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Evolution of the Caribbean subfamily Mussinae (Anthozoa: Scleractinia: Faviidae): transitions between solitary and colonial forms

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Understanding evolutionary transitions in scleractinian corals is fundamental to predicting responses of coral reefs to climate change. We examine transitions between solitary and colonial corals in the fossil record, focusing on the Caribbean solitary reef coral *Scolymia* and members of the subfamily Mussinae. Fossil specimens are selected from a large well-documented collection of Neogene Caribbean corals, and a total of 23 species are distinguished using 15 morphological features. Ten of the 23 species are extant Caribbean species, seven are previously described extinct Neogene species, and six other extinct species are formally described as new. The 7+6 extinct species are added to a morphological data set consisting of 30 extant molecularly characterized species plus seven additional extinct (five Eocene, two Neogene) species. In addition to the Caribbean subfamily Mussinae, the extant species include the Indo-Pacific families Merulinidae and Lobophylliidae, and the Caribbean subfamily Favinae. Phylogenetic analysis was performed on the data using maximum parsimony, and the results reveal four clades, which correspond with previously reported molecular clades. Solitary corals group most closely with Caribbean Mussinae and Indo-Pacific Lobophylliidae, whereas colonial corals are present in all four clades. Within Caribbean Mussinae, members of the colonial genera *Mycetophyllia* and *Isophyllum* form distinct subclades, as do the extinct solitary genera *Antillia* and *Antillophyllia*. The relationships within *Scolymia* are less well defined but its members appear more closely related to extinct solitary genera dating back to the Eocene. These results indicate that evolutionary transitions between solitary and colonial corals have been rare within the Mussinae. Except *Antillophyllia*, most Mussinae genera are restricted to the Caribbean. During the late Miocene, *Mycetophyllia* diversified and three other modern Mussinae genera (*Mussa*, *Scolymia*, *Isophyllum*) originated in association with increased Caribbean productivity. Mussinae that were more likely to survive Plio-Pleistocene extinction may have taken refuge in deep forereef habitats.

Keywords: reef corals; Neogene; systematics; phylogenetic analysis

Introduction

The question of whether solitary scleractinian corals are ancestral to colonial scleractinian corals, or vice versa, has long been controversial (Coates & Oliver 1973; Rosen 1986; Barbeitos *et al.* 2010). Solitary corals are defined as having only one mouth or centre – or, in other words, as consisting of a single corallite or individual. They are aclonal and have wider distributions both geographically and bathymetrically. On the other hand, colonial corals have more than one mouth and are polycentric; they have many corallites formed by corallite budding and are clonal. In general, most colonial corals tend to have symbiotic zooxanthellae and are reef-building, whereas most solitary corals lack zooxanthellae and are not reef-building (Coates & Oliver 1973; Coates & Jackson 1985, 1987). However, exceptions

have been reported (e.g. the solitary zooxanthellate *Scolymia* Haime, 1852, the colonial azooxanthellate *Lophelia* Milne Edwards & Haime, 1849, and colonial corals that are not reef-building such as *Goniopora stokesi* Milne Edwards & Haime, 1851, *Heteropsammia eupsammides* (Gray, 1849), and some polystomatous mushroom corals (Hoeksema 1989)). Moreover, coloniality has been interpreted as an adaptation for reef-building (Coates & Oliver 1973; Jackson 1979) and is therefore important for understanding how coral reefs respond to increasing anthropogenic threats and global warming.

The traditional view of scleractinian evolution is that most colonial forms arose via several pathways from one or more solitary ancestors, involving both intracalicular and extracalicular budding and various degrees of corallite integration (Wells 1956, p. F352, fig. 253). The pathways

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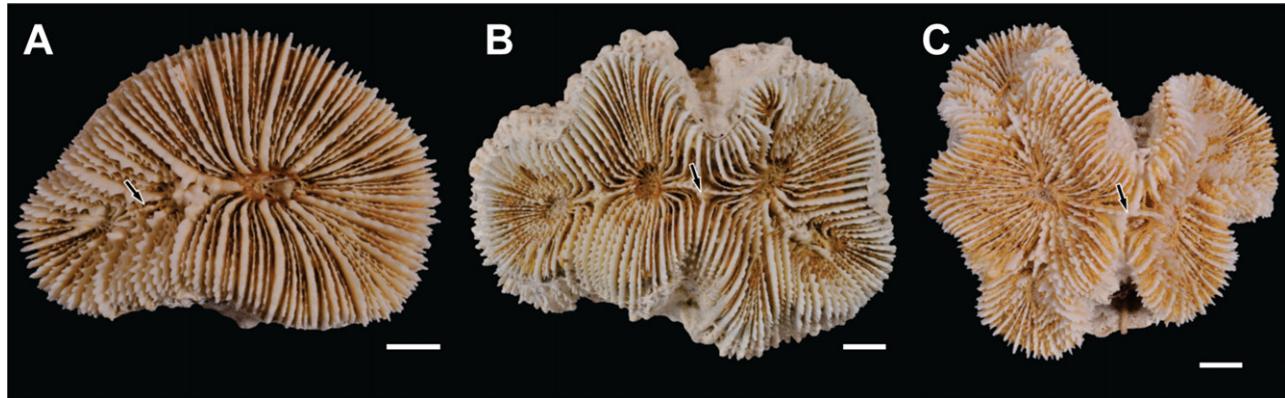


Figure 1. *Scolymia lacera* is almost always solitary, but rare colonial specimens, such as these, have been found. Note the lamellar linkage between centres (arrows). **A–C**, calical surfaces; **A**, USNM 87176; **B**, USNM 87176; **C**, USNM 84596. Scale bars: **A, B** = 2 cm; **C** = 1 cm.

include (a) hydnophoroid, (b) phaceloid-plocoid-ceriod, (c) flabellate and (d) dendroid or reptoid colony forms. However, only limited work has been done examining transformations from solitary to colonial forms within the context of a phylogenetic tree (but see Hoeksema & Best 1991; Arrigoni *et al.* 2014). Comprehensive molecular trees for the Order Scleractinia Bourne, 1900 (Fukami *et al.* 2008; Kitahara *et al.* 2010) show that most major clades are either solitary or colonial, but a few clades consist of a mixture of solitary and colonial forms. For example, the Indo-Pacific genera *Homophyllia* Brüggeman, 1877, *Micromussa* Veron, 2000, *Sclerophyllia* Klunzinger, 1879 and *Lobophyllia* de Blainville, 1830 in the family Lobophilliidae Dai & Horng, 2009 include both solitary and colonial species (Arrigoni *et al.* 2015, 2016; Huang *et al.* 2016), as do several genera in the families Agariciidae Gray, 1847 and Fungiidae Dana, 1846 (Hoeksema 1989; Gittenberger *et al.* 2011; Benzoni *et al.* 2012; Kitahara *et al.* 2012). Occasional colonial forms have also been reported *within* species of modern Indo-Pacific *Homophyllia australis* Milne Edwards & Haime, 1849 (see Arrigoni *et al.* 2016), *Micromussa pacifica* Benzoni & Arrigoni in Arrigoni *et al.*, 2016, and *Lobophyllia* (=*Parascolymia*) *vitiensis* (Brüggeman, 1877) (see Chevalier 1975). The production of additional centres may depend on the corallum size (Hoeksema 1991), for example in *Ctenactis echinata* (Pallas, 1766). Rare colonial forms have been observed in Caribbean *Scolymia lacera* (Pallas, 1766) (Fig. 1), but not *Scolymia cubensis* (Milne Edwards & Haime, 1849) (see Logan 1988). Preliminary ancestral state reconstructions based on molecular trees have indicated that loss of coloniality has occurred as frequently as gain of coloniality (Barbeitos *et al.* 2010).

Here we investigate the evolution of the solitary Atlantic reef coral *Scolymia* in order to better

understand its relationship with colonial members of the family Faviidae. Using both molecular and morphological data, modern members of the family have recently been found to be exclusively Atlantic and have been revised to contain two subfamilies (Mussinae, Faviinae), with the Mussinae consisting of the genera *Mussa* Oken, 1815, *Isophyllia* Milne Edwards & Haime, 1851, *Mycetophyllia* Milne Edwards & Haime, 1848 and *Scolymia* (see Fukami *et al.* 2008; Budd *et al.* 2012). Of these four genera, *Scolymia* has previously been interpreted to include both Atlantic and Indo-Pacific solitary reef corals (Veron 2000), but molecular analyses (Fukami *et al.* 2008) have shown that these solitary corals consist of four distinct clades: (1) Atlantic *Scolymia*; (2) Indo-Pacific *Parascolymia* (=*Lobophyllia*); (3) Indo-Pacific *Homophyllia*; and (4) Indo-Pacific *Micromussa*. Only the first clade (Atlantic *Scolymia*) belongs to the family Faviidae (previously referred to as ‘Mussidae’, in Budd *et al.* 2012).

Although molecular data are still lacking, Atlantic *Scolymia* has long been thought to be closely related to the colonial phaceloid genus *Mussa*. In fact, the two genera have sometimes been synonymized (Vaughan & Wells 1943, p. 195; Wells 1956, p. F418). However, the two genera differ in colony form, the structure of their thickening deposits and calcification centres, and the shape of their septal teeth. Moreover, *Mussa* has trabecular linkage between corallites, whereas *Scolymia* has lamellar linkage (Fig. 1). Thus, the two genera more likely represent separate but closely related taxa (Budd *et al.* 2012; Kitahara *et al.* 2016).

Our investigation focuses on the Caribbean fossil record dating back to the late Eocene, when solitary members of the Mussinae are first reported from the Caribbean. Colonial Atlantic Mussinae are believed to have first appeared during the early Oligocene (Frost & Langenheim 1974) and diversified during the Neogene. We perform

a phylogenetic analysis and revise the taxonomy of the Mussinae. Based on the results, we address the following questions: which taxa were the ancestors of the modern solitary Atlantic reef coral, *Scolymia*? Did *Scolymia* evolve from a fossil lineage of solitary corals, from colonial Mussinae or from Indo-Pacific Lobophylliidae? What is the nature of the relationship between Caribbean Mussinae and Indo-Pacific Lobophylliidae? We also examine patterns of origination and extinction and their association with environmental change.

Comment on nomenclature

The families Faviidae and Mussidae are synonyms (Budd *et al.* 2012). Authorship of the family Faviidae has traditionally been attributed to Gregory (1900), and authorship of the family Mussidae has traditionally been attributed to Ortmann (1890; see Vaughan & Wells 1943; Wells 1956). However, Milne Edwards & Haime (1857, p. 426) described the “Faviacées” as a family-level taxon called an “agèle”. Therefore, we have used ‘Faviidae’ Milne Edwards & Haime, 1857 as the name and authorship of the family in the present study.

Taxa

Repository abbreviations

CCD: Cenozoic Coral Database; **MCZ:** Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; **NMB:** Naturhistorisches Museum Basel, Basel, Switzerland; **NHMUK:** Natural History Museum, London, UK (formerly British Museum of Natural History, BMNH); **PMU:** Palaeontological collections, Museum of Evolution, Uppsala University, Sweden; **PRI:** Paleontological Research Institution, Ithaca, NY, USA; **SUI:** Paleontology Repository, University of Iowa, Iowa City, IA, USA; **UCMP:** University of California Museum of Paleontology, Berkeley, CA, USA; **USNM:** United States National Museum; now the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Fossil collections

Specimens. A total of 868 specimens (Supplemental material, Appendix A) were selected from a large collection of Neogene corals consisting of >15,000 specimens and ~230 species, which is deposited at the University of Iowa (SUI) and the US National Museum (USNM). Information about the specimens is contained in the Cenozoic Coral Database (CCD), available on request from JSK. The selections were made based on

the morphological characters of the subfamily Mussinae given in Budd *et al.* (2012), including medium to large calices with high relief (>6 mm), widely spaced septa (<6 per 5 mm), relatively small trabecular columella, reduced epitheca, well-developed endotheca, parathecal walls, and tall (>0.6 mm), widely spaced (1–2 mm), spine-shaped teeth.

In addition to the Caribbean Neogene, we also analysed type specimens of five species of Mussinae previously reported from the Caribbean Eocene (Fig. 2). These five species are exclusively solitary and consist of: *Antillia clarki* Durham in Clark & Durham, 1946; *Antilophyllum (?) olssoni* Durham in Clark & Durham, 1946; *Syzygophyllum hadleyi* Wells, 1934; *Syzygophyllum hayesi* Vaughan, 1919; and *Circophyllum clevei* Duncan, 1873. We did not include two other species, *Circophyllum compressa* Duncan, 1873 and *Antillia heueri* Frost & Langenheim, 1974, because they did not have the relatively small trabecular columella or a well-developed endotheca diagnostic of the Mussinae. *Antilophyllum (?) gesteri* Durham in Clark & Durham, 1946 is not as well preserved as *A. olssoni* but appears to be the same species.

Finally, we included representatives of two unnamed extinct Neogene species in the genus *Manicina* Ehrenberg, 1834 (Faviinae) in our analysis, because they are similar in macromorphology to modern *Isophyllum* (Mussinae).

Species recognition. As in previous work (Budd & Bosellini 2016), we qualitatively grouped our specimens of Neogene Mussinae into 23 species (Supplemental material, Appendix B) using the following macromorphological, micromorphological and microstructural criteria: corallum (colony shape; development of epitheca), corallite (length, width and structure of corallite series, ‘valleys’), development of coenosteum, costa continuity, septa (number, relative development), columella (size, structure, linkage), development of paliform lobes, relative abundance of dissepiments, and wall structure. Observations were made on calical surfaces using a stereoscope and on transverse thin sections using transmitted light. The resulting species were analysed in the phylogenetic analysis and are formally described in the systematic account.

Taxonomic names. We compared our specimens of the 23 species with type specimens of modern species in the subfamily Mussinae (Budd *et al.* 2012). Ten of the 23 species could be assigned to modern species (Supplemental material, Appendix B). These species include representatives of all species of Mussinae previously reported from the modern-day Caribbean.

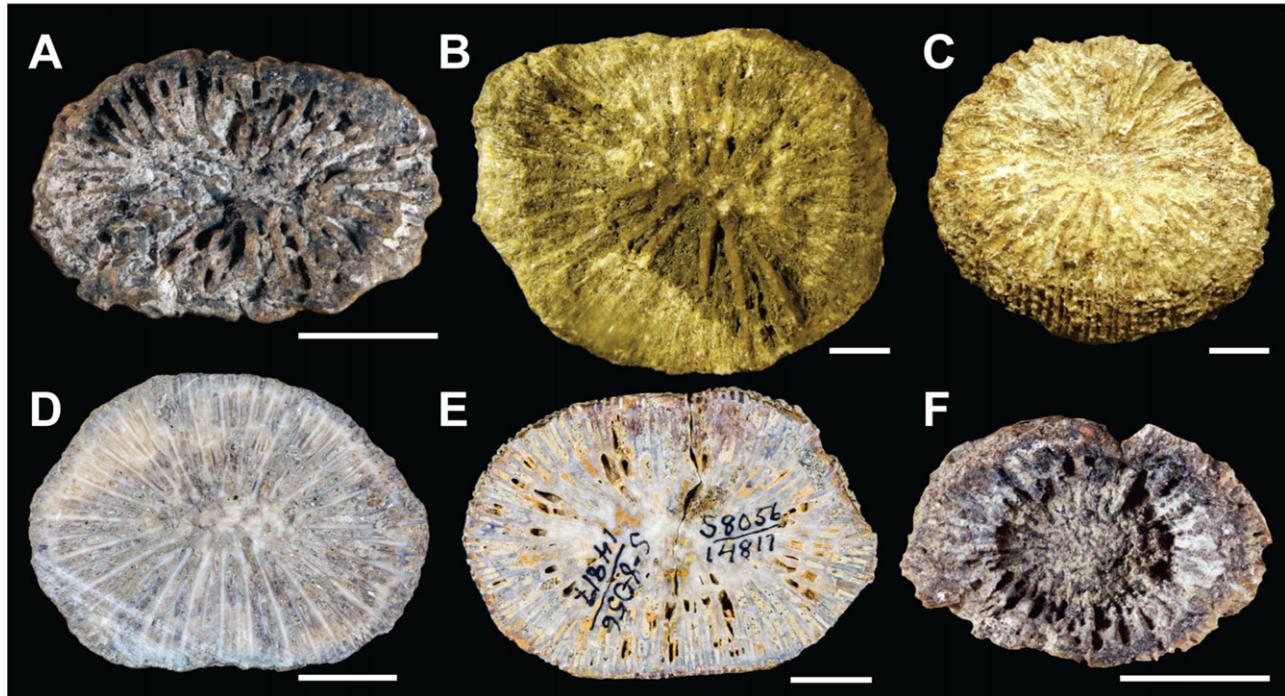


Figure 2. Type specimens of late Eocene solitary species that have been previously assigned to *Antillia* or *Antillophyllia*. Species figured in A–E belong to the subfamily Mussinae and are included in the phylogenetic analysis. F has a large, papillose columella not characteristic of the Mussinae, and is not included. A–C, calical surfaces; A, *Antillophyllia clevei* (Duncan, 1873), PMU 23618; B, *Antillia hayesi* Vaughan, 1919, USNM 325009; C, *Antillia hadleyi* (Wells, 1934), PRI 3781. D–E, transverse cuts; D, *Antillia clarki* Durham in Clark & Durham, 1946, UCMP 14814; E, *Antillophyllia olssoni* Durham in Clark & Durham, 1946, UCMP 14817. F, *Antillia compressa* (Duncan, 1873), PMU 23617, calical surface. Scale bars = 1 cm.

A total of 14 extinct species of Mussinae have been described previously from the Caribbean Neogene (Supplemental material, Appendix C). This number includes *Trachyphyllia* and *Antillophyllia*, two genera that are morphologically similar to and often confused with the genus *Antillia*. We examined type specimens of these 14 species and determined synonymies, reducing the number of previously described extinct species to seven. Specimens of the 13 extinct species in our collections were compared with type specimens of these seven species (Supplemental material, Appendix C), and assigned to each of the seven species. The six remaining extinct species in our collections were described as new.

The 23 recognized species are formally described in the Systematic palaeontology section, below. They are also illustrated in the online taxonomic database NMITA (Neogene Marine Biota of Tropical America) available at <http://nmita.iowa.uiowa.edu>.

Species included in the phylogenetic analysis

A total of 50 species were included in the phylogenetic analysis. They consist of: (1) 7 + 6 extinct Neogene species (Supplemental material, Appendix B); (2) the five Eocene Caribbean species mentioned above

(Fig. 2); (3) the two extinct *Manicina* species mentioned above; and (4) 30 modern species (10 Mussinae + 20 additional modern species; Supplemental material, Appendix D).

The 30 modern species were selected because they have been previously characterized molecularly and analysed in phylogenetic studies integrating molecular and morphological data. The selections were made to include representatives of an assortment of different clades on previous molecular trees. As in previous analyses (e.g. Budd *et al.* 2012), *Montastraea cavernosa* (Montastraeidae Yabe & Sugiyama, 1941) was chosen to be the outgroup because molecular analyses have shown it to be a sister group of the taxa analysed here (Fukami *et al.* 2008). The modern ingroup species (Fig. 3) in our analysis consisted of:

- Merulinidae Verill, 1865 (six species in four genera): *Trachyphyllia*, *Caulastraea* Dana, 1846, *Oulophyllia* Milne Edwards & Haime, 1848, *Dipsastraea* de Blainville, 1830 (Huang *et al.* 2014).
- Lobophylliidae (six species in four genera): *Lobophyllia*, *Homophyllia*, *Cynarina* Brüggeman, 1877, *Acanthastrea* Milne Edwards & Haime, 1848 (Huang *et al.* 2016).

