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## The family Faviidae (Anthozoa: Scleractinia)

## Part II. The genera *Caulastraea, Favia, Diploria, Thysanus, Hadrophyllia, Manicina,* and *Colpophyllia*

by

Ann F. Budd and Kenneth G. Johnson

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## PART II. THE GENERA *CAULASTRAEA, FAVIA, DIPLORIA, THYSANUS, HADROPHYLLIA, MANICINA,* AND *COLPOPHYLLIA*

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## ABSTRACT

Seventeen species and seven genera of the family Faviidae that bud intramurally are described in collections from the Neogene sequence in the Cibao Valley of the northern Dominican Republic. The material consists of 220 colonies from 85 localities along five river sections that range in age from Late Oligocene to Early Pliocene. Most of the specimens were collected along two river sections (39 localities in Río Gurabo, 37 localities in Río Cana) that expose an exceptionally continuous sequence extending from Late Miocene to Early Pliocene time.

Species are distinguished by sorting specimens into four qualitative groups based on colony form. Species within the *phaceloid* group (two specimens) are recognized by a principal component analysis including both primary types for all known Neogene and Quaternary Caribbean species of intramurally budding phaceloid faviids, and morphologically similar specimens collected in Plio-Pleistocene deposits near Limón, Costa Rica. Species within the *plocoid* group (five specimens) are determined by qualitative comparisons with type and non-type specimens of all known Neogene and Quaternary Caribbean species. Species within the *flabelloid* group that have bidirectional budding (154 specimens) are distinguished by principal component and average linkage cluster analyses; flabelloid species that have unidirectional budding (eight specimens) are recognized by adding specimens to the final cluster analysis for bidirectional flabelloid forms. Species within the *meandroid* group that have wide valleys (13 specimens) are determined by qualitative comparisons with specimens of all known Neogene and Quaternary Caribbean species. Meandroid species that have narrow valleys (32 specimens) are distinguished by canonical discriminant analyses comparing two qualitative groups of specimens with collections of three Recent Caribbean species.

The results suggest that 17 intramural faviid species lived in the northern Dominican Republic during Neogene time, eight of which are new. Six of the eight are represented by more than five specimens and are formally named (*Favia maoadentrensis, F. vokesae, Diploria zambensis, Hadrophyllia saundersi, Manicina geisteri, M. jungi*); names for the remaining two species are left in open nomenclature. Of the nine previously known species, one was described only as a subspecies and is therefore elevated to species rank (*Manicina puntagordensis* Weisbord, 1968). Two others consist of at least three previously named species that are synonymous. Eight of the 17 Dominican Republic species occur at fewer than four localities and are therefore considered uncommon.

The 17 Dominican Republic species are assigned to genera by studying the topology of a cladogram containing all known Cenozoic Caribbean faviid species with intramural budding (40 species total). The cladistic analysis was performed using 22 multistate characters (65 character states), nine of which are continuous. States for five of the nine continuous characters are determined statistically using multiple comparisons tests. The cladogram is a strict consensus tree of 78 equally parsimonious trees. The results suggest that seven genera lived in the northern Dominican Republic during Neogene time. One genus (*Hadrophyllia*), consisting of only one species, is new. Two others (*Manicina, Teleiophyllia*) are synonymized, resulting in a new combination for the name of one species (*Manicina grandis*). One previously described species (*Teleiophyllia navicula* Duncan, 1864) is shifted to the genus *Thysanus.*

Preliminary comparisons with other well-documented collections of Neogene and Quaternary Caribbean corals suggest that only four of the 17 described species are restricted to the Dominican Republic. Most species were fairly widely distributed across the Caribbean region. Origination rates appear to have been high among flabelloid and meandroid faviid species during the Late Miocene to earliest Pliocene; extinction rates were high in these species during the Plio-Pleistocene.

## RESUMEN

En base en las colleciones sequenciales del Neogeno del valle del Cibao, localizado al Norte de la República Dominicana, se describen 17 especies y siete géneros de la familia Faviidae con gemación intratentacular. Se collectaron 220 colonias en 85 localidades localizadas a lo largo de cinco secciones del río. Estas localidaes estan arregaldas cronologicamente desde el Oligoceno superior hasta el Plioceno inferior. La mayoria de los especimenes proviene de localidades en dos secciones de los ríos Gurabo y Cana (39 localidades en el río Gurabo y 37 en el río Cana). El estado de preservación de estas secciones es excepcionalmente bueno. La sequencia es continua y se extiende desde el Mioceno superior hasta el Plioceno inferior.

Las especies descritas fueron separadas en base a cuatro grupos cualitativos de acuerdo a la forma de la colonia. Las especies del grupo *faceloide* con gemación intratentacular (dos especimenes) se separan atraves de análisis de componentes principales. En este análisis se incluyó material tipológico de todas las especies conocidas del Neogeno y del Cuaternario del Caribe, así como especimenes colectados en depósitos del Plio-Pleistoceno de Limón, Costa Rica. Las especies del grupo *plocoide* (cinco especimenes) se separaron en base a comparaciones cualitativas con material tipológico y no tipológico de todas las especies conocidas del Neogeno y Cuaternario del Caribe. Las especies del grupo *flaveoloide* con gemación bidireccional (154 especimenes) han sido reconocidas a través de un análisis de componentes principales y de un análisis de cluster. Las especies del grupo *flaveoloide* con gemación unidireccional (ocho especimenes) se separan de las formas con gemación bidireccional cuando estos especimenes se adicionaran al cluster. Las especies del grupo *meandroide* poseedoras de valles amplios (13 especimenes) se determinaron en base a comparaciones cualitativas con todo el material conocido del Neogeno y Cuaternario del Caribe. Las especies pertenecientes a éste grupo pero que tienen valles estrechos (32 especimenes) han sido diferenciadas por análisis canónico discriminante, comparando dos grupos cualitativos de especimenes con material pertenenciente a tres especies recientes del Caribe.

Los resultados sugieren la existencia de 17 especies con gemación intratentacular de la familia Faviidae en el Norte de la República Dominicana durante el Neogeno. Ocho de estas especies son nuevas y descritas por primera vez en el presente trabajo. Seis de estas ocho especies son representadas por mas de cinco especimenes y son formalmente nominadas: *Favia maoadentrensis, F. vokesae, Diploria zambensis, Hadrophyllia saundersi, Manicina geisteri, M. jungi.* Los nombres de las otras dos especies han sido colocados en nomenclatura abierta. De las nueve especies previamente conocidas, una fue descrita como subespecie y posteriormente elevada a la categoría de especie (*Manicina puntagordensis* Weisbord, 1968). Otras dos especies corresponden, al menos, a tres especies nominadas previamente convirtiendose en sinónimos. Ocho de las 17 especies de la República Dominicana se encuentran en menos de cuatro localidades y son consideradas poco comunes.

La asignación genérica de las 17 especies mencionadas se hizo por métodos cladísticos. Para el análisis cladístico se utilizaron todas las especies con gemación intratentacular pertenecientes a la familia Faviidae conocidas en el Cenozoico del Caribe (40 especies). Se utilizaron 22 caracteres multiestado (un total de 65 estados de caracteres). Nueve de estos caracteres son continuos; los estados de cinco de estos nueve caracteres han sido determinados estadísticamente por comparaciones múltiples. El cladograma resultante, un árbol de consensus de 78 árboles igualmente parsimoniosos, sugiere que siete géneros vivieron en el Norte de la República Dominicana durante el Neogeno. Uno de estos géneros, *Hadrophyllia,* es monotípico y esta especie se describe por primera vez. Los géneros *Teleiophyllia* y *Manicina* han sido sinonimizados, resultando en una combinación nueva para una especie (*Manicina grandis*). Una especie descrita previamente (*Teleiophyllia navicula* Duncan, 1864) ha sido transferida al género *Thysanus.*

Comparaciones preliminares utilizando las colecciones existentes del Neogeno y Cuaternario del Caribe sugieren que tan solo cuatro de las 17 espcies descritas estan restringidas a la República Dominicana. La mayoria de las especies se encuentran ampliamente distribuidas a lo largo de la región del Caribe. Los grupos flaveoloide y meandroide presentan altas tazas de originación de nuevas especies durante el Mioceno superior y el Plioceno inferior. Las tazas de extinción son igualmente altas durante el Plio-Pleistoceno para estos dos grupos.

## INTRODUCTION

This monograph is part of a multidisciplinary project on the paleontology and stratigraphy of the northern Dominican Republic, coordinated by P. Jung and J. B. Saunders of the Naturhistorisches Museum in Basel, Switzerland. It is the fourth in a series on the systematics and evolutionary history of the reef corals from the Middle Miocene through Lower Pliocene of the northern Dominican Republic. It is the second and final paper on the family Faviidae Gregory, 1900, and covers 17 species of seven genera that bud intramurally. As in previous monographs (Foster, 1986, 1987; Budd, 1991), the material was collected between 1978 and 1980 by J. Geister, P. Jung, J. B. Saunders, and co-workers as part of their large-scale multidisciplinary project on the paleontology and stratigraphy of the Neogene deposits of the Cibao Valley region (Saunders *et al.*, 1982; Saunders *et al.*, 1986), and is deposited at the Naturhistorisches Museum in Basel, Switzerland (NMB). The sampled sequence is one of the longest, most continuous, and best-studied Neogene sequences in the Caribbean region. Although it is composed primarily of siliciclastics and large reefal accumulations and carbonates are rare (Evans, 1986), the sequence contains a suite of abundant, exceptionally well-preserved reef corals, including more than 80 species of 33 genera (Budd *et al.*, 1994b). The corals were collected as part of a larger macrofossil sampling program in which individual specimens in closely spaced horizons were extracted systematically from the face of the outcrop. The samples have been keyed into detailed stratigraphic sections, whose age dates have been determined by study of microfossils (Saunders *et al.*, 1986).

Of the seven genera treated in the present monograph, three (*Thysanus* Duncan, 1863, *Manicina* Ehrenberg, 1834, and *Hadrophyllia,* n. gen.) have distributions restricted to the Neogene to Recent of the Caribbean region, while two others (*Diploria* Milne Edwards and Haime, 1848, and *Colpophyllia* Milne Edwards and Haime, 1848) are known only from the

Table 1.—Distinguishing characteristics of four scleractinian families exhibiting convergent evolution in the Neogene of the northern Dominican Republic (after Vaughan and Wells, 1943; Wells, 1956; as modified by Veron et al., 1977).

| Family | Septal teeth | Trabecular fan systems | Septal lobes | Columella | Coenosteum |
|---|---|---|---|---|---|
| Faviidae Gregory, 1900 | acute | 1–2 | small or absent | mostly spongy | mostly porous |
| Meandrinidae Gray, 1847 | minute | 1–2 | small or absent | mostly lamellar | mostly solid |
| Mussidae Ortmann, 1890 | large | multiple | absent | spongy | rare |
| Trachyphylliidae Verrill, 1901 | acute | 2 | prominent | spongy | rare |

Paleogene to Recent of the Caribbean and Mediterranean regions. Only the two remaining genera (*Caulastraea* Dana, 1846, and *Favia* Oken, 1815) have broad geographic distributions that extend into the Indo-Pacific. Both of these latter two genera also have relatively long stratigraphic ranges; *Favia* ranges from the Cretaceous to Recent, and *Caulastraea* from Paleogene to Recent. Three of the seven genera (*Caulastraea, Thysanus, Hadrophyllia*) are currently extinct in the Caribbean region, and so are all but one (*Colpophyllia natans* [Houttuyn, 1772]) of the 17 species. These extinctions occurred during an episode of Plio-Pleistocene turnover in reef communities throughout the Caribbean region, which affected approximately 75% of the entire reef-coral fauna (Budd *et al.,* 1996; Johnson *et al.,* 1995; Johnson, 1998). All of the species in the present monograph have first occurrences in the Caribbean during the Middle to Late Miocene, and most appear to have had geographic distributions that extend across the Caribbean region (Budd *et al.,* 1994b).

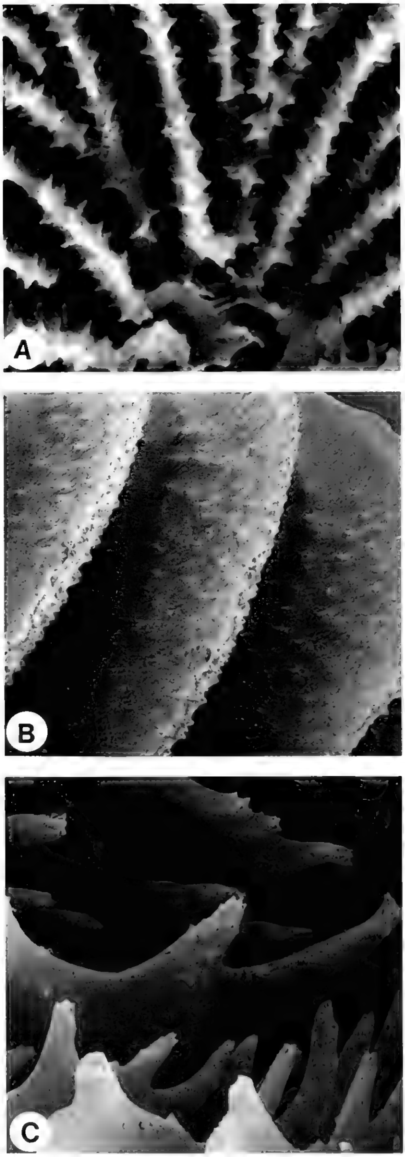
In the NMB collections, members of the seven genera exhibit a wide array of colony forms, and many are free-living. Included among the colony forms are: 'phaceloid' (= corallites separated by void space), 'plocoid' (= corallites separated by coenosteum), 'flabelloid' (= corallites arranged in single series), and 'meandroid' (= corallites arranged in multiple series), but not 'cerioid' (= corallites juxtaposed). Many species, especially in the genera *Thysanus, Hadrophyllia,* and *Manicina,* are more common on soft-bottom substrates and in reef-associated seagrass flats than in reef framework environments, and are important components of the recurrent Neogene grass flat assemblages discussed by Budd *et al.* (1996). They are often associated with similar flabelloid and meandroid forms and large solitary forms belonging to the families Meandrinidae Gray, 1847, Mussidae Ortmann, 1890, and Trachyphylliidae Verrill, 1901. In fact, the convergence in colony form among families is so striking that, in some cases, genera belonging to different families are difficult to distinguish without detailed microscopic examination. Special emphasis will be given to this convergence in the present monograph and in two monographs that will follow later in the series (one on the Meandrinidae, and the other on the Mussidae and Trachyphylliidae).

