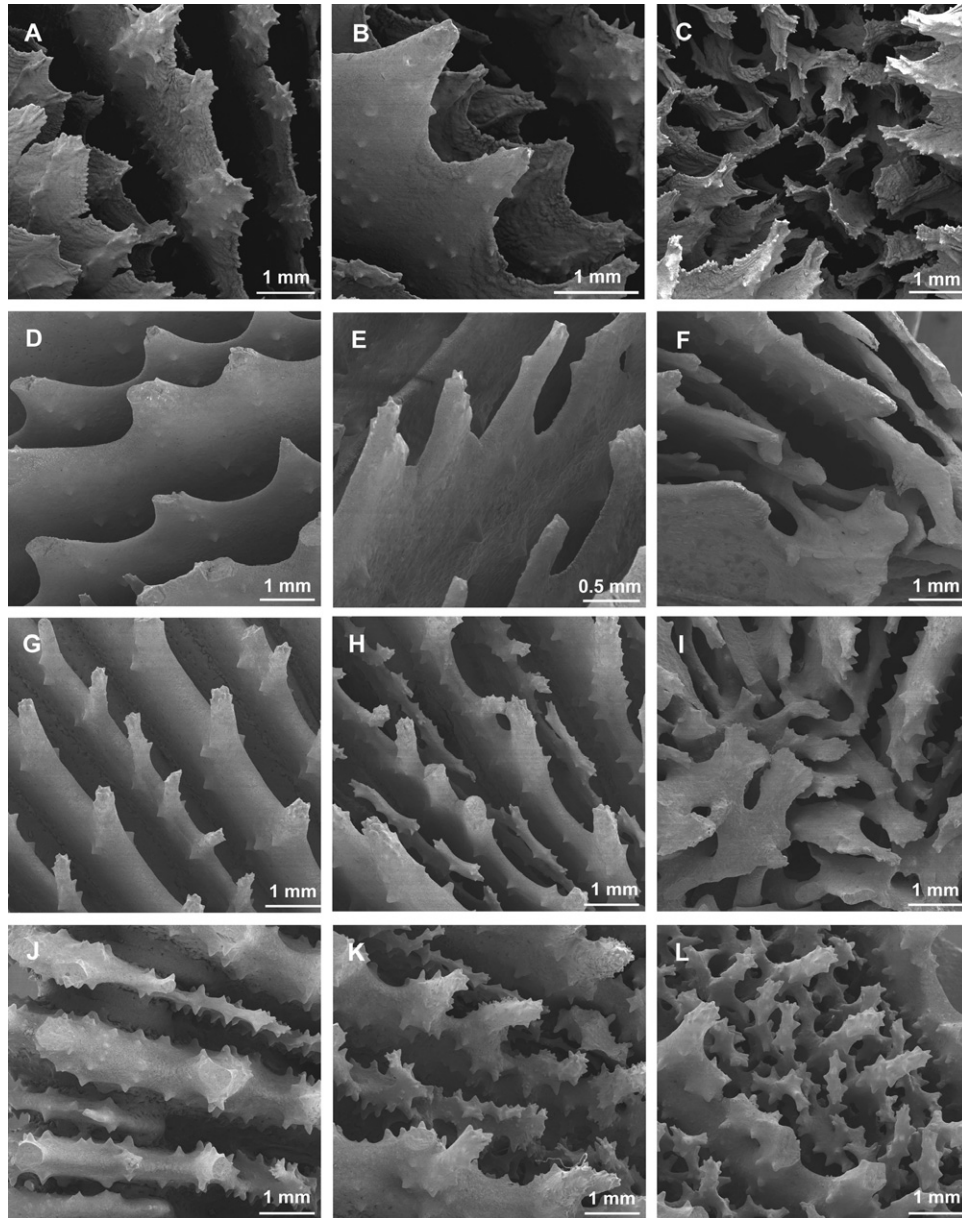


Figure 18. *Mussa* and *Scolymia* micromorphology (scanning electron microscopy): left column, wall; middle column, mid-septum; right column, columella. Both *Mussa* and *Scolymia* have high, spine-shaped teeth. *Mussa* is distinguished by thinner septa, and a distinctively horizontally layered interarea. The columellae of *Scolymia* have thick, paddle-shaped teeth, in comparison to the thinner platy teeth of *Mussa*. A–C, *Mussa angulosa* (Pallas, 1766); figured specimen = SUI102761 (FA1012), Bocas del Toro, Panama. D–F, *Scolymia lacera* (Pallas, 1766); figured specimen = USNM84920, Discovery Bay, Jamaica. G–I, *Scolymia cubensis* (Milne Edwards & Haime, 1849); figured specimens = USNM84940, Maria Buena Bay, Jamaica (G, H); SUI102777 (FA1097, SCUB16), Bocas del Toro, Panama (I). J–L, *Scolymia wellsi* (Laborel, 1967); figured specimen = USNM84926, Angel Reef, Tobago.

coenosteum and incomplete corallite walls, mostly confluent septa; absent or feeble discontinuous columella with lamellar linkage; reduced epitheca; pali-form lobes; abundant endotheca (Figs 9E, F, 14A–J).

Micromorphology: high (> 0.6 mm), widely spaced (1–2 mm), spine-shaped teeth, regularly arranged,

with spiked tips resembling a Medieval spiked mace weapon; layered (banded) interarea of septal teeth; feeble or absent columella; pali-form lobes; fine granules along the sides of teeth (Fig. 19G–O).

Microstructure: parathecal wall with trabeculothecal elements. Well-developed clusters of calcification

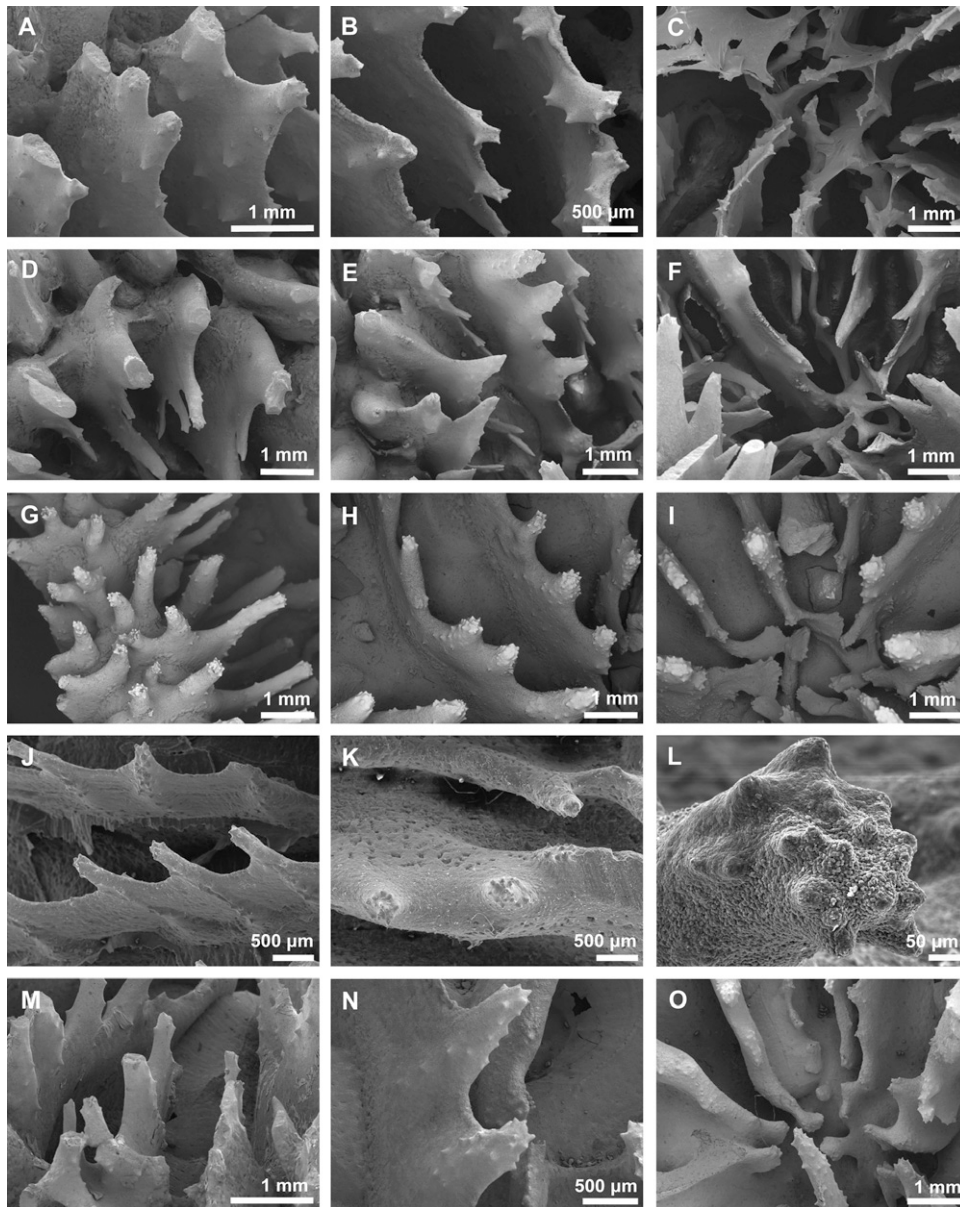


Figure 19. *Isophyllia* and *Mycetophyllia* micromorphology (scanning electron microscopy): left column, wall; middle column, mid-septum; right column, columella. *Isophyllia* and *Mycetophyllia* have high (>0.6 mm), widely spaced (1–2 mm), spine-shaped teeth; a horizontally layered interarea of septal teeth; and fine granules on the sides of teeth. A–C, *Isophyllia sinuosa* (Ellis & Solander, 1786); figured specimen = SUI102757 (FA1014), Bocas del Toro, Panama. D–F, *Isophyllia rigida* (Dana, 1846); figured specimen = SUI102753 (FA1074), Bocas del Toro, Panama. G–I, *Mycetophyllia lamarchiana* (Milne Edwards & Haime, 1849); figured specimen = SUI102773 (FA1133), Discovery Bay, Jamaica. J–L, *Mycetophyllia aliciae* (Wells, 1973); figured specimen = SUI102769 (FA1006), Bocas del Toro, Panama. M–O, *Mycetophyllia danaana*? (Milne Edwards & Haime, 1849); figured specimen = SUI102771 (FA1002), Bocas del Toro, Panama.

centres encircled by concentric rings of fibrous thickening deposits; clusters cross medial lines; reduced thickening deposits (Fig. 23G–O).

Included species: *Mycetophyllia lamarchiana* Milne Edwards & Haime, 1849: 258 [holotype = MNHN-Scle910, Fig. 9E, F, unknown locality].

Mycetophyllia aliciae Wells, 1973: 41, figs 25–28 [holotype = USNM53496, Fig. 14C, D, Discovery Bay, Jamaica].