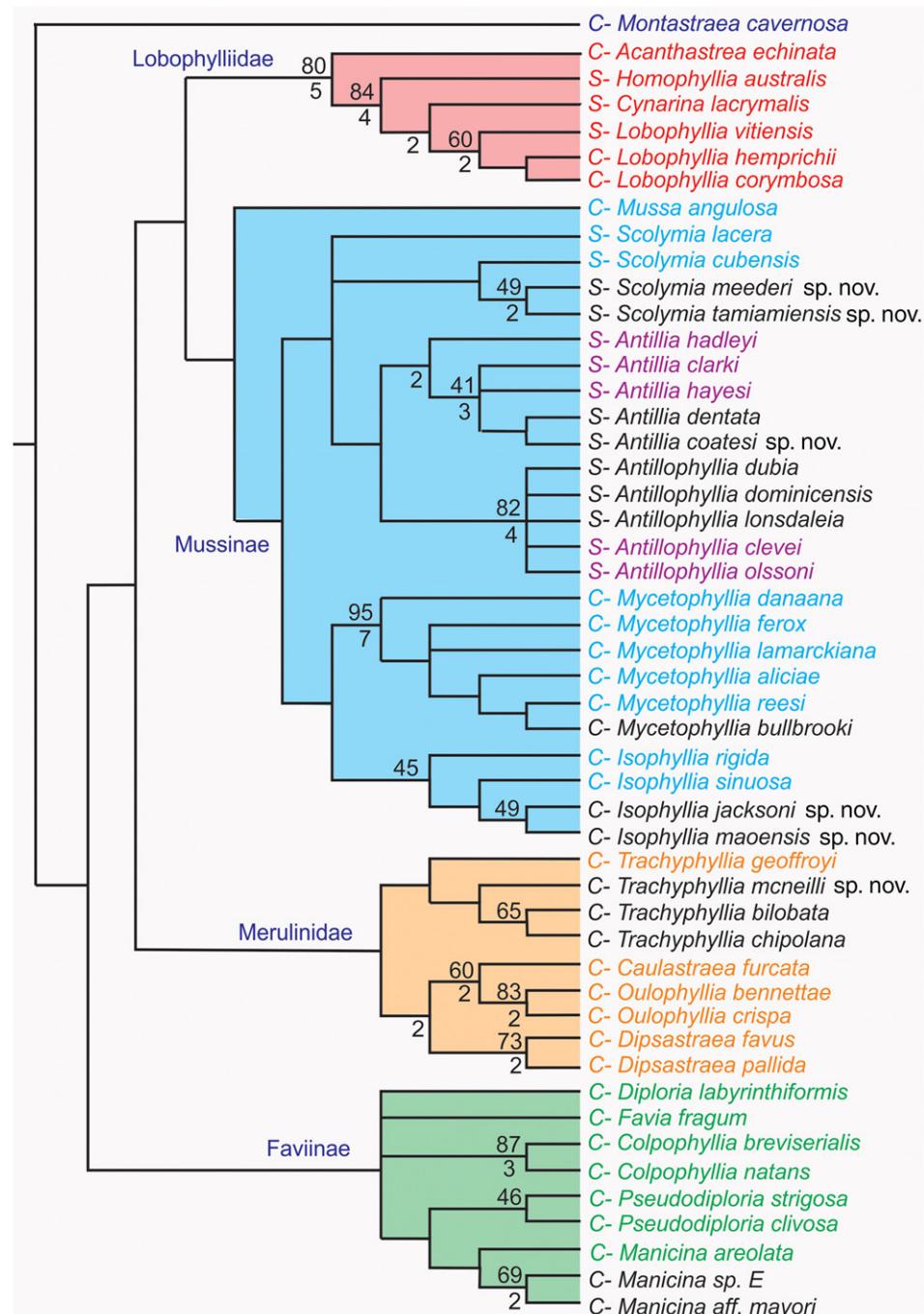


Figure 3. Strict consensus tree for morphological phylogenetic analysis (maximum parsimony) including modern and extinct species. The results suggest four major clades, which agrees with the molecular analyses of Fukami *et al.* (2008). Red species names are modern Lobophylliidae; blue species names are modern Mussinae; orange species names are modern Merulinidae; green species names are modern Faviinae; black species names are extinct Neogene species; purple species names are extinct Eocene species. Preceding each species name, 'S' is solitary; 'C' is colonial. Numbers above and below nodes are bootstrap values (>40) and Bremer support values (>1), respectively.

- Faviidae, Mussinae (10 species in four genera): *Mussa*, *Scolymia*, *Isophyllia*, *Mycetophyllia* (all modern Mussinae: Budd *et al.* 2012).
- Faviidae, Faviinae (seven species in five genera): *Colpophyllia* Milne Edwards & Haime, 1848,

Diploria Milne Edwards & Haime, 1848, *Pseudodiploria* Fukami, Budd & Knowlton in Budd *et al.*, 2012, *Favia* Milne Edwards & Haime, 1857, *Manicina* (representative modern Faviinae) (Budd *et al.* 2012).

Localities

The specimens in this study (Supplemental material, Appendix A) consist of samples extracted from outcrop exposures at ~ 811 localities in ~ 15 countries (Johnson *et al.* 2008; Budd *et al.* 2011). Some of the most intensively sampled stratigraphical units include: the late Miocene of Curaçao (Budd *et al.* 1998) and Panama (Klaus *et al.* 2012); the Mio–Pliocene of the Dominican Republic (Budd *et al.* 1994, 1996; Klaus & Budd 2003; Klaus *et al.* 2008, 2011); and the Plio–Pleistocene of Jamaica (Budd & McNeill 1998), Costa Rica and Panama (Budd *et al.* 1999; Klaus *et al.* 2012), Curaçao (Budd *et al.* 1998) and Florida (Klaus *et al.* 2017). A list of formations and their current age dates is provided in the Supplemental material, Appendix E.

Analytical methods

Characters

Following Budd & Stolarski (2009, 2011) and Budd *et al.* (2012), we selected 40 characters (Supplemental material, Appendix E), and coded the 50 species (20 extinct +30 extant) for phylogenetic analysis (Fig. 3). The characters consist of three sets of features: (1) macromorphology (using a stereoscope, at magnifications $<\times 50$); (2) micromorphology (using a scanning electron microscope, at magnifications ranging from $\times 50$ to $\times 200$); and (3) microstructure (using transverse thin sections, at magnifications $<\times 100$). Budd & Bosellini (2016) provide a glossary of morphological terms.

Macromorphological features serve as the primary diagnostic characters in traditional classification (Vaughan & Wells 1943; Wells 1956). They are architectural in nature, including colony form (solitary vs colonial, corallite budding and integration, the length and shape of calical series), the 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.

Micromorphological features, most notably 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 emphasize the three-dimensional 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. In the present study, micromorphological features could not be examined in extinct taxa due to inadequate preservation, and therefore were coded

as missing in the character matrix (Supplemental material, Appendices G and H).

With the exception of corallite wall structure, microstructural features were not used in the traditional classification of Vaughan & Wells (1943) and Wells (1956), although they were included in the classification systems of Alloiteau (1952, 1957) and Chevalier & Beauvais (1987). They involve the internal structure (i.e. the arrangement of calcification centres and fibres) within the wall, septa and columella, and consist of observations made primarily using transmitted light on petrographic thin sections. As in Budd *et al.* (2012), we focus 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), and on the costosepta and columella. In the latter observations, we consider the degree to which calcification centres are clustered, the distinctiveness of costoseptum medial lines, and the presence of transverse structures or clusters of centres crossing medial lines. Despite recrystallization, these features could be observed in fossil taxa for which we have thin sections.

The main difference between the characters used in the present study and those in previous work (e.g. Budd & Bosellini 2016) is the inclusion of features that pertain to solitary corals, and the exclusion of characters that pertain to meandroid corals. Examples of included new characters are: solitary, free-living, calice shape and septa shape. Examples of excluded characters are: extra-calicular budding, monticles, series width, series sinuosity, series forking, coenosteum structure, calice or valley width, calice depth, columella size, columella continuity and fibres.

Phylogenetic analysis

Maximum parsimony analysis was performed on the 50-taxon by 40-character data matrix using TNT v. 1.1 (Goloboff 1999; Nixon 1999; Goloboff *et al.* 2008). Heuristic searches were conducted with 1000 random addition replicates, each employing 100 cycles of sectorial searches, ratcheting, drifting and tree fusing. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. To assess clade support, heuristic searches were performed on 1000 bootstrap pseudoreplicate data sets (Felsenstein 1985). In addition, Bremer support values (Bremer 1988) were calculated for each node in the strict consensus of the most parsimonious trees (MPTs) using TreeRot 3 (Sorenson & Franzosa 2007), executed in PAUP* 4.0b10 (Swofford 2003). The number of random addition sequence replicates performed for each constrained analysis was set to 1000, with a rearrangement limit of 1 million per replicate.

Results

The phylogenetic analysis recovers 40 MPTs with tree lengths of 193 steps, a consistency index of 0.332 and a retention index of 0.802. The strict consensus tree is shown in Figure 3. Four main clades are recovered as monophyletic, but with low support among them. In general, the four clades agree with the previously defined molecular clades of Fukami *et al.* (2008): (1) molecular clade XVIII + XIX + XX (Lobophylliidae); (2) molecular clade XXI (Faviidae – Mussinae); (3) molecular clade XVII (Merulinidae); and (4) molecular clade XXI (Faviidae – Faviinae).

Nearly all of the extinct taxa in the analysis group with either Mussinae or Merulinidae. With the exception of the two extinct *Manicina* species, no extinct taxa occur in Faviinae and Lobophylliidae. The two extinct genera, *Antillia* and *Antillophyllia*, form distinct groups within Mussinae. The three extinct species of *Trachyphyllia* group with modern *T. geoffroyi* within Merulinidae. The remaining 10 extinct species are recovered within Mussinae – two group with *Scolymia*, two with *Antillia*, three with *Antillophyllia*, one with *Mycetophyllia* and two with *Isophyllia*. Of the five Eocene species, three group with *Antillia* and two with *Antillophyllia*. These results are used to assign species to families and genera in the Systematic palaeontology section below.

With respect to solitary-to-colonial transitions and vice versa, the tree shows that solitary corals only occur in the Lobophylliidae and Mussinae; whereas colonial corals occur in all four clades. In Lobophylliidae, the solitary corals group together with colonial corals and transitions between solitary and colonial corals appear to occur in both directions. In contrast, the solitary corals in Mussinae occur within solitary subclades that are distinct from colonial subclades.

Systematic palaeontology

In the systematic account that follows genera are based on clades in the phylogenetic analysis and their synapomorphies (Fig. 3); species are based on characters in Supplemental material, Appendices G and H. The synonymies are abbreviated. Only the first time a species name is used is considered in the synonymies for each species. Question marks indicate species whose type specimens are lost and that were not figured or the figures are inadequate. Only Caribbean Neogene species are given in synonymies. Non-Neogene and non-Caribbean synonyms are treated in Remarks sections. The term ‘non-type’ refers to specimens that are not primary types. Species diagnoses and descriptions focus

on dimensions and differences among species within genera. Micromorphology and microstructure of extant taxa are described and illustrated in Budd *et al.* (2012). Micromorphology and microstructure of fossil taxa are described herein as preservation permits.

Family Merulinidae Verrill, 1865

Genus *Trachyphyllia* Milne Edwards & Haime, 1848

1848 *Trachyphyllia* Milne Edwards & Haime: 492.

Type species. *Manicina amaranthum* Dana, 1846, p.189, pl. 9, fig. 1; syntypes USNM 85, YPM IZ 1974 [= *Turbinolia geoffroyi* Audouin, 1846, p. 233, pl. 4, figs 1.1, 1.2].

Type locality. ‘Habite les mers de la Chine’ (Milne Edwards & Haime 1848, p. 492), Singapore (Verrill 1864, p. 48); modern

Diagnosis. After Huang *et al.* (2014, fig. 26) based on the type species, *Trachyphyllia geoffroyi*.

Macromorphology: colonial and sometimes free-living, with intracalicular budding only. Often phaceloid (flabello-meandroid). Calice width large (>15 mm) and high relief (>6 mm). Septa in ≥4 cycles (≥48 septa) in six systems, compact and nonconfluent. Free septa present but irregular. Septa spaced 5–6 septa per 5 mm. Costosepta subequal or equal in relative thickness. Columella trabecular and spongy (>3 threads), <1/4 of calice width, and continuous (trabecular) among adjacent corallites. Septal (multiaxial) lobes well developed. Epitheca well developed and endotheca low-moderate (tabular).

Micromorphology: tooth base at mid-calice, circular. Tooth tip at mid-calice, irregular; tip orientation, perpendicular to septum. Tooth height low (<0.3 mm) and tooth spacing narrow (<0.3 mm), with >6 teeth per septum. Granules aligned on septal face, perpendicular to septal margin; irregular in shape. Interarea palisade.

Microstructure: Walls usually formed by dominant paratheca and partial septotheca; trabeculothecal elements may be present or even dominant; abortive septa absent. Thickening deposits fibrous, reduced. Costa centre clusters weak; 0.3–0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines strong. Transverse crosses present. Columella centres clustered.

Distribution. Extant. Modern: Indo-Pacific only, although absent east of Fiji. Fossil: late Eocene to present of the Indo-Pacific; early Miocene to early Pleistocene of the Caribbean.

Remarks. Wells (1956) assigned *Trachyphyllia* to the subfamily Trachyphylliinae Verrill, 1901, family Faviidae Gregory, 1900. Budd *et al.* (2012) transferred *Trachyphyllia* to the family Merulinidae, based on molecular data and micromorphology (the shape of its septal teeth: see also Huang *et al.* 2014). According to molecular data, the genus *Trachyphyllia* is most closely related to *Coelastrea* Verrill, 1866 and to a lesser degree *Dipsastraea* de Blainville, 1830. *Trachyphyllia* is distinguished primarily by its phaceloid (flabello-meandroid) colony form, its reduced, closely spaced teeth, and its aligned granules, perpendicular to the septal face (Huang *et al.* 2014).

Wells (1956) assigned both *Trachyphyllia* and *Antillophyllia* to the same subfamily, Trachyphylliinae Verrill, 1901, because of the presence of septal lobes. Veron *et al.* (1977) considered the two genera to be synonymous. On the other hand, Best & Hoeksema (1987) considered *Antillophyllia* and *Antillia* to be synonymous. The present phylogenetic analysis (Fig. 3) shows that the three genera are distinct and that *Trachyphyllia* belongs to a different family.

Assuming that *Trachyphyllia geoffroyi* and *T. radiata* (Pichon, 1980) are synonyms (as per Veron & Hodgson 1989), *Trachyphyllia* is monotypic today, but as evidenced by the grouping in the phylogenetic tree (Fig. 3), the genus consisted of at least three species in the geologic past. Modern *Trachyphyllia geoffroyi* differs from the three fossil species described herein by having longer series, septa subequal in thickness, fewer dissepiments and a septo-parathecal wall.

Modern *Trachyphyllia*, including the type species and its type specimens, is described in Huang *et al.* (2014). Unlike many of the other modern genera in this paper, *Trachyphyllia* is a broadcast spawner.

Trachyphyllia bilobata (Duncan, 1864) (Fig. 4A–I)

1864 *Antillia bilobata* Duncan: 31, pl. 3, fig. 3 (holotype NHMUK PI R28753; ‘Nivajé shale’, Dominican Republic, Neogene).

1864 *Antillia ponderosa* Milne Edwards & Haime in Duncan: 28, pl. 5, fig. 5 (holotype NMHUK PI R40412; Jamaica, Neogene).

1865 *Antillia walli* Duncan in Duncan & Wall: 11, pl. 2, fig. 4a–c (holotype NHMUK PI R28942; Bowden, Jamaica, Neogene).

Material. Holotype; holotypes of the two synonyms and 205 non-type specimens. Five non-type specimens are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Bilobate colony, wide calices (25–40 mm wide) containing 90–150 septa with septal lobes; elongate spongy columella; trabeculothecal wall.

Description. Macromorphology: colonial (usually two centres), free-living as adult; bilobate (constricted), conical corallum with ‘V’-shaped base, corallum height 3–5 cm (height approximately the same as calice length). Calice width = 25–40 mm; length = 35–65 mm; depth <6 mm. Five–six septal cycles (four complete), 96–150 septa total (>48 septa per calicular lobe), arranged according to the formula $S1 = S2 > S3 \gg S4 > S5 > S6$, with $S5$ and $S6$ being better developed in systems along the greater calicular diameter; septa subequal in thickness, curved; five septa per 5 mm. Elongate, narrow (<5 mm), spongy columella with trabecular linkage. Well-developed septal lobes. Abundant endotheca, moderately developed epitheca.

Micromorphology: finely dentate septa with scattered granules.

Microstructure: trabeculothecal wall, reduced thickening deposits; closely spaced (0.2–0.25 mm) centres of rapid accretion; moderate costal medial lines, moderate septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

Occurrence. Late Miocene–early Pleistocene: Cercado, Gurabo and Mao formations of the Dominican Republic; Tamiami Formation of Florida; Bowden and Hope Gate formations of Jamaica; Old Bank Formation of Panama (1–5.6 Ma).

Remarks. *Trachyphyllia bilobata* overlaps morphologically with *Trachyphyllia chipolana* but is distinguished by having more septal cycles and wider calices than *T. chipolana*. The degree to which the corallum is pinched varies among specimens (Foster *et al.* 1988). *Trachyphyllia bilobata* and *T. chipolana* are similar in calical shape to juvenile *T. geoffroyi* (Foster *et al.* 1988). The overall colony shape is similar to Mediterranean *Placosmilia* and Caribbean *Placocyathus*, both of which have lamellar columellae.

Trachyphyllia chipolana (Weisbord, 1971) (Fig. 5A–F)

1971 *Antillophyllia chipolana* Weisbord: 35–40, pl. 8, figs 1–8 (lectotype selected herein USNM66232, USGS2564; Chipola Formation, Florida, early Miocene).

Material. Holotype and 137 non-type specimens. Three non-type specimens are thin-sectioned (Supplemental material, Appendix A).