In addition to convergence in colony form, another interesting aspect of the evolution of the families Faviidae, Meandrinidae, and Mussidae is that at least one Neogene Dominican Republic species in each of the three families (*Favia dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925, in the Faviidae; *Meandrina braziliensis* [Milne Edwards and Haime, 1849] in the Meandrinidae; and *Mussismilia* n. sp. aff. *hartti* [Verrill, 1868] in the Mussidae) is morphologically similar to a species whose distribution is restricted today to Brazil. This similarity suggests that Brazil may have served as a refuge during the Plio-Pleistocene environmental perturbations that may have caused increased extinctions in the Caribbean fauna. Further morphometric comparisons are needed to test this hypothesis.

Following the terminology and classification system of Vaughan and Wells (1943) and Wells (1956) as modified by Veron *et al.* (1977) and Veron (1986), the families Faviidae, Meandrinidae, Mussidae, and Trachyphylliidae are generally characterized by laminar septa composed of simple trabeculae. Members of the four families usually lack synapticulae, and have relatively large corallites (*i.e.,* greater than 2 mm in diameter) with more than two septal cycles. The Faviidae are distinguished by numerous acute teeth formed at the tips of a simple fan system of trabeculae on their upper septal margins, and by a coenosteum consisting of vesicular or tabular exothecal dissepiments. The Meandrinidae are distinguished by minute teeth formed similarly by a simple trabecular fan on their upper septal margins, by a heavy coenosteum, and usually by a lamellar columella. The Mussidae are distinguished by large, coarse teeth formed by a fan system of multiple trabeculae on their upper septal margins, and by septa that appear ragged in horizontal section. The Trachyphylliidae are distinguished by prominent septal lobes and numerous acute teeth on their upper septal margins (Table 1; Text-fig. 1). In the present monograph, septal lobes are defined as internal lobes formed only in scleractinians with lamellar septa composed of simple trabeculae. They are constructed by a second smaller trabecular fan system that develops in addition to the main fan system forming the septa (Text-fig. 2). Paliform lobes differ from septal lobes in that they are not constructed by a second fan system. They are formed instead by vertical extensions of one or more trabecular bundles within the main fan system.

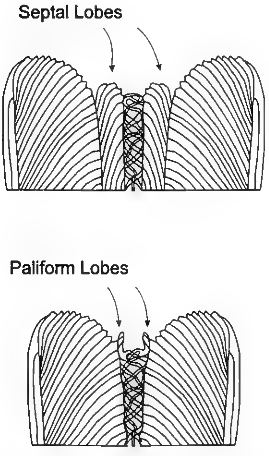
Convergence occurs among phaceloid forms in the NMB collections in the Faviidae (*Caulastraea*) and Mussidae (*Mussismilia* Ortmann, 1890); among plocoid forms in the Faviidae (*Favia*) and Meandrinidae (*Dichocoenia* Milne Edwards and Haime, 1848); among flabelloid forms in the Faviidae (*Thysanus, Manicina, Hadrophyllia*) and Meandrinidae (*Placocyathus* Milne Edwards and Haime, 1848); among meandroid forms in the Faviidae (especially, *Manicina*), Meandrinidae (*Meandrina* Lamarck, 1801), and Mussidae (*Isophyllia* Milne Edwards and Haime, 1851); and among pseudo-solitary forms in the Mussidae (*Antillia* Duncan, 1863, *Scolymia* Haime, 1852) and Trachyphylliidae (*Trachyphyllia* Milne Edwards and Haime, 1848, *Antillophyllia* Vaughan, 1932).

Taxa have been recognized in the present monograph using a combination of qualitative and quantitative techniques, including multivariate statistical analyses and cladistic analysis. Specimens in the NMB collections were first sorted into qualitative groups based on colony form (*i.e.,* phaceloid, plocoid, flabelloid, and meandroid). Within each colony form group, a set of morphologic characters was selected that facilitated subdivision of the group into finer morphologic subgroups. In most cases, these characters consisted of linear distance measures of corallite architecture and septal counts. Subdivision into morphologic subgroups was accomplished without regard to position in the stratigraphic sequence, following the approach of Cheetham (1986) and Budd and Coates (1992). Many of the taxa examined in the present monograph are uncommon or rare. In cases where the original colony form group consisted of more than 10 specimens, this subdivision was accomplished quantitatively by average linkage cluster analysis and a series of iterative canonical discriminant analyses (see Budd *et al.,* 1994a, for discussion of statistical methods).



Text-figure 1.—Scanning electron micrographs showing the differences in septal teeth among the families Faviidae, Meandrinidae, and Mussidae, × 20. (**A**) The family Faviidae which is characterized by acute septal teeth formed by single trabecular fan systems; SUI 84993 (J-111), figured specimen of *Manicina mayori* Wells, 1936, Recent, Discovery Bay, Jamaica; (**B**) The family Meandrinidae which is characterized by minute septal teeth formed by single trabecular fan systems; USNM 325304 (NF507), figured specimen of *Meandrina meandrites* (Linnaeus, 1758), Recent, Discovery Bay, Jamaica; (**C**) The family Mussidae which is characterized by large septal teeth formed by multiple trabecular fan systems; SUI 54924 (J-114), figured specimen of *Isophyllia sinuosa* (Ellis and Solander, 1786), Recent, Discovery Bay, Jamaica.

←



Text-figure 2.—Schematic drawings of vertical cuts through calices comparing septal lobes and paliform lobes. Both types of lobes are continuations of the inner ends of lamellar septa which are composed of simple trabeculae. Septal lobes are constructed by an additional trabecular fan system, whereas paliform lobes are formed by vertical extensions of one or more trabecular bundles from the main fan system. Pali, by contrast, are physically distinct vertical pillars that remain after septal substitution.

Differences among final subgroups were assessed by one-way analyses of variance and Duncan's multiple comparisons tests. The statistical methods were performed using S-plus (version 3.3) and SAS (version 6.10).

If the original colony form group consisted of fewer than 10 specimens, the subgroups were distinguished by comparison with morphologic differences among Recent or fossil species. These comparisons are preliminary, because genetic studies have recently shown that one abundant and widely known faviid species in the Caribbean, *Montastraea annularis* (Ellis and Solander, 1786), is actually a complex of sibling species (Knowlton *et al.*, 1992; Weil and Knowlton, 1994), and the same may be true of *Manicina areolata* (Linnaeus, 1758) and other closely related species (Johnson, 1991) that are treated herein. Most Recent scleractinian species in the Caribbean were originally described in the late 1700s and 1800s on the basis of very few specimens and few characters. Although Vaughan (1901), in particular, attempted to revise all of the shallow-water species by qualitative examination of large collections and comparisons with the results of transplant experiments, little comprehensive work based on large collections (except Roos, 1971; Cairns, 1982; Zlatarski and Martinez Estalella, 1982) has been published in recent decades, and none has incorporated the newer molecular and morphometric protocols. The systematics of Recent Caribbean reef-coral species, therefore, are greatly in need of re-evaluation and revision.

Species names were assigned to morphologic subgroups in the present monograph by quantitative comparisons with holotypes of all formally described faviid species (except forms with extramural budding, including *Montastraea* Blainville, 1830, *Solenastrea* Milne Edwards and Haime, 1848, *Agathiphyllia* Reuss, 1864; see Budd, 1991, table 3) from the late Early Miocene to Pliocene of the Caribbean region (Table

Table 2.—List of all previously described species of Faviidae with intramural budding in the upper Lower Miocene through Pliocene of the Caribbean region, and their synonyms.

1. *Calamophyllia portoricensis* Coryell in Coryell & Ohlsen, 1929, p. 199–200, pl. 30, fig. 4; holotype = AMNH 23000. [=*Caulastraea portoricensis*]
2. *Maeandra bowersi* Vaughan, 1917, p. 374, pl. 51, figs. 1a, b; holotype = USNM 68289. [=*Diploria bowersi*]
3. *Diploria sarasotana* Weisbord, 1974, p. 351–353, pl. 35, figs. 1, 2; pl. 36, fig. 1; holotype = FMNH 8279.
4. *Favia dominicensis* Vaughan *in* Vaughan & Hoffmeister, 1925, p. 325, pl. 2, figs. 4, 6, 7; holotype = MCZ 103512.
5. *Goniastrea trinitatis* Vaughan *in* Vaughan & Hoffmeister, 1926, p. 123–124, pl. 4, figs. 2, 2a. [=*Goniastrea canalis*]
6. *Goniastrea canalis* Vaughan, 1919, p. 416–417, pl. 91, fig. 4; holotype = USMN 324996.
7. *Manicina pliocenica* Gane, 1895; p. 10; holotype = USNM (lost); neotype selected herein = NMB D6165.
8. *Manicina areolata puntagordensis* Weisbord, 1968, p. 51–57; pl. 4, fig. 5; pl. 5, figs. 1–5; pl. 12, fig 4; holotype = PRI 27560. [=*Manicina puntagordensis*]
9. *Teleiophyllia grandis* Duncan, 1864, p. 35–35; pl. 3, figs. 5a, b; holotype = BM(NH) R28754. [=*Manicina grandis*]
10. *Teleiophyllia navicula* Duncan, 1864, p. 36; pl. 4, figs. 1a, b; holotype = BM(NH) R28766. [=*Thysanus navicula*]
11. *Thysanus crassicostatus* Vaughan *in* Vaughan & Hoffmeister, 1925, p. 326; pl. 3, figs. 5–8; holotype = MCZ 9280. [? =*Hadrophyllia saundersi*]
12. *Thysanus excentricus* Duncan, 1863, p. 439–440; pl. 16, figs. 3a–c; holotype = BM(NH) B.M.46814.
13. *Thysanus corbicula* Duncan, 1863, p. 430; pl. 15, figs. 3a, b; holotype = BM(NH) R28795.
14. *Thysanus elegans* Duncan *in* Duncan & Wall, 1865, p. 10; pl. 2, figs. 2a, b; holotype = BM(NH) R28918. [=*Thysanus excentricus*]
15. *Thysanus vaughani* Weisbord, 1971, p. 22–23; pl. 5, figs. 3–5; holotype = FMNH 8294. [? =*Thysanus corbicula*]
16. *Thysanus hayesi* Vaughan, 1919, p. 424; pl. 77, fig. 3, a, b; holotype = USNM 324994. [=*Thysanus excentricus*]
17. *Thysanus floridanus* Weisbord, 1974, p. 356–358; pl. 24, figs. 1–3; holotype = USNM 79812. [=*Thysanus corbicula*]

Table 3.—List of all currently accepted Recent species of Faviidae with intramural budding in the Caribbean region (Wells and Lang, 1973) and in Brazil (Laborel, 1969).

1. *Colpophyllia amaranthus* (Houttuyn, 1772), p. 128, pl. 127, fig. 1; holotype = lost (Matthai, 1928).
2. *Colpophyllia breviserialis* Milne Edwards & Haime, 1849, p. 267; holotype = BM(NH) 1840.5.29.6.
3. *Colpophyllia natans* (Houttuyn, 1772), p. 124; holotype = lost (Matthai, 1928).
4. *Diploria clivosa* (Ellis & Solander, 1786), p. 163; holotype = lost (Kerr, 1910).
5. *Diploria labyrinthiformis* (Linnaeus, 1758), p. 794–795; holotype = lost (Matthai, 1928).
6. *Diploria strigosa* (Dana, 1848), p. 257–258, pl. 14, figs. 4a, b; holotype = USNM 00005.
7. *Favia fragum* (Esper, 1795), p. 79, pl. 64, figs. 1, 2; holotype = lost (Scheer, 1990).
8. *Favia gravida* Verrill, 1868, p. 354; holotype = YPM 9081.
9. *Favia leptophylla* Verrill, 1868, p. 353; holotype = YPM 9084.
10. *Manicina areolata* (Linnaeus, 1758), p. 795; holotype = BM(NH) 28.3.1.32.
11. *Manicina mayori* Wells, 1936, p. 104–105; (=*Manicina gyrosa* Ehrenberg, 1834, p. 326, holotype = MB 2859 [figured in Matthai, 1928, pl. 63, fig. 6]).

2). In instances where holotypes were not readily available for study, these comparisons were made using the text of original species descriptions. Stratigraphic ranges were determined by comparisons with samples of traditionally recognized Recent species from the Caribbean region (Wells and Lang, 1973) and Brazil (Laborel, 1969) (Table 3), and with occurrences in 39 Miocene to Pleistocene localities that are scattered across the Caribbean region (Table 4).

Finally, genera and evolutionary relationships among taxa were re-assessed by using the results of cladistic analyses on the resulting species using parsimony (Johnson, 1998). The analyses were performed using 40 Eocene to Recent Caribbean faviid species and 22 multistate characters with a total of 65 states. The taxa include all known Cenozoic species with intramural budding, and the characters include all possible diagnostic morphologic features, including both continuous and discontinuous character types. Genera were defined as holophyletic groups of species that a modified jackknife procedure revealed as having high clade stability.