Mycetophyllia danaana Milne Edwards & Haime, 1849: 259 [holotype is from an unknown locality, and is lost (A Andouche, pers. comm., 2007). We herein designate specimen SUI102772 (FA1003) (Fig. 14E,

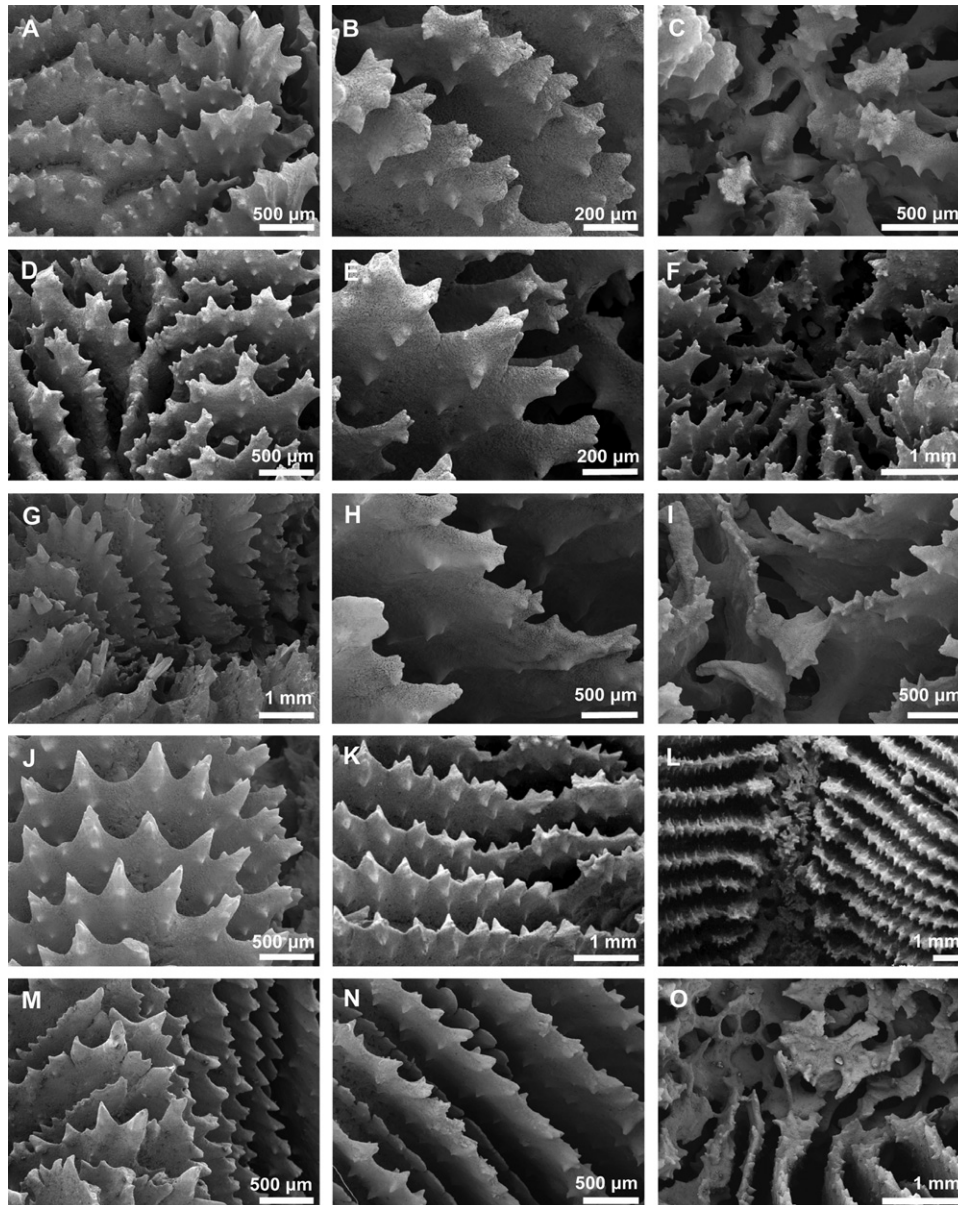


Figure 20. *Favia*, *Diploria*, and *Pseudodiploria* micromorphology (scanning electron microscopy): left column, wall; middle column, mid-septum; right column, columella. *Favia*, *Diploria*, and *Pseudodiploria* have paddle-shaped to tricorne teeth with elliptical bases orientated perpendicular to the septal plane. The interarea of teeth is smooth, and granules are spiked and aligned. Teeth in different septal cycles differ slightly in *Favia*, but are equal in *Diploria* and *Pseudodiploria*. A–C, *Favia fragum* (Esper, 1795); figured specimen = SUI122816 (FA1065), Bocas del Toro, Panama. D–F, *Favia gravida* (Verrill, 1868); figured specimen = YPM4518, Rio Grande Do Norte State, Fernando de Noronha Archipelago, Brazil. G–I, *Diploria labyrinthiformis* (Linnaeus, 1758); figured specimen = SUI122810 (FA1061), Bocas del Toro, Panama. J–L, *Pseudodiploria strigosa* (Dana, 1846); figured specimens = SUI122813 (FA1062), Bocas del Toro, Panama (J, K); SUI122815 (FA1103), Discovery Bay, Jamaica (L). M–O, *Pseudodiploria clivosa* (Ellis & Solander, 1786); figured specimen = SUI122807 (FA1060), Bocas del Toro, Panama.

F) collected by H. Fukami at Bocas del Toro, Panama as the neotype.]

Mycetophyllia ferox Wells, 1973: 40, figs 22–24 [holotype = USNM53494, Fig. 14G, H, Eaton Hall, Jamaica].

Mycetophyllia reesi Wells, 1973: 36, figs 19–21 [holotype = USNM53493, Fig. 14I, J, West Bull, Jamaica]

Remarks: In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Mycetophyllia*

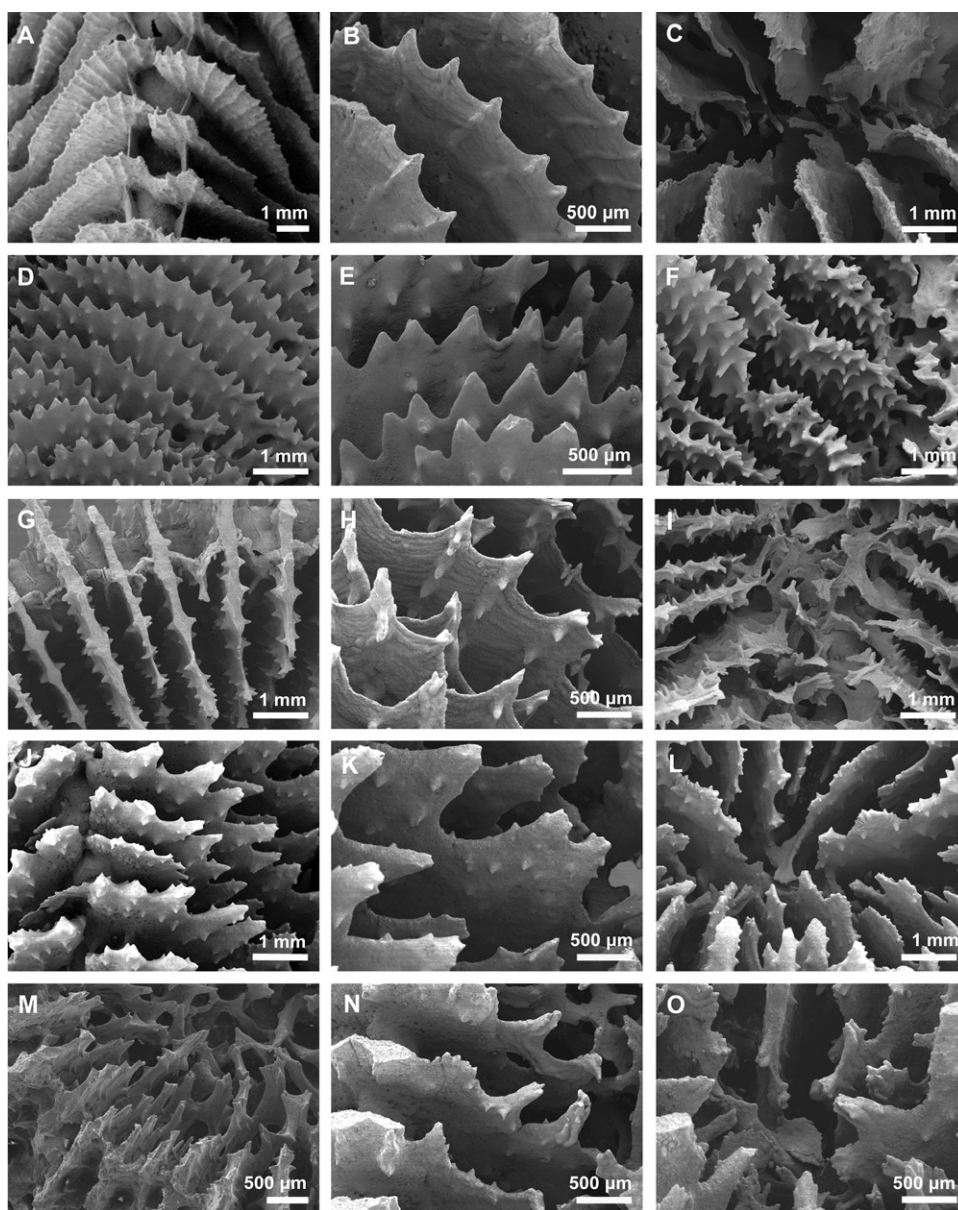


Figure 21. *Colpophyllia*, *Manicina*, and *Mussismilia* micromorphology (scanning electron microscopy): left column, wall; middle column, mid-septum; right column, columella. *Colpophyllia*, *Manicina*, and *Mussismilia* have paddle-shaped to tricorne teeth with elliptical bases orientated perpendicular to the septal plane. Tooth height is low (<0.3 mm) in *Colpophyllia* and *Manicina*, and medium to high (>0.3 mm) in *Mussismilia*. The interarea of teeth is smooth in *Manicina* but horizontally banded in *Colpophyllia* and *Mussismilia*. Granules are spiked and aligned. A–C, *Colpophyllia natans* (Houttuyn, 1772); figured specimens = SUI122804 (FA1100) Discovery Bay, Jamaica (A); SUI122802 (FA1071), Bocas del Toro, Panama (B, C). D–F, *Manicina areolata* (Linnaeus, 1758); figured specimen = SUI122824 (FA1107), Bocas del Toro, Panama. G–I, *Mussismilia hartti* (Verrill, 1868); figured specimen = YPM4516, Maria Farinha, Pernambuco, Brazil. J–L, *Mussismilia braziliensis* (Verrill, 1868); figured specimen = YPM9104, Santa Barbara Island, Abrolhos Archipelago, Bahia, Brazil. M–O, *Mussismilia leptophylla* (Verrill, 1868); figured specimen = SUI99645 (FA1029), Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil (M); YPM9087, Lixa Reef, Abrolhos Archipelago, Bahia, Brazil. (N, O).

is distinguished by having a meandroid colony form, long series, centres with lamellar linkage, discontinuous collines enclosing one or more continuous series, and a reduced or absent columella; colonies form

initially by circumoral budding (Vaughan & Wells, 1943: 193, 196). Our observations indicate that it also has paliform lobes. *Mycetophyllia* is generally similar to *Isophyllia* in microstructure and micromorphology.