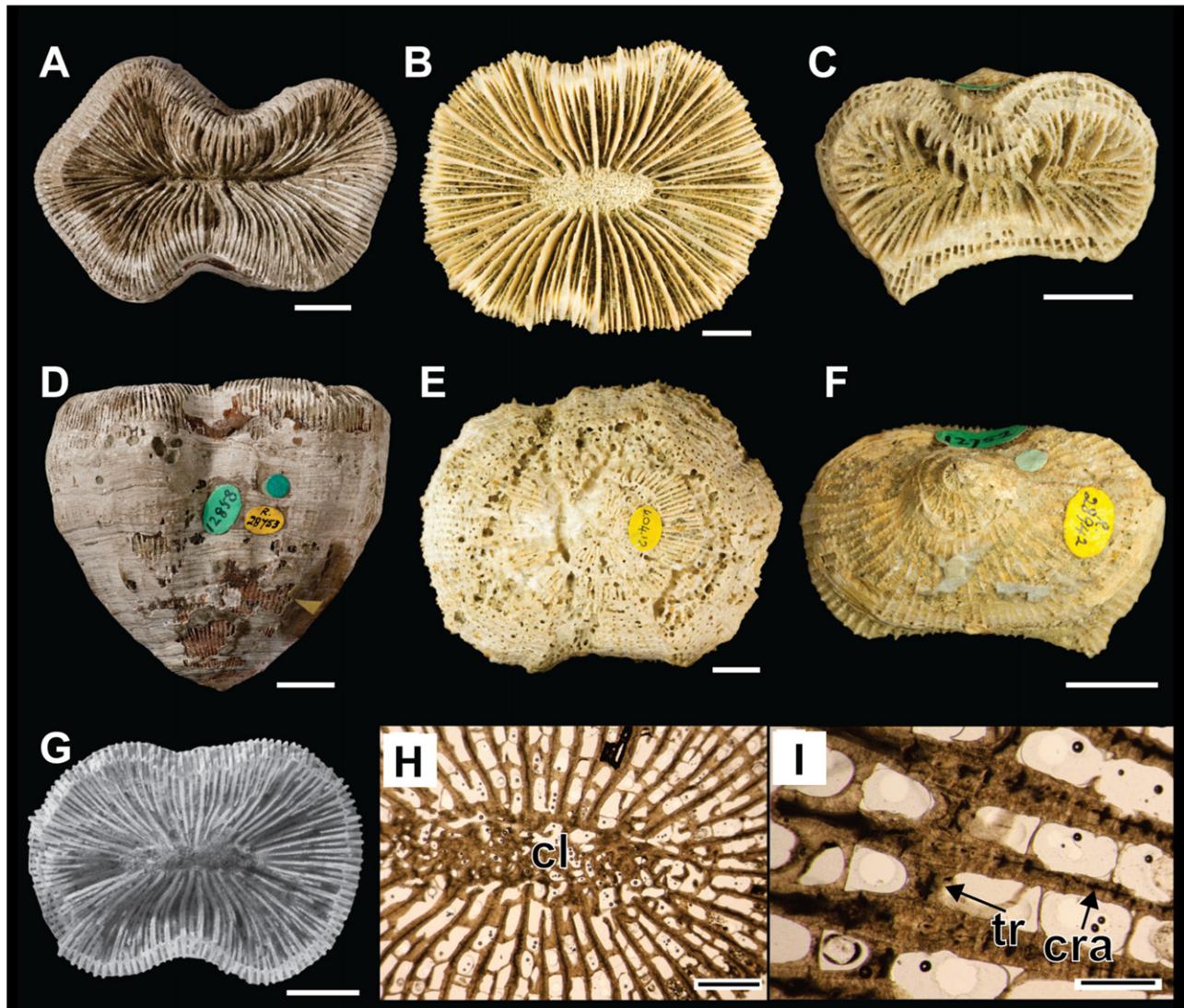


Figure 4. *Trachyphyllia bilobata* is distinguished by having a bilobate, free-living colony form; a wide calice; septal lobes; a spongy columella; and a trabeculothecal wall. **A, B**, holotype, NHMUK PI R28753; **A**, calical surface; **B**, corallum side. **C, D**, calical surfaces; **C**, synonym, holotype of *Antillia walli*, NHMUK PI R28942; **D**, synonym, holotype of *Antillia ponderosa*, NHMUK PI R40412. **E, F**, corallum bases; **E**, synonym, holotype of *Antillia ponderosa*, NHMUK PI R40412; **F**, synonym, holotype of *Antillia walli*, NHMUK PI R28942. **G**, hypotype, NMB D5905 (CCD12242), calical surface showing septal lobes. **H, I**, hypotype, SUI 129437 (CCD 47767): **H**, transverse thin section showing an elongate spongy columella (cl); **I**, transverse thin section showing a trabeculothecal corallite wall (tr) and closely spaced centres of rapid accretion (cra). Scale bars: A–G = 1 cm; H = 3 mm; I = 1 mm.

Diagnosis. Elongate colony composed of a single valley (15–25 mm wide) containing 80–130 septa with small septal lobes; trabeculothecal wall.

Description. Macromorphology: colonial (>2 centres), free-living as adult; long, irregular corallum with ‘V’-shaped base; one valley, often constricted (pinched); conical corallum (flabellate), corallum height 3–5 cm (height approximately the same as calice length). Calice width = 15–25 mm; length = 40–60 mm; depth 6–12 mm. Five septal cycles (three complete); 80–130 septa total, arranged according to the formula $S1 = S2 > S3 >$

$S4 > S5$, with $S4$ and $S5$ being better developed in systems along the greater calicular diameter; septa subequal in thickness, curved; five septa per 5 mm. Elongate, narrow (<5 mm), spongy trabecular columella. Well-developed septal lobes. Abundant endotheca, moderately developed epitheca.

Micromorphology: finely dentate septa with scattered granules.

Microstructure: trabeculothecal wall, reduced thickening deposits; closely spaced (0.2–0.25 mm) centres of rapid accretion; moderate costal medial lines, moderate

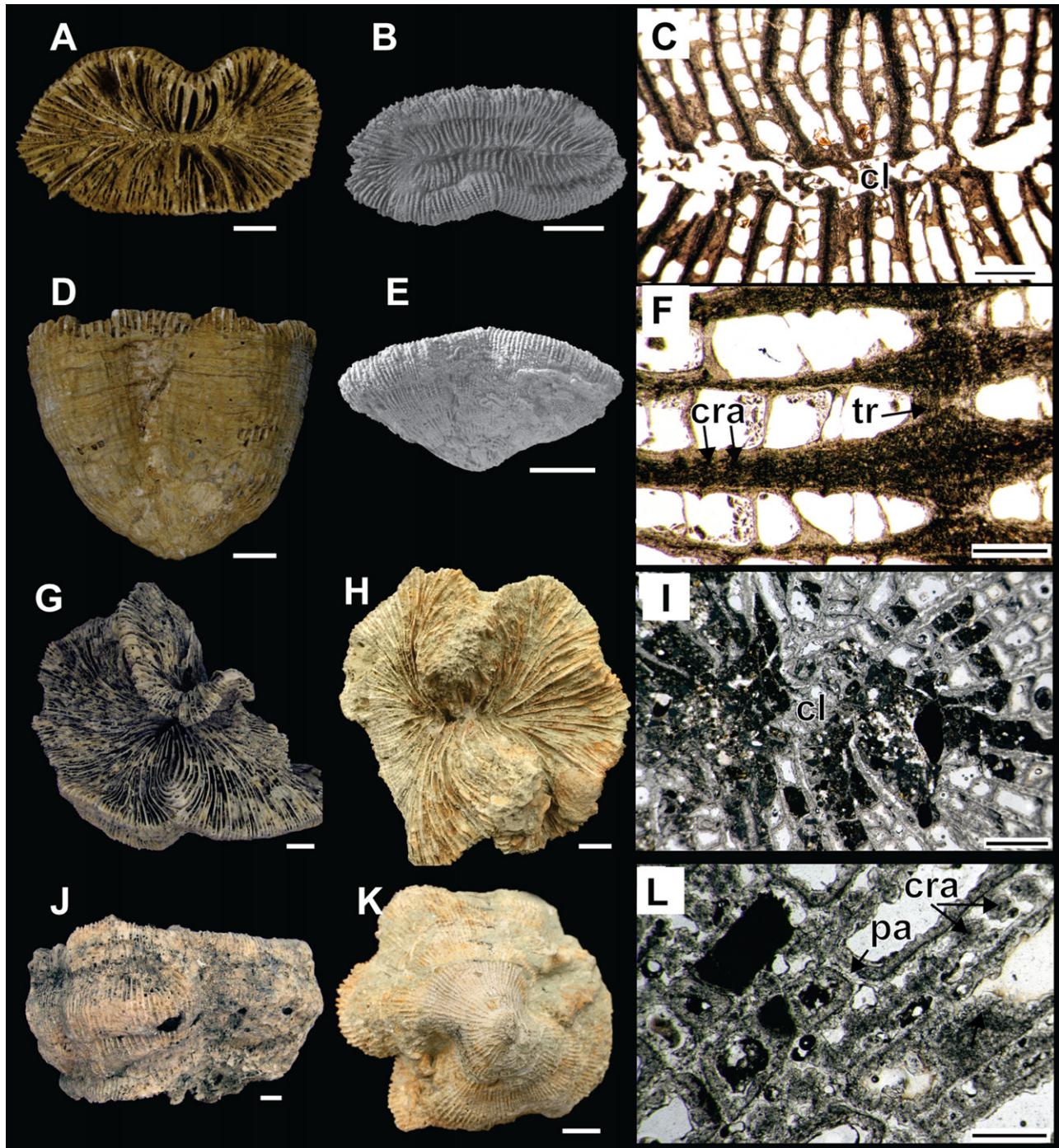


Figure 5. *Trachyphyllia chipolana* and *T. mcneilli* Budd & Klaus sp. nov. *Trachyphyllia chipolana* is similar to *T. bilobata* in bilobate colony form and trabeculothecal wall (tr) with closely spaced centres of rapid accretion (cra) but has a distinctively narrower calice and columella (cl). *Trachyphyllia mcneilli* has an irregular multilobate form and partially parathecal wall (pa). A–F, *Trachyphyllia chipolana*. A, holotype, USNM 66232, calical surface; B, hypotype, NMB D6613 (CCD12201), calical surface showing septal lobes; C, hypotype, SUI 137213, transverse thin section showing narrow columella; D, holotype, USNM 66232, corallum side; E, hypotype specimen, NMB D6613 (CCD12201), calical surface; F, hypotype, SUI 137213, transverse thin section showing trabeculothecal corallite wall. G–L, *Trachyphyllia mcneilli*; G, holotype, SUI 102824 (CCD9584), calical surface; H, paratype, SUI 146467 (CCD54758), calical surface; I, paratype, SUI 140400 (CCD9617), transverse thin section showing spongy columella; J, holotype, SUI 102824 (CCD9584), corallum side; K, paratype, SUI 146467 (CCD54758), corallum base; L, paratype, SUI 140400 (CCD9617), transverse thin section showing trabeculothecal corallite wall. Scale bars: A, B, D, E, G, H, J, K = 1 cm; C, I = 3 mm; F, L = 1 mm.

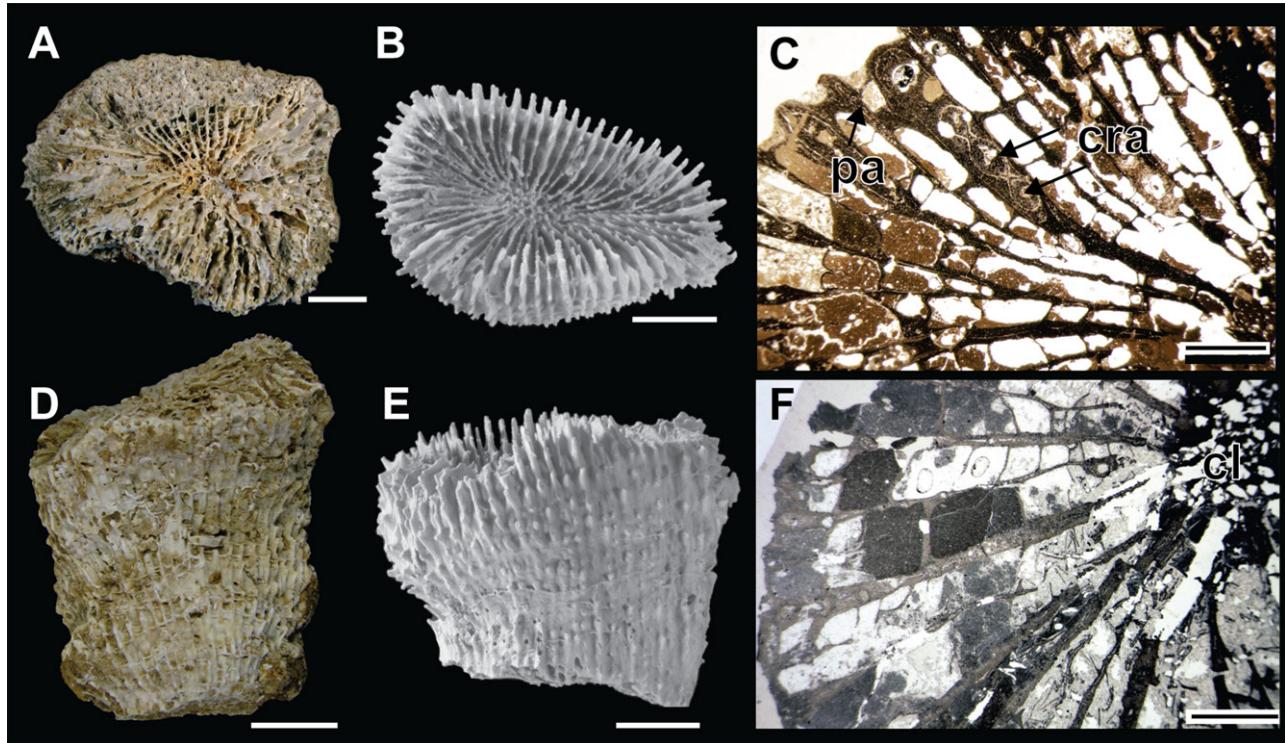


Figure 6. Fossil *Mussa angulosa*. *Mussa angulosa* has a phaceloid colony form; its large calices and spine-shaped teeth are similar to those of the solitary coral *Scolymia lacera*. However, it has fewer septa, and trabecular linkage instead of lamellar linkage (Fig. 1). Its centres of rapid accretion (cra) are widely spaced, its wall is parathecal (pa), and its columella (cl) is spongy. A, hypotype, USNM 14780765 (CCD3550), calical surface; B, hypotype, NMB D6609, calical surface; C, hypotype, SUI 146152 (CCD 53520), transverse thin section showing parathecal (pa) coralite wall; D, hypotype, USNM 14780765 (CCD3550), corallite side; E, hypotype, NMB D6609, corallite side; F, hypotype, SUI 146152 (CCD 53520), transverse thin section showing spongy columella (cl). Scale bars: A, B, D, E = 1 cm; C, F = 3 mm.

septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

Occurrence. Early Miocene–late Pliocene: Gurabo Formation of the Dominican Republic; Chipola and Tamiami formations of Florida; it also possibly occurs in the Tamana Formation of Trinidad (2.8–18.3 Ma).

Remarks. *Trachyphyllia chipolana* has previously been lumped together with *T. bilobata*, but it has a distinctively narrow calice. It has previously been referred to as ‘*Trachyphyllia* sp. A’ (Budd *et al.* 1994).

***Trachyphyllia mcneilli* Budd & Klaus sp. nov.
(Fig. 5G–L)**

Material. Holotype, five paratypes and 31 non-type specimens. One non-type specimen is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Multilobate (>2 large calicular lobes emanating from one or more centres) colony, large calices containing 170–190 septa with septal lobes, trabeculothecal wall.

Description. Macromorphology: colonial (>2 centres), usually free-living but may be attached as adult; irregular multilobate (often bilobate), conical corallum with constrictions, corallum height >7 cm (height approximately the same as calice width). Calice width = 6–7 cm; length = ~11 cm; depth = 1–2 cm. Six septal cycles (four complete); >180 septa total (>60 septa per calicular lobe), arranged according to the formula S1 = S2 > S3 ≫ S4 > S5 > S6, with S5 and S6 better developed in systems along the greater lobe diameter; septa subequal in thickness, curved; five septa per 5 mm. Elongate, spongy (width = 4 mm) columella. Well-developed septal lobes. Abundant endotheca, moderately developed epitheca.

Micromorphology: finely dentate septa with small aligned granules.

Microstructure: trabeculothecal wall, partially parathecal; reduced thickening deposits; well-developed, closely spaced (<0.5 mm) centres of rapid accretion; moderate costal medial lines, moderate septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

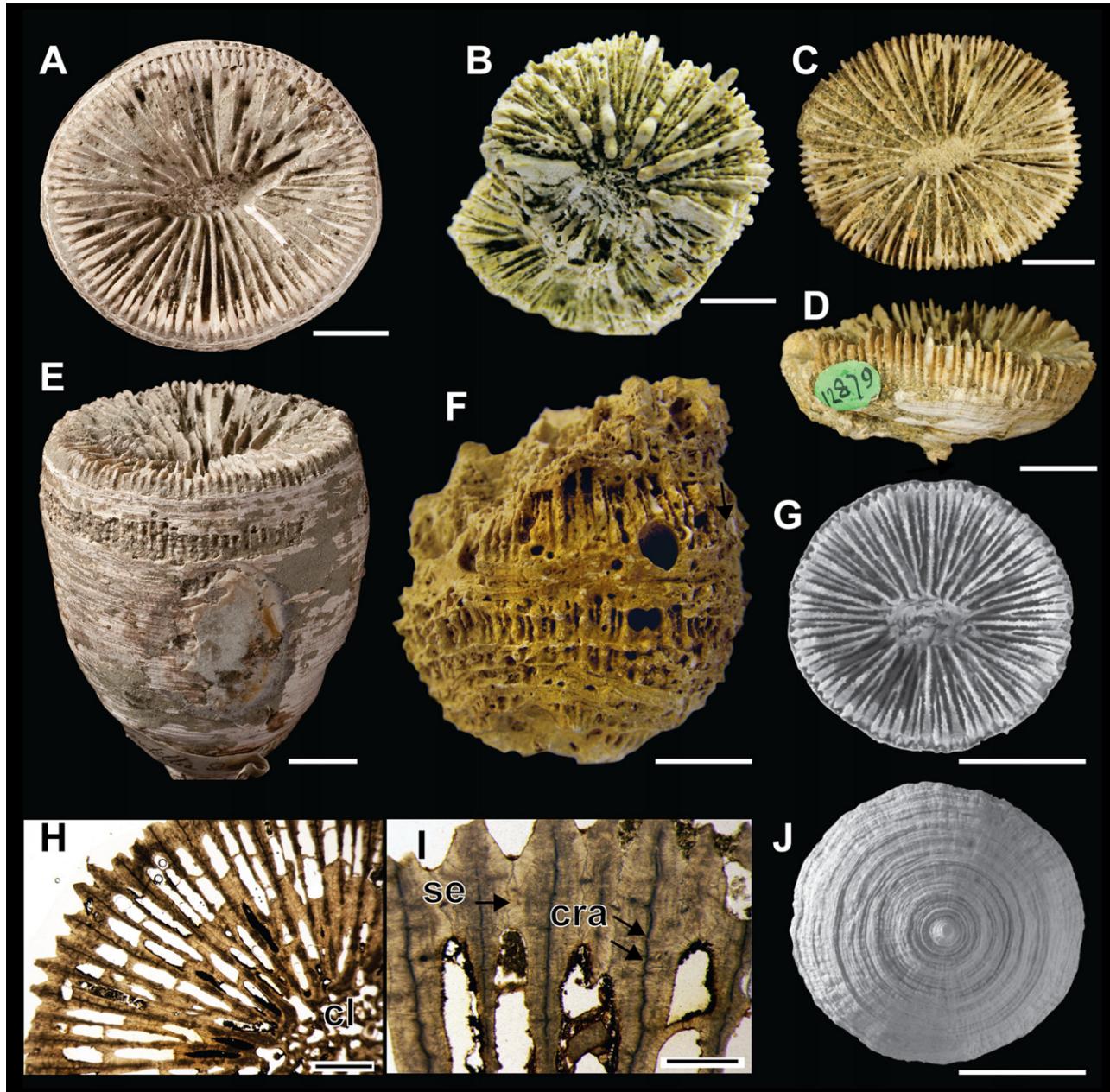


Figure 7. *Antillia dentata* is solitary with a medium-sized calice and no septal lobes; its septa are subequal in thickness and straight; it has a well-developed epitheca and septothecal (se) corallite wall. **A**, holotype, NHMUK PI R28761, calical surface; **B**, syntype of the colonial coral *Syzygophyllia brevis* Reuss, 1860, NHMW 1872/0013/0037, calical surface showing unequal septa and paliform lobes. **C**, **D**, synonym, Duncan's figured specimen of *Montlivaltia ponderosa* Milne Edwards & Haime of Duncan, 1863, NHMUK PI R28794; **C**, calical surface; **D**, corallum side; **E**, holotype, NHMUK PI R28761, corallum side; **F**, syntype of the colonial coral *Syzygophyllia brevis* Reuss, 1860, NHMW 1872/0013/0037, corallum side; **G**, hypotype, NMB D6612 (CCD10198), calical surface. **H**, **I**, hypotype, SUI 140412 (CCD140412); **H**, transverse thin section showing subequal septa in thickness and spongy columella (cl); **I**, transverse thin section showing septothecal (se) corallite wall and moderately spaced centres of rapid accretion (cra). **J**, hypotype, NMB D6612 (CCD10198), corallum base. Scale bars: A–G = 1 cm; H = 3 mm; I = 1 mm.