Based on the cladistic results, the following genera and species are described:

Genus *Caulastraea* Dana, 1846
*Caulastraea portoricensis* (Coryell *in* Coryell and Ohlsen, 1929)
Genus *Favia* Oken, 1815
*Favia dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925
*Favia* n. sp. aff. *dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925
*Favia vokesae,* n. sp.
*Favia maoadentrensis,* n. sp.
Genus *Diploria* Milne Edwards and Haime, 1848
*Diploria zambensis,* n. sp.
Genus *Thysanus* Duncan, 1863
*Thysanus corbicula* Duncan, 1863
*Thysanus excentricus* Duncan, 1863
*Thysanus navicula* (Duncan, 1864)
Genus *Hadrophyllia,* n. gen.
*Hadrophyllia saundersi,* n. sp.
Genus *Manicina* Ehrenberg, 1834
*Manicina geisteri,* n. sp.
*Manicina grandis* (Duncan, 1864)
*Manicina jungi,* n. sp.
*Manicina pliocenica* Gane, 1895
*Manicina puntagordensis* Weisbord, 1968
*Manicina* n. sp. aff. *mayori* Wells, 1936
Genus *Colpophyllia* Milne Edwards and Haime, 1848
*Colpophyllia natans* (Houttuyn, 1772)

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Table 4.—List of fossil localities whose faunas have been examined in addition to the localities treated herein, to estimate the geographic distributions of species and their overall stratigraphic ranges. Age dates for Bahamas localities are modified after McNeill et al. (1993). Age dates for Jamaican localities are after Aubry (1993) and Land (1973, 1991). Age dates for Costa Rican localities are preliminary and determined by D. F. McNeill (pers. comm. 1996). Sources for all other ages are given in Budd et al. (1994b). fbmp = feet below mud pit.

| Collecting locality | Absolute age dates | Faunal description | Repository |
|---|---|---|---|
| Early to Middle Miocene: | | | |
| 1. Tampa Formation, Florida | 22–23.7 Ma | Weisbord, 1973 | FMNH |
| *2. Emperador Limestone, Panama | 17.6–22 Ma | Vaughan, 1919 | USNM |
| *3. Anguilla Formation, Anguilla | 16.2–22 Ma | Budd *et al.*, 1995 | SUI |
| 4. Chipola Formation, Florida | 15–18 Ma | Weisbord, 1971 | FMNH |
| 5. Brasso and Tamana Formations, Trinidad | 11.2–15 Ma | Vaughan and Hoffmeister, 1926 | USNM |
| *6. Unda (1228–1236 fbmp), Bahamas | 11.6–11.7 Ma | Budd and Kievman, 1993 | U. Miami |
| Late Miocene to Early Pliocene: | | | |
| *1. Manzanilla Formation, Trinidad | 5.3–11.2 Ma | Vaughan and Hoffmeister, 1926 | USNM |
| 2. Lirio Limestone, Isla de Mona | 5.3–11.2 Ma | Gonzalez *et al.*, 1992 | SUI |
| *3. Unda (1030–1063 fbmp), Bahamas | 5.3–5.4 Ma | Budd and Kievman, 1993 | U. Miami |
| *4. Unda (978–1030 fbmp), Bahamas | 5.2–5.3 Ma | Budd and Kievman, 1993 | U. Miami |
| 5. Brasso Seco, Rio Banano Formation, Costa Rica | 4–5.3 Ma | Budd *et al.*, 1999 | USNM, SUI |
| 6. Quebrada Chocolate reef trend, Q. Chocolate Formation, Costa Rica | 3–3.6 Ma | Budd *et al.*, 1999 | USNM, SUI |
| 7. Buenos Aires reef trend, Q. Chocolate Formation, Costa Rica | 3–4 Ma | Budd *et al.*, 1999 | USNM, SUI |
| Late Pliocene: | | | |
| 1. Pinecrest Sandstone, Florida | 3–3.5 Ma | Meeder, 1987 | USNM |
| 2. Bowden Formation, Jamaica | 2–3.5 Ma | Budd collections | USNM, SUI |
| 3. La Cruz Marl, Cuba | 1.6–3.5 Ma | Vaughan, 1919 | USNM |
| 4. Empalme reef trend, Moin Formation, Costa Rica | 1.6–1.9 Ma | Budd *et al.*, 1999 | USNM, SUI |
| 5. Matanzas, Cuba | 1–3.5 Ma | Vaughan, 1919 | USNM |
| 6. Old Pera Beds, Jamaica | 1.8–2.5 Ma | Budd collections | USNM, SUI |
| 7. Hope Gate Formation, Jamaica | 1.8–2.5 Ma | Budd collections | USNM, SUI |
| 8. Unda (342–355 fbmp), Bahamas | 2.1–2.2 Ma | Budd and Kievman, 1993 | U. Miami |
| 9. Clino (606–648 fbmp), Bahamas | 2.1–2.2 Ma | Budd and Kievman, 1993 | U. Miami |
| 10. Unda (272–342 fbmp), Bahamas | 1.9–2.1 Ma | Budd and Kievman, 1993 | U. Miami |
| 11. Clino (514–539 fbmp), Bahamas | 1.9–2.0 Ma | Budd and Kievman, 1993 | U. Miami |
| 12. Unda (259–272 fbmp), Bahamas | 1.8–1.9 Ma | Budd and Kievman, 1993 | U. Miami |
| 13. Clino (445–484 fbmp), Bahamas | 1.8–1.9 Ma | Budd and Kievman, 1993 | U. Miami |
| 14. Lomas del Mar, Costa Rica | 1.6–1.9 Ma | Budd *et al.*, 1999 | USNM, SUI |
| 15. Unda (209–259 fbmp), Bahamas | 1.7–1.8 Ma | Budd and Kievman, 1993 | U. Miami |
| 16. Clino (394–445 fbmp), Bahamas | 1.6–1.8 Ma | Budd and Kievman, 1993 | U. Miami |
| 17. Caloosahatchee Formation, Florida | 1.6–1.8 Ma | Weisbord, 1974 | USNM, FMNH |
| Early Pleistocene: | | | |
| 1. Manchioneal Formation, Jamaica | 0.8–1.8 Ma | Budd collections | USNM, SUI |
| 2. Clino (321–394 fbmp), Bahamas | 1.3–1.6 Ma | Budd and Kievman, 1993 | U. Miami |
| 3. Glades Formation, Florida | 1–1.6 Ma | Weisbord, 1974 | USNM, FMNH |
| Middle to Late Pleistocene: | | | |
| 1. Clino (86–278 fbmp) | 200–900 Ka | Budd and Kievman, 1993 | U. Miami |
| *2. Unda (127–164 fbmp) | 500–700 Ka | Budd and Kievman, 1993 | U. Miami |
| 3. Santo Domingo, Dominican Republic | 100–500 Ka | Geister, 1982 | U. Bern |
| 4. San Andrés | 100–500 Ka | Geister, 1975 | U. Bern |
| 5. Key Largo Limestone, Florida | 100–500 Ka | Weisbord, 1974 | USNM |
| 6. Falmouth Formation, Jamaica | 120–150 Ka | Budd collections | USNM, SUI |

* None of the genera treated herein were found to be present.

[BM(NH)]; R. Portell, Florida Museum of Natural History (FMNH); R. Chamberlain, American Museum of Natural History (AMNH); F. Collier, Museum of Comparative Zoology, Harvard University (MCZ); W. L. Taylor, Paleontological Research Institution (PRI); D. Blake and S. D. Sroka, University of Illinois at Urbana-Champaign; E. Lazo-Wasem, Yale Peabody Museum (YPM).

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## ABBREVIATIONS OF REPOSITORY INSTITUTIONS

AMNH = American Museum of Natural History, New York, NY, U.S.A.
BM(NH) = The Natural History Museum, London, England, U.K.
CCD = Cenozoic Coral Database, specimen database available at http://porites.geology.uiowa.edu
FMNH = Florida Museum of Natural History, University of Florida, Gainesville, FL, U.S.A.
MB = Museum für Naturkunde, Berlin, Germany
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
NF = Nancy Foster coral collection specimen numbers (specimens deposited at USNM)
NMB = Naturhistorisches Museum, Basel, Switzerland
NMITA = Neogene Marine Biota of Tropical America, biotic database available at http://porites.geology.uiowa.edu
PPP = Panama Paleontology Project, coordinated by Jeremy Jackson and Anthony Coates at the Smithsonian Tropical Research Institute
PRI = Paleontological Research Institution, Ithaca, NY, U.S.A.
SUI = University of Iowa (formerly the State University of Iowa), Iowa City, IA, U.S.A.
TU = Tulane University, New Orleans, LA, U.S.A.
USGS = United States Geological Survey, Reston, VA, U.S.A.
USNM = United States National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
YPM = Yale Peabody Museum, New Haven, CT, U.S.A.

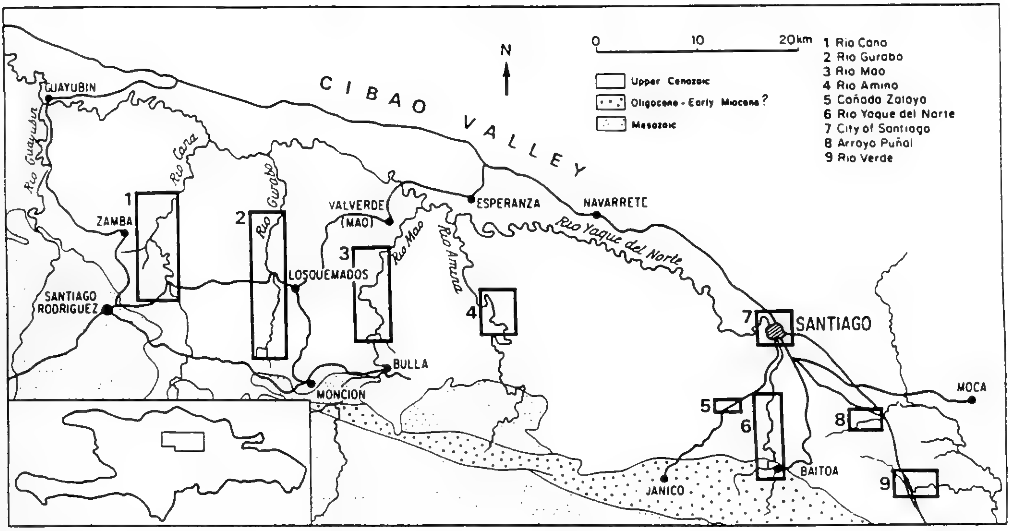
## PREVIOUS WORK

As reviewed in Budd (1991), the first major study of the systematics of Neogene reef corals from the northern Dominican Republic was done by Duncan (1863, 1864, 1868) using the Heneken collection (Heneken, 1853), now deposited at The Natural History Museum in London, U.K. [BM(NH)]. Among the faviids with intramural budding in this collection, Duncan (1863, 1864) recognized a total of four new flabelloid species from the Dominican Republic. He also described one new flabelloid species from the Neogene of Jamaica (Duncan and Wall, 1865). Based on Duncan's initial work, Pourtalès (1875) noted one flabelloid species and three meandroid species in his list of fossil corals collected by W. M. Gabb in the northern Dominican Republic, but all were previously described. The only other nineteenth century publications on the systematics of Neogene Caribbean reef corals were written by Gane (1895, 1900), who described one new species of meandroid coral from the Caloosahatchee River of Florida.

Despite an extensive survey of Oligocene and Miocene Caribbean reef corals, Vaughan (1919) described only one additional Neogene faviid species with intramural budding (*Thysanus hayesi*), in his study of collections from a range of different Cenozoic Caribbean locations. This one species was found in the Maury collections from the Neogene of the Dominican Republic (Maury, 1917; deposited at the U.S. National Museum). He described a second species in his subsequent study of the Gabb collection (Vaughan and Hoffmeister, 1925). Following these initial works on coral systematics, very little has been done on Neogene Dominican Republic material, although additional species have been described from the Middle to Late Miocene of Trinidad (Vaughan and Hoffmeister, 1926), the Late Miocene of south central California (Vaughan, 1917), the Late Pliocene of Venezuela (Weisbord, 1968), and the Plio-Pleistocene of Florida (Weisbord, 1974) (Table 2).