Isophyllia differs from *Mycetophyllia* in that *Mycetophyllia* lacks a coenosteum, and has confluent costosepta, centres with lamellar linkage, and paliform lobes, as described above.

Following Wells (1973), Cairns, Hoeksema & Land (1999) and Veron (2000) recognized five species of *Mycetophyllia*, whereas Zlatarski & Estalella (1982) recognized two (*Mycetophyllia lamarckiana*, *Mycetophyllia? reesi*), the latter one of which was only questionably assigned to *Mycetophyllia*. Lang's (1973) experimental studies of aggressive interactions found that *Mycetophyllia ferox* was the most aggressively superior, followed by *Mycetophyllia reesi*, but there was no interaction amongst *Mycetophyllia lamarckiana*, *Mycetophyllia aliciae*, and *Mycetophyllia danaana*. The five species of *Mycetophyllia* are distinguished primarily on the basis of colony form, which may be highly variable within species. *Mycetophyllia reesi* is distinguished by circumoral budding and no collines (Fig. 14I, J); and *Mycetophyllia ferox* by intracalicular budding and narrow (~10 mm), meandering, sometimes discontinuous valleys with continuous forked collines (Fig. 14G, H). *Mycetophyllia aliciae*, *Mycetophyllia danaana*, and *Mycetophyllia lamarckiana* all initially have circumoral budding (less pronounced in *Mycetophyllia danaana*), followed by intracalicular budding, and straight, continuous valleys. The valleys in *Mycetophyllia aliciae* are multiseriate and the collines discontinuous (Fig. 14C, D), whereas the valleys in *Mycetophyllia danaana* and *Mycetophyllia lamarckiana* are uniseriate. *Mycetophyllia danaana* and *Mycetophyllia lamarckiana* also tend to have less pronounced paliform lobes than the other three species (J. Lang, pers. comm.). *Mycetophyllia danaana* has deep valleys (10–12 mm), sometimes forming monticules (superficial 'hydnochoroid pillars' sensu Wells, 1973), discontinuous collines, and more septa (12–16 per cm; Fig. 14E, F); whereas *Mycetophyllia lamarckiana* has broad, shallow (< 10 mm) valleys, continuous collines, and fewer septa (six to seven per cm; Fig. 14A, B). Danaher (1998) interpreted *Mycetophyllia lamarckiana* and *Mycetophyllia danaana* as being synonymous based on analyses of skeletal variation caused by environmental gradients related to energy and nutrient acquisition (functional plasticity).

GENUS *SCOLYMIA* HAIME, 1852: 279 (FIGS 9G, H, 12A, B, 18A–C, 22A–C)

Synonyms: *Lithophyllia* Milne Edwards, 1857: 290 [type species = *Madrepora lacera* Pallas, 1766, by subsequent designation (Felix, 1925: 100)].

Type species: *Madrepora lacera* Pallas, 1766: 298; by subsequent designation, Vaughan, 1901: 6. Holotype

is lost. We herein designate specimen YPM9036 collected by J. C. Lang in 1968 at Rio Bueno, Jamaica, as the neotype.

Original type species locality: 'Mare Americanum' (Pallas, 1766: 298) [Recent].

Original descriptions:

1. 'Je propose donc de laisser le nom de *Caryophyllia* à tous les polypiers qui présentent les caractères reconnus en 1828 par M. Stokes, et que M. Ehrenberg et nous-mêmes avons décrits depuis celui de *Cyathina*, en assignant au genre *Caryophyllia*, Milne Edw. et J. Haime (Compt. rend. de l'Ac. des sc., t. XXVII: 491, 1848 – non Stokes), si tant est que cette division mérite d'être conservée la dénomination de *Scolymia* que lui donne M. Jourdan dans la collection du Musée de Lyon. Cette restauration est d'autant plus importante, qu'il n'y a pour ainsi dire pas deux auteurs qui aient attribué la même un terme à cette regrettable confusion.' (Haime, 1852: 279)
2. 'Coral cylindro-turbinata, cylindrical, or almost prismatical, in all ages attached to the ground by an expanded base, without a distinct epitheca. Costae prominent, roughly spinose, the uppermost spines being the strongest. Calicle shallow, circular, rarely oblong, rectangular or lobate. Septa of first and second cycles with their free edges lacero-dentate, the teeth increasing in size from within outwards. Columella oblong in outline, consisting of thin trabeculae, its surface finely papillose or imbricate.' (Brüggemann, 1877: 301)

Subsequent morphological descriptions (Matthai, 1928, and later): = *Mussa* in Matthai (1928: 202–208); = *Mussa* in Vaughan & Wells (1943: 195); = *Mussa* in Wells (1956: F418); Wells (1964: 375–384); Laborel (1969: 217–222); Lang (1971: 952–959); Wells (1971: 960–962); Walton Smith (1971: 92); Zlatarski & Estalella (1982: 157–165); Veron (2000: vol. 3: 66–71); Neves *et al.* (2006: 45–54).

Diagnosis: Macromorphology: solitary, with rare intracalicular budding; large calices (> 4 cm), more than four septal cycles, unequal; well-developed, spongy (> three threads) columella with lamellar linkage; reduced epitheca; no septal or paliform lobes; abundant endotheca (Figs 9G–H, 12C–H).

Micromorphology: high (> 0.6 mm), widely spaced (1–2 mm), spine-shaped, pointed teeth, regularly arranged; smooth interarea of septal teeth; teeth in major and minor septal cycles differ in size; spongy columella, with columellar teeth differing in size and shape from septal teeth; spiky, aligned granules (Fig. 18D–L).

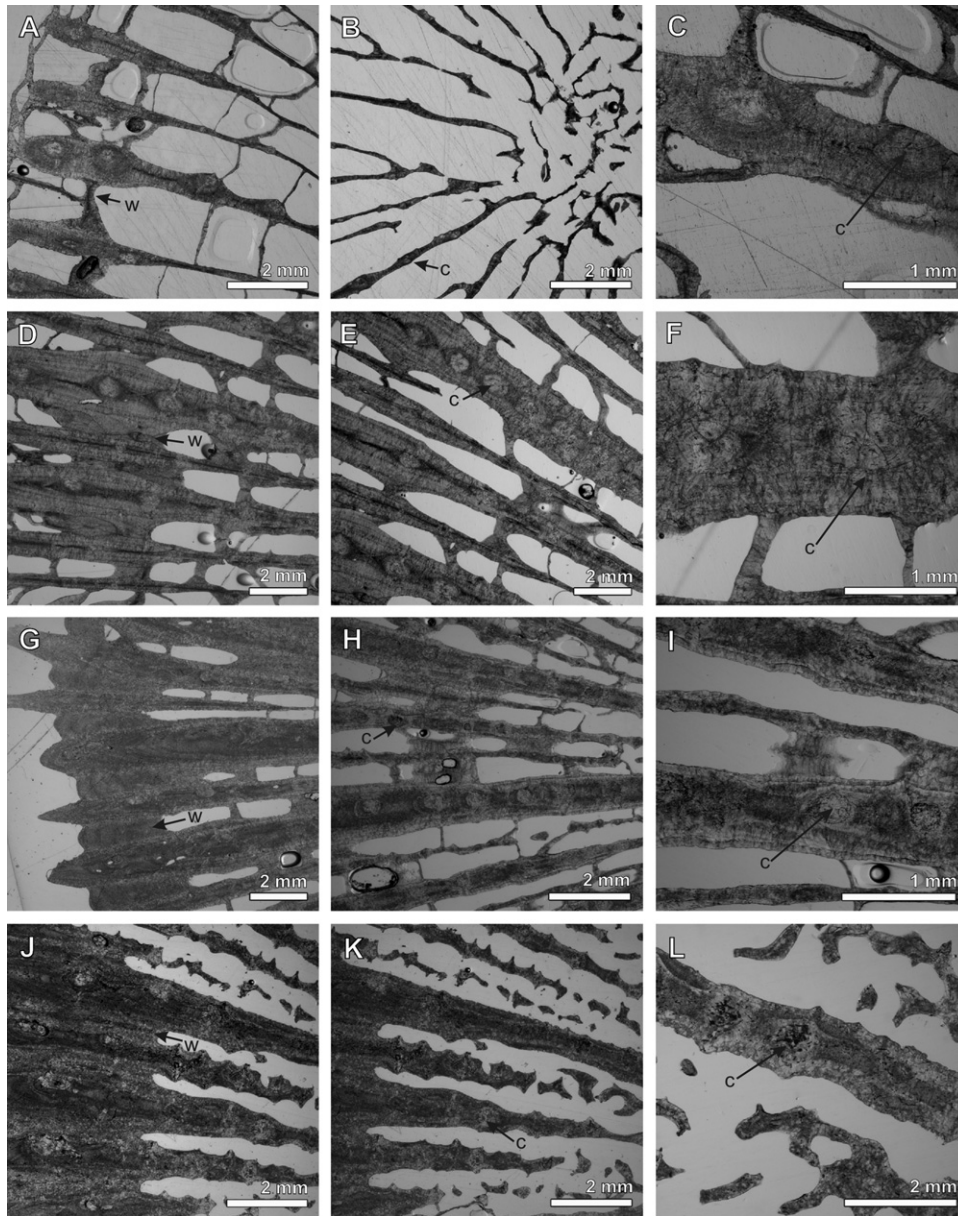


Figure 22. *Mussa* and *Scolymia* microstructure (transverse thin section): left column, wall; middle column, mid-septum; right column, close-up of clusters. Both *Mussa* and *Scolymia* have parathecal walls (w); however, trabeculothecal elements and thickening deposits are better developed in *Scolymia*. Both genera form well-developed clusters of calcification centres (c) that cross medial lines. These clusters are more closely spaced in *Scolymia*. A–C, *Mussa angulosa* (Pallas, 1766); figured specimen = SUI102761 (FA1012), Bocas del Toro, Panama. D–F, *Scolymia lacera* (Pallas, 1766); figured specimen = USNM1090899, Bahia Concha, Colombia. G–I, *Scolymia cubensis* (Milne Edwards & Haime, 1849); figured specimen = USNM84939, Maria Buena Bay, Jamaica. J–L, *Scolymia wellsii* (Labrel, 1967); figured specimen = USNM84926, Angel Reef, Tobago.

Microstructure: parathecal wall with trabeculothecal elements. Widely separated (> 1.2 mm), well-developed clusters of calcification centres encircled by concentric rings of fibrous thickening deposits; clusters cross weak medial lines; moderate thickening deposits (Fig. 22D–L).

Included species: Scolymia lacera (Pallas, 1766: 298) [holotype is from ‘Mare Americanum’, and is lost; neotype (herein designated) = YPM9036, Fig. 9G, H, Rio Bueno, Jamaica].