Derivation of name. After Donald F. McNeill, who first discovered specimens of this species in Curaçao, Netherlands Antilles, for establishing chronostratigraphical and palaeoenvironmental constraints on Cenozoic coral-bearing strata.

Occurrence. Late Miocene–late Pliocene: Seroe Domi Formation of Curaçao; Cercado, Gurabo and Mao formations of the Dominican Republic; and Old Bank Formation of Panama (3–6.45 Ma).

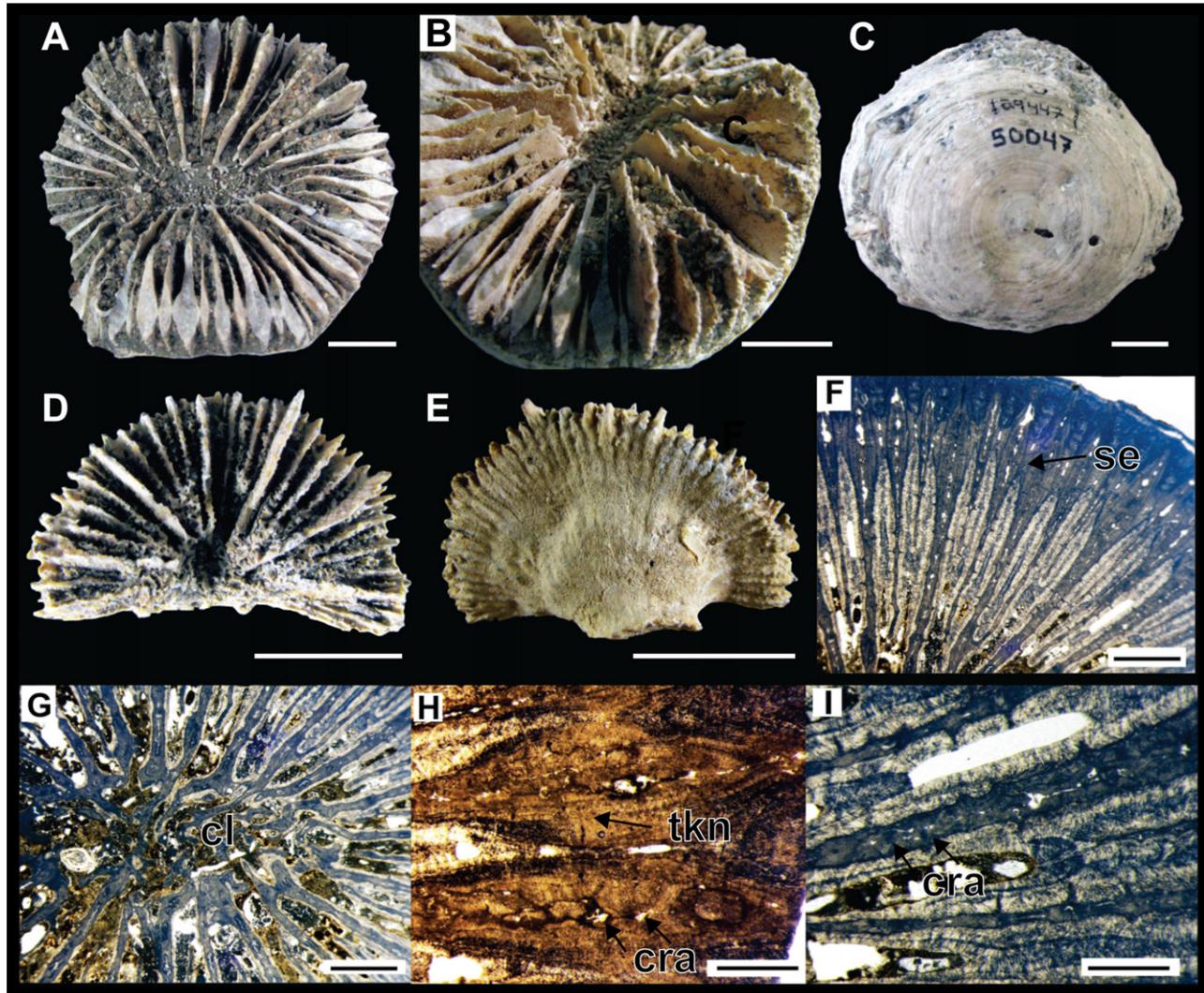


Figure 8. *Antillia coatesi* Budd & Klaus sp. nov. *Antillia coatesi* is solitary with a large corallite and distinctive large, widely spaced teeth; its septa are unequal and straight; its centres of rapid accretion (cra) are widely spaced and surrounded by extensive thickening deposits (tkn). Like *A. dentata*, it has a well-developed epitheca and septothecal (se) corallite wall and spongy columella (cl). **A, B**, holotype, SUI 127788 (CCD50045); **A**, calical surface; **B**, calical surface showing large septal teeth. **C**, paratype, SUI 129447 (CCD50047), corallum side showing epitheca. **D, E**, holotype of *Syzygophyllia tampae* Weisbord, 1973, a possible synonym, USNM 68312; **D**, calical surface; **E**, corallum base. **F–I**, paratype, SUI 127794 (CCD 50051); **F**, transverse thin section showing septothecal (se) corallite wall; **G**, transverse thin section showing spongy columella (cl); **H**, transverse thin section, close-up of corallite wall showing thickening deposits (tkn) and widely spaced centres of rapid accretion (cra); **I**, transverse thin section, close-up of septa showing widely spaced centres of rapid accretion (cra). Scale bars: A–E = 1 cm; F, G = 3 mm; H, I = 1 mm.

Remarks. *Trachyphyllia mcneilli* is similar to *A. dominicensis* in its large calices, numbers of septa and septal lobes, but it differs by having a variable multilobate form, intracalicular budding, a moderately well-developed columella and a trabeculothecal corallite wall. It has previously been referred to as ‘*Trachyphyllia* sp. B’ (Budd *et al.* 1998).

Family **Faviidae** Milne Edwards & Haime, 1857

Subfamily **Mussinae** Ortmann, 1890

Genus **Mussa** Oken, 1815

1815 *Mussa* Oken: 73.

Type species. *Madrepora angulosa* Pallas: 299; neotype YPM 9035, Port Royal, Jamaica (figured in Budd *et al.* 2012, fig. 9A, B).

Type locality. ‘Mare Americanum’ (Pallas 1766, p. 300); modern.

Diagnosis. After Budd *et al.* (2012, figs 12, 18, 22). Macromorphology: colonial; intracalicular budding.

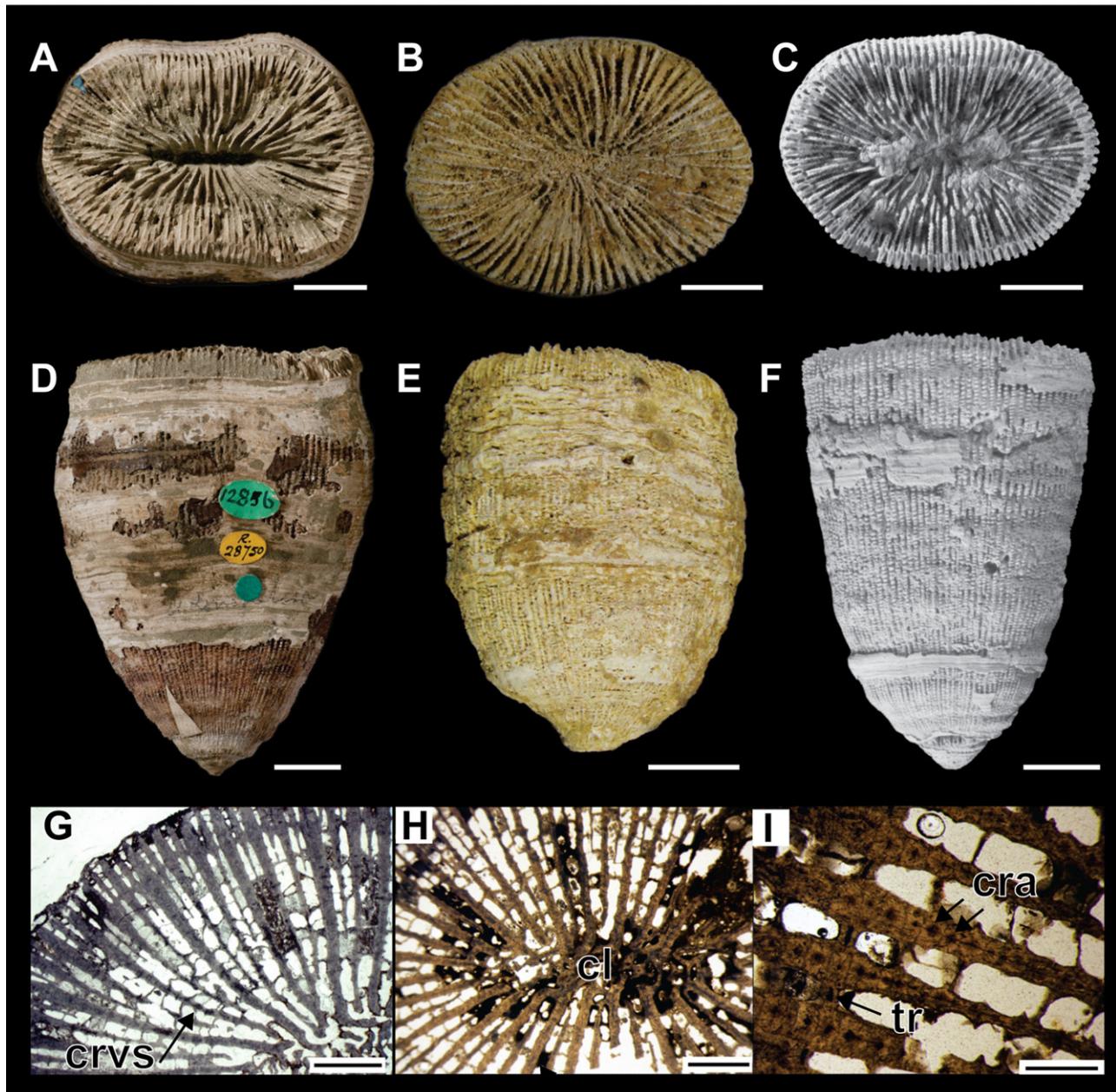


Figure 9. *Antillophyllia lonsdaleia* is solitary and barrel-shaped, with an elliptical corallite and well-developed septal lobes. It has numerous curved septa (crvs), a compact columella (cl), and a trabeculothecal (tr) corallite wall. A, lectotype, NHMUK PI R28750, calical surface; B, holotype of *Antillia sawkinsi*, USNM M353652, calical surface; C, hypotype, NMB D6611 (CCD10102), calical surface; D, lectotype, NHMUK PI R28750, corallum side; E, holotype of *Antillia sawkinsi*, USNM M353652, corallum side; F, hypotype, NMB D6611 (CCD10102), corallum side; G, hypotype, USNM 72808, transverse thin section showing curved septa (crvs); H, I, hypotype, SUI 106630 (CCD43216); H, transverse thin section showing compact columella (cl); I, transverse thin section showing trabeculothecal (tr) corallite wall and closely spaced centres of rapid accretion (cra). Scale bars: A–F = 1 cm; G, H = 3 mm; I = 1 mm.

Phaceloid to fasciculate, with short series (usually 1–3 centres per series); large calices (2.5–4.5 cm) with high relief (>6 mm), four complete septal cycles in six systems, subequal in thickness; thin, curved septa, with wide septal spacing; continuous, spongy (>3 threads) columella with trabecular linkage; reduced epitheca; no septal or paliform lobes; abundant endotheca.

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

Microstructure. Parathecal wall. Widely spaced (>1.2 mm), well-developed centres of rapid accretion that cross medial lines; reduced thickening deposits.

Distribution. Extant. Modern: Caribbean only. Fossil: late Miocene–Recent, Caribbean only.

Remarks. According to molecular data, *Mussa* belongs to the family Faviidae, subfamily Mussinae, which is distinguished by the size and shape of its septal teeth and abundant internal dissepiments (Budd *et al.* 2012). Its teeth are distinctively large (>0.6 mm tall), widely spaced (1–2 mm) and spine-shaped (circular base) (see Budd *et al.* 2012). According to the phylogenetic tree in the present study (Fig. 3), *Mussa* is not closely related to other modern genera assigned to the Mussinae (e.g. *Isophyllumia*, *Mycetophyllumia*, *Scolymia*). *Mussa* differs from these other genera in its distinctive phaceloid colony form, its reduced thickening deposits and the well-developed microstructural medial lines within its costosepta. Nevertheless, it is similar to the solitary genus *Scolymia* in having large calices with numerous septa, to the colonial genus *Mycetophyllumia* by having parathecal corallite walls, and to the colonial genus *Isophyllumia* in having a spongy columella with trabecular linkage (Budd *et al.* 2012). Juvenile *Mussa* are especially difficult to distinguish from juvenile *Scolymia*, because they both have concave calices and awl-shaped teeth (Wells 1971). In fact, Fenner (1993) found a complete morphological series joining *S. lacera* and *M. angulosa*.

Mussa is similar in overall colony shape to the Indo-Pacific genus *Lobophyllumia* de Blainville, 1830 and to the Mediterranean Oligocene genus *Leptomussa* d'Achiardi, 1867. *Leptomussa* differs from *Mussa* by being primarily solitary (ceratoid), lacking a columella and epitheca, and having a septothecal wall. *Lobophyllumia* differs from *Mussa* by having well-developed thickening deposits, lamellar linkage between centres and longer series. Like *Leptomussa*, *Lobophyllumia* lacks an epitheca and has a septothecal wall. Images of modern species (macromorphology, micromorphology, microstructure) are given in Budd *et al.* (2012, figs 9, 12, 18, 22).

***Mussa angulosa* (Pallas, 1766)**
(Fig. 6A–F)

1766 *Madrepore angulosa* Pallas: 299 (neotype: YPM 9035; Port Royal, Jamaica, modern).

Material. Fifteen non-type specimens, one of which is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Phaceloid, attached; short, uniserial series with wide, deep valleys. Few septa, exsert up to 6 mm. Continuous, trabecular columella. Tall, thin, widely spaced teeth, spine-shaped.

Description. Three to five centres per series, irregular calical shape. Valley width = 4–5 cm, valley depth = 10–20 mm. Four complete septal cycles arranged according to the formula S1 = S2 > S3 > S4; septa subequal in thickness; 3–5 septa per 5 mm. Elliptical, spongy columella. Parathecal wall, reduced thickening deposits, reduced epitheca.

Occurrence. Late Miocene–Recent: Moín and Quebrada Chocolate formations of Costa Rica; Gurabo and Mao formations of the Dominican Republic; Tamiami Formation of Florida; Manchioneal Formation of Jamaica (0–3.7 Ma).

Remarks. The genus *Mussa* is monotypic today and was monotypic in the geologic past. Only one species, *Mussa angulosa*, is known. The type specimen is described in Budd *et al.* (2012).

Genus *Antillia* Duncan, 1864

1864 *Antillia* Duncan: 28.

Type species. *Antillia dentata* Duncan, 1864, p. 29, pl. 3 (fig. 2a–c); holotype NHMUK PI R28761.

Type locality. Nivajé Shale, Dominican Republic; Neogene.

Diagnosis. Solitary, circular corallum, bowl-shaped base; free-living; medium sized calices (< 50 mm); > 4 septal cycles in six systems; spongy columella with paliform lobes; no septal lobes; well-developed epitheca. Septothecal wall, moderate to extensive thickening deposits.

Distribution. Extinct, Caribbean-only. Eocene–early Pleistocene.

Remarks. *Antillia* is an extinct, exclusively Caribbean solitary genus. According to the phylogeny (Fig. 3), it consists of two Neogene species and is closely related to the solitary genus *Scolymia*. *Antillia* differs from *Scolymia* by being free-living and having smaller calices, a strong epitheca and a septothecal corallite wall. *Antillia* differs from the solitary genus *Antillophyllia* by having a bowl-shaped corallum, well-developed epitheca, circular calices, straight septa, paliform lobes and a septothecal corallite wall. Unlike *Antillophyllia* it lacks septal lobes.

The present authors do not consider *Antillia* to be a synonym of the Mediterranean Neogene genus *Syzygophyllia* Reuss, 1860, p. 216 (type species *Syzygophyllia brevis* Reuss, 1860, NHMW 1872/13/37, Neogene, Ruditz, Czech Republic) as has been indicated by Vaughan (1932). *Antillia* differs from *Syzygophyllia* in that it is solitary whereas *Syzygophyllia* is primarily colonial. Although the type specimen of *S. brevis* consists of a single corallite, *Syzygophyllia* is phaceloid with lamellar linkage (Vaughan & Wells 1943), similar to modern *Lobophyllia* de Blainville, 1830 but having epitheca.

We also do not consider *Antillia* to be a synonym of *Trachyphyllia* as has been indicated in the Paleobiology Database (paleobiodb.org). *Antillia* is solitary, with a well-developed epitheca and septothecal corallite wall; *Trachyphyllia* is colonial.

Antillia also differs from the solitary Mediterranean Eocene genus *Circophyllia* Milne Edwards & Haime, 1848, p. 491 (type species *Anthophyllum truncatum* Goldfuss, 1826), which is turbinate and has a septothecal wall and no epitheca (Vaughan & Wells 1943).

In addition to the Neogene species treated herein, three species are reported from the Caribbean Eocene: *Antillia clarki* Durham in Clark & Durham, 1946, p. 79 (Colombia), *A. compressa* (Duncan, 1873, p. 556) (St. Bartholomew) and *Antillia hayesi* Vaughan, 1919, p. 424 (Nicaragua); and two species are reported from the Caribbean Oligocene: *Antillia hadleyi* (hadleyi) Wells, 1934, p. 79 (Cuba), and *Antillia heueri* Frost & Langenheim, 1974, p. 291 (Chiapas). *Antillia compressa* and *A. heueri* have smooth exsert septa and well-developed thickening deposits. They appear to be azooxanthellate corals, possibly in the family Caryophyllidae, and unrelated to the species treated herein.

***Antillia dentata* Duncan, 1864**
(Fig. 7A, C–E, G–J)

1863 *Montlivaltia ponderosa* Milne Edwards & Haime in Duncan: 441–442, pl. 16, fig. 6a, b; (figured specimen NHMUK PI R28794; Jamaica, Neogene).