## CIBAO VALLEY OCCURRENCES AND PRELIMINARY PALEOECOLOGICAL INTERPRETATIONS

The seven genera treated in this monograph occur in five (Río Amina, Río Cana, Río Gurabo, Río Mao, Río Yaque del Norte) of the nine river sections collected by Saunders *et al.* (1986) through the Neogene of the Cibao Valley (Text-fig. 3). By far, the most abundant genus is *Manicina* Ehrenberg, 1834, which occurs at a total of 61 NMB localities. *Thysanus* Dun-

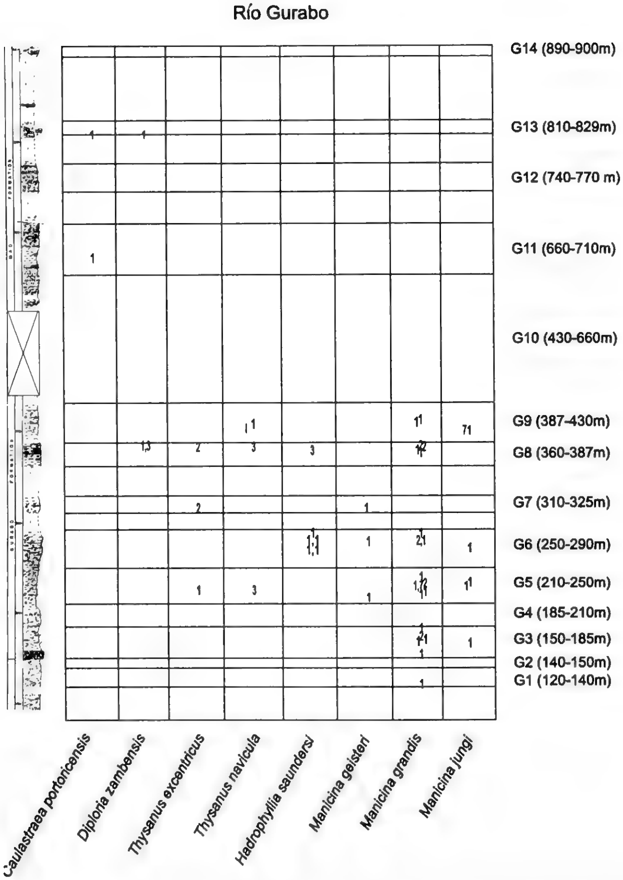


Text-figure 3.—Map showing the location of the river sections sampled. The seven genera treated herein were found in only five of the nine sampled sections: Río Amina, Río Cana, Río Gurabo, Río Mao, Río Yaque del Norte (after Saunders *et al.*, 1986, text-fig. 3).

can, 1863 (11 NMB localities), *Diploria* Milne Edwards and Haime, 1848 (nine NMB localities), *Hadrophyllia,* n. gen. (eight NMB localities), and *Favia* Oken, 1815 (four NMB localities) occur in fewer NMB localities; whereas *Caulastraea* Dana, 1846 (two NMB localities) and *Colpophyllia* Milne Edwards and Haime, 1848 (one NMB locality) are rare. The most abundant species is *M. grandis* Duncan, 1864, which occurs at 45 NMB localities. Other common species include: *M. jungi,* n. sp. (17 NMB localities), *M. geisteri,* n. sp. (11 NMB localities), *D. zambensis,* n. sp. (nine NMB localities), *H. saundersi,* n. sp. (eight NMB localities), *T. navicula* (Duncan, 1864) (seven NMB localities), *T. excentricus* Duncan, 1863 (five NMB localities), and *M. puntagordensis* (Weisbord, 1968) (four NMB localities). The nine remaining species are rare and occur at fewer than four NMB localities each.

Members of five of the seven genera in this monograph were found at 39 NMB localities along Río Gurabo (Text-fig. 4). They consist of a total of eight species (one *Caulastraea,* one *Diploria,* one *Hadrophyllia,* three *Manicina,* and two *Thysanus*). Two of the eight species (*C. portoricensis* and *D. zambensis*) are framework-building corals with large colony sizes; the other six consist of smaller free-living flabelloid forms that are often found in silty soft bottom areas (see Budd *et al.*, 1996). These six free-living species occur only within the lower 430 m of the section measured in Río Gurabo, and all but *M. grandis* occur above 150 m in the section (Text-fig. 4). *M. grandis* appears to be the only species in this monograph that occurs in an *in situ* patch reef of the Cercado Formation located within the Río Gurabo section at 150–155 m (G3) (Evans, 1986), and in the nearshore sands that underlie it. The patch reef occurs within a unit that contains impressions of seagrass cells on the attachment bases of bryozoans (Cheetham and Jackson, 1996). This seagrass may have extended from shallow water (< 10 m) to depths as great as 20–30 m during Mio-Pliocene time. In general, the six free-living species within the Río Gurabo section are most abundant in two units between 210 and 290 m (G5, G6) and in two units between 360 and 430 m (G8, G9), and four to five of the six species usually occur together in the same unit. Between 210 and 290 m (G5, G6), they are associated with an assemblage of branching *Porites* and *Stylophora* interpreted as having been deposited under moderately deep marine conditions in 10–30 m of water. Between 360 and 430 m (G8, G9) within the Río Gurabo section, the six free-living species are associated with 20–30 cm thick beds of reefal carbonates that contain abundant agariciid and platy corals characteristic of deep reef conditions (20–30 m) and appear to have been transported into deeper water (>> 30 m) (see Budd *et al.*, 1996).

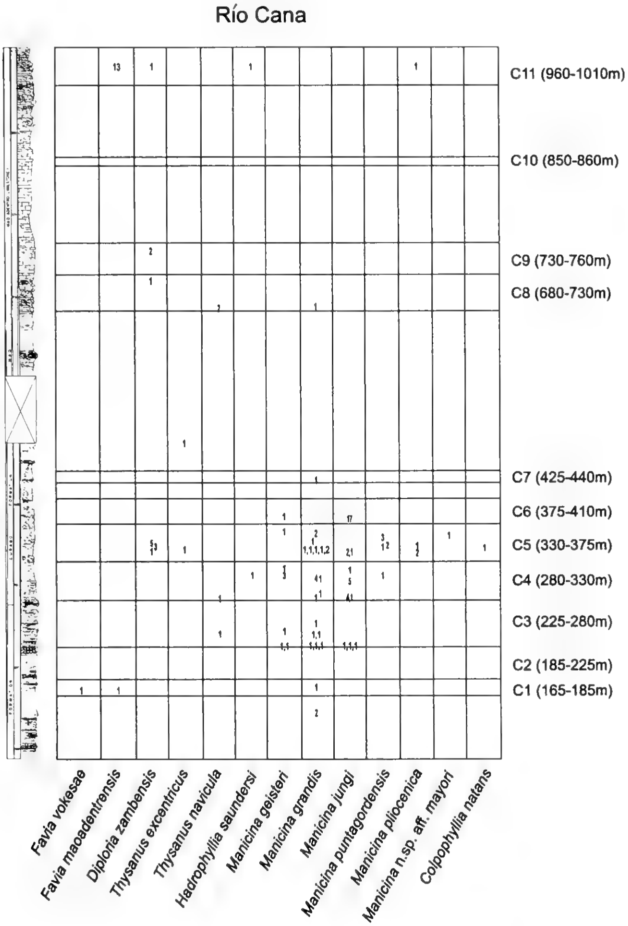
The two larger reef-building corals (*C. portoricensis*



Text-figure 4.—Columnar section of Río Gurabo showing the occurrences of species treated in this monograph (columnar section modified after Saunders *et al.*, 1986, text-fig. 6). The horizontal lines delineate horizons that have distinctive assemblages of reef corals (see Budd *et al.*, 1996). Cluster analyses of collections of the total reef-coral fauna in the lower eight horizons indicate that G3 contains a soft bottom community characteristic of reef-associated grass flats at moderate to deep water depths (10–30 m), whereas G5, G6, G7, and G8 contain more reefal communities characteristic of relatively deep water depths (20–30 m). The numbers within the grid represent numbers of specimens of each species collected within each horizon.

and *D. zambensis*) occur in slump deposits of reefal material in the middle and upper part of the Río Gurabo section (above 360 m). Ostracode assemblages associated with these units suggest that they may have been deposited in water deeper than 100 m (Bold, 1988). *C. portoricensis* occurs in two higher units in the Río Gurabo section (674 m, 808 m) in association with abundant calcified branching corals. *D. zambensis* occurs in the higher of these two units (808 m), but is also found near the middle of the Río Gurabo section (381 m) in the 20–30 cm thick beds of transported reefal carbonates described above.

Members of six of the seven genera in this monograph were found at 37 NMB localities in Río Cana (Text-fig. 5). They consisted of a total of 13 species (two *Favia,* one *Diploria,* six *Manicina,* one *Hadrophyllia,* two *Thysanus,* and one *Colpophyllia*). In general, higher numbers of large framework-building corals occur in Río Cana, especially near the mouth of the Cañada de Zamba (330–375 m within



Text-figure 5.—Columnar section of Río Cana showing the occurrences of species treated in this monograph (columnar section modified after Saunders *et al.*, 1986, text-fig. 16). The horizontal lines delineate horizons that have distinctive assemblages of reef corals (see Budd *et al.*, 1996). Cluster analyses of all reef corals found in the lower six assemblages indicate that C1 contains a reef community characteristic of shallow water depths (< 10 m), C3 and C4 contain soft bottom communities characteristic of reef-associated grass flats at moderate to deep water depths (10–30 m), and C5 contains a reef community characteristic of relatively deep water depths (20–30 m). The numbers within the grid represent numbers of specimens of each species collected within each horizon.

the Río Cana section, C5) where a more than 15 m thick *in situ* assemblage of deep reef agariciid and platy corals crops out (Saunders *et al.*, 1986; Budd *et al.*, 1996). Large massive framework-building corals are also found at 960–1010 m (C11) within the section in the steeply dipping, 1–2 m thick beds of the Mao Adentro Limestone that were transported as slump deposits.

Beginning at the base of the Río Cana section (Text-fig. 5), *Manicina grandis* is the only free-living flabelloid coral found in the shallow (< 10 m water depth) nearshore portion of the section (165–185 m; C1); however, unlike Río Gurabo, it is accompanied by two species of *Favia*. The overlying 150 m of section (especially 225–330 m; C3, C4) contains a diverse assemblage of free-living flabelloid corals including three species of *Manicina,* one of *Hadrophyllia,* and one of *Thysanus.* Study of the bases of bryozoans in these two units (Cheetham and Jackson, 1996) has revealed unmistakable impressions of seagrass rhizomes. The seagrass units are overlain by the Cañada de Zamba reef (330–375 m, C5), which contains large massive corals such as *D. zambensis, C. natans,* and the three meandroid species of *Manicina.* Four free-living flabelloid species (*T. excentricus, M. geisteri, M. grandis,* and *M. jungi*) and platy and branching corals are also common. Free-living flabelloid species continue to be abundant in beds (375–440 m; C6) above the Cañada de Zamba reef which also contain evidence of seagrass. Although less diverse, they also occur in transported slump deposits in the Mao Adentro Limestone (680–760 m [C8] and 960–1010 m [C11]). *D. zambensis* and *F. maoadentrensis* are especially abundant in these younger transported beds.

In addition to the Río Gurabo and Río Cana, members of the seven genera in this monograph were also found at three NMB localities in Río Yaque del Norte, two NMB localities in Río Mao, and one NMB locality in Río Amina. In Río Yaque del Norte, *Favia dominicensis* Vaughan, 1925 and *F.* n. sp. aff. *dominicensis* occur in the older portions of the section (the Oligocene Tabera Group and the Lower to Middle Miocene Baitoa Formation), and these two species only occur in the Dominican Republic in these sections. Also in Río Yaque del Norte, *Manicina jungi,* n. sp. occurs at La Barranca (NMB locality 17268) in the Lower Pliocene Gurabo Formation. Only three free-living flabelloid species (*Thysanus corbicula* Duncan, 1863, *M. grandis,* and *M. geisteri*) were found in the Gurabo Formation in Río Mao; and one free-living flabelloid species (*M. grandis*) was found in the Gurabo Formation in Río Amina.

## TAXONOMIC METHODS

### SPECIES RECOGNITION

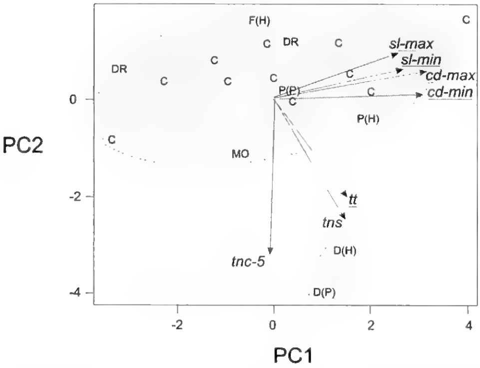
### Phaceloid colony forms

Approximately 40 specimens in the NMB collections have phaceloid growth forms, intramural budding, moderately well-developed spongy columellae, and well-developed costae. Species with these traits have been reported in the Caribbean Neogene in three genera (*Caulastraea* Dana, 1846, *Mussismilia* Ortmann, 1890, and *Eusmilia* Milne Edwards and Haime, 1848), each of which belongs to a different scleractinian family (Table 5; Pls. 1, 2). Of these three genera, only two NMB specimens belong to the faviid genus *Caulastraea,* as evidenced by their relatively small corallite size (corallite diameter = 5–10 mm), elliptical corallite shape, numerous equal-sized costae, reduced

Table 5.—Distinguishing characteristics of three morphologically similar, phaceloid genera that belong to different scleractinian families and occur in the Neogene of the Dominican Republic. All three genera possess intramural budding and spongy columellae. Ranges of corallite sizes and shapes overlap among genera.

| Family | Genus | Type species | Corallite size | Corallite shape | Septal margins | Calical relief | Costae | Endotheca | Epitheca |
|---|---|---|---|---|---|---|---|---|---|
| Faviidae | *Caulastraea* | *furcata* Dana, 1846 | 5–15 mm | circular to elliptical | acute teeth | shallow | many equal | reduced | reduced |
| *Mussidae | *Mussismilia* | *hartti* (Verrill, 1868) | 12–30 mm | irregular | med.–large teeth | sloping | high, equal | well-developed | reduced |
| Caryophylliidae | *Eusmilia* | *fastigiata* (Pallas, 1766) | 8–35 mm | elongate | smooth | exsert septa | low, subequal | vesicular | well-developed |

* Note: *Mussa* is also phaceloid, but it has thicker septa with fewer but larger teeth, a reduced columella, and more intramural centers per branch.



Text-figure 6.—Biplot of principal component (PC) scores for *Caulastraea.* Principal component analysis transforms the data into a new set of axes (principal components) which consist of combinations of the original variables. The new axes are selected successively to maximize the amount of variance and at the same time be uncorrelated with one another. In the present analysis, two measures of corallite size and septum length are most heavily weighted on PC1; and the inverse of numbers of septa and costae are most heavily weighted on PC2 (Table 7). As described in the text, nineteen specimens were included in the analyses: two NMB specimens (DR), the holotype (P[H]) and paratype (P[P]) of *C. portoricensis*; the holotype (D[H]) and paratype (D[P]) of *C. dendroidea*; the holotype (P[H]) of *C. furcata*, one specimen (MO) from the Upper Miocene of the nearby Island of Mona, and 11 specimens (C) from the Upper Pliocene Moín Formation of Costa Rica. Abbreviations for variables (underlined and in italics) are given in Table 6. Two clusters representing the species *C. portoricensis* and *C. furcata* (above) and *C. dendroidea* (below) were detected.

endotheca, and reduced epitheca. The other specimens belong primarily to *Mussismilia* (Pl. 1, figs. 3, 6) and, possibly, *Eusmilia* (Pl. 1, figs. 4, 5).