Scolymia cubensis (Milne Edwards & Haime, 1849: 238) [holotype is from Cuba, and is lost (A. Andouche,

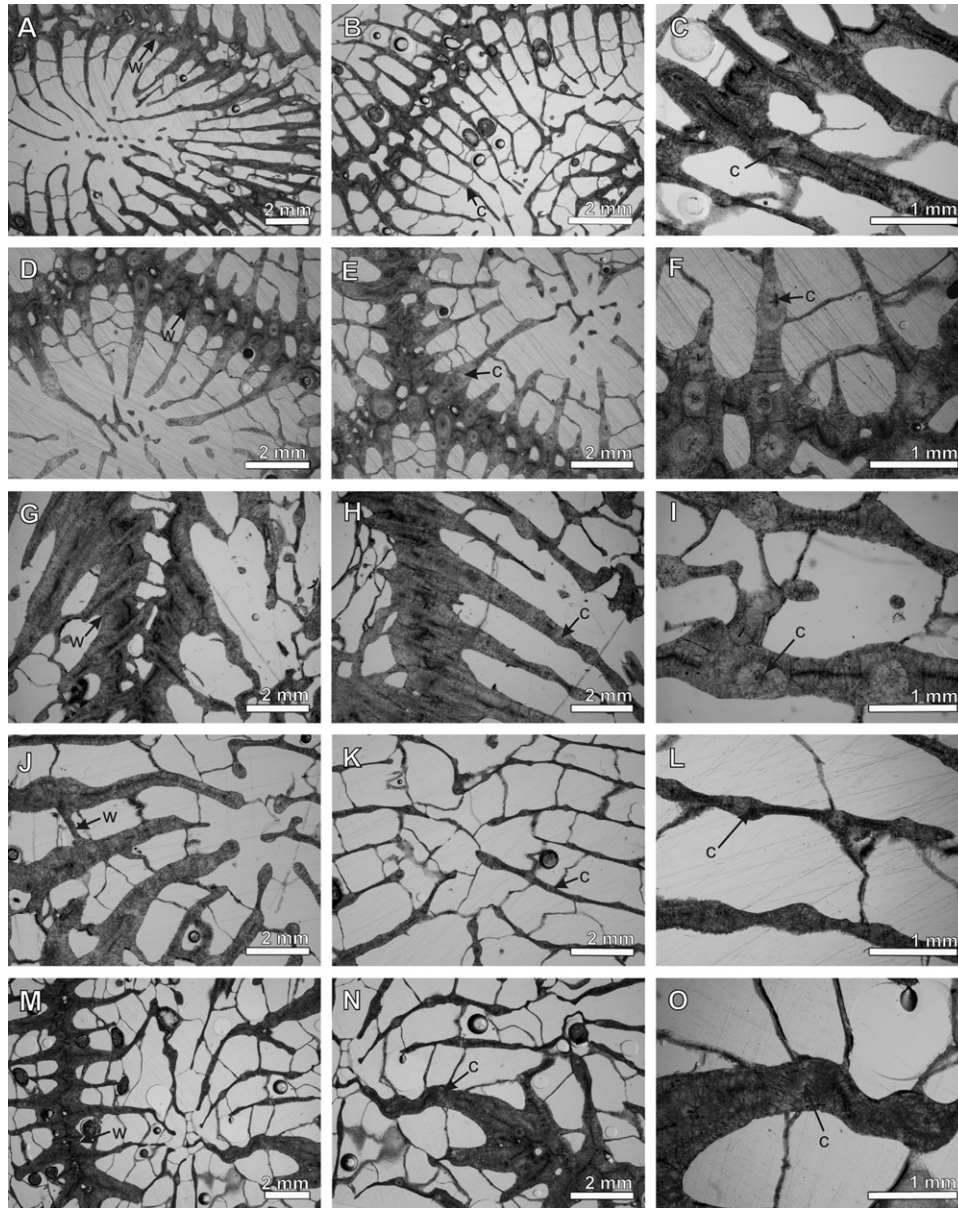


Figure 23. *Isophyllia* and *Mycetophyllia* microstructure (transverse thin section): left column, wall; middle column, mid-septum; right column, close-up of clusters. Both *Isophyllia* and *Mycetophyllia* have parathecal walls (w) with trabeculothecal elements, well-developed clusters of calcification centres (c) that cross medial lines, and reduced thickening deposits. A–C, *Isophyllia sinuosa* (Ellis & Solander, 1786); figured specimen = SUI102757 (FA1014), Bocas del Toro, Panama. D–F, *Isophyllia rigida* (Dana, 1846); figured specimen = SUI102752 (FA1009), Bocas del Toro, Panama. G–I, *Mycetophyllia lamarchiana* (Milne Edwards & Haime, 1849); figured specimen = SUI102773 (FA1133), Discovery Bay, Jamaica. J–L, *Mycetophyllia aliciae* (Wells, 1973); figured specimen = SUI102768 (FA1005), Bocas del Toro, Panama. M–O, *Mycetophyllia danaana?* (Milne Edwards & Haime, 1849); figured specimen = SUI102771 (FA1002), Bocas del Toro, Panama.

pers. comm., 2009); neotype (herein designated) = YPM7569, Fig. 12E, F, Runaway Bay, Jamaica].

Scolymia wellsii (Laborel, 1967: 107, figs 1–3) (holotype = MNHN-Scle20175, Fig. 12G, H, Abrolhos Archipelago, Brazil).

Remarks: Following Zlatarski & Estalella (1982), Veron (2000) synonymized *Scolymia lacera* (Pallas) with *Mussa angulosa* (Pallas), and redesignated *Scolymia cubensis* (Milne Edwards & Haime, 1849) as the type species of *Scolymia*. Our observations

indicate that *Scolymia lacera* and *Mussa angulosa* are distinct. *Scolymia* differs from *Mussa* in its colony form, more extensive thickening deposits, more closely spaced clusters of calcification centres (< 1.8 mm), smooth interarea of septal teeth, and distinctive paddle-shaped columellar teeth. When budding, it also has lamellar linkage, in contrast to trabecular linkage in *Mussa*. We therefore retain *Madrepora lacera* Pallas, 1766, as the type species of *Scolymia*.

As described by Wells (1964: 375–376), the genus *Scolymia* is characterized by wholly dentate septal margins, dentations four to six (per) cm on larger septa, large calices (> 4 cm), centres with trabecular linkage, and sparse septal granules. *Scolymia* is distinguished from the genus *Homophyllia* [type species = *Homophyllia australis* (Milne Edwards & Haime, 1849)] on the basis of number of dentations [ten to 12 (per) cm in *Homophyllia*] and calice size (< 4 cm in *Homophyllia*). *Scolymia* is distinguished from the genus *Parascolymia* [type species = *Parascolymia vitiensis* (Brüggemann, 1877)] on the basis of septal granulation (more numerous and thicker in *Parascolymia*). Wells (1964) also indicates that *Scolymia* has trabecular linkage amongst centres, as opposed to *Parascolymia*. However, our observations show that linkage in *Scolymia* is indeed lamellar. Veron (2000: vol. 3: 66–71) later assigned *Homophyllia australis* and *Parascolymia vitiensis* to the genus *Scolymia*, presumably because of their monocentric colony form, and their 'large, regular, blunt teeth'. Following the molecular results of Fukami *et al.* (2004), we restrict the definition of the genus to include only Atlantic taxa. The genus, therefore, does not include the following species described in Veron (2000): *Scolymia australis* (Milne Edwards & Haime, 1849: 310) [= *Homophyllia* Brüggemann, 1877]; *Scolymia vitiensis* Brüggemann, 1877: 304–305 [= *Parascolymia* Wells, 1964].

Wells (1971) recognized two species of *Scolymia* (*Scolymia lacera*, *Scolymia cubensis*), which were supported by Lang's (1971) experiments on aggressive interactions. Laborel (1967) described a third species, *Scolymia wellsi* from Brazil. Although Zlatarski & Estalella (1982) synonymized the three species, Cairns, Hoeksema & Land (1999) and Neves *et al.* (2006) recognized them as being distinct. As described by Neves *et al.* (2006), the three species can be distinguished on the basis of septal dentation. *Scolymia wellsi* has irregular teeth that are sometimes fused forming porous septa (Fig. 12G, H); *Scolymia cubensis* has long and slim teeth (> five per cm) that are awl-shaped (Fig. 12E, F); *Scolymia lacera* has large and stout teeth (< five per cm) that are subtriangular (Fig. 12C, D). Wells (1971) and Lang (1971) further noted that differences between lower and higher cycle

septa are more pronounced in *Scolymia lacera*, its calices are more concave, and its maximum calice diameters are larger (15 cm as opposed to 10 cm in *Scolymia cubensis*). The corallum of *Scolymia wellsi* is similar to *Scolymia cubensis*, although even smaller (< 6 cm). Given the morphological similarities amongst the three species, we have designated neotypes for *Scolymia lacera* and *Scolymia cubensis* using material collected and studied by Lang (1971).

SUBFAMILY FAVIINAE GREGORY, 1900: 29.

Type genus: Favia Milne Edwards, 1857

Original description: 'Compound Aporosa in which the corallum is massive or dendroid; the septa are numerous, imperforate, radial and usually hexamerous. The endotheca is dissepimental. Growth is in the main by fission.' (Gregory, 1900: 29).

Diagnosis: Macromorphology: colonial only; corallites discrete or arranged in uniaxial series (includes plocoid, meandroid, and phaceloid forms); coenosteum usually present, although limited; costosepta not confluent; epitheca reduced or well developed; septal lobes (except *Mussismilia*) (Fig. 2).

Micromorphology: regular, narrowly spaced (< 1 mm), tricornate or fan-shaped septal teeth (never spine-shaped or triangular), with elliptical bases orientated transverse to the septal plane; interarea of teeth smooth or consisting of horizontal bands; septal granules strong and aligned (Figs 3, 4).

Microstructure: septothecal or parathecal corallite walls, containing occasional trabeculothecal elements; clusters of centres of calcification within the costosepta and columella weakly developed (except *Mussismilia*), narrowly separated (< 0.6 mm), and connected by medial lines; carinae usually well developed (Figs 5, 6).

Genera included:

Favia Milne Edwards, 1857

Colpophyllia Milne Edwards & Haime, 1848

Diploria Milne Edwards & Haime, 1848

Manicina Ehrenberg, 1834

Mussismilia Ortmann, 1890

Pseudodiploria Fukami, Budd & Knowlton gen. nov.

Remarks: In the classification system of Vaughan & Wells (1943: 153) and Wells (1956: F400), the family Faviidae is distinguished by having a septothecal or parathecal wall; simple trabeculae, in one or two fan systems; dentate septal margins; dissepiments; and relatively small corallites (< 10 mm in diameter). As herein defined, the subfamily Faviinae is monophyletic (Fig. 7) and restricted to taxa whose septal teeth

are regular and narrowly spaced, with elliptical bases orientated transverse to the septal plane (i.e. paddle-shaped), and whose septal granules are strong, spiky, and aligned.

Unlike the subfamily Mussinae, which possesses spine-shaped or triangular teeth and diffuse granulation, the septal teeth of the Faviinae are tricorne or fan-shaped (elliptical bases); and septal granulation is well developed (evenly scattered or organized in lines).

Traditional Atlantic 'faviids' (including *Montastraea cavernosa* and the *Orbicella annularis* complex) are also distinguished from traditional Indo-Pacific 'faviids' on the basis of tooth shape. Indo-Pacific taxa have irregular spine-shaped or multidirectional teeth (often lacerate); whereas Atlantic taxa (excluding the *Orbicella annularis* complex) have regular, blocky teeth that are often paddle-shaped (see description in Budd & Stolarski, 2011).