1864 *Antillia dentata* Duncan: 29, pl. 3 (fig. 2a–c) (holotype NHMUK PI R28761; Dominican Republic, Neogene).

1901 *Antillia gregorii* Vaughan: 6 (new name for *Montlivaltia ponderosa* Milne Edwards & Haime in Duncan, 1863).

Material. Holotype, holotype of synonym and 74 non-type specimens. Eight non-type specimens are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Medium-size calices (2–3 cm), with septa subequal in thickness and moderate-sized teeth.

Description. Macromorphology: solitary, free-living as adult, circular calices, bowl- to barrel-shaped corallum, usually with ‘U’-shaped base, corallum height 2–6 cm. Calice width = 20–30 mm; depth < 6 mm. Four to five septal cycles (four complete) arranged according to the formula $S1 = S2 > S3 > S4$; 72–96 septa total; septa subequal in thickness; four septa per 5 mm. Elliptical, spongy trabecular columella; weak paliform lobes. Moderate endotheca, well-developed epitheca.

Micromorphology: moderately developed teeth (five teeth per 4 mm).

Microstructure: septothecal wall, moderate thickening deposits; well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion; moderate costal medial lines, moderate septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

Occurrence. Late Miocene–early Pleistocene: Cercado, Gurabo and Mao formations, Los Haitises Formation, Dominican Republic; Old Pera Beds, Jamaica (0.8–6.45 Ma).

Remarks. Vaughan (1919) considered *A. dentata* and *A. gregorii* to be separate species; however, our observations of the type specimens indicate that they are similar in corallum size and shape, costosepta development, columella, paliform lobes, wall structure, development of endotheca and epitheca, and septal dentition. We therefore have synonymized the two species.

***Antillia coatesi* Budd & Klaus sp. nov.**
(Fig. 8A–I)

1973 ?*Syzygophyllia tampae* Weisbord: 60–61, pl. 28, figs 1–3, pl. 29, fig. 1 (holotype USNM 68312; Arcadia Formation (Tampa Member), Florida, early Miocene).

Material. Holotype, 29 paratypes and seven non-type specimens, plus one questionable synonym (Supplemental material, Appendix A). The holotype and 13 paratypes are thin-sectioned.

Diagnosis. Large calices (3–5 cm) with unequal septa and large teeth.

Description. Macromorphology: solitary, free-living as adult, circular calices, bowl- to barrel-shaped corallum, usually with ‘U’-shaped base, corallum height 1.5–4 cm. Calice width = 30–50 mm; depth < 6 mm. Four to five septal cycles (four complete) arranged according to the formula $S1 = S2 > S3 \gg S4$; 72–96 septa total; septa unequal in thickness; four septa per 5 mm. Circular,

spongy trabecular columella; weak paliform lobes. Moderate endotheca, well-developed epitheca.

Micromorphology: large, widely spaced teeth with round bases and tips (two teeth per 4 mm), distinctively unequal in lower (primary – tertiary) and higher septal cycles; moderately abundant, spiky granules, strongly aligned.

Microstructure: septothecal wall, extensive thickening deposits; well-developed, widely spaced (0.7–1.8 mm) centres of rapid accretion; weak costal medial lines, weak septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

Derivation of name. After Anthony G. Coates for his pioneering work to unravel the geological and palaeontological history of the Central American Isthmus.

Occurrence. Late Miocene–late Pliocene: Old Bank Formation, Panama; Gurabo and Mao formations, Dominican Republic; Bowden Formation, Jamaica (2.7–6.15 Ma).

Remarks. This species has distinctively large primary and secondary septa ('regular subequal lobular dentations' *sensu* Vaughan & Wells 1943), similar to *Syzygophyllia brevis*, but is distinguished by its strong epitheca and solitary bowl- to barrel-shaped corallum.

Weisbord's (1973) holotype of '*Syzygophyllia tampae*' may be a juvenile because it has a smaller calice width of 22–25 mm and a small pedicle. However, it also has 96 septa and the primary and secondary septal cycles are notably thicker and better developed than the higher cycles; the wall is mostly septothecal, and the teeth are relatively large, similar to the material described as *Antillia coatesi*. Due to its smaller size, *Antillia tampae* is only questionably synonymized with *Antillia coatesi*. In previous work, this species has been mistakenly referred to as '*Antillia gregorii*' (Vaughan 1901, 1932; Budd *et al.* 1994; Budd & McNeill 1998).

Genus *Antillophyllia* Vaughan, 1932

1932 *Antillophyllia* Vaughan: 506.

Type species. *Antillia lonsdaleia* Duncan, 1864, p. 30–31, pl. 3 (fig. 4) (syntype NHMUK PI R28750–52).

Type locality. Nivajé Shale, Dominican Republic; Neogene.

Diagnosis. Solitary, turbinate (conical) corallum, elliptical calice; free-living; medium to large calices (<60 mm in width); curved septa, >5 septal cycles in six systems; small septal lobes; reduced to moderate epitheca; trabeculothecal wall, reduced to moderate thickening deposits.

Distribution. Extinct. ?Cretaceous (Maastrichtian) or Eocene–early Pleistocene of the Caribbean, and possibly the Mio-Pliocene of the Indo-Pacific and the Oligocene of the Mediterranean (see Discussion).

Remarks. *Antillophyllia* is an extinct, primarily Caribbean solitary genus. It was first described by Vaughan (1932), who distinguished it from *Antillia* on the basis of its having septal lobes. Vaughan (1932) considered the fossil members of *Trachyphyllia* described herein as also belonging to *Antillophyllia*. However, *Antillophyllia* differs from *Trachyphyllia* by having more septal cycles, thicker septa, smaller septal lobes, a more compact columella and better developed septal teeth. It is exclusively solitary and does not form the meandroid colonies possessed by some variants of *Trachyphyllia geoffroyi* (Best & Hoeksema 1987).

In addition to the Neogene species treated herein, two species are reported from the Caribbean Eocene: *Antillophyllia clevei* (Duncan, 1873, p. 556) (St. Bartholomew), and *Antillophyllia* (?) *olssoni* Durham in Clark & Durham, 1946, p. 80 (Colombia). A third species, *Antillophyllia* (?) *gesteri* Durham in Clark & Durham, 1946, p. 79 (Colombia), is similar in overall dimensions to *Antillia clarki*, but is too poorly preserved to characterize. Baron-Szabo (2006) also reports possible *Trachyphyllia sawkinsi* (=*Antillophyllia lonsdaleia*) in USNM collections from the Maastrichtian of Jamaica.

Antillophyllia lonsdaleia (Duncan, 1864) (Fig. 9A–I)

1864 *Antillia lonsdaleia* Duncan: 30–31, pl. 3, fig. 4 (syntypes NHMUK PI R28750–52; Nivajé Shale, Dominican Republic, Neogene; lectotype designated herein NHMUK PI R28750).

1926 *Antillia sawkinsi* Vaughan in Vaughan & Hoffmeister: 118, pl. 2, fig. 6, 6a (holotype USNM M353652; USGS 8299, Manzanilla Formation, Trinidad, late Miocene).

Material. Lectotype, two paralectotypes, synonym and 86 non-type specimens. Five non-type specimens are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Solitary, elliptical calice (30–40 mm) containing 120–140 septa, septal lobes, moderate epitheca, trabeculothecal wall.

Description. Macromorphology: solitary (one centre), free-living as adult, elliptical calices (not constricted), barrel-shaped (cuneiform) corallum with 'V'-shaped base, corallum height 3–7 cm (height

approximately the same as calice length). Calice width = 30–40 mm; length = 30–50 mm; depth ~6 mm; six septal cycles arranged according to the formula S1 = S2 > S3 > S4 ≫ S5 > S6, with S5 and S6 being better developed in systems along the greater calicular diameter; 120–140 septa total; septa subequal in thickness, curved; six septa per 5 mm. Elliptical, narrow (<3 mm), compact trabecular columella. Small septal lobes. Abundant endotheca, moderate epitheca.

Micromorphology: coarsely dentate septa (seven teeth per 4 mm). Sparse, spiky granules, weakly aligned.

Microstructure: trabeculothecal wall, moderate thickening deposits; weakly developed, closely spaced (0.4–0.5 mm) centres of rapid accretion; weak costal medial lines, moderate septal medial lines, transverse structures cross medial lines (carinae); clustered columella centres.

Occurrence. Late Miocene–early Pleistocene: Moín Formation of Costa Rica; Cercado, Gurabo, and Mao formations of the Dominican Republic; Uraccá and Old Bank formations of Panama; Tamana and Manzanilla formations of Trinidad (0.8–9.2 Ma).

Remarks. *Antillophyllia lonsdaleia* is most similar to *Antillophyllia dubia*, but it has more and thinner septa, and better developed teeth.

***Antillophyllia dominicensis* (Vaughan in Vaughan & Hoffmeister, 1925)**
(Fig. 10A–F)

1925 *Antillia dominicensis* Vaughan in Vaughan & Hoffmeister: 324–325, pl. 3, fig. 9, pl. 4, figs 1, 2 (holotype MCZ 9278 = 103511; Dominican Republic, Neogene).

Material. Holotype and 14 non-type specimens. One non-type specimen is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Solitary, large, elliptical calices (50–60 mm) containing 170–190 curved septa, septal lobes, little or no epitheca, parathecal wall.

Description. Macromorphology: solitary (one centre), free-living as adult, elliptical calices (sinuous margins but not constricted), conical (turbinate) corallum with ‘V’-shaped base, corallum 5–6 cm height (height approximately the same as calice width). Calice width = 50–60 mm; length = 70–100 mm; depth <6 mm. Six septal cycles (five complete) arranged according to the formula S1 = S2 > S3 > S4 ≫ S5 > S6, with S5

and S6 being better developed in systems along the greater calicular diameter; 170–190 septa total; septa subequal in thickness, curved; five septa per 5 mm. Reduced (<3 mm), elliptical, compact trabecular columella. Small septal lobes. Abundant endotheca, little or no epitheca.

Micromorphology: finely dentate septa. Sparse, spiky granules, weakly aligned.

Microstructure: trabeculothecal wall with parathecal elements, moderate thickening deposits; weakly developed, moderately spaced (1.5–2 mm) centres of rapid accretion; weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Late Miocene–late Pliocene: Gurabo and Mao formations of the Dominican Republic, Tamiami Formation of Florida (2.8–6.15 Ma).

Remarks. *Antillophyllia dominicensis* is similar in its large calice size, numbers of septa, and septal lobes to *T. mcneilli*, but is distinguished by its exclusively solitary form (i.e. lack of intracalicular budding) and parathecal wall.

***Antillophyllia dubia* (Duncan, 1863)**
(Fig. 10G–L)

1863 *Flabellum dubium* Duncan: 429 (holotype NHMUK PI R28837; Nivajé Shale, Dominican Republic, Neogene).

1926 *Antillia bullbrookii* Hoffmeister in Vaughan & Hoffmeister: 119, pl. 2, figs 7, 7a, 8, 8a (holotype USNM M353675; USGS 9286, Tamana Formation, Trinidad, middle Miocene).

Material. Holotype, holotype of synonym, and six non-type specimens. One non-type specimen is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Solitary, small, elliptical calices (20–30 mm) containing 90–100 septa, septal lobes, moderate epitheca, trabeculothecal wall.

Description. Macromorphology: solitary (one centre), free-living as adult, elliptical calices (not constricted), conical (turbinate) corallum with ‘V’-shaped base, corallum height 2–3 cm (height approximately the same as calice width). Calice width = 20–30 mm; length = 30–40 mm; depth <6 mm. Five septal cycles arranged according to the formula S1 = S2 > S3 > S4 > S5, with S4 and S5 being better developed in systems along the greater calicular diameter; 90–100 septa total; septa subequal in thickness; four septa per 5 mm. Weak (<3 mm) trabecular, compact

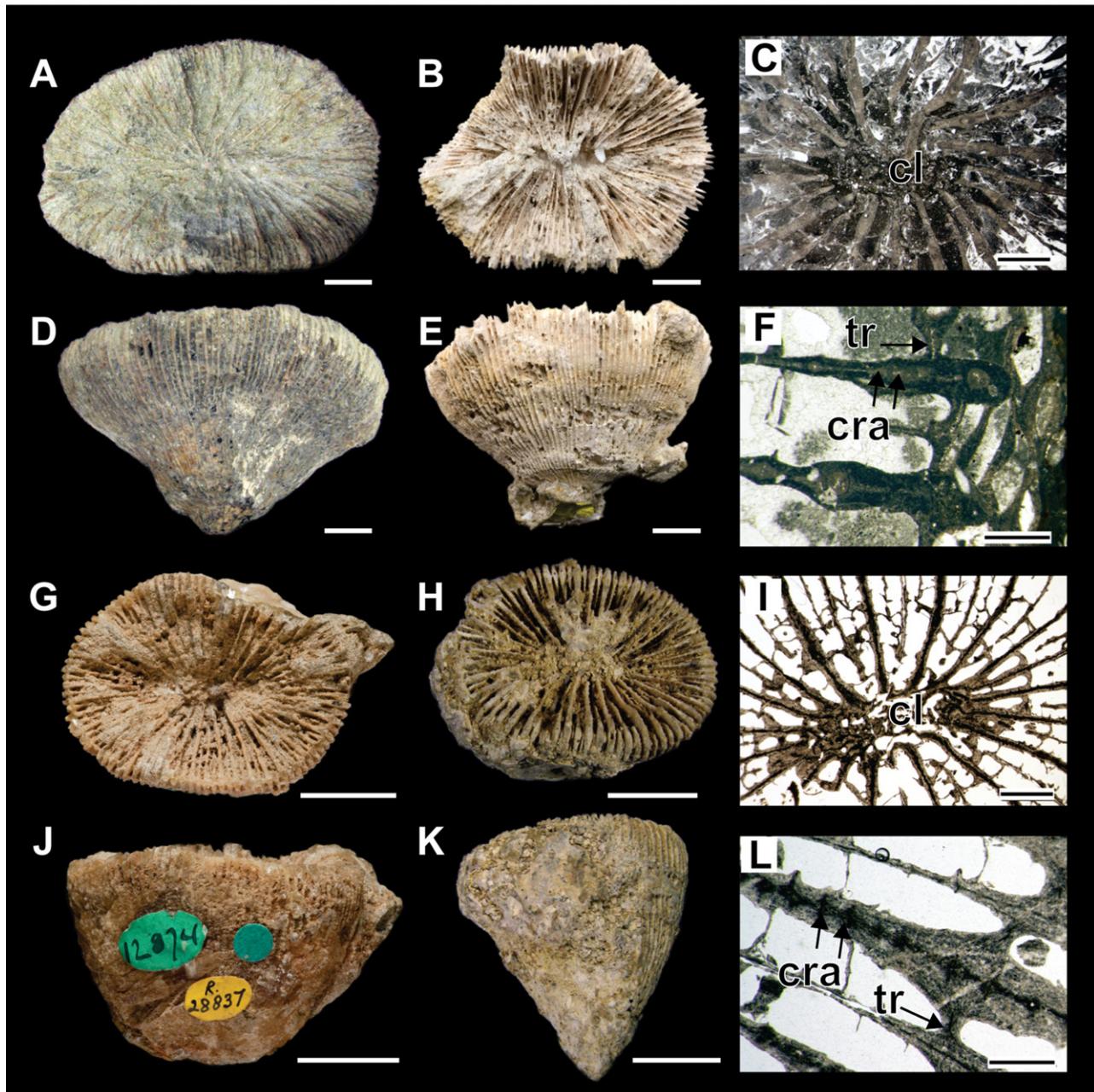


Figure 10. *Antillophyllia dominicensis* and *A. dubia*. *Antillophyllia dominicensis* (large corallite) and *A. dubia* (small corallite) are solitary and conical with an elliptical corallite and limited or moderate epitheca. Septa curve near the columella, which is compact, and the corallite wall is trabeculothecal. **A–F**, *Antillophyllia dominicensis*; **A**, holotype, MCZ 103511, calical surface; **B**, hypotype, SUI 146058 (CCD53031), calical surface; **C**, hypotype, SUI 140399, transverse thin section showing compact columella (cl); **D**, holotype, MCZ 103511, corallum side; **E**, hypotype, SUI 146058 (CCD53031), corallum side; **F**, hypotype, SUI 140399, transverse thin section showing trabeculothecal (tr) corallite wall and moderately spaced centres of rapid accretion (cra). **G–L**, *Antillophyllia dubia*; **G**, holotype, NHMUK PI R28837, calical surface; **H**, holotype of *Antillia bullbrookii*, USNM M353675, calical surface; **I**, hypotype, SUI 129443, transverse thin section showing compact columella (cl); **J**, holotype, NHMUK PI R28837, corallum side; **K**, holotype of *Antillia bullbrookii*, USNM M353675, corallum side; **L**, hypotype, SUI 129443, transverse thin section showing trabeculothecal (tr) corallite wall and closely spaced centres of rapid accretion (cra). Scale bars: A, B, D, E, G, H, J = 1 cm; C, I = 3 mm; F, L = 1 mm.

columella. Small septal lobes. Abundant endotheca, poorly developed epitheca.

Micromorphology: finely dentate septa. Sparse, spiky granules, weakly aligned.

Microstructure: trabeculothecal wall, moderate thickening deposits; weakly developed, closely spaced (0.5 mm) centres of rapid accretion; moderate costal medial lines, moderate septal medial lines, transverse

structures cross medial lines (carinae); aligned columella centres.

Occurrence. Late Oligocene–early Pleistocene: Moín Formation of Costa Rica; ‘Nivajé Shale’ of the Dominican Republic; Arcadia, Chipola and Tamiami formations of Florida; Tamana Formation of Trinidad (0.8–26 Ma).

Remarks. As indicated above, *Antilophyllum dubia* has thicker and fewer septa than *Antilophyllum lonsdaleia*. It is similar to late Oligocene “*Antillia?* willcoxi (Dana Vaughan” of Weisbord, 1973, p. 56 (=*Desmophyllum willcoxi* Gane) from the Arcadia Formation (Tampa Member) of Florida, but it has more septa.

Genus ***Isophyllia*** Milne Edwards & Haime, 1851

1851 *Isophyllia* Milne Edwards & Haime: 87.
1928 *Isophyllastrea* Matthes: 262 (type species: *Astraea rigida* Dana, 1846: 237; pl. 12, fig. 8a–d; modern).

Type species. *Oulophyllum? spinosa* Milne Edwards & Haime, 1849, p. 269; holotype: MNHN-Scle866 (Budd *et al.* 2012, fig. 9C, D) (=*Madrepora sinuosa* Ellis & Solander, 1786, p. 160).

Type locality. ‘Patrie inconnue’ (Milne Edwards & Haime, 1849, p. 269); modern.

Diagnosis. After Budd *et al.* (2012, figs 9, 13–19, 23). Macromorphology: colonial. Intracalicular budding; initially circumoral. Meandroid (uniserial), usually short series (<5 centres per series) with distinct valleys; medium calices (1–2.5 cm) with high relief (>6 mm); three or more septal cycles per centre in six systems, equal; reduced, costate coenosteum, with or without an ambulacrum; costae not continuous; weak, moderately spongy, discontinuous columella with trabecular linkage; reduced epitheca; no septal or paliform lobes; abundant endotheca.

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

Microstructure: parathecal wall with trabeculothecal elements. Well-developed centres of rapid accretion encircled by concentric rings of fibrous thickening deposits; transverse structures cross medial lines; moderate thickening deposits.

Distribution. Extant. Modern: Caribbean only. Fossil: late Miocene–Recent of the Caribbean.