To determine the species of the two NMB specimens of *Caulastraea,* linear distance measurements and counts were made on 19 colonies including: the two NMB specimens (NMB D6140 [CCD 0057], NMB D6141 [CCD 2334]); the holotype (AMNH 23000) and paratype (AMNH 23001) of *Caulastraea portoricensis* (Coryell *in* Coryell and Ohlsen, 1929) from the Upper Oligocene to Lower Miocene of Puerto Rico; the holotype (AMNH 23003) and paratype (AMNH 23004) of *C. dendroidea* (Coryell *in* Coryell and Ohlsen, 1929) from the Upper Oligocene to Lower Miocene of Puerto Rico; one specimen of Late Miocene *Caulastraea* from the Isla de Mona (SUI 84532); 11 specimens of Late Pliocene *Caulastraea* from the Quebrada Chocolate Formation near Limón, Costa Rica (CCD 0141, 0423, 0768, 0770, 3429, 3423, 3435, 3443, 3445, 3447, 3456); and the syntype of *Caulastraea furcata* Dana, 1846 (USNM 80) from the Recent of Fiji. Many of these specimens are illustrated in Plates 1 and 2.

A total of seven characters (Table 6) were measured or counted on one corallite from each colony using a binocular microscope with an optical micrometer: maximum corallite diameter (CD-MAX), minimum corallite diameter (CD-MIN), total number of septa (TNS), major septum length (SL-MIN, SL-MAX), theca thickness (TT), and number of costae per 5 mm (TNC-5). More corallites per colony could not be measured owing to inadequate preservation. The ranges of these characters differed greatly in magnitude; therefore, the data were analyzed by performing a principal component analysis using the correlation matrix. The

Table 6.—List summarizing all morphological measurements and counts used in this monograph and their abbreviations.

| Measurement or count | Abbreviation | Applicable colony forms |
|---|---|---|
| 1. Minimum corallite diameter (mm) | CD-MIN | phaceloid, plocoid |
| 2. Maximum corallite diameter (mm) | CD-MAX | phaceloid, plocoid |
| 3. Valley width (mm) | IVW | flabelloid, meandroid |
| 4. Corallum width (mm) | OVW | flabelloid |
| 5. Total number of septa | TNS | phaceloid, plocoid |
| 6. Total number of septa per 5 mm | TNS-5 | flabelloid, meandroid |
| 7. Number of major septa | NMS | phaceloid, plocoid |
| 8. Number of major septa per 5 mm | NMS-5 | flabelloid, meandroid |
| 9. Total number of costae per 5 mm | TNC-5 | phaceloid |
| 10. Distance between adjacent corallites (mm) | NND | phaceloid, plocoid, meandroid |
| 11. Theca thickness (mm) | TT | all |
| 12. Major septum length† (mm) | SL | meandroid |
| 13. Major septum thickness* (mm) | ST | meandroid, phaceloid |
| 14. Colony height (cm) | CL-HT | all |
| 15. Minimum colony diameter (cm) | CL-MIN | phaceloid, plocoid, meandroid |
| 16. Maximum colony diameter or length (cm) | CL-MAX | all |

* Measured only in thin section.
† In phaceloid forms, SL-MIN and SL-MAX were distinguished.

Table 7.—Pearson's correlations among original variables and principal component axes (PC) in multivariate statistical analyses of *Caulastraea*.

| Original variable | PC1 | PC2 | PC3 | PC4 | PC5 |
|---|---|---|---|---|---|
| Min. corallite diameter (CD-MIN) | 0.8881* | 0.0445 | −0.2621 | −0.0475 | −0.3651 |
| Max. corallite diameter (CD-MAX) | 0.9335* | 0.1598 | 0.1164 | 0.2159 | −0.0034 |
| Total no. of septa (TNS) | 0.4443 | −0.8063* | −0.3036 | 0.1382 | 0.0734 |
| Total no. of costae per 5 mm (TNC-5) | −0.0264 | −0.9680* | −0.0285 | 0.1661 | 0.0356 |
| Theca thickness (TT) | 0.3852 | −0.5702* | 0.6074* | −0.3936 | −0.0404 |
| Min. septum length (SL-MIN) | 0.7796* | 0.1734 | −0.4398 | −0.3109 | 0.2613 |
| Max. septum length (SL-MAX) | 0.7651* | 0.2986 | 0.4798 | 0.2322 | 0.1406 |
| % variance explained | 45.71 | 29.41 | 13.82 | 5.73 | 3.28 |

* Heavily weighted characters.

plot of the first two principal components (Text-fig. 6) suggests that two distinct clusters exist among the measured specimens: (1) a small cluster consisting of the two types of *C. dendroidea,* and (2) a large cluster consisting of the remaining 17 specimens including the types of *C. portoricensis* and *C. furcata.* The second principal component is most important in distinguishing the two clusters, and is most strongly correlated with total number of septa (TNS) and total number of costae per 5 mm (TNC-5) and, to a lesser degree, with theca thickness (TT) (Table 7). The first principal component is most strongly correlated with four characters related to overall corallite size (CD-MIN, CD-MAX, SL-MIN, SL-MAX), theca thickness (TT) (Table 7), and scores on it did not differ significantly among clusters (Text-fig. 6). The third principal component is most strongly correlated with theca thickness (TT) (Table 7), and scores on it also did not differ among clusters.

If the two clusters are interpreted to represent species with names corresponding to their constituent Neogene types, these results indicate that, although two species of *Caulastraea* (*C. dendroidea, C. portoricensis*) may have lived in the Caribbean during the Late Oligocene, only one (*C. portoricensis*) survived through the Mio-Pliocene, and it is morphologically similar to the living Indo-Pacific species *C. furcata* (see "Systematic Paleontology," p. 38). Despite the abundance of *C. portoricensis* at other similar-aged Caribbean sites, it was very rare in the Mio-Pliocene of the Dominican Republic.

### Plocoid colony forms

Five specimens in the NMB collections (CCD 2043–2047) have plocoid growth forms, mono- to tricentric corallites formed by intramural budding, numerous acute septal teeth, and porous coenostea. The latter two characters indicate that these specimens belong to the family Faviidae (Table 1). The five specimens can be visually subdivided into three distinct groups based on corallite diameter. Three specimens (CCD 2045–2047) with "large" corallite diameters (7–10 mm) have relatively thin septa and thin parathecal walls. One specimen (CCD 2044) with "mid-sized" corallite diameters (5–7 mm) has closely spaced corallites and angular shaped corallites. One specimen (CCD 2043) with "small" corallite diameters (3.5–5 mm) has thicker, more numerous septa, septothecal walls, and well-developed costae. The distinctiveness of the three groups is further supported by qualitative examination of five additional specimens (USNM 95212, 95251, 95266, 95278, 95319) in collections made by Emily and Harold Vokes of Tulane University within the same Dominican Republic horizons. One of the Tulane specimens clearly belongs to the "large" corallite group, and four belong to the "small" corallite group.

Only one faviid genus with a plocoid colony form, *Favia* Oken, 1815, is known to form mono- to tricentric corallites in the Neogene to Recent of the Caribbean. One species, *F. fragum* (Esper, 1795), occurs today in the Caribbean region; and two other species, *F. gravida* Verrill, 1868, and *F. leptophylla* Verrill, 1868, occur today in Brazil (Table 3). A fourth species, *Favia dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925, has been reported from the Neogene of the Dominican Republic (Table 2). Qualitative comparisons among specimens of these four species and the three NMB groups (Table 8) suggest that, although similar to *Favia fragum,* the NMB group with "small" corallites differs by possessing slightly larger corallite diameters of 3.5–5 mm (Pls. 4, 5). This NMB group is therefore described as a new species, *Favia vokesae,* n. sp. This "small" corallite group is strikingly similar morphologically to the Pliocene to Recent meandrinid species *Dichocoenia stokesi* Milne Edwards and Haime, 1848, from which it differs by having a more porous coenosteum, well-developed costae, and acute septal teeth (Text-fig. 7).

The NMB group with "large" corallites is morpho-

Table 8.—Distinguishing characteristics of four previously reported Neogene to Recent Caribbean species of *Favia* and three morphologic groups of *Favia* in the NMB collections.

| Species | CD-MIN | Corallite shape | # Centers per corallite | TNS-5 | Colony diameter |
|---|---|---|---|---|---|
| *F. dominicensis* Vaughan, 1925 | 5–8 | angular | 1–2 | 6 | mid (5–15 cm) |
| *F. fragum* (Esper, 1795) | 2.5–3.5 | rounded | 1–2 | 12 | small (5 cm) |
| *F. gravida* Verrill, 1868 | 2.5–4 | rounded | <6 | 12 | small-mid (5–15 cm) |
| *F. leptophylla* Verrill, 1868 | 5–7 | rounded | 1–3 | 6 | large (>15 cm) |
| NMB—small corallites (*F. vokesae*, n. sp.) | 3.5–5 | rounded | 1–2 | 12 | small (5 cm) |
| NMB—mid-sized corallites (*F.* n. sp. aff. *dominicensis*) | 5–7 | angular | 1–2 | 6 | mid (5–15 cm) |
| NMB—large corallites (*F. dominicensis*) | 8–10 | rounded | 1–2 | 6 | mid (5–15 cm) |

logically identical to the holotype of *Favia dominicensis* (MCZ 103512, Table 8). It is also similar to the holotype of *Favia leptophylla* (YPM 517) from the Recent of Brazil (Pl. 3), but specimens in the NMB group have larger, more closely spaced corallites with fewer centers and more septa. Larger samples are needed to determine the taxonomic relationships between *F. dominicensis* and *F. leptophylla,* so they are treated as separate species in the present monograph. The one NMB specimen with "mid-sized" corallites is not similar to any of the four known species (Table 8), and is therefore described as a separate species. Because there is only one specimen, this new species is left in open nomenclature.

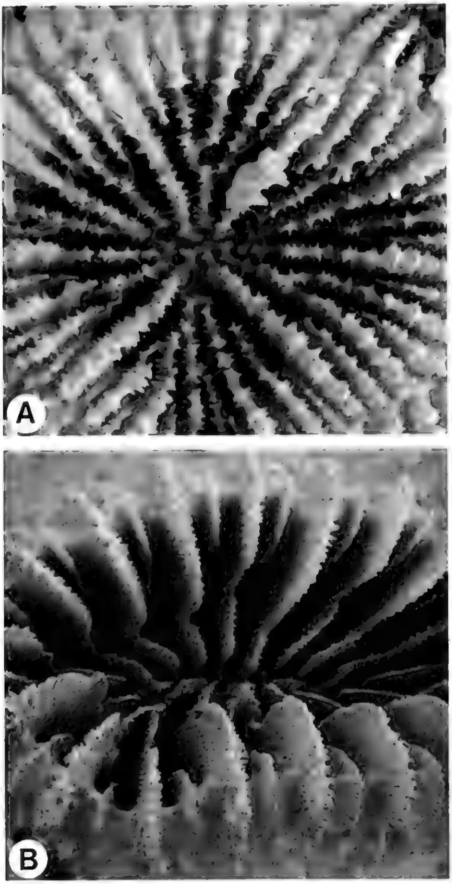
A second species of *Favia* from the Recent of Brazil, *Favia gravida,* is similar morphologically to yet another morphologic group in the Neogene of the Dominican Republic. This group consists of 14 NMB specimens (herein named *Favia maoadentrensis,* n. sp.), and possesses a colony form intermediate between plocoid forms with one to three centers per corallite and meandroid forms whose corallites are arranged in series containing more than six centers (Pls. 6, 8). Because of the strong tendency of this NMB group to form long branching corallite series, it is treated later in the section on meandroid colony forms. Like *Favia gravida,* however, its valleys are 3–4 mm in diameter and rounded in shape, and it has 24–28 septa per centimeter and forms small to medium-sized colonies (5–15 mm in diameter). It therefore is intermediate in overall morphology between *Favia* and *Diploria.* Cladistic analyses including this species (see "Genus Recognition") indicate, however, that it groups more closely with *Favia.*

### Flabelloid colony forms

Of the more than 300 specimens in the NMB collections with elongate, flabelloid colony forms, 162 have numerous acute septal teeth and a continuous trabecular columella, two diagnostic characteristics of the family Faviidae (Table 1). These 162 specimens can be separated into two groups: one with bidirectional budding (154 specimens) and the other with unidirectional budding (eight specimens). Morphologic subgroups were distinguished within the bidirectional group using multivariate statistical analyses. Sixty-eight well-preserved specimens were selected for analysis, and two linear distance measurements (corallum width [OVW] and valley width [IVW]) and two septal counts (total septal number per 5 mm [TNS-5], number of major septa per 5 mm [NMS-5]) were made on the calical surface of each specimen using a binocular microscope with an ocular micrometer (Text-fig. 8). No other measures of overall colony shape or sinuosity or of corallite architecture could be performed owing to the fragmentary nature of much of the material.

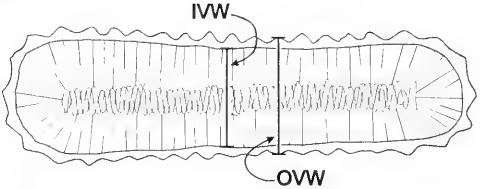
Because the two linear distance measures are confounded and high correlations exist among the four variables (Table 9), a principal component analysis was first performed on the 68 observations. The ranges for these characters differ greatly in magnitude; therefore, the analysis was performed using the correlation matrix. The results (Table 9) show that three principal components are needed in order to account for more than 95% of the variation among samples (PC1 = 64.3%, PC2 = 21.6%, PC3 = 11.6%). A combination of variables related to corallite size (OVW, IVW) are correlated with the first principal component, number of major septa per 5 mm (NMS-5) is most strongly correlated with the second principal component, and total number of septa per 5 mm (TNS-5) is most strongly correlated with the third principal component.