Distribution: Atlantic only.

GENUS *FAVIA* MILNE EDWARDS, 1857: 426
(FIGS 10A–D, 15A–D, 20A–F, 24A–F)

[not Oken, 1815: 67, because all taxa in Oken book rejected by ICZN opinion 417 (ICZN Commission, 1956)]

Synonyms: None.

Type species: *Madrepora fragum* Esper, 1795: 79, pl. 64, figs 1, 2 [= *Madrepora ananas* Pallas, 1766]; by subsequent designation, Verrill, 1901: 88–91. Holotype is lost (Scheer, 1990; Cuif & Perrin, 1999). We herein designate specimen MNHN-scleFAV560 collected by Mr Ricord in Haiti (Cuif & Perrin, 1999) as the neotype (Fig. 10C, D).

Original type species locality: 'südlichen Americanischen Meeren' (Esper, 1795: 80) [Recent].

Original descriptions:

1. 'Röhren (=walls) in einem kitt, öffnen sich oben gleich hoch, laufen in leinen gemeinschaftlichen Stamm zusammen.' (Oken, 1815: 67).
2. 'Le polypier se compose de polypiérites unis entre eux par des côtes plus ou moins développées et une exothèque celluleuse. Les calices coservant des bords libres, soit subcirculaires, soit ovalaires. La columelle est spongieuse. Les cloisons sont débordantes; leurs dents internes sont les plus grandes et souvent même simulent des palis. L'endothèque est bien développée.' (Milne Edwards, 1857: 426–427).

Subsequent morphological descriptions (Matthai, 1928 and later): Not in Matthai, 1928 (but see Matthai, 1919); Vaughan & Wells (1943: 163, 166); Wells (1956: 402); Labrel (1969: 191–198); Cuif & Perrin (1999: 137–156); Walton Smith (1971: 79–80); Zlatarski & Estalella (1982: 61–66); Veron (2000: vol. 3: 100–131).

Diagnosis: Macromorphology: plocoid; discrete (one to three centres per series); costate coenosteum; small calices (< 4 mm) with three or more septal cycles; continuous, compact trabecular columella; well-developed epitheca; moderate endothea; small septal lobes (Figs 10A–D, 15A–D).

Micromorphology: distinctive paddle-shaped teeth, occasionally tricorne, with elliptical bases orientated transverse to the septal plane; smooth interarea of teeth; spiked granules organized in lines; teeth in major and minor septal cycles differ slightly in size (Fig. 20A–F).

Microstructure: septothecal wall; small (< 0.6 mm), well-defined clusters of calcification centres within costosepta, forming carinae orientated transverse to the septal plane; layered fibrous thickening deposits (Fig. 24A–F).

Species included: *Favia fragum* (Esper, 1795: 79, pl. 64, figs 1, 2). Holotype is from 'südlichen Americanischen Meeren', and is lost; neotype (herein designated) = MNHN-scleFAV560, Figure 10C, D, Haiti.

Favia gravida Verrill, 1868: 354 [syntypes = YPM1465A, B; Fig. 15C, D, Abrolhos Archipelago, Brazil] (= *Favia conferta* Verrill, 1868: 355) [syntypes = YPM1466A, B; YPM8268, Abrolhos Archipelago, Brazil].

Remarks: The genus *Favia* was originally described by Oken (1815: 67), who listed '*Favia ananas*' first as belonging to the genus. However, according to ICZN opinion 417 (ICZN Commission, 1956), the names originally proposed by Oken (1815) are rejected. Therefore authorship is based on subsequent use of the name. Ehrenberg (1834) was the second to use the name, but assigned an assortment of species to the genus, all of which have been subsequently assigned to other genera. Cuif & Perrin (1999) indicate 'Milne-Edwards, 1857' as the author of *Favia*, after Verrill (1901). This usage is followed here.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Favia* is distinguished by having a plocoid colony form; a costate coenosteum; a parietal (= trabecular) columella; and intracalicular budding. Septal margins are strongly dentate; trabeculae are usually simple, in one or two fan systems; and corallites are relatively

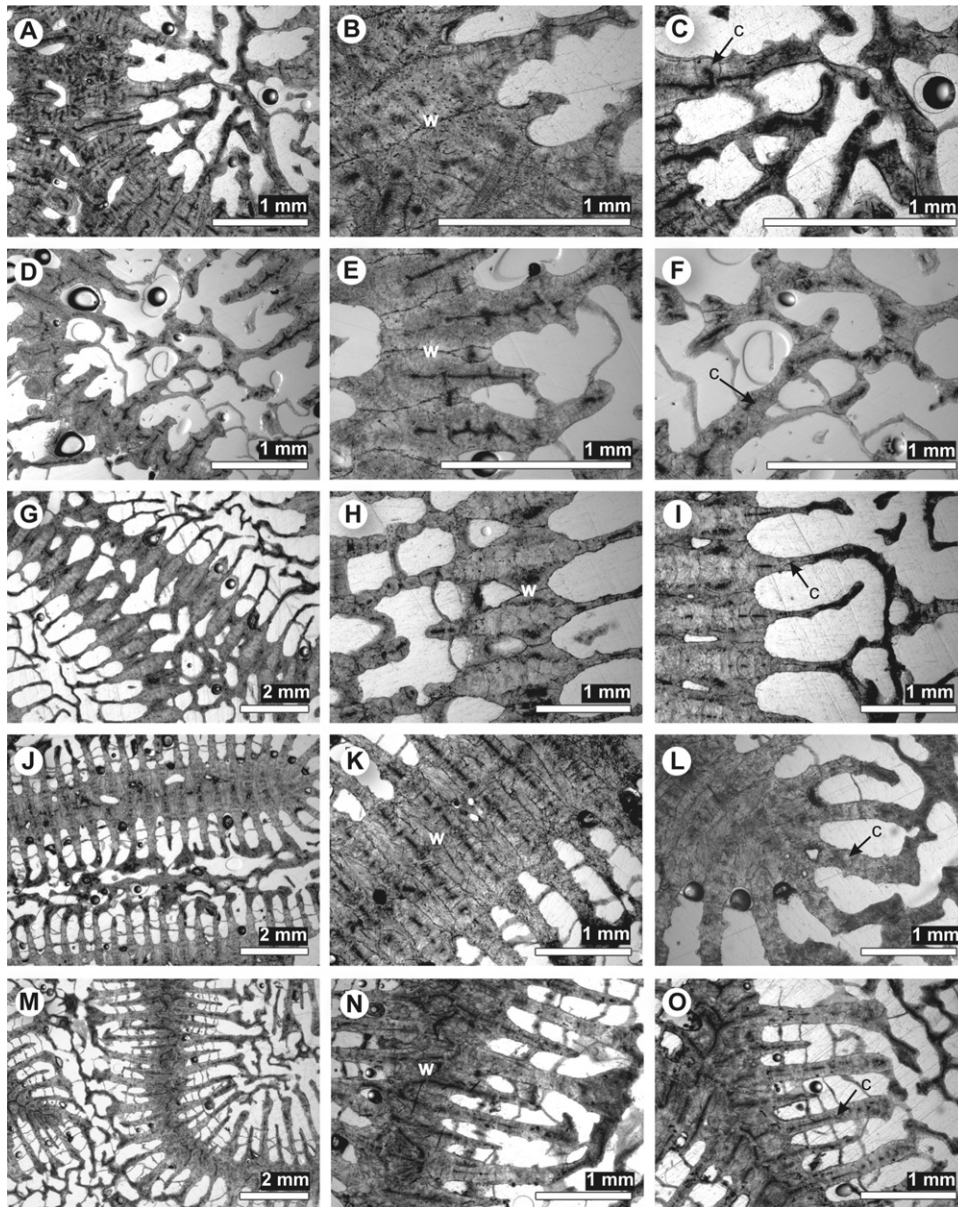


Figure 24. *Favia*, *Diploria*, and *Pseudodiploria* microstructure (transverse thin section): left column, whole corallite; middle column, wall; right column, columella. *Favia*, *Diploria*, and *Pseudodiploria* all have septothecal walls (w). In *Pseudodiploria*, there are also trabeculothecal components, and *Pseudodiploria strigosa* has abortive septa. Clusters of calcification centres (c) are well defined in *Favia*, moderately well defined in *Diploria*, and weak in *Pseudodiploria*; however, *Pseudodiploria* has better defined medial lines. Carinae are well developed in *Favia*, but not in the other two genera; thickening deposits are moderately developed in all three genera. A–C, *Favia fragum* (Esper, 1795); figured specimen = SUI122816 (FA1065), Bocas del Toro, Panama. D–F, *Favia gravida* (Verrill, 1868); figured specimen = YPM9085, Rio Formoso, Pernambuco, Brazil. G–I, *Diploria labyrinthiformis* (Linnaeus, 1758); figured specimen = SUI122810 (FA1061), Bocas del Toro, Panama. J–L, *Pseudodiploria strigosa* (Dana, 1846); figured specimen = SUI122813 (FA1062), Bocas del Toro, Panama. M–O, *Pseudodiploria clivosa* (Ellis & Solander, 1786); figured specimen = SUI122807 (FA1060), Bocas del Toro, Panama.

small (< 10 mm) (Vaughan & Wells, 1943: 153–154, 163, 166). As discussed above, it is distinguished from Indo-Pacific '*Favia*', herein referred to as *Dipstraera* de Blainville, 1830, on the basis of its

paddle-shaped septal teeth and septothecal corallite wall structure.

Our work shows that species traditionally assigned to the genus vary considerably in corallite wall struc-

ture (including parathecal, septothecal, and trabeculothecal walls) and in the shape of their septal teeth. We hereby restrict the definition of the genus to species with septothecal walls and multicentred paddle-shaped teeth orientated transverse to the septal plane, three characters that the genus *Favia* shares with *Manicina* as defined below. *Favia* is distinguished from *Manicina* on the basis of its short corallite series (= valleys), small calice width (< 4 mm) with low relief, its regular minor septa, and its compact (one to three threads) columella. In addition, the corallite walls of *Favia* are exclusively septothecal, whereas those of *Manicina* contain trabeculothecal elements.

Following Laborel (1969), Cairns, Hoeksema & Land (1999) listed two species of *Favia* (*Favia fragum*, *Favia gravida*) with septothecal walls from the Caribbean and Brazil; however, both Zlatarski & Estalella (1982) and Veron (2000) synonymized the two species. Walton Smith (1971) recognized *F. fragum* as distinct, and further split *F. gravida* into two species (*F. gravida*, *F. conferta*). Here we list and illustrate two species of *Favia* (*F. fragum*, *F. gravida*) following Nunes *et al.* (2008), who showed *F. fragum* and *F. gravida* to be genetically distinct. *Favia gravida* (Fig. 15C, D) is distinguished from *F. fragum* (Fig. 15A, B) on the basis of its more numerous septa (four complete septal cycles), somewhat longer series, higher calice elevation, and taller, more widely spaced septal teeth.