Remarks. According to molecular data, *Isophyllia* belongs to the family Faviidae, subfamily Mussinae, which is distinguished by the size and shape of its septal teeth and abundant internal dissepiments (Budd *et al.* 2012). Species of *Isophyllia* are distinguished primarily on the basis of series length, corallite/valley width and numbers of septa. See Budd *et al.* (2012, figs 13, 19, 23) for images of modern species (macromorphology, micromorphology, microstructure). *Isophyllastrea* was synonymized with *Isophyllia* in Budd *et al.* (2012).

Isophyllia is similar in colony shape to the Indo-Pacific genus *Sympyllum* Milne Edwards & Haime, 1848, which has recently been synonymized with *Lobophyllum* (Huang *et al.* 2016). It differs by having shorter series, centres with trabecular linkage, an epitheca, less developed thickening deposits, and similar teeth in higher and lower septal cycles. It is distinguished from *Mycetophyllum* by having coenosteum, a well-developed spongy columella, and centres with trabecular linkage, and by lacking paliform lobes. Images of modern species (macromorphology, micromorphology, microstructure) are given in Budd *et al.* (2012, figs 14, 19, 23). Like other Mussinae, *Isophyllia* is a brooder.

Isophyllia sinuosa (Ellis & Solander, 1786)
(Fig. 11H, I)

1786 *Madrepora sinuosa* Ellis & Solander: 160.
1849 *Oulophyllum? spinosa* Milne Edwards & Haime, 1849, p. 269; holotype: MNHN-Scle866.

Material. Ten non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive colonies. Uniserial valleys (>3 corallites), which radiate from one (or more) central corallite; narrow valleys. Reduced coenosteum, corallites juxtaposed.

Description. Macromorphology: three to five centres per series. Valley width 10–25 mm, valley depth 8–10 mm. Three to four septal cycles (three complete) per centre arranged according to the formula S1 = S2 > S3 ≫ S4, 24–36 septa per centre, 7–9 septa per cm, septa equal in thickness, long tertiary septa. Discontinuous spongy columella with trabecular linkage. Reduced coenosteum.

Microstructure: parathecal wall with trabeculothecal elements. Moderate thickening deposits, transverse structures cross medial lines (carinae), well-developed, closely spaced (<0.4 mm) centres of rapid accretion.

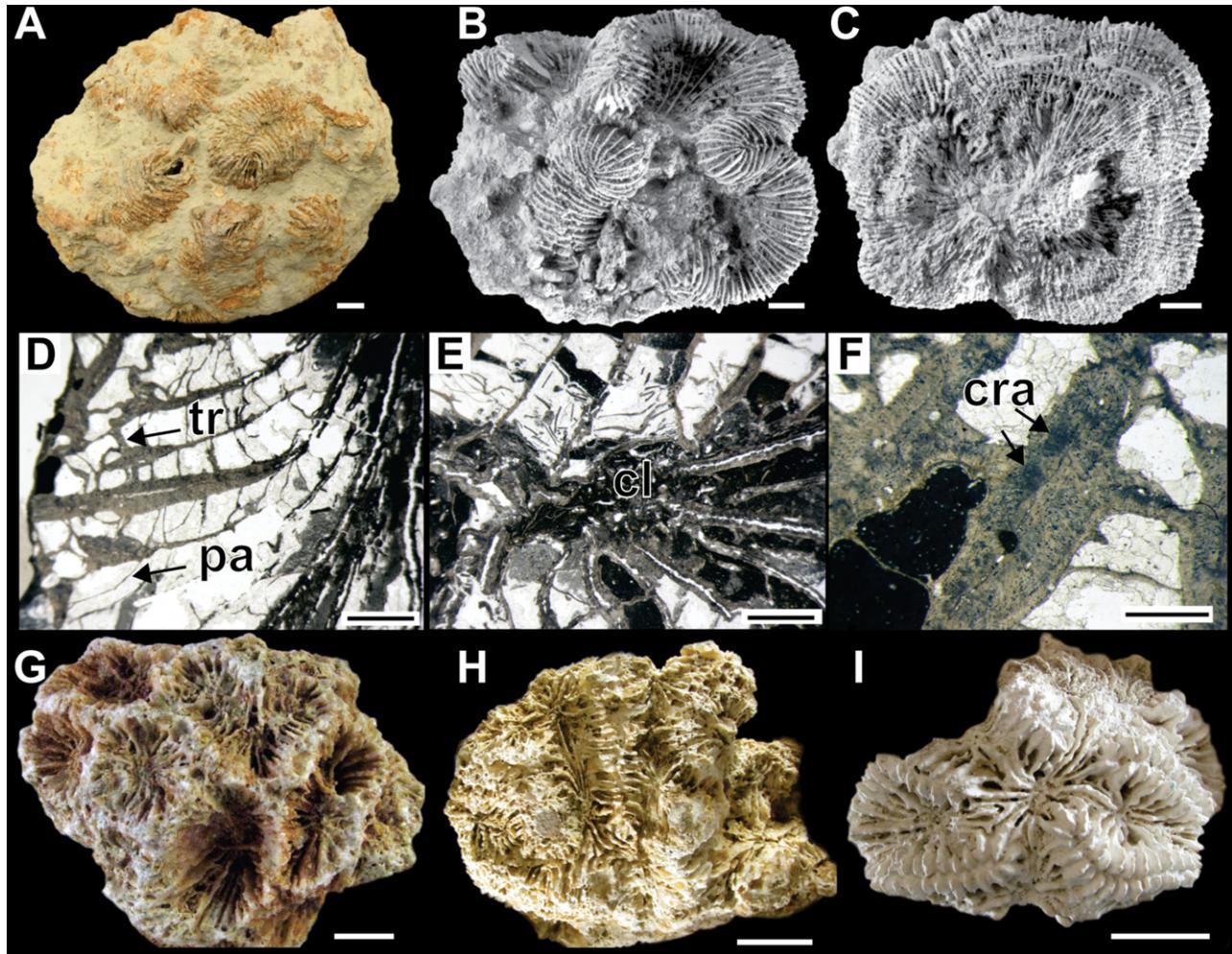


Figure 11. Fossil *Isophyllia*. *Isophyllia* is colonial and differs from *Mycetophyllia* by having coenosteum and mostly trabecular linkage between valley centres. Corallite walls in both genera are parathecal (pa) with trabeculothecal (tr) elements. Unlike *Isophyllia sinuosa* and *I. maoensis*, *I. rigida* and *I. jacksoni* have short valleys (< 3 centres). *Isophyllia jacksoni* is often free-living and its calices are multilobate. A–F, *Isophyllia jacksoni* Budd & Klaus sp. nov.; A, holotype, SUI 146114 (CCD49277), calical surface; B, paratype, NMB D6614 (CCD10001), calical surface; C, paratype, NMB D6614 (CCD10001), corallum bottom; D, paratype, SUI 140419 (CCD47496), transverse thin section showing mostly parathecal (pa) corallite wall; E, paratype, SUI 140419 (CCD47496), transverse thin section showing spongy columella (cl); F, paratype, SUI 140419 (CCD47496), transverse thin section showing closely spaced centres of rapid accretion (cra). G, *I. rigida*, hypotype, SUI 102842, calical surface; H, *I. sinuosa*, hypotype, SUI 118736 (CCD3554), calical surface; I, *I. sinuosa*, hypotype, USNM 1437457, calical surface. Scale bars: A–C, G–I = 1 cm; D, E, = 3 mm; F = 1 mm.

Moderate costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Early Pliocene–Recent: Moín Formation of Costa Rica; Los Haitises Formation of the Dominican Republic; Tamiami Formation of Florida; Falmouth Formation of Jamaica; Isla Colon Formation of Panama (0–3.6 Ma).

Remarks. *Isophyllia sinuosa* and *I. maoensis* have longer valleys (>3 centres) than *I. rigida* and *I. jacksoni*. *Isophyllia sinuosa* is distinguished from *I. maoensis* by having a reduced coenosteum and lacks an

ambulacrum. Type specimens are described in Budd *et al.* (2012).

***Isophyllia jacksoni* Budd & Klaus sp. nov.**
(Fig. 11A–F)

Material. Holotype, eight paratypes and 46 non-type specimens. Seven paratypes are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive colonies, often free-living. Short series (<3 corallites) in wide, deep, multilobate valleys with numerous septa.

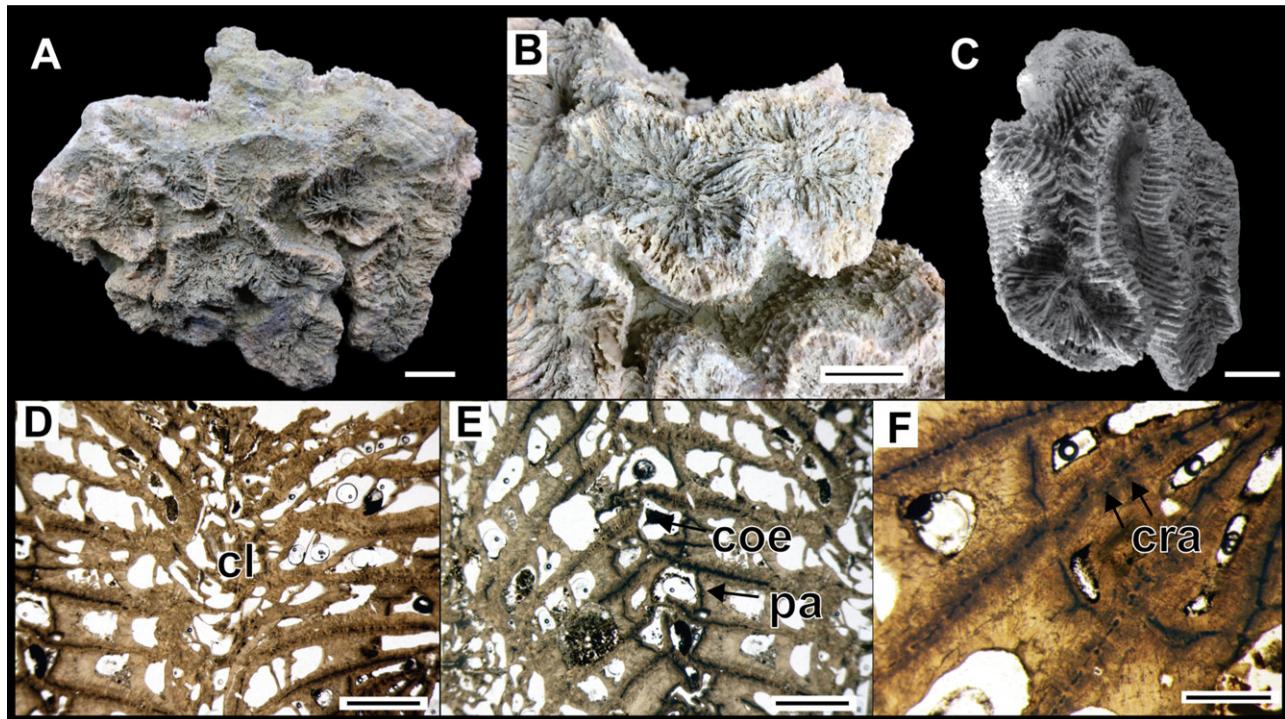


Figure 12. *Isophyllia maoensis* Budd & Klaus sp. nov. *Isophyllia maoensis* has long valleys (> 3 centres), and a more extensive coenosteum with a better developed, unusually deep ambulacrum in comparison with *I. sinuosa*. **A, B**, holotype, SUI 146140 (CCD47050); **A**, calical surface; **B**, close-up of calical surface. **C**, paratype, NMB D6610 (CCD10025), calical surface; **D–F**, holotype, SUI 107983 (CCD42540); **D**, transverse thin section showing spongy columella (cl); **E**, transverse thin section showing moderately developed coenosteum (coe) and parathecal (pa) wall; **F**, transverse thin-section close-up of corallite wall showing closely spaced centres of rapid accretion (cra). Scale bars: A–C = 1 cm; D, E = 3 mm; F = 1 mm.

Description. Macromorphology: one to three centres per series. Valley width 25–35 mm, valley depth 10–20 mm. Four to five septal cycles per centre (four complete), arranged according to the formula $S1 = S2 > S3 \gg S4 > S5$, 48–72 septa per centre, six to nine septa per cm; septa subequal in thickness. Discontinuous spongy columella with trabecular linkage. Little or no coenosteum.

Microstructure: parathecal wall with trabeculothecal elements. Moderate thickening deposits, transverse structures cross medial lines (carinae), well-developed, closely spaced (<0.4 mm) centres of rapid accretion. Moderate costal medial lines, weak septal medial lines; clustered columella centres.

Derivation of name. After Jeremy B. C. Jackson for his groundbreaking work on the adaptive significance of solitary versus colonial growth strategies and the evolutionary patterns associated with closure of the Central American Seaway.

Occurrence. Late Miocene–early Pleistocene: Seroe Domi Formation (Ridges) of Curaçao; Cercado, Gurabo and Mao formations and Los Haitises Formation of the Dominican Republic (0.8–6.45 Ma).

Remarks. *Isophyllia jacksoni* and *I. rigida* have shorter valleys (<3 centres) than *I. sinuosa* and *I. maoensis*. *Isophyllia jacksoni* is distinguished from the other species by its large, deep, multilobate valleys and greater number of septal cycles. This species has also previously been referred to as '*Isophyllastrea* sp. B' (Budd *et al.* 1999).

***Isophyllia maoensis* Budd & Klaus sp. nov.
(Fig. 12A–F)**

Material. Holotype, six paratypes and five non-type specimens. Four paratypes are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive colonies. Uniserial valleys (>3 corallites), which radiate from one (or more) corallite centres; raised, narrow zigzag valleys; well-developed ambulacrum.

Description. Macromorphology: three to five centres per series. Valley width 15–30 mm, valley depth 8–10 mm. Valleys raised as much as 5–10 mm above coenosteal surface. Three to four septal cycles (three complete), arranged according to the formula $S1 = S2 > S3 \gg S4$, 24–36 septa

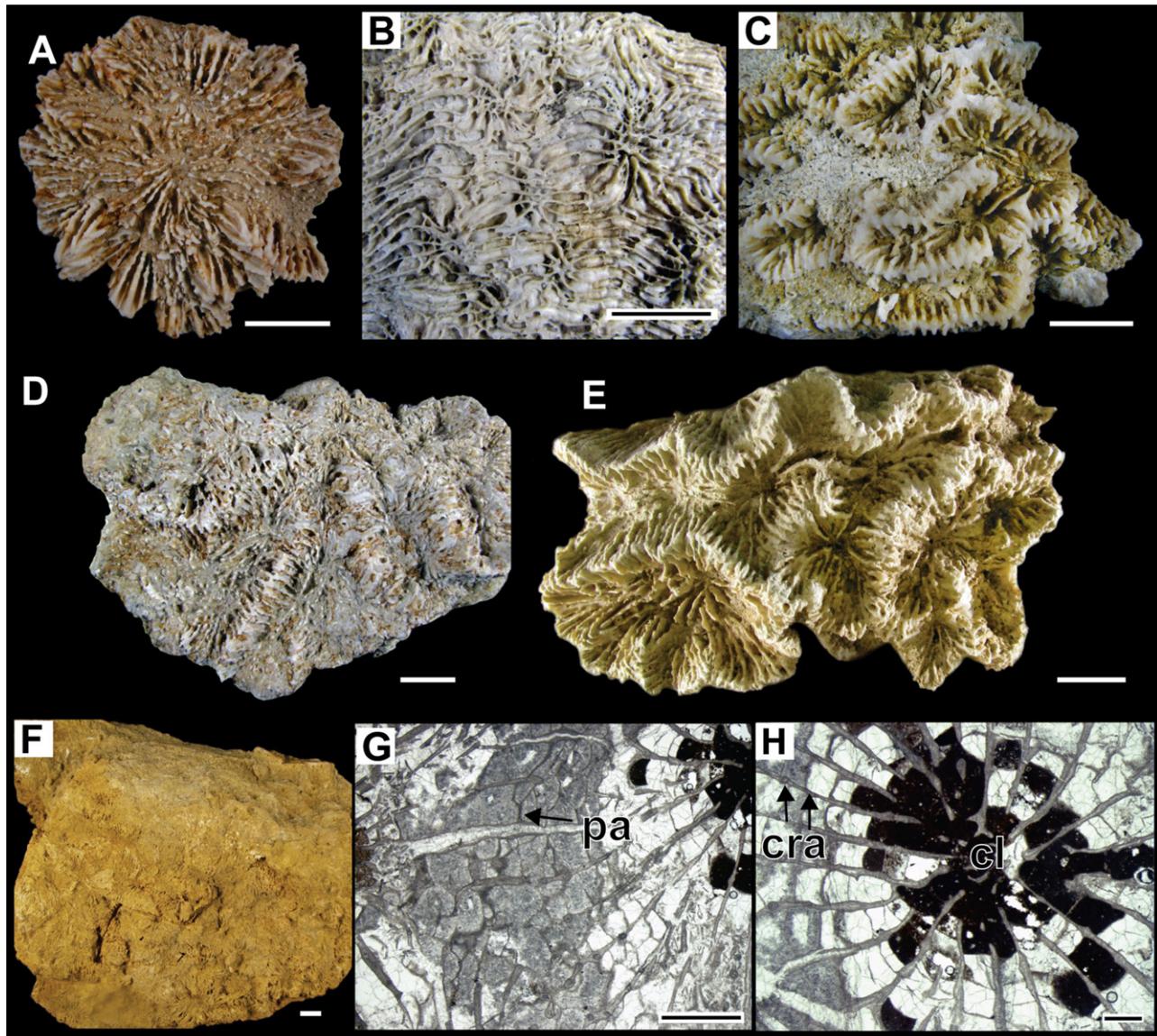


Figure 13. Fossil *Mycetophyllia* is colonial with both uniserial and multiserial valleys. There is no coenosteum and septa are confluent with <24 septa. The columella is reduced and paliform lobes are usually well developed. *Mycetophyllia lamarckiana* is uniserial with long, straight, radiating valleys; *M. reesi* (small corallites) and *M. bullbrooki* (large corallites) lack valleys and collines; *M. ferox* has narrow, winding valleys; *M. aliciae* is multiserial and *M. danaana* has short, deep, irregular valleys. A–E, calical surfaces; A, *M. lamarckiana*, hypotype, USNM 14780822 (CCD0181); B, *M. reesi*, hypotype, USNM 14780832 (CCD0738); C, *M. ferox*, hypotype, USNM 14780814 (CCD0949); D, *M. aliciae*, hypotype, USNM 14780774 (CCD6979); E, *M. danaana*, hypotype, USNM 14780804 (CCD4804). F–H, *M. bullbrooki*, holotype, USNM M353663; F, corallum surface; G, transverse thin section showing parathecal (pa) wall; H, transverse thin section showing reduced columella (cl) and well-developed, moderately spaced centres of rapid accretion (cra). Scale bars: A–F = 1 cm; G = 3 mm; H = 1 mm.

per corallite, five to seven septa per cm, septa equal in thickness, long tertiary septa. Discontinuous spongy columella with trabecular linkage. Well-developed coenosteum, up to 10 mm in thickness. Well-developed costal teeth.

Microstructure: parathecal wall with trabeculothecal elements. Moderate thickening deposits, transverse structures cross medial lines (carinae), well-developed, closely spaced (<0.4 mm) centres of rapid accretion.

Moderate costal medial lines, weak septal medial lines; clustered columella centres.

Derivation of name. After the Mao Adentro Limestone, the unit in which this species is most abundant.