Standardized scores for these three principal components were input into an average linkage cluster analysis using squared euclidean distances. Study of r-square values associated with the cubic clustering criterion revealed that as many as three clusters (cutoff distance = 1.003) have r-square values less than 0.500 and are thus significant (Text-fig. 9). Two of the clusters, later identified as *Thysanus navicula* and *Had-*



Text-figure 7.—Scanning electron micrographs showing two species in different scleractinian families, with similar plocoid colony forms and corallite architectures. Both species have corallites that are budded intramurally, have 1–3 centers and spongy columellae, and are 3–4 mm in diameter. *Favia,* however, has distinctive acute septal teeth and lacks septal lobes; whereas *Dichocoenia* has minute teeth and prominent lobes. Both photos, × 10. (**A**) Figured specimen of *Favia fragum* (Esper, 1795), family Faviidae, SUI 54923, Recent, La Parguera, Puerto Rico; (**B**) Figured specimen of *Dichocoenia stokesi* (Milne Edwards and Haime, 1848), family Meandrinidae, SUI 54925, Recent, Discovery Bay, Jamaica.

*rophyllia saundersi,* were sufficiently distinct that their members were removed from the data set, and the cluster analysis was rerun with only specimens of *Manicina* following the same procedure as the first. The second analysis (Text-fig. 10) revealed four clusters (cutoff distance = 1.011) with r-square values less than 0.500. Because one of the four clusters was composed of only one specimen (CCD 2069), only three clusters (later identified as *M. geisteri, M. grandis,* and *M. jungi*) were considered further, thereby yielding a total of five clusters among the flabelloid forms with bidirectional budding.



Text-figure 8.—Diagram showing two measurements made on bidirectional flabelloid colony forms: IVW, valley width, and OVW, corallum width. In addition to these two measurements, total number of septa per 5 mm (TNS-5) and number of major septa per 5 mm (NMS-5) were also counted. "Major septa" are septa that extend completely to the columella.

Differences among the five clusters were examined using canonical discriminant analysis and Duncan's multiple comparisons tests comparing means for each variable. An initial discriminant analysis revealed that three of the 68 specimens (CCD 2186, 2073, 2069) were incorrectly classified, so these specimens were reassigned and the analysis rerun. The results showed that: (1) four canonical variables have significant values for Wilks' Lambda, suggesting five significantly distinct groups, (2) 100% of the specimens are correctly classified, and (3) the clusters do not overlap on plots for the first three canonical variables (Text-fig. 11). A combination of variables related to septal spacing (TNS-5 and the inverse of OVW and IVW) is most strongly correlated with the first canonical variable which distinguished between the clusters for *H. saundersi* (cluster #2) and *M. jungi* (cluster #5); a combination of variables related to corallite size (TNS-5, OVW) is most strongly correlated with the second canonical variable which distinguished clusters for *T. navicula* (cluster #1) and *M. grandis* (cluster #4) from clusters for *H. saundersi* (cluster #2), *M. geisteri* (cluster #3), and *M. jungi* (cluster #5); and number of major septa per 5 mm (NMS-5) is most strongly correlated with the third canonical variable which distinguished the cluster for *T. navicula* (cluster #1) from the other four clusters (Table 10).

Univariate comparisons among the five species (Table 11, Text-fig. 12) further showed that *H. saundersi* (cluster #2) is distinguished by a large corallum width, whereas *M. geisteri* (cluster #3) is distinguished by a proportionally large corallite width relative to corallum width (Pls. 12, 13). *M. grandis* (cluster #4) and *M.*

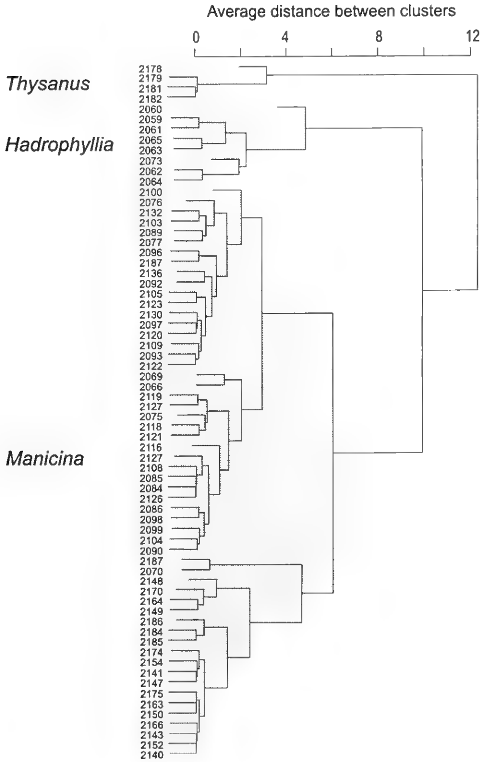
Table 9.—Pearson's correlations among original variables and principal components (PC) in multivariate statistical analyses of specimens with bidirectional flabelloid colony forms.

| Original variable | NMS-5 | TNS-5 | OVW | PC1 | PC2 | PC3 |
|---|---|---|---|---|---|---|
| No. of major septa per 5 mm (NMS-5) | — | | | −0.383 | 0.753* | −0.535 |
| Total no. of septa per 5 mm (TNS-5) | 0.490 | — | | −0.484 | 0.330 | 0.809* |
| Corallum width (OVW) | −0.336 | 0.534 | — | 0.562* | 0.385 | 0.139 |
| Valley width (IVW) | 0.317 | 0.495 | 0.898 | 0.551* | 0.420 | 0.198 |

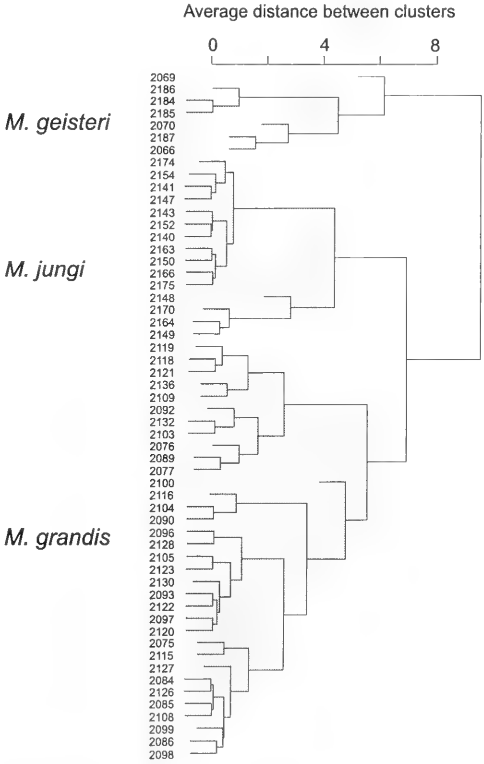
* Heavily weighted characters.

*jungi* (cluster #5) have high numbers of major septa per 5 mm, although *M. grandis* has relatively few minor septa and thus a relatively low total number of septa per 5 mm (Pls. 14–17). *T. navicula* (cluster #1) has a very low number of major septa per 5 mm (Pl. 11).

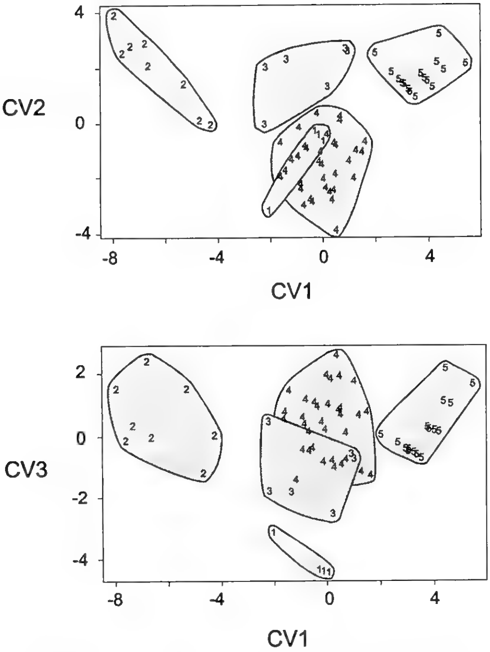
Exclusively flabelloid colony forms do not occur in the family Faviidae today, and only two fossil species with bidirectional growth have been described in the Caribbean, "*Teleiophyllia grandis*" Duncan, 1864 and



Text-figure 9.—UPGMA dendrogram for all colonies with bidirectional flabelloid colony forms. The cluster analysis was based on squared Euclidean distances. Each branch of the dendrogram represents a colony, and is labelled using the colony's CCD number. The cubic clustering criterion revealed three clusters that are determined later in the monograph to represent the genera *Thysanus*, *Hadrophyllia*, and *Manicina*.



Text-figure 10.—UPGMA dendrogram for a subset of bidirectional flabelloid colony forms, having small to intermediate corallite sizes and intermediate to high numbers of major septa. This subset is recognized later in the monograph as belonging to *Manicina*. Each branch of the dendrogram represents a colony, and is labelled using the colony's CCD number. The cubic clustering criterion revealed three clusters that represent the species *M. geisteri*, *M. jungi*, and *M. grandis*.



Text-figure 11.—Plots of scores on the first three canonical variables in the final canonical discriminant analysis distinguishing species of bidirectional flabelloid colony forms. Each point represents one colony. The polygons enclose clusters of colonies belonging to the following species: 1 = *Thysanus navicula*, 2 = *Hadrophyllia saundersi*, 3 = *Manicina geisteri*, 4 = *M. grandis*, and 5 = *M. jungi*.

"*Teleiophyllia navicula*" Duncan, 1864, both of which are from the Neogene of the northern Dominican Republic. Qualitative comparisons of measurements made on holotypes of these two species suggest that "*T. grandis*" can be assigned to cluster #4, and "*T. navicula*" to cluster #1 (Tables 11, 12; Pls. 11, 14). The other three clusters (#2, 3, 5) are unique, and therefore are described as new (respectively *Hadrophyllia saundersi*, n. sp.; *Manicina geisteri*, n. sp.; *Manicina jungi*, n. sp.) in the present monograph. Bidirectional flabelloid forms also occur in the Meandrinidae in the Caribbean during the Neogene, and some have morphologies convergent with the five faviid species with bidirectional flabelloid forms. Cluster #4 (*Manicina grandis*), for example, is morphologically similar to the late Miocene to early Pleistocene meandrinid species, *Placocyathus variabilis* (Duncan, 1864), from which it differs by having well-developed costae, spongy columellae, and more numerous septa (Text-fig. 13).

In contrast to bidirectional flabelloid colony forms, only eight specimens in the NMB collections have unidirectional flabelloid forms. Five of the eight specimens were poorly preserved or fragmentary; therefore, measurements and counts could only be made on three specimens (CCD 2193, 2194, 2198). The same four variables (Text-fig. 8; Table 6) were measured as on the bidirectional flabelloid colony forms. The data were then added to the data set with the specimens having bidirectional flabelloid growth forms, and the same sequence of statistical analyses as described above (*i.e.*, principal component analysis followed by avearage linkage cluster analysis) was performed. The results showed that two of the three specimens (CCD 2193, 2194) were most similar to *M. grandis* (cluster #4); whereas the third specimen (CCD 2198) was most similar to *M. jungi* (cluster #5). These similarities can be attributed primarily to the two variables involving septal counts (total number of septa per 5 mm [TNS-5], number of major septa per 5 mm [NMS-5]), because corallum width (OVW) and, to a lesser extent, valley width (IVW) are notably smaller in the unidirectional flabelloid colony forms (Tables 11, 12). The most important characteristic distinguishing the two unidirectional flabelloid groups (*i.e.*, CCD 2198 vs. [CCD 2193, 2194]) is total number of septa per 5 mm (TNS-5). Other important distinguishing characteristics that were not measured involve the length of the corallum and the shape of the growing tip (Pl. 10).

A total of seven species with unidirectional growth forms have been described from the late Early Mio-

Table 10.—Pearson's correlations among the original variables and canonical variables (CV) in the final canonical discriminant analysis distinguishing species with bidirectional flabelloid colony forms.

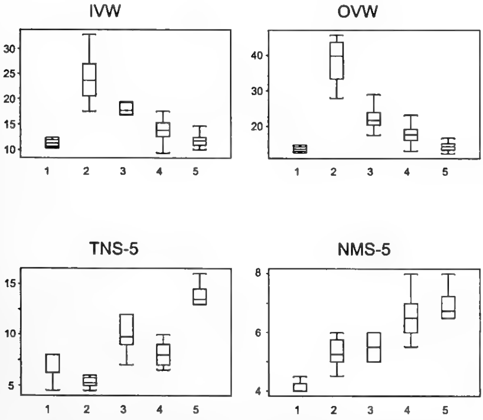
| Original variable | CV1 | CV2 | CV3 |
|---|---|---|---|
| Valley width (IVW) | −0.801* | 0.394 | 0.210 |
| Corallum width (OVW) | −0.867* | 0.420* | 0.266 |
| Total no. of septa per 5 mm (TNS-5) | 0.874* | 0.478* | 0.088 |
| No. of major septa per 5 mm (NMS-5) | 0.562 | −0.150 | 0.812* |
| % variance explained | 66.3 | 22.7 | 10.3 |

* Heavily weighted characters.