Following the molecular results of Fukami *et al.* (2004, 2008), we restrict the definition of the genus *Favia* to include only Atlantic taxa. The emended genus does not include the following species, which were assigned to it by Veron (2000) and are herein assigned to the genus *Dipsastraea* de Blainville, 1830 [type species: *Madrepora favus* Forskål, 1775 (SD: Wells, 1936)].

Species Assigned to Dipsastraea:

- Favia favus* (Forskål, 1775: 132) [lectotype = ZMK28, unknown locality]; not seen but illustrated in Veron *et al.*, 1977: 26 (fig. 28).
- Favia albida* Veron, 2000 (3): 112 ['Holotype' in Veron, 2002: 140 = G55788 (MTQ), Sharm al-Sheikh, Sinai Peninsula, Egypt], seen.
- Favia danai* (Milne Edwards, 1857: 442) [holotype = USNM00032, Tonga-Tabou], seen.
- Favia helianthoides* Wells, 1954: 458 [holotype = USNM44980, Bikini Atoll], seen.
- Favia lacuna* Veron, Turak & DeVantier; in Veron, 2000 (3): 111 ['holotype' in Veron, 2002: 139 = G55836 (MTQ), northern Red Sea coast of Saudi Arabia], seen.
- Favia laxa* (Klunzinger, 1879: 49) [holotype = ZMB-Cni2193, Red Sea]; seen.
- Favia lizardensis* Veron & Pichon; in Veron *et al.* (1977: 45 [holotype = BM(NH)1977.1.1.2, MacGillivray, eastern Australia], seen.
- Favia maritima* (Nemenzo, 1971: 169) [syntypes = UP C-859, C-861, Puerto Princesa Bay, Palawan, Philippines]; not seen.
- Favia marshae* Veron, 2000 (3): 122 ['holotype' in Veron, 2002: 145 = WAM Z12910], Ashmore Reef, north-west Australia, not seen.
- Favia matthaii* Vaughan, 1918: 109 [holotype = USNM38381, Indian Ocean], seen.
- Favia maxima* Veron & Pichon; in Veron *et al.* (1977): 43 [holotype = BM(NH)1977.1.1.1, Hook Island, Whitsunday Islands, Great Barrier Reef], seen.
- Favia pallida* (Dana, 1846: 224) [syntype = USNM00076, 'Feejee Islands'], seen.
- Favia rosaria* Veron, 2000 (3): 119 ['holotype' in Veron, 2002: 143 = G55822 (MTQ), Milne Bay, eastern Papua New Guinea], seen.
- Favia rotumana* (Gardiner, 1899: 750) [Neotype = ZMA Coel. 5686, Rotumana, Fiji], not seen but illustrated in Wijsman-Best, 1972: pl. 3, fig. 2.
- Favia rotundata* (Veron & Pichon); in Veron *et al.* (1977): 64 [holotype = BM(NH)1977.1.1.6, south-west Swain Reefs, eastern Australia], not seen.
- Favia speciosa* Dana, 1846: 220 [syntype = USNM00037, 'East Indies'], seen.
- Favia stelligera* (Dana, 1846: 216) [syntype = USNM00055, 'Feejee Islands'], seen.
- Favia truncata* Veron, 2000 (3): 113 ['holotype' in Veron, 2002: 142 = G55836 (MTQ), Milne Bay, eastern Papua New Guinea], seen.
- Favia veroni* Moll & Borel Best, 1984: 48 [holotype = RMNH 15209, Kudigareng Keke, Spermonde Archipelago, Indonesia], seen.
- Favia vietnamensis* Veron, 2000 (3): 127 ['holotype' in Veron, 2002: 146 = G55859 (MTQ), Nha Trang, Vietnam], seen.

Note: Following ICZN Commission (2011: 162–166), the species named in Veron, (2000) are valid. However, the type specimens designated in Veron (2002) are not valid.

The Atlantic species *Favia leptophylla* Verrill, 1868: 353 [holotype = YPM1517, Abrolhos Archipelago, Brazil] is transferred for the first time to the genus *Mussismilia*, as described below under *Mussismilia*.

GENUS *COLPOPHYLLIA* MILNE EDWARDS & HAIME, 1848: 492 (FIGS 10E, F, 15E–J, 21A–C, 25A–C)

Synonyms: None.

Type species: *Meandrina gyrosa* de Lamarck, 1816: 247 [= *Madrepora natans* Houttuyn, 1772: 124]; by

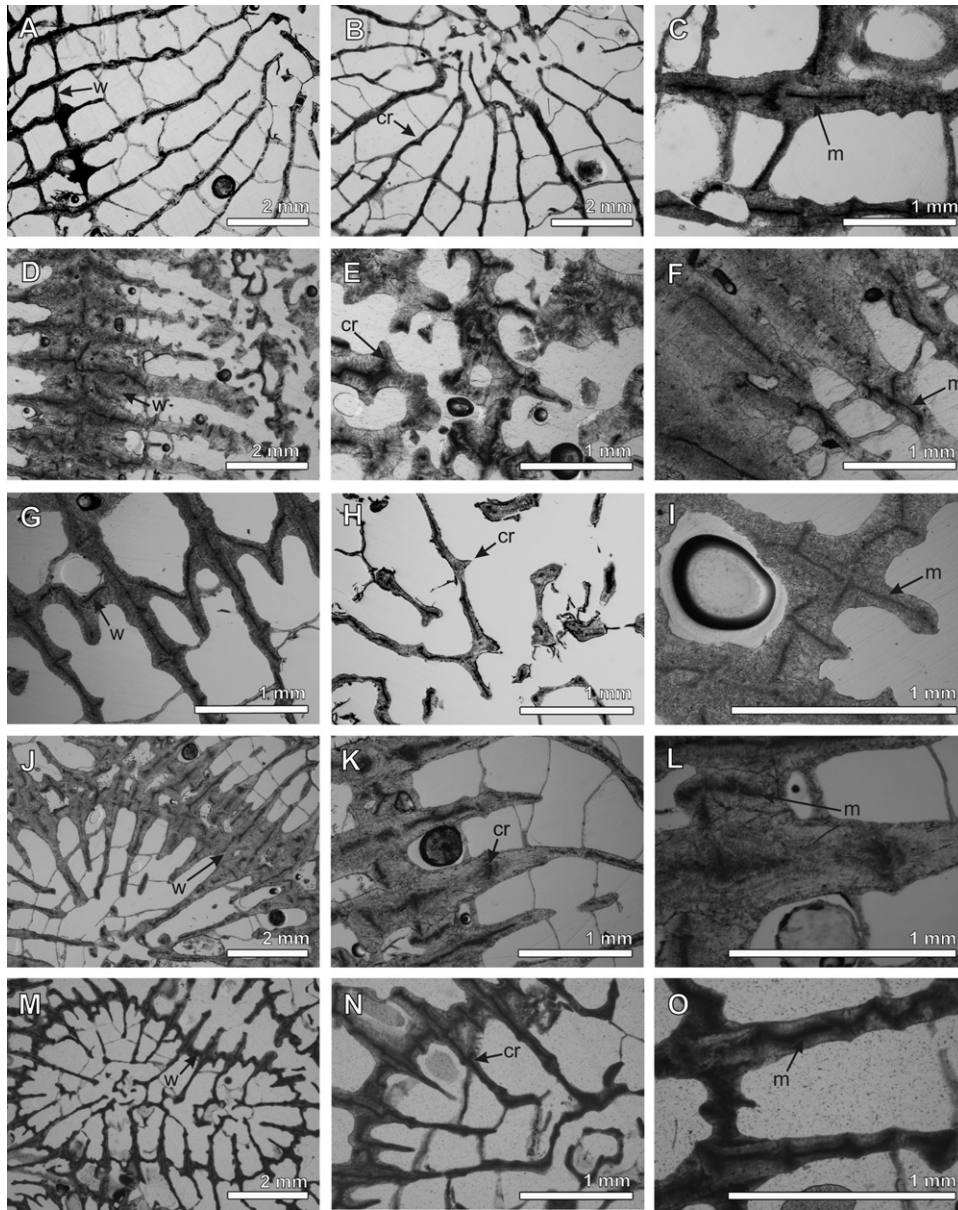


Figure 25. *Colpophyllia*, *Manicina*, and *Mussismilia* microstructure (transverse thin section): left column, wall; middle column, corallite interior; right column, close-up of septa. Corallite walls (w) in *Colpophyllia* and *Mussismilia* are parathecal; whereas in *Manicina* they are septothecal with trabeculothecal elements. Trabeculothecal elements are also present in *Mussismilia braziliensis* and to a lesser extent in *Mussismilia leptophylla*. Moderately well-defined costoseptal medial lines (m) and well-developed carinae (cr) occur in all three genera. A–C, *Colpophyllia natans* (Houttuyn, 1772); figured specimen = SUI122802 (FA (FA1071), Bocas del Toro, Panama (A); SUI122804 (FA1100, J115), Discovery Bay, Jamaica (B, C). D–F, *Manicina areolata* (Linnaeus, 1758); figured specimen = SUI122822 (FA1067), Bocas del Toro, Panama. G–I, *Mussismilia hartti* (Verrill, 1868); figured specimen = YPM4516, Maria Farinha, Pernambuco, Brazil. J–L, *Mussismilia braziliensis* (Verrill, 1868); figured specimen = YPM9104, Santa Barbara Island, Abrolhos Archipelago, Bahia, Brazil. M–O, *Mussismilia leptophylla* (Verrill, 1868); holotype = YPM1517A, Abrolhos Reef, Abrolhos Archipelago, Bahia, Brazil.

original designation. The holotype MNHN-scle105 is lost (A. Andouche, pers. comm., 2009). Also lost are (1) Milne Edwards & Haime's specimen of '*Colpophyllia fragilis* Dana', which was described and illustrated by

Matthai (1928: 103–104) (A. Andouche, pers. comm. 2009); and (2) Esper's (1795) figured specimen of *Madrepora natans*, which Matthai (1928: 102, pl. 67, figs 1, 2) designated as the 'type' of *Colpophyllia*

natans (Müller, 1775) (Scheer, 1990). We herein designate specimen SUI130588 (Carlon #828), collected by D. B. Carlon in 2007 at Crawl Cay, Bocas del Toro, Panama, as the neotype of *Colpophyllia natans* (Houttuyn, 1772) (Fig. 10E, F).

Original type species locality: Unknown [Recent].

Original description: 'Polypier composé, massif. Les séries de polypières étant intimement soudées entre elles par les côtes. Columelle rudimentaire ou nulle. Cloisons serrées, excessivement minces, à bord très-finement denticulé et faiblement échancré dans son milieu, de manière à simuler inférieurement un lobe peu marqué. Endothèque vésiculaire très-abondante' (Milne Edwards & Haime, 1848: 492).

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai (1928: 99–109); Vaughan & Wells (1943: 171); Wells (1956: F403); Walton Smith (1971: 82–83); Zlatarski & Estalella (1982: 83–85); Veron (2000: vol. 3: 210–211).

Diagnosis: Macromorphology: meandroid (uniserial), with large valleys (> 15 mm); limited costate coenostem forming a distinctive 'double wall'; discontinuous, compact trabecular columella with lamellar linkage between centres; reduced epitheca; abundant vesicular endothea; septal lobes (Figs 10E–F, 15E–J).