Occurrence. Late Miocene–early Pleistocene: Cercado, Gurabo and Mao formations of the

Dominican Republic; Isla Colon Formation of Panama (1.4–6.45 Ma).

Remarks. *Isophyllum maoensis* has longer valleys (>3 centres) than *I. jacksoni* and *I. rigida*. It differs from *I. sinuosa* by having a more extensive coenosteum with a deep ambulacrum. This species has also previously been referred to as ‘*Isophyllum* sp. A’ (Budd *et al.* 1994, 1998).

***Isophyllum rigida* (Dana, 1846)**
(Fig. 11G)

1846 *Astraea rigida* Dana: 237, pl. 12, fig. 8a–d (holotype YPM 4297, West Indies, modern).

Material. Nine non-type specimens, one of which is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive colonies. Monocentric corallites, small in diameter. Reduced coenosteum. Thickening deposits form well-developed concentric rings associated with septal teeth, and smooth interareas between septal teeth.

Description. Macromorphology: monocentric. Corallite diameter 10–15 mm, corallite depth 5–15 mm. Three to four septal cycles (three complete) arranged according to the formula $S1 = S2 > S3 > S4$, 25–30 septa per corallite, seven to nine septa per cm, septa equal in thickness, relatively short tertiary septa.

Microstructure: parathecal wall with trabeculothecal elements. Moderate thickening deposits, transverse structures cross medial lines (carinae), well-developed, closely spaced (<0.4 mm) centres of rapid accretion. Moderate costal medial lines, weak septal medial lines; clustered columella centres. Well-developed concentric rings associated with septal teeth.

Occurrence. Late Miocene–Recent: Moín and Quebrada Chocolate formations of Costa Rica; Falmouth and Manchioneal formations of Jamaica; Old Bank Formation of Panama (0–5.8 Ma).

Remarks. *Isophyllum rigida* is distinguished from the other species by its small, monocentric corallites and reduced coenosteum. Type specimens are described in Budd *et al.* (2012). Fossils of this species have also previously been referred to as ‘*Mycetophyllum* sp. A’ (Budd *et al.* 1999).

Genus ***Mycetophyllum*** Milne Edwards & Haime, 1848

1848 *Mycetophyllum* Milne Edwards & Haime: 491–492.

Type species. *Mycetophyllum lamarckiana* Milne Edwards & Haime, 1849, p. 258; holotype MNHN Scle910 (figured in Budd *et al.* 2012, fig. 9E, F).

Type locality. “Patrie inconnue” (Milne Edwards & Haime 1849, p. 258); modern.

Diagnosis. After Budd *et al.* (2012, figs 14, 19, 23). Macromorphology: colonial, often platy. Intracalicular budding; often circumoral. Meandroid (uniserial and multiserial), with and without collines, often long series; centres spaced 5–15 mm apart; < 24 septa per centre, equal; no coenosteum and incomplete corallite walls, confluent septa; absent or feeble, discontinuous columella with lamellar linkage; reduced epitheca; paliform lobes; abundant endotheca.

Micromorphology: high (>0.6 mm), widely spaced (1–2 mm), spine-shaped teeth, regularly arranged, with spiked tips resembling those of a Medieval spiked mace weapon; layered (banded) interarea of septal teeth; fine granules along the sides of teeth.

Microstructure: parathecal wall, if present, with occasional trabeculothecal elements. Well-developed centres of rapid accretion encircled by concentric rings of fibrous thickening deposits; transverse structures (carinae) cross medial lines; usually reduced thickening deposits.

Distribution. Extant. Modern: Caribbean only. Fossil: Early Oligocene–Recent: Caribbean only.

Remarks. According to molecular data, *Mycetophyllum* belongs to the family Faviidae, subfamily Mussinae, which is distinguished by the size and shape of its septal teeth and abundant internal dissepiments (Budd *et al.* 2012). Species of *Mycetophyllum* are distinguished primarily on the basis of colony form, which may be highly variable within species. With the possible exception of *M. bullbrookii*, which has reduced thickening deposits, microstructure is the same across species. Images of modern species (macromorphology, micromorphology, microstructure) are given in Budd *et al.* (2012, figs 9, 14, 19, 23). Like other Mussinae, *Mycetophyllum* is a brooder.

Mycetophyllum lamarckiana Milne Edwards & Haime, 1849
(Fig. 13A)

1849 *Mycetophyllum lamarckiana* Milne Edwards & Haime, 1849: 258 (holotype MNHN Scle910; unknown locality, modern).

Material. Nine non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive or platy colonies. Series radiate from colony centre; straight, continuous, uniserial valleys. Continuous, radiating collines (absent centrally). Reduced paliform lobes.

Description. Macromorphology: valley width 10–20 mm, valley depth 5–12 mm. Centre spacing 8–11 mm; six to seven septa per cm; 10–15 septa per centre (approx. two septal cycles) with $S1 > S2 > S3$.

Microstructure: parathecal walls with trabeculothecal elements, reduced thickening deposits, transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Late Pliocene–Recent: Moín Formation of Costa Rica, Los Haitises Formation of the Dominican Republic; Hope Gate and Manchioneal formations of Jamaica; Uraccá Formation of Panama (0–3.6 Ma).

Remarks. *Mycetophyllum lamarckiana* differs from other *Mycetophyllum* species by having deep uniserial valleys (>5 centres). Modern species including type specimens are described in Budd *et al.* (2012).

***Mycetophyllum aliciae* Wells, 1973**
(Fig. 13D)

1973 *Mycetophyllum aliciae* Wells: 41, figs 25–28 (holotype = USNM 53496: Discovery Bay, Jamaica, modern).

Material. Five non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Platy colonies. Series radiate from colony centre; straight, wide, continuous, multiserial valleys; discontinuous collines. Well-developed paliform lobes.

Description. Macromorphology: valley width 30–80 mm, valley depth 3–7 mm. Centre spacing 10–15 mm; six to seven septa per cm; 10–12 septa per centre (approx. two septal cycles) with $S1 > S2$.

Microstructure: parathecal walls with trabeculothecal elements, reduced thickening deposits, transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Late Pliocene–Recent: Moín Formation of Costa Rica; Mao Formation of the Dominican Republic (0–3.7 Ma).

Remarks. *M. aliciae* differs from other *Mycetophyllum* species by having long, multiserial valleys (> 5 centres). Modern species including type specimens are described in Budd *et al.* (2012).

***Mycetophyllum bullbrooki* Vaughan in Vaughan & Hoffmeister, 1926**
(Fig. 13F–H)

1926 *Mycetophyllum bullbrooki* Vaughan in Vaughan & Hoffmeister: 124–125, pl. 4, fig. 3 (holotype USNM353663; Trinidad, USGS 8299, middle Miocene).

Material. Holotype and 11 non-type specimens. Holotype is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive colonies. Intracalicular budding only (not circumoral). Non-serial; no valleys or collines. Large, shallow corallites (centres spaced >15 mm apart). Numerous septa 28–30 septa per centre), costae not confluent; reduced paliform lobes.

Description. Macromorphology: centre spacing 14–26 mm, calical depth <3 mm; six to nine septa per cm; ~28–30 septa per centre (~three septal cycles) with $S1 > S2 > S3 \gg S4$.

Microstructure: parathecal wall, with no trabeculothecal elements. Little or no thickening deposits, lacking concentric rings. Transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Early Oligocene–early Pleistocene: Seroe Domi Formation (Flatiron, Ridges) of Curaçao; Cercado and Mao formations of the Dominican Republic; Uraccá Formation of Panama; Tamana and Manzanilla formations of Trinidad; Culebra Formation (Emperador) of Panama (0.8–34 Ma).

Remarks. *Mycetophyllum bullbrooki* differs from other *Mycetophyllum* species by large corallites and lacking valleys (nonserial) and collines, and by not having confluent septa. With regard to microstructure, it has reduced thickening deposits. Nevertheless, the results of the phylogenetic analysis (Fig. 3) clearly show that *M. bullbrooki* groups with the five modern species of *Mycetophyllum*.

***Mycetophyllum danaana* Milne Edwards & Haime, 1849**
(Fig. 13E)

1849 *Mycetophyllum danaana* Milne Edwards & Haime: 259 (neotype SUI 102772; Bocas del Toro, Panama, modern).

Material. Thirty-eight non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Massive or platy colonies. Circumoral followed by intracalicular budding; sinuous continuous valleys; short, discontinuous collines. Deep valleys, sometimes forming monticules (superficial ‘hydnophoroid pillars’ *sensu* Wells 1973). Reduced paliform lobes.

Description. Macromorphology: valley width 10–20 mm, valley depth 10–12 mm. Centre spacing 10–15 mm; 10–12 septa per cm; 12–16 septa per centre (approx. two septal cycles) with S1 > S2 > S3.

Microstructure: parathecal walls with trabeculothecal elements, reduced thickening deposits, transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, and weak septal medial lines; clustered columella centres.

Occurrence. Late Miocene–Recent: Moín Formation of Costa Rica; Seroe Domi Formation (Ridges, Sea Cliff) and Lower and Middle Terraces of Curaçao; Mao Formation of the Dominican Republic; Falmouth and Manchioneal formations of Jamaica; Old Bank and Uraccá formations of Panama (0–5.8 Ma).

Remarks. *Mycetophyllum danaana* differs from other *Mycetophyllum* species by having short and deep valleys (< 3 centres). Modern species including type specimens are described in Budd *et al.* (2012).

***Mycetophyllum ferox* Wells, 1973**
(Fig. 13C)

1973 *Mycetophyllum ferox* Wells: 40, figs 22–24 (holotype USNM 53494; Eaton Hall, Jamaica, modern).

Material. Sixteen non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Platy colonies. Intracalicular budding only (not circumoral). Narrow (~10 mm), meandering, sometimes discontinuous uniserial valleys with continuous forked collines. Well-developed paliform lobes.

Description. Macromorphology: valley width 10 mm, valley depth 3–5 mm. Centre spacing 5–10 mm; 9–11 septa per cm; 18–20 septa per centre (two to three septal cycles) with S1 > S2 > S3.

Microstructure: parathecal walls with trabeculothecal elements, reduced thickening deposits, transverse

structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Early Pliocene–Recent: Moín Formation of Costa Rica; Mao Formation of the Dominican Republic; Isla Colon Formation of Panama (0–3.7 Ma).

Remarks. *Mycetophyllum ferox* differs from other *Mycetophyllum* species by having long, narrow, sinuous valleys (> 5 centres). Modern species including type specimens are described in Budd *et al.* (2012).

***Mycetophyllum reesi* Wells, 1973**
(Fig. 13B)

1973 *Mycetophyllum reesi* Wells: 36, figs 19–21 (holotype USNM 53493; West Bull, Jamaica, modern).

Material. Twenty-seven non-type specimens, none of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Platy colonies. Circumoral budding; no valleys or collines. Well-developed paliform lobes.

Description. Macromorphology: centre spacing 7–15 mm, calical depth <3 mm; 9–11 septa per cm; 10–15 septa per centre (~two septal cycles) with S1 > S2 > S3.

Microstructure: parathecal walls with no trabeculothecal elements, reduced thickening deposits. Transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, weak septal medial lines; clustered columella centres.

Occurrence. Early Pleistocene–Recent: Moín Formation of Costa Rica, Hope Gate Formation of Jamaica (0–2.4 Ma).

Remarks. *Mycetophyllum reesi* differs from other *Mycetophyllum* species by lacking valleys (nonserial) and collines and having confluent septa. Modern species including type specimens are described in Budd *et al.* (2012).

Genus *Scolymia* Haime, 1852

1852 *Scolymia* Haime: 279.

Type species. *Madrepora lacera* Pallas, 1766: 298; neotype YPM 9036 (figured in Budd *et al.* 2012, fig. 9G, H).

Type locality. “Mare Americanum” (Pallas, 1766, p. 298); modern.

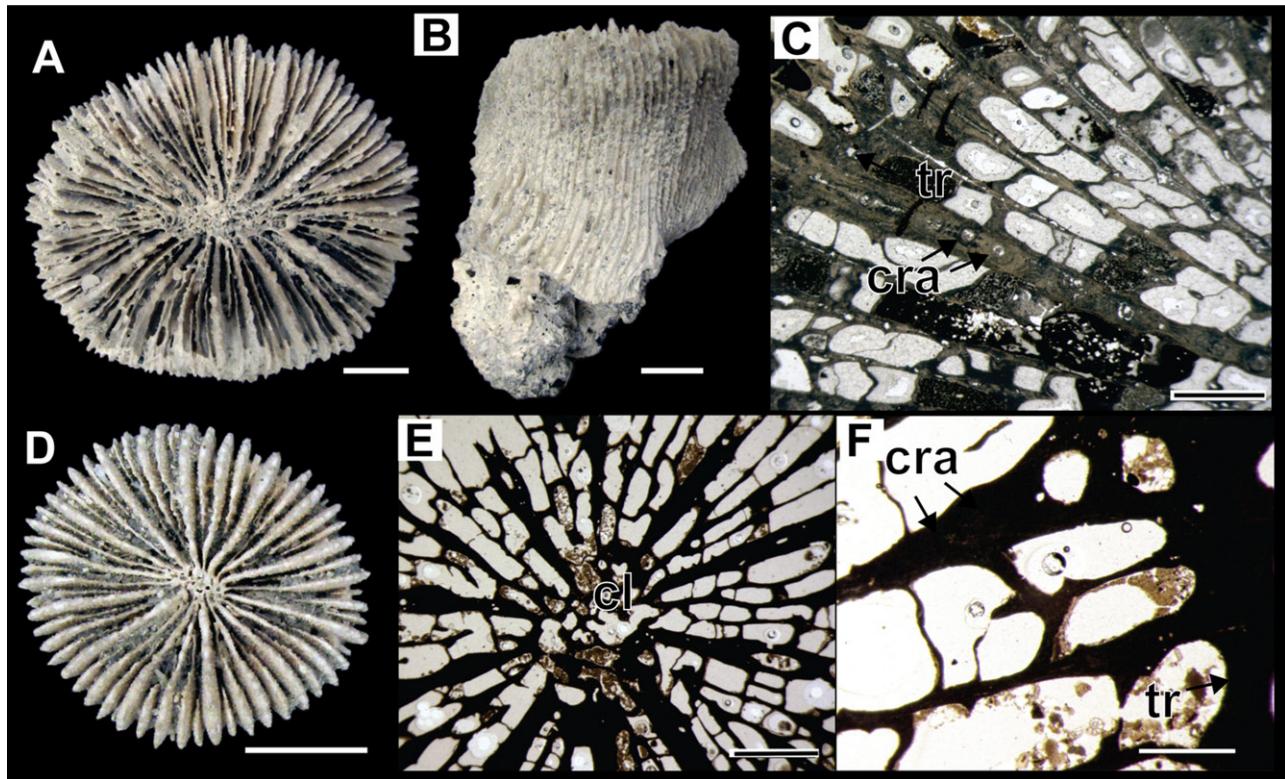


Figure 14. Fossil *Scolymia lacera* and *S. cubensis*. *Scolymia* is solitary and attached; the two modern species (*S. lacera* and *S. cubensis*) have large cylindrical corallites. *Scolymia lacera* has a concave calice and distinctively unequal septa, whereas *S. cubensis* has a convex calice and septa more subequal in thickness. Both species have a parathecal wall with trabeculothecal elements. A–C, *Scolymia lacera*; A, B, hypotype, SUI 146169 (CCD53249); A, calical surface; B, corallum side; C, hypotype, SUI 101409 (CCD44768), transverse thin section showing mostly parathecal corallite wall with trabeculothecal elements (tr) and moderately spaced centres of rapid accretion (cra). D–F, *Scolymia cubensis*, hypotype, SUI 146167 (CCD54494); D, calical surface; E, transverse thin section showing spongy columella (cl); F, transverse thin section showing mostly parathecal corallite wall with trabeculothecal elements (tr) and moderately spaced centres of rapid accretion (cra). Scale bars: A, B, D = 1 cm; C, E = 3 mm; F = 1 mm.

Diagnosis. After Budd *et al.* (2012, figs 12, 18, 22). Macromorphology: solitary, attached, with aberrant forms exhibiting rare intracalicular budding; large (>4 cm), irregular calices, >four septal cycles in six systems; well-developed, spongy (>3 threads) columella with lamellar linkage; reduced epitheca; usually lacking septal lobes; abundant endotheca.

Micromorphology: large (>0.6 mm high), 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.

Microstructure: trabeculothecal to parathecal wall. Widely separated (>1.2 mm), well-developed centres of rapid accretion encircled by concentric rings of fibrous thickening deposits; transverse structures cross weak medial lines; moderate thickening deposits.

Distribution. Extant. Modern: Caribbean only. Fossil: Late Miocene–Recent.

Remarks. According to molecular data, *Scolymia* belongs to the family Faviidae, subfamily Mussinae, which is distinguished by the size and shape of its septal teeth and abundant internal dissepiments (Budd *et al.* 2012). The genus is not related to the Indo-Pacific solitary corals *Cynarina*, *Homophyllia*, *Lobophyllia* (=*Parascolymia*) and *Micromussa* in the family Lobophilliidae (Arrigoni *et al.* 2016; Huang *et al.* 2016), from which it differs by having more closely spaced, pointed (not lobate) teeth; more prominent granules; less well-developed centres of rapid accretion; and less well-developed thickening deposits. The three modern species (*S. lacera*, *S. cubensis* and *S. wellsi*) are distinguished primarily by the size and shape of their teeth.

Scolymia differs from *Antillia* by having larger calices that are attached to the substrate; a weak epitheca; large, more widely spaced teeth; and a trabeculothecal to parathecal wall. Images of modern species (macromorphology, micromorphology, microstructure) are given in Budd *et al.* (2012, figs 9, 12, 18, 22). Like other Mussinae, *Scolymia* is a brooder.

***Scolymia lacera* (Pallas, 1766)**
(Fig. 14A–C)

1766 *Madrepora lacera* Pallas: 298 (neotype YPM 9036; Rio Bueno, Jamaica, modern).

Material. Fifteen non-type specimens, two of which are thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Solitary, attached, cylindrical corallum; large, circular, concave calice (averaging ~75 mm wide). Unequal septa. Large and stout teeth (< 5 per cm) that are subtriangular.

Description. Macromorphology: maximum calice width = 10–15 cm (with an average of ~75 mm), calice depth = 10–20 mm. Five to six septal cycles arranged according to the formula $S1 = S2 > S3 > S4 > S5 \gg S6$, ~110 septa per calice, unequal. Circular, spongy columella. No internal lobes, weak epitheca.

Microstructure: parathecal wall with trabeculothecal elements; moderate thickening deposits. Transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, moderate septal medial lines; clustered columella centres.

Occurrence. Late Miocene–Recent: Moín Formation of Costa Rica; Cercado, Gurabo, Los Haitises and Mao formations of the Dominican Republic; Tamiami, Bowden and Manchioneal formations of Florida; Uraccá Formation of Panama (0–6.45 Ma).

Remarks. *Scolymia lacera* and *S. cubensis* have much larger calices with more septa than the two extinct species *S. meederi* and *S. tamiamiensis*. *Scolymia lacera* differs from *S. cubensis* primarily in calice shape and septal tooth shape. *S. lacera* has a concave calice and large subtriangular teeth. Modern species including type specimens are described in Budd *et al.* (2012).

***Scolymia cubensis* (Milne Edwards & Haime, 1849)**
(Fig. 14D–F)

1849 *Caryophyllia cubensis* Milne Edwards & Haime: 238 (neotype YPM7569; Runaway Bay, Jamaica, modern).