Table 11.—Descriptive statistics for characters measured on species with flabelloid colony forms. Means and standard errors of means (in parentheses) are given for species with ≥10 specimens. Medians and ranges (in parentheses) are given for species with <10 specimens.

| Species | No. of NMB specimens | Corallum width (OVW) | Valley width (IVW) | Total no. of septa per 5 mm (TNS-5) | No. of major septa per 5 mm (NMS-5) |
|---|---|---|---|---|---|
| Bidirectional: | | | | | |
| *M. geisteri* | 6 | 21.70 (11.50) | 17.70 (2.60) | 8.7 (5.0) | 5.5 (0.6) |
| *M. grandis* | 34 | 17.706 (0.430) | 13.812 (0.369) | 8.22 (0.19) | 6.63 (0.10) |
| *M. jungi* | 16 | 14.775 (0.483) | 11.938 (0.318) | 13.88 (0.27) | 6.94 (0.14) |
| *T. navicula* | 4 | 13.65 (2.30) | 11.25 (2.10) | 8.0 (3.5) | 4.0 (0.5) |
| *H. saundersi* | 8 | 39.90 (18.20) | 23.65 (15.40) | 5.2 (1.5) | 5.2 (1.5) |
| Duncan's test | | 2>3>4>(5=1) | 2>3>(4=5=1) | 5>3>(4=1)>2 | (4=5)>(3=2)>1 |
| Unidirectional: | | | | | |
| *T. corbicula* | 1 | 12.3 | 10.9 | 26 | 13 |
| *T. excentricus* | 2 | 12.85 (3.10) | 11.05 (0.90) | 6.25 (0.50) | 6.25 (0.50) |

cene through Pliocene of the Caribbean region (Table 12; Pl. 9). Two species are from the Neogene of the Dominican Republic (*Thysanus corbicula* Duncan, 1863, and *Thysanus crassicostatus* Vaughan *in* Vaughan and Hoffmeister, 1925), two are from the Pliocene Bowden shell beds of Jamaica (*Thysanus excentricus* Duncan, 1863, and *Thysanus elegans* Duncan *in* Duncan and Wall, 1865), one is from the Late Pliocene of Matanzas, Cuba (*Thysanus hayesi* Vaughan, 1919), one is from the late Early Miocene Chipola Formation of Florida (*Thysanus vaughani* Weisbord, 1971), and one is from the Late Pliocene Caloosahatchee Formation of Florida (*Thysanus floridanus* Weisbord, 1974). Of these seven, the holotypes of *T. corbicula* and *T. floridanus* have values for total number of septa per 5 mm (TNS-5) and corallum widths (OVW) similar to CCD 2198 (Tables 11, 12), and are therefore synonymized. The holotypes for *T. excentricus, T. elegans,* and *T. hayesi* have values for total number of septa per 5 mm (TNS-5) and corallum widths (OVW) similar to specimens CCD 2193 and 2194 (Tables 11, 12), and are synonymized. The holotype of *T. vaughani* is an unusually tiny specimen; its high values for TNS-5, however, are more similar to CCD 2198; therefore, it is questionably synonymized.



Text-figure 12.—Box plots showing medians, first and third quantiles, and ranges for measurements and counts made on species with bidirectional flabelloid colony forms: 1 = *Thysanus navicula*, 2 = *Hadrophyllia saundersi*, 3 = *Manicina geisteri*, 4 = *M. grandis*, and 5 = *M. jungi*. IVW, valley width; OVW, corallum width; TNS-5, total number of septa per 5 mm; NMS-5, number of major septa per 5 mm.

## Meandroid colony forms

Four faviid genera with meandroid colony forms have been reported for the entire Cenozoic of the Caribbean region: *Colpophyllia* Milne Edwards and Haime, 1848, *Diploria* Milne Edwards and Haime, 1848, *Leptoria* Milne Edwards and Haime, 1848, and *Manicina* Ehrenberg, 1834. Of these four, only *Leptoria* has ever occurred in the Indo-Pacific, and its last occurrence in the Caribbean is restricted to the Late Oligocene (Budd *et al.*, 1992). *Leptoria* also differs from *Colpophyllia, Diploria, Manicina,* and many other faviids by having a lamellar (instead of spongy) columella. *Colpophyllia, Diploria,* and *Manicina* differ from one another in valley width and in the structure of the columella and wall (Table 13; Text-fig. 14). The columella is a plate formed by elongation of a protoseptum into the corallite center ("lamellar"), or a spongy mass formed by intermingling threads of loose trabeculae and paliform lobes extending from the septa ("spongy"). The wall is either parathecal and formed by dissepiments, or septothecal and formed by thickening of the septo-costal trabeculae. *Colpophyllia* has very thin septa, abundant dissepiments, reduced la-

Table 12.—Measurements and counts made on holotypes of all previously described species of "*Teleiophyllia*" and *Thysanus*. "*T. grandis*" and "*T. navicula*" have bidirectional flabelloid forms; the other seven species have unidirectional flabelloid forms.

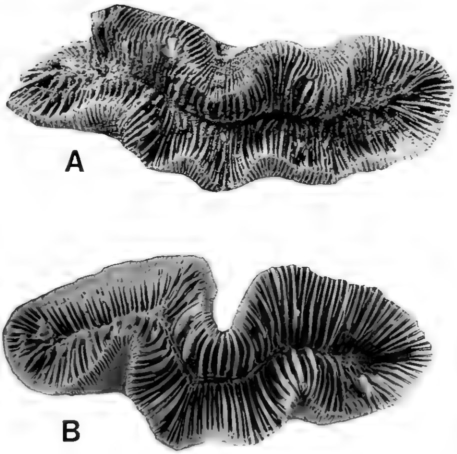
| Species name | Museum catalog number | Valley width (IVW) | Corallum width (OVW) | Total no. of septa per 5 mm (TNS-5) | No. of major septa per 5 mm (NMS-5) | Colony height (CL-HT) | Max. colony length (CL-MAX) |
|---|---|---|---|---|---|---|---|
| *Teleiophyllia grandis* Duncan, 1864 | BM(NH) R28754 | 18 | 23 | 11 | 6 | 4.1 | 13.0* |
| *Teleiophyllia navicula* Duncan, 1864 | BM(NH) R28766 | 9 | 13.9 | 3–4 | 4 | 1.2 | 3.2* |
| *Thysanus corbicula* Duncan, 1863 | BM(NH) R28795 | 7.5 | 9.1 | 10 | 5 | 0.5 | 1.2 |
| *Thysanus crassicostatus* Vaughan *in* Vaughan and Hoffmeister, 1925 | MCZ 9280 | — | — | 6 | 6 | 3.1 | 6.9* |
| *Thysanus elegans* Duncan *in* Duncan and Wall, 1865 | BM(NH) R28918 | 6 | 8.9 | 6 | 5 | 0.8 | 1.4 |
| *Thysanus excentricus* Duncan, 1863 | BM(NH) 46814 | 8 | 11.7 | 6–8 | 5–6 | 1.5 | 3.7 |
| *Thysanus floridanus* Weisbord, 1974 | USNM 79812 | 6.9 | 9.5 | 9 | 5 | 0.6 | 2.2* |
| *Thysanus hayesi* Vaughan, 1919 | USNM 324994 | 8.9 | 13.5 | 5 | 5 | 1.2 | 1.8* |
| *Thysanus vaughani* Weisbord, 1971 | FMNH 8294 | 1.8 | 2.5 | 10 | 5 | 0.3 | 0.8 |

* Broken.

mellar and discontinuous columellae, and distinctive parathecal double walls (Text-fig. 14A, B). *Diploria* has narrow valleys, spongy and continuous columellae, and thick septothecal walls (Text-fig. 14C). *Manicina* has wide valleys, spongy and continuous columellae, and thick septothecal walls, some double, that are reinforced by dissepiments (Text-fig. 14D).

Only one specimen in the NMB collections possesses characteristics diagnostic of the genus *Colpophyllia* as outlined in Table 13, and only one species (*Colpophyllia mexicanum* Frost and Langenheim, 1974, from the Early Miocene of Chiapas, Mexico) has been reported from the Miocene and Pliocene of the Caribbean region. Morphologic comparisons between the NMB specimen, the three currently accepted Recent Caribbean species (Table 3; Pl. 21), another possible Recent species (*C. fissa* [Ehrenberg, 1834]), and *C. mexicanum* indicate that the NMB specimen is morphologically very similar to *C. natans* (Houttuyn, 1772) (Table 14), and in the absence of more material, is therefore considered synonymous.

Twelve specimens in the NMB collections possess characteristics diagnostic of the genus *Manicina,* as outlined in Table 13. Because of the low sample size, these specimens were qualitatively grouped on the basis of colony form: group #1 (*M. pliocenica*) consisted of *four* small to intermediate-sized free-living colonies with single valley systems, group #2 (*M.* n. sp. aff. *mayori*) consisted of *one* large attached colony with a multiple valley system, and group #3 (*M. puntagordensis*) consisted of *seven* large ellipsoidal, free-living colonies with highly regular single valley systems. Of the two known modern Caribbean species of *Manicina* (*M. areolata* [Linnaeus, 1758] and *M. mayori* Wells, 1936, see Table 3), the colony form of group #1 (*M. pliocenica*) is most similar to *M. areolata,* and the colony form of group #2 (*M.* n. sp. aff. *mayori*) is most similar to *M. mayori.* To compare the three NMB groups with the two modern species, transverse thin sections were prepared of five NMB specimens (one of group #1 [*M. pliocenica*], one of group #2 [*M.* n. sp. aff. *mayori*], three of group #3 [*M. puntagordensis*]), and five variables were measured on each thin section (Table 6): number of major septa per 5 mm (NMS-5), total number of septa per 5 mm (TNS-5), valley width (IVW), distance between valleys (NND), and theca thickness (TT). Two replicates were measured on two of the five specimens. The first three measurements (NMS-5, TNS-5, IVW) were made as in flabelloid colony forms (Text-fig. 8). Distance between valleys (NND) was measured from the outer margin of the wall of one valley, to the outer edge of the wall of an adjacent valley. Theca thickness (TT) was measured from the inner to outer edge of the wall. Similarly, thin sections were prepared of three Recent specimens (two *M. areolata* [USNM 96241–NF497,



Text-figure 13.—Calical surfaces of two species (*Manicina grandis, Placocyathus variabilis*) in different scleractinian families, with similar bidirectional flabelloid colony forms and corallite architectures. *M. grandis* has acute septal teeth, small septal lobes, and a spongy columella; whereas *P. variabilis* has minute septal teeth, no septal lobes, and a lamellar columella. *M. grandis* also has more numerous septa with well-developed costae. Both photos, × 1. (**A**) Figured specimen of *Manicina grandis* (Duncan, 1864), family Faviidae, SUI 90996 (KJ87–10), Upper Miocene, Río Cana, Cercado Formation, Dominican Republic. (**B**) Figured specimen of *Placocyathus variabilis* Duncan, 1864, family Meandrinidae, NMB D6250 (CCD 1034), Upper Miocene, locality NMB 16824, Río Cana, Gurabo Formation, Dominican Republic.

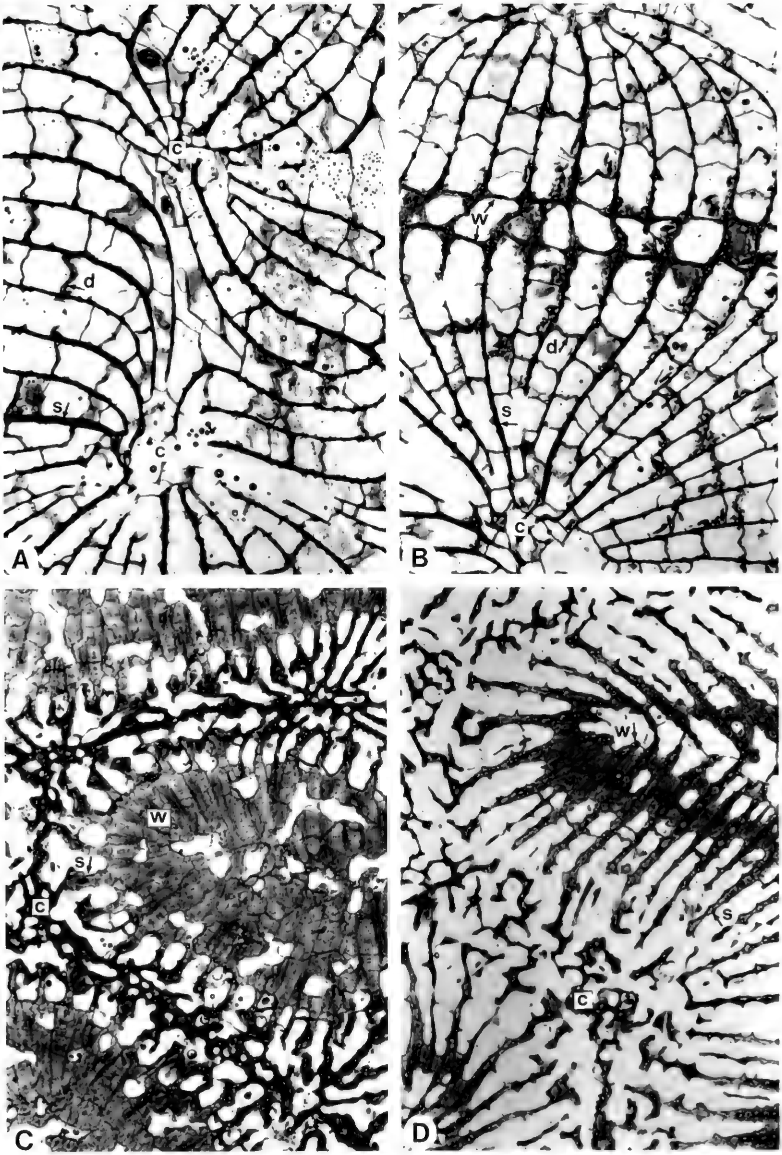
498], and one *M. mayori* [SUI 84989]), and the same five variables were measured on each thin section. Qualitative examination of the resulting data (Table 15) suggests that modern *M. areolata* have more septa per 5 mm than NMB group #1 (*M. pliocenica*), and that modern *M. mayori* have narrower, more widely separated valleys than NMB group #2 (*M.* n. sp. aff. *mayori*) (Pls. 18, 19).