Micromorphology: regular fan-shaped septal teeth with elliptical bases orientated transverse to the septal plane; spiky septal granules organized in lines; interarea of teeth along a septum is distinctively horizontally layered (banded); teeth in different septal cycles and along individual septa similar in size and shape (Fig. 21A–C).

Microstructure: parathecal corallite wall; centres of calcification within costosepta and columella form a well-developed medial line crossed by carinae; limited thickening deposits (Fig. 25A–C).

Species included: *Colpophyllia natans* (Houttuyn, 1772) [holotype is from an unknown locality, and is lost; neotype (herein designated) = SUI130588 (Carlon #828), Fig. 10E, F, Bocas del Toro, Panama].

Colpophyllia amaranthus (Houttuyn, 1772) [holotype is from an unknown locality, and is lost (Matthai, 1928); neotype (herein designated) = USNM100498, Fig. 15G, H, Venezuela].

Colpophyllia breviserialis Milne Edwards & Haime, 1849 [holotype = BM(NH)18.40.5.29.6, Fig. 15I, unknown locality].

Remarks: As explained by Wells (1936), there are two different species that have been assigned the name 'gyrosa': (1) *Madrepora natans* Houttuyn, 1772 =

Madrepora gyrosa Ellis & Solander, 1786 = *Meandrina gyrosa* de Lamarck, 1816 = *Colpophyllia natans* Matthai, 1928; (2) *Manicina gyrosa* Ehrenberg, 1834 = *Manicina gyrosa* Matthai, 1928 = *Manicina mayori* Wells, 1936. The first is the type species of *Colpophyllia*, and its type specimen is lost. A neotype (SUI130588) has been therefore designated for *Colpophyllia natans*. Wells (1936: 105) proposed the name *Manicina mayori* to replace the second species, *Manicina gyrosa* Ehrenberg, because Ellis & Solander (1786) had already named the first species *Madrepora gyrosa*.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Colpophyllia* is distinguished by having a meandroid colony form; a 'double' wall; small septal lobes; discontinuous series and collines; centres linked by lamellae; a spongy, parietal (= trabecular) columella. Septal margins are strongly dentate; trabeculae are usually simple, in one or two fan systems (Vaughan & Wells, 1943: 153, 154, 163, 171). Our observations agree. In addition, the genus has a distinctive parathecal wall (dissepimental), and centres of calcification in the costosepta and columella form well-defined medial lines that are crossed by distinct carinae (or short transverse lines). Septal teeth are small and fan-shaped, orientated transverse to the plane of the septum. The genus *Colpophyllia* is distinguished from *Mussismilia* by its meandroid colony form, lamellar centre linkage, septal lobes, and smaller septal teeth. It is distinguished from *Favia*, *Diploria*, and *Manicina* by its lamellar linkage, reduced epitheca, abundant vesicular endothea, and parathecal wall. *Colpophyllia* is distinguished from its meandroid Indo-Pacific counterpart, *Oulophyllia* Milne Edwards & Haime, 1848, on the basis of its double wall, lamellar linkage, and septal lobes; its parathecal walls (trabeculothecal in *Oulophyllia*), its regular tricorn septal teeth with elliptical-perpendicular bases (irregular multiaxial in *Oulophyllia*); and its strong, aligned granules.

Cairns, Hoeksema & Land (1999) recognized three species of *Colpophyllia* (*Colpophyllia natans*, *Colpophyllia amaranthus*, *Colpophyllia breviserialis*), which differ in valley length, depth, and numbers of septa per cm. *Colpophyllia amaranthus* (Fig. 15G, H) is characterized by deep discontinuous valleys (up to 30 mm) and more numerous septa (ten to 12 centres per cm). *Colpophyllia breviserialis* (Fig. 15I, J) is characterized by short valleys having fewer than five centres. *Colpophyllia natans* (Figs 10E, F, 15E, F) is characterized by longer and more continuous valleys, a distinctive double wall, and eight to nine septa per cm. Both Zlatarski & Estalella (1982) and Veron (2000) synonymized the three species; Walton Smith (1971) recognized only *Colpophyllia natans* and *Colpophyllia amaranthus*.

GENUS *DIPLORIA* MILNE EDWARDS & HAIME, 1848: 493 (FIGS 10G, H, 16A, B, 20G–I, 24G–I)

Type species: Meandrina cerebriformis de Lamarck, 1816: 246, holotype = MNHN-Scle102 [= *Madrepora labyrinthiformis* Linnaeus, 1758: 794–795]; by original designation.

Type species locality: ‘Habite les mers d’Amérique’ (de Lamarck, 1816: 246) [Recent].

Original description: ‘Les séries de polypiérites soudées entres elles par les côtes et l’exothèque qui sont très-développées. Collines doubles et très-larges. Cloisons serrées, très-débordantes et dont les dents supérieures sont les plus fortes.’ (Milne Edwards & Haime, 1848: 493)

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai (1928: 50–54); Wells (1936: 118–119, 1956); Vaughan & Wells (1943: 163–164, 166, 171: F402–403); Zlatarski & Estalella (1982: 66–83); Walton Smith (1971: 80–82); Veron (2000: vol. 3: 206–209).

Diagnosis: Macromorphology: meandroid (uniserial), with medium valleys (4–15 mm); well-developed costate coenosteum; continuous, trabecular columella; well-developed epitheca; moderately developed tabular endotheca; small septal lobes (Figs 10G, H, 16A, B).

Micromorphology: regular tricornate teeth with pointed tips and elliptical bases orientated transverse to the septal plane; smooth interarea of teeth; spiked granules organized in lines; teeth in different septal cycles and across individual septa similar in size and shape (Fig. 20G–I).

Microstructure: septothecal wall; moderately well-developed clusters of calcification centres within costosepta, which are connected by faint or absent medial lines; no carinae; fibrous thickening deposits containing layers (Fig. 24G–I).

Species included: [monotypic genus]: Diploria labyrinthiformis (Linnaeus, 1758) [holotype is from an unknown locality, and is lost (Matthai, 1928); neotype (herein designated) = SUI1228814 (FA1078) collected by H. Fukami in Boca del Toro, Panama, Fig. 16A, B].

Remarks: Milne Edwards & Haime (1849) originally designated *Meandrina cerebriformis* as the type species of *Diploria* based on a specimen in the Lamarck collection (MNHN-Scle102). As indicated in Matthai (1928: 63), this species has subsequently been synonymized with *Diploria labyrinthiformis*

(Linnaeus), the type specimen of which is lost. A neotype (SUI1228814) has been therefore designated for *Diploria labyrinthiformis*.

In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Diploria* is distinguished by having a meandroid colony form; long sinuous series; a continuous parietal (= trabecular) columella, and a septothecal corallite wall. Septal margins are strongly dentate; trabeculae are usually simple, in one or two fan systems (Vaughan & Wells, 1943: 153–154, 163, 166). It is distinguished from its meandroid Indo-Pacific counterpart, *Platygyra* Ehrenberg, 1834, on the basis of its well-developed columella, septal lobes, septothecal walls (trabeculothecal in *Platygyra*), its regular tricornate septal teeth with elliptical-perpendicular bases (irregular multi-axial in *Platygyra*), and its well-developed aligned granules.

Cairns, Hoeksema & Land (1999), Zlatarski & Estalella (1982), Walton Smith (1971), and Veron (2000) all recognized three species of *Diploria* (*Diploria labyrinthiformis*, *Diploria strigosa*, *Diploria clivosa*), which differ in valley width, numbers of septal cycles, and development of coenosteum. *Diploria labyrinthiformis* is distinguished by a well-developed coenosteum with a distinctive grooved ambulacrum, valley widths of ~5 mm, and 14–17 septa per cm (Fig. 16A, B). *Diploria strigosa* has limited coenosteum, valley widths of ~6 mm, and 15–20 septa per cm (Fig. 16C, D). *Diploria clivosa* has no coenosteum, valley widths of ~3.75 mm, and 30–40 septa per cm (Fig. 16E, F). However, the molecular analyses (nuclear β -tubulin exon and intron; mitochondrial *cox1-trnM* intergenic region) of Nunes *et al.* (2008) show that *Diploria labyrinthiformis* is more closely related to *Manicina areolata* than to the other two species. Mitochondrial data show *Diploria strigosa* and *Diploria clivosa* as grouping together in the same genus-level clade, but nuclear data do not. We therefore separate the three traditional species of *Diploria* into two genera: one (*Diploria*) containing *labyrinthiformis* and the other (*Pseudodiploria*) containing *strigosa* and *clivosa*. The two genera can be distinguished on the basis of the development of coenosteum, wall structure, and the distinctiveness of medial lines.

GENUS *MANICINA* EHRENBERG, 1834: 325 (FIGS 11A, B, 16G–J, 21D–F, 25D–F)

Synonyms: *Podasteria* Ehrenberg, 1834: 326 [type species = *Manicina mayori* Wells, 1936 (= *Manicina gyrosa* Ehrenberg, 1834)]; see Wells, 1936: 125–126.

Type species: Madrepora areolata Linnaeus, 1758: 795; by subsequent designation, Milne Edwards & Haime, 1848: 493. Holotype is lost (Matthai, 1928).

We herein designate specimen ZMB-Cni673 from St. Thomas, US Virgin Islands, in the Ehrenberg collection (Berlin Museum) as the neotype. This specimen was identified by Ehrenberg (1834: 324) as '*Manicina areolata* Ehrenberg'.

Original type species locality: 'O. Asiatico' (Linnaeus, 1758) [Recent].

Original descriptions:

1. 'Manshetten-Coralle' (Ehrenberg, 1834: 325);
2. 'Se distingue du précédent par son épithèque incomplète et pars ses cloisons (= septa) très-fortement granulées latéralement, qui offrent près de la columelle un lobe paliforme.' (Milne Edwards & Haime, 1848: 493).

Subsequent morphological descriptions (Matthai, 1928 and later): Matthai (1928: 78–95); Wells (1936: 118–119, 1956); Vaughan & Wells (1943: 163–164, 166, 171: F402–403); Walton Smith (1971: 83–84); Zlatarski & Estalella (1982: 85–92); Veron (2000: vol. 3: 99).

Diagnosis: Macromorphology: meandroid (uniserial), with large valleys (12–15 mm); continuous, spongy trabecular columella; reduced epitheca; tabular endothea; well-developed septal lobes; sometimes free-living (Figs 11A, B, 16G–H).

Micromorphology: tricornate teeth orientated transverse to the septal plane; smooth interarea of teeth; spiked granules organized in lines; columellar teeth similar in size and shape to septal teeth (Fig. 21D–F).

Microstructure: septothecal wall with trabeculothecal elements; well-defined clusters of calcification centres within costosepta, which are connected by medial lines; carinae; fibrous thickening deposits containing layers (Fig. 25D–F).

Species included: *Manicina areolata* (Linnaeus, 1758: 795) [holotype is from an unknown locality, and is lost (Matthai, 1928); neotype (herein designated) = ZMB-Cni673, Fig. 11A, B, St. Thomas, US Virgin Islands].