Material. Twenty-seven non-type specimens, one of which is thin-sectioned (Supplemental material, Appendix A).

Diagnosis. Solitary, attached, cylindrical corallum; large, circular, convex calice (averaging ~75 mm wide). Equal septa. Long and slim teeth (>5 per cm) that are awl-shaped.

Description. Macromorphology: maximum calice width = 8–10 cm (with an average of ~75 mm), calice depth = 10–20 mm. Five to six septal cycles arranged according to the formula $S1 = S2 > S3 > S4 > S5 \gg S6$, ~110 septa per calice.

Microstructure: parathecal wall with trabeculothecal elements; moderate thickening deposits. Transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, moderate septal medial lines; clustered columella centres.

Occurrence. Late Miocene–Recent: Moín Formation of Costa Rica; Cercado, Gurabo, Los Haitises and Mao formations of the Dominican Republic; Tamiami, Bowden and Manchioneal formations of Florida; Uraccá Formation of Panama (0–6.45 Ma).

Remarks. *Scolymia cubensis* is distinguished by having a convex calice and thin, awl-shaped septal teeth. Modern species including type specimens are described in Budd *et al.* (2012).

***Scolymia meederi* Klaus & Budd sp. nov.**
(Fig. 15A–F)

Material. Holotype and two paratypes (Supplemental material, Appendix A).

Diagnosis. Solitary, attached, cylindrical corallum. Small circular calices. Unequal septa, with unusually thick primary and secondary septa and paliform lobes. Large teeth, three per 5 mm, differing in development among septal cycles.

Description. Macromorphology: corallum height 3–4 cm. Maximum corallite diameter 2–3 cm (with an average of ~25 mm), calice depth 3–5 mm. Three to four septal cycles arranged according to the formula $S1 = S2 > S3 \gg S4$, ~48 per calice, eight septa per 5 mm.

Microstructure: trabeculothecal wall, moderate thickening deposits. Transverse structures cross medial lines (carinae); well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, moderate septal medial lines; clustered columella centres.

Derivation of name. After John F. Meeder who first discovered the Golden Gate Reef Member of the Tamiami Formation in Florida, and specimens of this species.

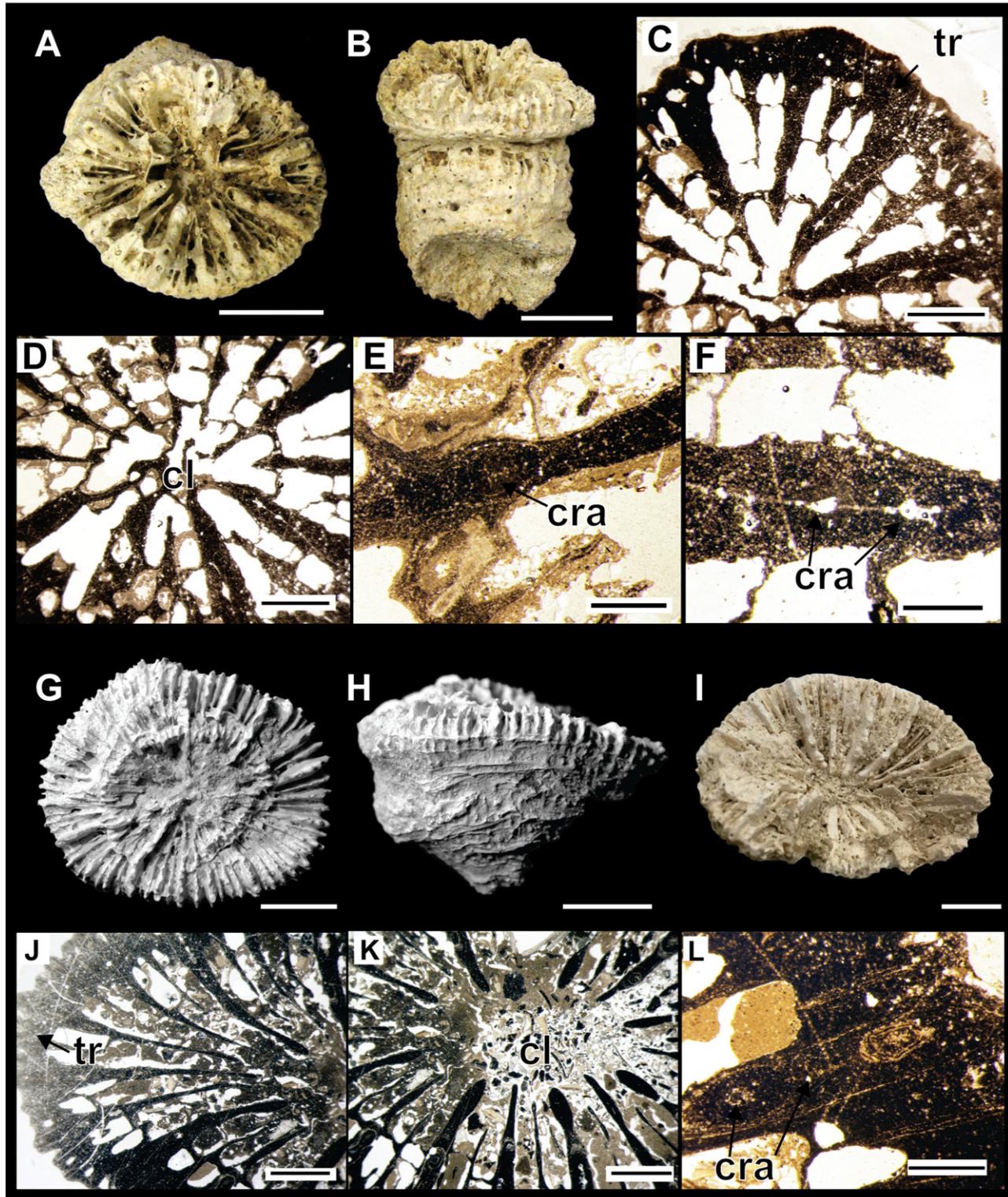


Figure 15. *Scolymia meederi*, Klaus & Budd sp. nov. and *S. tamiamiensis* Klaus & Budd sp. nov. These two extinct species differ from extant *Scolymia* species in corallite size and shape, the presence of paliform lobes, and a trabeculothecal wall. *Scolymia meederi* has a relatively small corallite with exceptionally well-developed primary and secondary septa and paliform lobes; *S. tamiamiensis* has a conical corallum with an elliptical corallite and unequal septa. A–F, *Scolymia meederi*; A, B, holotype, SUI 146175 (CCD 53545); A, calical surface; B, corallum side; C–F, paratype, SUI 146176 (CCD54222); C, transverse thin section showing trabeculothecal (tr) corallite wall; D, transverse thin section showing reduced trabecular columella (cl); E, transverse thin section of

Occurrence. Late Pliocene: Tamiami Formation of Florida (2.8–3.2 Ma).

Remarks. *Scolymia meederi* is distinguished by having a small calice, fewer septal cycles, unusually thick S1 and S2, and well-developed paliform lobes. This species has also previously been called *Scolymia* sp. A (Klaus *et al.* 2017).

***Scolymia tamiamiensis* Klaus & Budd sp. nov.**
(Fig. 15G–I)

Material. Holotype and four paratypes (Supplemental material, Appendix A).

Diagnosis. Solitary, attached; conical (turbinate) corallum with ‘V’-shaped base. Elliptical calices. Unequal septa, unusually thick primary and secondary septa, with paliform lobes. Large teeth, three per 5 mm, differing in development among septal cycles.

Description. Macromorphology: corallum height 1.5–2.5 cm. Maximum corallite diameter 4–5 cm (with an average of ~35 mm), calice depth 5–15 mm. Five septal cycles arranged according to the formula S1 = S2 > S3 > S4 > S5, with S4 and S5 being better developed in systems along the greater calicular diameter; ~96 per calice, eight to nine septa per 5 mm.

Microstructure: trabeculothecal wall, moderate thickening deposits. Transverse structures cross medial lines (carinae), well-developed, moderately spaced (0.7–1.8 mm) centres of rapid accretion. Weak costal medial lines, moderate septal medial lines; clustered columella centres.

Derivation of name. After the Tamiami Formation, in which it occurs.

Occurrence. Late Pliocene: Tamiami Formation of Florida (2.8–3.2 Ma).

Remarks. *Scolymia tamiamiensis* is characterized by having intermediate sized calices and numbers of septal cycles along with paliform lobes. Its calices may be slightly elliptical. This species has also previously been called *Scolymia* sp. B (Klaus *et al.* 2017).

Discussion

Our results indicate that six genera of the subfamily Mussinae inhabited the Caribbean over the past 40 million years (Fig. 3). Phylogenetic analysis shows that five of the six genera have moderate to strong bootstrap and/or Bremer support. Three of the six genera in the present study (*Antillia*, *Antilophyllia*, *Scolymia*) are solitary and three (*Isophyllia*, *Mussa*, *Mycetophyllia*) are exclusively colonial. Relationships among the six genera are poorly resolved, as are relationships among species within genera. The one genus that is less well defined is *Scolymia*. Within *Scolymia*, *S. lacera* does not group closely with the other species of *Scolymia* suggesting that the genus may be composed of disparate taxa and in need of further molecular work. To date, molecular data are published only for *Mussa angulosa*, *Scolymia cubensis*, *Isophyllia sinuosa*, *Mycetophyllia danaana*, *Mycetophyllia aliciae* and *Mycetophyllia lamarckiana* (Kitahara *et al.* 2016). Analyses of these data show that these six species belong to a distinct subclade (Mussinae) within the family Faviidae and are nested as follows: ‘*Scolymia* (*Isophyllia* (*Mussa*, *Mycetophyllia*))’ (Kitahara *et al.* 2016).

Within Mussinae, evolutionary transitions between solitary and colonial taxa are rare and poorly supported (Fig. 3). Not only are genera either solitary or colonial, but both solitary (*Antillia*, *Antilophyllia*) and colonial (*Mycetophyllia*) taxa first occurred during the Eocene (or possibly earlier) and their lineages remain distinct throughout their subsequent evolution (Fig. 16). This result, along with molecular analyses (Kitahara *et al.* 2016), disagrees with previous interpretations that *Mussa angulosa* (colonial) and *Scolymia lacera* (solitary) may be closely related or even the same species (Matthai 1928; Vaughan & Wells 1943; Wells 1956). Although not well resolved, *Scolymia* appears to be more closely related to extinct solitary genera such as *Antillia* and *Antilophyllia*. The rarity of evolutionary transitions between solitary and colonial species within the Mussinae contrasts with observations described earlier in several Indo-Pacific genera, including *Cycloseris*, *Lithophyllum*, *Homophyllia*, *Micromussa*, *Sclerophyllia* and *Lobophyllia* (Hoeksema & Best 1987; Gittenberger *et al.* 2011; Benzoni *et al.* 2012; Arrigoni *et al.* 2014, 2015, 2016; Huang *et al.* 2016).

septum showing well-developed centre of rapid accretion (cra) encircled by thickening deposits; **F**, transverse thin section of septum showing moderately spaced centres of rapid accretion (cra). **G–L**, *Scolymia tamiamiensis*; **G, H**, holotype, SUI 146181 (CCD53544); **G**, calical surface; **H**, corallum side; **I**, paratype, SUI 146179 (CCD53517), calical surface; **J–L**, paratype, SUI 146178 (CCD 53293); **J**, transverse thin section showing trabeculothecal (tr) corallite wall; **K**, transverse thin section showing reduced trabecular columella (cl); **L**, transverse thin section close-up of corallite wall showing moderately spaced centres of rapid accretion (cra). Scale bars: A, B, G, I = 1 cm; C, D, J, K = 3 mm; L = 1 mm.

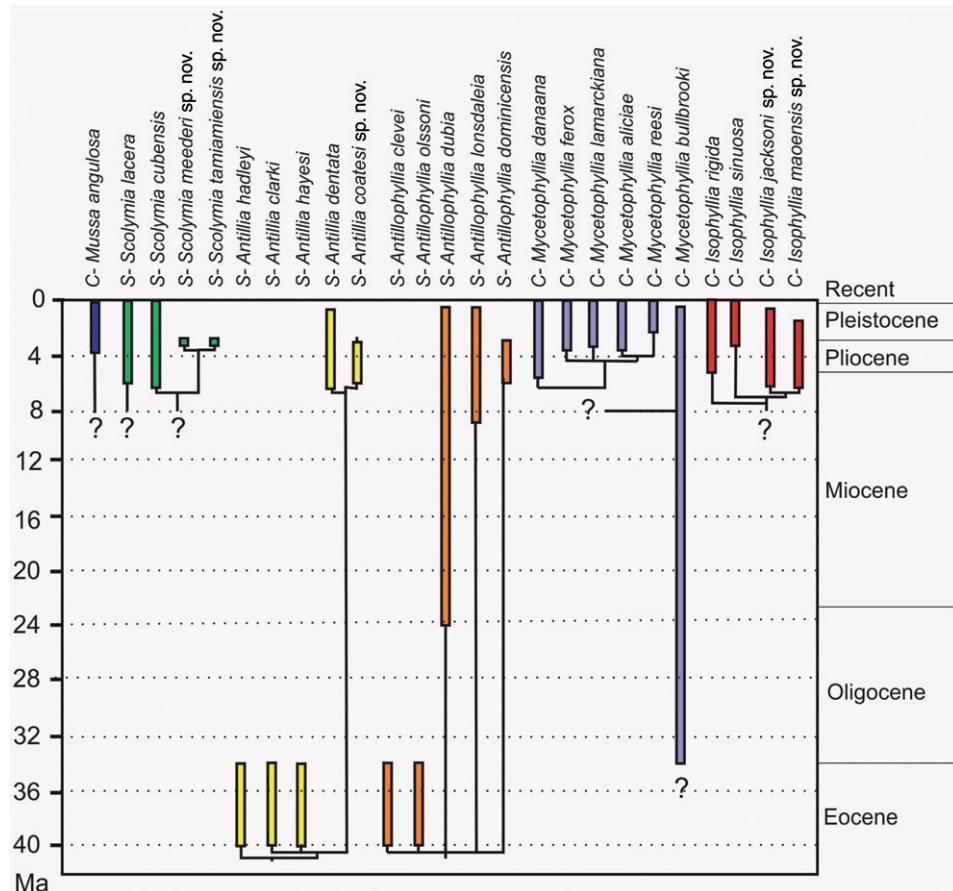


Figure 16. Stratigraphical ranges of species of Mussinae over the past 40 million years. Ranges for each species are maximums based on the age dates of the formations in which they occur (Supplemental material, Appendix E). Relationships among species are schematic, based on the phylogenetic analysis (Fig. 3).

Our results suggest that Caribbean and Indo-Pacific members of the clade Faviidae + Lobophylliidae + Merulinidae (i.e. the suborder Faviina of Wells 1956) were for the most part distinct from one another by Neogene time. One exception is the three species in our analysis that group more closely with members of the Indo-Pacific merulinid genus *Trachyphyllia*. In addition, *Antillophyllia* has been found in the Oligocene of France (Cahuzac & Chaix 1993, 1994) as well as the Mio–Pliocene of Indonesia (Santodomingo *et al.* 2014; Johnson *et al.* 2015). In previous work, *Trachyphyllia* and *Antillophyllia* have been interpreted to be closely related due to the presence of septal lobes (Wells 1956). Our phylogenetic analysis shows this not to be the case, with *Antillophyllia* clearly grouping with members of Mussinae. Both genera are cosmopolitan and have long histories dating back to the Eocene (see Santodomingo *et al.* 2014 for *Trachyphyllia*).

In contrast, high bootstrap and Bremer support values indicate that the Indo-Pacific family Lobophylliidae is a distinct and cohesive evolutionary unit. No lobophylliid

species are closely related to species of Mussinae. The distinctiveness of the Lobophylliidae was also found by Budd & Bosellini (2016) in their study of relationships between the Oligocene Mediterranean and modern Indo-Pacific meandroid corals and by Santodomingo *et al.* (2014) in their study of Miocene Indo-Pacific corals.

Preliminary comparisons also suggest that five of the six Mussinae genera in the present study are distinct from morphologically similar Mediterranean genera indicating that the subfamily is largely restricted to the Caribbean. *Mussa* has not been previously reported from the Mediterranean, but *Scolymia*, *Antillia*, *Isophyllia* and *Mycetophyllia* all have previously reported occurrences (Chevalier 1962). Preliminary morphological examination suggests that Mediterranean *Scolymia* and *Antillia* may be *Lobophyllia* (*Parascolymia*), *Leptomussa* or *Syzgophyllia*; Mediterranean *Isophyllia* and *Mycetophyllia* may be *Acanthastraea*, *Lobophyllia* (*Sympyphilla*) or *Hydnophyllia* (Budd 2018, pers. obs.).

Stratigraphical ranges show that diversification of both solitary and colonial taxa within the Mussinae

occurred during the late Miocene, and extinction of both solitary and colonial taxa occurred during the Plio–Pleistocene (Fig. 16). Three genera (*Mussa*, *Scolymia*, *Isophyllum*) and 11 of the 25 Mussinae species have first occurrences during the late Miocene. Two genera (*Antillia*, *Antillophyllia*) and 10 of the 25 Mussinae species became extinct during the Plio–Pleistocene. Mussinae diversification occurred at roughly the same time as previously reported for free-living solitary and flabellito-meandroid (FSFM) corals, in response to increased palaeoproductivity, and the extension of broad shallow-dipping shelf margins (Klaus *et al.* 2011). In addition to solitary corals, five species first occurred in the colonial genus *Mycetophyllum*, and four species first occurred in the colonial genus *Isophyllum*; modern species of both *Mycetophyllum* and *Isophyllum* occur in the deep fore reef (Reed *et al.* 2017).

Mussinae extinctions also coincided with high extinction rates of FSFM corals associated with the onset of Northern Hemisphere glaciation (Klaus *et al.* 2011). Seven of the 10 Mussinae species that became extinct were solitary. This extinction has been interpreted as a response to a transition from mesotrophic to oligotrophic conditions (Jain & Collins 2007) and the development of steepened reefal shelf margins. In general, during the high extinction episode, large, fast-growing corals that build extensive shallow reef flats were most likely to survive (Budd & Johnson 1999). The results of our present study suggest in addition that deep-fore reef attached colonial corals such as *Mycetophyllum* and *Isophyllum* that are common on steep fore reef slopes also persisted and that the deep fore reef may be a refuge for them. Except for *Mussa*, which is unstudied, all of the species that survived the extinction episode (*Isophyllum*, *Mycetophyllum*, *Scolymia*) are attached and have a brooding reproductive mode (Soto & Weil 2016).

Despite the adaptive significance of solitary versus colonial growth strategies in the ecological and evolutionary success of corals in response to varying environmental conditions, our results indicate transitions between solitary and colonial Mussinae are rare. Future transitions within Mussinae in response to increased temperature, ocean acidification or other types of environmental change are unlikely. Our results also suggest that Caribbean and Indo-Pacific corals may respond differently due to the different evolutionary histories of corals in the two regions, with most modern Caribbean taxa originating during the late Miocene. The geological record suggests the fore reef may have at times been a diversity ‘hot spot’ for solitary and flabellito-meandroid corals. However, like their shallow-water counterparts, corals inhabiting fore reef environments were still

vulnerable to extinction during periods of environmental change.

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Supplemental material

Supplemental material for this article can be accessed at <http://dx.doi.org/10.1080/14772019.2018.1541932>.

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