Manicina mayori Wells, 1936 (= *Manicina gyrosa* Ehrenberg, 1834: 326); holotype = ZMB-Cni2859, unknown locality, Fig. 16I, J (also figured by Matthai, 1928: pl. 63, fig. 6).

Not *Madrepora gyrosa* Ellis & Solander, 1786 [= *Colpophyllia natans* (Houttuyn, 1772)].

Remarks: In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Manicina* is distinguished by 'reduced epitheca, broader and more open corallum, longer series, usually continuous, with ambulacra. Inner septal lobes small and narrow'

(Vaughan & Wells, 1943: 171). The genus *Diploria* is 'meandroid. . . , forming massive or subencrusting colonies with long series and thick collines with narrow or broad ambulacra. Septa of some species with small internal lobes. Columella continuous, parietal' (Vaughan & Wells, 1943: 166). In the key to genera (Vaughan & Wells, 1943: 162), the two genera are distinguished by the presence of internal lobes (*Manicina*: present; *Diploria*: absent) and by corallite wall structure (*Manicina*: 'parathecal'; *Diploria*: septothecal). Contrary to these distinctions, our examination showed that *Diploria labyrinthiformis* and the two species of *Pseudodiploria* (*Pseudodiploria strigosa*, *Pseudodiploria clivosa*) sometimes have small septal lobes (like *Manicina*) and the wall of the two *Pseudodiploria* species is partially trabeculothecal (like *Manicina*). Both characters are therefore highly variable, as are other characters that have been cited as diagnostic, including valley width and development of epitheca. Similar macromorphological characters include (1) uniserial, meandroid form; (2) continuous, trabecular columella; and (3) tabular endothea. Our study of microstructural and micromorphological characters shows that *Manicina*, *Diploria*, and *Pseudodiploria* have similar septal teeth and interareas between teeth. However, in contrast to *Diploria* and to a lesser extent *Pseudodiploria*, *Manicina* forms distinct clusters of calcification centres that are connected by medial lines, carinae are present, septal teeth are especially well developed, and the columella is spongy.

Cairns, Hoeksema & Land (1999), Zlatarski & Estalella (1982), and Veron (2000) only recognized one species of *Manicina*, *Manicina areolata*; whereas Walton Smith (1971), following Matthai (1928) and Wells (1936), recognized two species, *Manicina areolata* and *Manicina mayori*, which are distinguished on the basis of colony form. *Manicina areolata* forms small, free-living colonies composed of one continuous valley (Fig. 16G, H), whereas *Manicina mayori* has larger, attached colonies with many discontinuous valleys (Fig. 16I, J).

GENUS *MUSSISMILIA* ORTMANN, 1890: 292
(FIGS 11C–F, 17A–H, 21G–O, 25G–O)

Synonyms: *Protomussa* Matthai, 1928: 268 [type species = *Acanthastraea braziliensis* Verrill, 1868: 355].

Type species: *Mussa harttii* Verrill, 1868: 357, syntypes = YPM1468A–C, 1469; by original designation. We herein designate YPM1468A collected by C. F. Hartt (1867) on Abrolhos Reef in Brazil, as the lectotype of *Mussismilia harttii* (Verrill).

Type species locality: Abrolhos Reef, Abrolhos Archipelago, Brazil [Recent].

Original description: 'Dieses Verhalten macht es nothwendig, die *Mussa harti* von der Gattung *Mussa* zu trennen and dieselbe den folgenden Formen anzuschließen. Wegen der eigenthümlichen, stark bedornen Rippen wird sie wohl eine eigene Gattung bilden müssen, für die ich die Namen *Mussismilia* vorschlagen möchte' (Ortmann, 1890: 292).

Subsequent morphological descriptions (Matthai, 1928 and later): = *Protomussa* in Matthai (1928: 268–272); Vaughan & Wells (1943: 192–193); Wells (1956: F417); Laborel (1969: 195–198); Veron (2000: vol. 3: 118); Walton Smith (1971: 80).

Diagnosis: Macromorphology: short series (one to three centres per series); discontinuous columella with trabecular linkage; abundant vesicular endotheca; no paliform lobes (Figs 11C–F, 17A–H).

Micromorphology: regular lacerate (twisted threads; multicentred, multidirectional) teeth; evenly scattered, spine-shaped septal granulation; porous septa; teeth in major and minor septal cycles are equal in size and shape; spongy columella, with columellar teeth different in size and shape from septal teeth (Fig. 21G–O).

Microstructure: parathecal (dissepiments only) corallite wall, sometimes containing trabeculothecal elements; centres of calcification within the wall, septa, and columella form a medial line broken by distinct clusters of centres; fibrous thickening deposits containing layers (Fig. 25G–O).

Included species: *Mussismilia hartti* (Verrill, 1868: 357) [lectotype = YPM1468A, Fig. 11C–F, Abrolhos, Brazil].

Mussismilia braziliensis (Verrill, 1868: 355) [holotype = YPM1467, Fig. 17C, D, Abrolhos, Brazil].

Mussismilia hispida (Verrill, 1901: 127) [holotype = YPM4287, Fig. 17E, F, Abrolhos, Brazil].

Mussismilia leptophylla (Verrill, 1868: 353) [holotype = YPM1517A, Fig. 17G, H, Abrolhos, Brazil] (= *Heliastrea aperta* Verrill, 1868: 356) [holotype = YPM1518, Abrolhos, Brazil].

Remarks: In the classification system of Vaughan & Wells (1943) and Wells (1956), the genus *Mussismilia* was placed within the family Mussidae because of its 'ragged' septal dentations and because its septa are formed by several (> two) trabecular fan systems. Our examination of micromorphology shows that the shape of its septal teeth is indeed unique. The teeth are medium to high and formed by multiple twisted threads, which are uniform in arrangement but vary

in size and orientation. The septa are usually thin and often porous near the columella. In addition, the genus differs from *Manicina* and *Favia* in its abundant vesicular endotheca, its parathecal (dissepiments only) wall, its costoseptal microstructure (well-developed clusters of calcification centres), and its interarea of septal teeth (horizontally banded). The genus is currently restricted to Brazil, but was common across the Caribbean region during the Miocene and Pliocene (Budd, Stemmann & Johnson 1994; Budd, Petersen & McNeill, 1998; Budd *et al.*, 1999).

In the classification system of Vaughan & Wells (1943) and Wells (1956), the species *Mussismilia leptophylla* was placed in the genus *Favia*, presumably because of the lack of multiple trabecular fan systems. However, our observations indicate that *Mussismilia leptophylla* also has more than one fan system (Fig. 21M–O). In addition, its parathecal wall structure, septal microstructure, and the shape of its septal teeth and granules are similar to those of *Mussismilia*. Moreover, based on nuclear and mitochondrial markers, Nunes *et al.* (2008) found that *Mussismilia leptophylla* groups more closely with the three *Mussismilia* species than it does with *Favia fragum* or *Favia gravida*. We therefore transfer *Mussismilia leptophylla* for the first time to the genus *Mussismilia*.

Cairns, Hoeksema & Land (1999) and Veron (2000) recognized three species of *Mussismilia*, which differ in colony form, calice size, and septal thickness (as does *Mussismilia leptophylla*, per our observations). *Mussismilia hartti* has a phaceloid colony form, calice diameters of 12–30 mm, 12–14 septa per cm, and thin septa (Fig. 17A, B); whereas *Mussismilia hispida*, *Mussismilia braziliensis*, and *Mussismilia leptophylla* are all subplooid. *Mussismilia hispida* has calice diameters of 14–15 mm, more than four septal cycles, thin septa, and a well-developed columella (Fig. 17E, F); *Mussismilia braziliensis* has calice diameters of 8–10 mm, fewer than four septal cycles, thick septa, and a weak columella (Fig. 17C, D); and *Mussismilia leptophylla* has calice diameters of ~6 mm, fewer than four septal cycles, thin septa, and a well-developed columella (Fig. 17G, H).

GENUS **PSEUDODIPLORIA** FUKAMI, BUDD & KNOWLTON GEN. NOV. (FIGS 11G, H, 16C–F, 20J–O, 24J–O)

Synonyms: *Maeandrina* Link, 1807, sensu Matthai, 1928: 50–54;

Type species: *Meandrina strigosa* Dana, 1846: 257–258; pl. 14, fig. 4a–b; holotype = USNM00005 (= *Meandrina cerebrum* Ellis & Solander, 1786: 163; Matthai, 1928: 55–63).

Type species locality: 'West Indies' (Dana, 1846) [Recent].

Diagnosis: Macromorphology: meandroid (uniserial), with medium valleys (4–15 mm); little or no coenosteum; continuous, trabecular columella; well-developed epitheca; moderately developed tabular endotheca; small septal lobes (Fig. 11G, H, 16C–F).

Micromorphology: regular tricorne teeth with pointed tips and elliptical bases orientated transverse to the septal plane; smooth interarea of teeth; spiked granules organized in lines; teeth in different septal cycles and across individual septa similar in size and shape (Fig. 20J–O).

Microstructure: septothecal wall with trabeculothecal elements; weak clusters of calcification centres within costosepta, which are connected by medial lines; no carinae; fibrous thickening deposits containing layers (Fig. 24J–O).

Species included: *Pseudodiploria strigosa* (Dana, 1846: 257–258; pl. 14, fig. 4a–b) [holotype = USNM00005, Fig. 11G, H, West Indies] [= *Maeandrina cerebrum* (Ellis & Solander) of Matthai, 1928].

Pseudodiploria clivosa (Ellis & Solander, 1786: 163) [holotype is from 'Oceano Indiae occidentalis', and is lost (Matthai, 1928); neotype (herein designated) = SUI122811, Fig. 16E, F, Bocas del Toro, Panama].

Remarks: Matthai (1928) indicated that *Maeandrina cerebrum* (Ellis & Solander) is the type species of *Maeandrina* Link, 1807. However, given that *Meandrina* de Lamarck, 1801 predates *Maeandrina* Link, 1807 and is a valid genus name (Table 1, Family Meandrinidae), we herein name a new genus, *Pseudodiploria*.

As explained above under *Diploria*, *Pseudodiploria* can be distinguished from *Diploria* by its limited or absent coenosteum, the presence of trabeculothecal elements in the otherwise septothecal corallite wall, and its often well-developed medial lines. The two species of *Pseudodiploria* (Fig. 16C–F) differ in the presence of coenosteum (*Pseudodiploria strigosa* has limited coenosteum but *Pseudodiploria clivosa* has no coenosteum), valley width (*Pseudodiploria strigosa* has valley widths of ~6 mm but *Pseudodiploria clivosa* has valley widths of ~3.75 mm), and number of septa per cm (*Pseudodiploria strigosa* has 15–20 but *P. clivosa* has 30–40 septa per cm).

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SUPPORTING INFORMATION

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

Appendix S1. List of specimens.

Appendix S2. Glossary of morphological terms.

Appendix S3. Illustrations of morphological characters and states.

Appendix S4. Character matrix used in morphological phylogenetic analyses.

Appendix S5. Additional phylogenetic character maps (macromorphology).

Appendix S6. Additional phylogenetic character maps (micromorphology).

Appendix S7. Additional phylogenetic character maps (microstructure).

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