Other than the two Recent species, only one species (*Manicina pliocenica* Gane, 1895, from the late Pliocene of Florida) and one subspecies (*Manicina areolata puntagordensis* Weisbord, 1968, from the Pliocene of Venezuela) have been reported from the Neogene to Recent of the Caribbean region. The holotype of *M. pliocenica* is lost; however, the original description (Gane, 1895) states that it has slightly wider valleys and fewer septa per 5 mm than *M. areolata,* and thereby suggests that it has strong affinities with NMB group #1 (Table 15). Measurements made on the calical surface of the holotype of *M. areolata puntagordensis* (PRI 27560; NMS-5 = 5, TNS-5 = 7, IVW = 15.2) are similar to those of NMB group #3 (*M. puntagordensis*); and it is therefore considered synonymous (Table 15). Since the holotype of *M. pliocenica* cannot be measured and its original description is vague, NMB groups #1 and #2 are described as separate species: NMB group #1 is given the name *M. pliocenica,* whereas NMB group #2 is left in open nomenclature with affinities to *M. mayori* because of the lack of material. A neotype is assigned for *M. pliocenica.*

Thirty-two specimens in the NMB collections possess meandroid colony forms with narrow (< 10 mm wide) valleys, two features that are generally characteristic of the genus *Diploria* as outlined in Table 13. These specimens can qualitatively be separated into two very distinct groups: (1) 18 specimens that consist primarily of large colonies with valley widths greater than 4 mm; and (2) 14 rounded colonies consisting of unattached coralliths with valley widths less than 4 mm. Three Recent species (Table 3) are currently recognized in the Caribbean region, and two additional exclusively Neogene species (Table 2) from the Caribbean and Eastern Pacific regions have also been described. The three living species are generally distinguished by differences in valley width, distance between neighboring valleys, and number and spacing of major and minor septa (Text-fig. 15).

Table 13.—Distinguishing characteristics of three meandroid genera of the family Faviidae in the Neogene to Recent of the Caribbean region.

| Genus | Author | Type species | Valleys | Columella | Septal lobes | Wall |
|---|---|---|---|---|---|---|
| *Colpophyllia* | Milne Edwards and Haime, 1848 | *Meandrina gyrosa* Lamarck, 1816 (=*natans*) | wide (>10 mm); thin septa | discontinuous; reduced, lamellar | small or absent | parathecal; double |
| *Diploria* | Milne Edwards and Haime, 1848 | *Meandrina cerebriformis* Lamarck, 1816 (=*labyrinthiformis*) | narrow (3.5–9 mm); thick septa | continuous; spongy | absent | septothecal; single |
| *Manicina* | Ehrenberg, 1834 | *Madrepora areolata* Linnaeus, 1758 | wide (>10 mm); mod. thick septa | continuous; spongy | small | septothecal but reinforced by dissepiments; sometimes double |



Text-figure 14.—Transverse thin sections showing diagnostic characteristics of three meandroid genera of the family Faviidae in the Neogene to Recent of the Caribbean region. The three genera can be distinguished by the structure of the columella and wall. *Colpophyllia* has a discontinuous, lamellar columella and a double parathecal wall; *Diploria* has a continuous, spongy columella and a single septothecal wall; *Manicina* has a continuous, spongy columella and a septothecal wall that is reinforced by dissepiments. *c* = columella, *d* = endothecal dissepiment, *s* = primary septum, *w* = wall. All photos, × 8. (**A**, **B**) Figured specimen of *Colpophyllia natans* (Houttuyn, 1772), USNM 3937 (NF504), Recent, Dry Tortugas. (**C**) Figured specimen of *Diploria labyrinthiformis* (Linneaus, 1758), USNM 36727 (NF500), Recent, Hog Island, Bahamas. (**D**) Figured specimen of *Manicina areolata* (Linneaus, 1758), USNM 96241 (NF497), Recent, Florida Keys.

Table 14.—Distinguishing characteristics of five Neogene to Recent Caribbean species of *Colpophyllia* and the one NMB specimen of *Colpophyllia*.

| Species | Author | Valley width (IVW) | Valley continuity | No. centers per valley | Valley depth | No. septa per 5 mm (TNS-5) | Distance bet. valleys (NND) | Colony size |
|---|---|---|---|---|---|---|---|---|
| *C. amaranthus* | (Houttuyn, 1772) | 15–30 mm | discontinuous | 4–7 | 15–30 mm | 5–6 | 2–3 mm | small |
| *C. breviserialis* | Milne Edwards and Haime, 1849 | 10–20 mm | discontinuous | 2–3 | 10–15 mm | 5–6 | 3–5 mm | huge |
| *C. fissa* | (Ehrenberg, 1834) | 8–15 mm | continuous | >10 | 6–10 mm | 5–7 | 2–3 mm | large |
| *C. natans* | (Houttuyn, 1772) | 15–30 mm | continuous | >10 | 10–15 mm | 4–5 | 3–5 mm | huge |
| *C. mexicanum* | Frost and Langenheim, 1974 | 10–14 mm | discontinuous | ?4–7 | 6–8 mm | 3–4 | 2–3 mm | ?large |
| NMB D6022 | | 15–20 mm | continuous | >10 | 5–10 mm | 4–5 | | ?large |

Canonical discriminant analysis and Duncan's multiple comparisons tests were performed to determine if the two NMB groups were the same as the three Recent species of *Diploria*. Seven characters were measured or counted on transverse thin sections of: eleven NMB colonies with large valley widths (*Diploria zambensis*), three NMB colonies with small valley widths (*Favia maoadentrensis*), three SUI colonies (SUI 90999–91001) of Recent *Diploria clivosa* (Ellis and Solander, 1786), five SUI colonies (SUI 91002–91006) of Recent *Diploria labyrinthiformis* (Linnaeus, 1758), and six SUI colonies (SUI 91007–91012) of Recent *Diploria strigosa* (Dana, 1848). The colonies of Recent species were collected from four reef sites near Carrie Bow Cay, Belize, in 1986, and from Crocus Bay, Anguilla, in 1987 (Table 16). The seven characters included five linear distance measurements of features (IVW, NND, TT, SL, ST) shown in Text-fig. 16, and linear distances (mm) within valleys near the wall extending (1) across ten major and minor septa (TNS) and (2) across ten major septa (NMS). The measurements were made using an image analysis system with a video camera attached to a dissecting microscope. Each measurement was made five times, and medians were used as final estimates. The two septal measurements (SL, ST) were made by calculating the distance between the position of the medial axes of ten adjacent septa. Bivariate plots of different pairwise combinations of the seven characters were examined for potential outlying and influential measures. Several cases were significantly separated from the majority of the data on these plots and subsequently remeasured.

Multivariate analysis of variance (Wilks' Lambda = 0.007, F = 6.7 [d.f. = 28, 62.27], p-value < 0.001), and plots of the first three canonical variables (Text-fig. 17) indicate that significant differences exist among the five groups (two NMB [*Diploria zambensis, F. maoadentrensis*]; three Recent [*D. clivosa, D. labyrinthiformis, D. strigosa*]). The first canonical variable is strongly correlated with distance between valleys (NND) and, to a lesser extent, with two measures related to overall valley size (IVW, SL) (Table 16). Scores on this variable for specimens of *Diploria zambensis* (NMB group #1) are clearly distinguished from

Table 15.—Measurements and counts made on transverse thin sections of *Manicina*. NMB group #1 was assigned to *Manicina pliocenica*; NMB group #2 was assigned to *Manicina* n. sp. aff. *mayori*; NMB group #3 was assigned to *Manicina puntagordensis*.

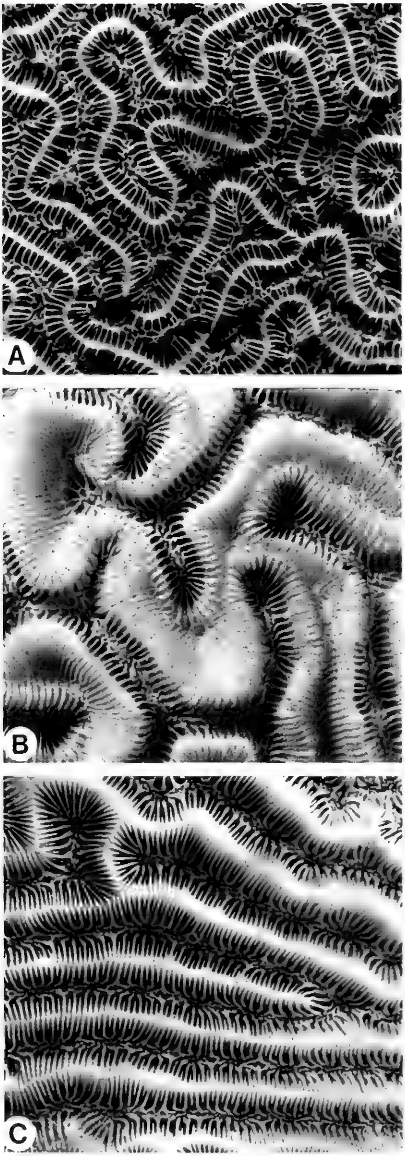
| Specimen | NMB group # or species | Valley width (IVW) | Total no. of septa per 5 mm (TNS-5) | No. of major septa per 5 mm (NMS-5) | Distance bet. adjacent corallites (NND) | Theca thickness (TT) |
|---|---|---|---|---|---|---|
| NMB D6165 | #1 | 10.0 | 7 | 5 | 6.4 | 0.7 |
| NMB D6166 | #2 | 18.6 | 7 | 5 | 1.7 | 0.5 |
| NMB D6166 | #2 | 19.0 | 7 | 5 | 1.1 | 0.7 |
| NMB D6019 | #3 | 14.6 | 6–7 | 5 | 2.9 | 0.3 |
| NMB D6169 | #3 | 15.8 | 7–8 | 6 | 3.3 | 0.8 |
| NMB D6169 | #3 | 17.2 | 7–8 | 6–7 | 1.4 | 0.5 |
| NMB D6107 | #3 | 12.9 | 6 | 6 | 3.3 | 0.4 |
| USNM 96241 (NF498) | *M. areolata*[1] | 11.9 | 9 | 7 | 4.4 | 1.1 |
| USNM 96241 (NF497) | *M. areolata*[1] | 9.1 | 8–9 | 6–7 | 4.0 | 0.6 |
| SUI 84989 | *M. mayori*[1] | 10.2 | 7–8 | 4–5 | 2.2 | 0.4 |

[1] Recent specimens.

those of the other taxa (Text-fig. 17), suggesting that valleys of *D. zambensis* are more widely separated and larger than those of the other four groups. The second canonical variable is strongly correlated with theca thickness (TT) (Table 16). Scores on the second canonical variable for *D. labyrinthiformis* are clearly separated from the other four taxa (Text-fig. 17), suggesting that *D. labyrinthiformis* is distinguished from the other groups by a relatively thick theca. The third canonical variable is correlated with the two measures of numbers of septa (NMS, TNS) and overall valley size (IVW, SL) (Table 16). Scores on the third canonical variable for specimens of *D. strigosa* are higher than for specimens of *D. clivosa* or *F. maoadentrensis* (NMB group #2), indicating that *D. strigosa* is distinguished from *D. clivosa* or *F. maoadentrensis* (NMB group #2) by its more numerous septa and larger valleys. Study of univariate means and 95% confidence intervals for the seven characters (Text-fig. 18, Table 17) further confirm these results (Table 18). In addition, *D. clivosa* and *F. maoadentrensis* differ significantly in distances between valleys (NND).

Holotypes for the two described Neogene species, *Diploria bowersi* (Vaughan, 1917) and *Diploria sarasotana* Weisbord, 1974, differ significantly from the five groups that were analyzed statistically. The holotype of *D. bowersi* (USNM 68289) is similar in valley width and spacing to *D. labyrinthiformis,* but has a total of four septa per 5 mm and no minor septa. The holotype of *D. sarasotana* (FMNH 8279) has narrowly spaced valleys that are extremely wide (7 to 13 mm) and contain numerous septa (11 major and minor septa per 5 mm), and is thus very unlike the five statistical groups treated here. As a result of the statistical analyses and these comparisons, the two NMB groups are therefore described here as new species, *Favia maoadentrensis* n. sp. (NMB group #2) and *Diploria zambensis* n. sp. (NMB group #1).

Meandroid forms with wide (> 10 mm thick) valleys and continuous columellae also occur in the Meandrinidae in the Caribbean during the Neogene, and some have morphologies convergent with the species of *Manicina* described above. *Manicina pliocen-*



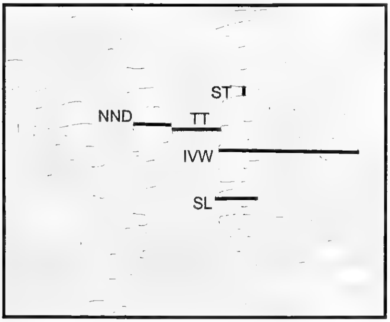
Text-figure 15.—Calical surfaces of three modern species of *Diploria. D. strigosa* is characterized by wide valleys (IVW = 4.5–6); a reduced coenosteum (NND << 1); and occasional minor septa (TNS-5 = 7–10, NMS-5 = 6–8). *D. labyrinthiformis* is characterized by mid-sized valleys (IVW = 3.5–5); a well-developed coenosteum (NND > 1); and no minor septa (TNS-5 = 6–8, NMS-5 = 6–8). It possesses a distinctive ambulacral groove along the axis of each colline. *D. clivosa* is characterized by long, narrow valleys (IVW = 2.5–3.5); a reduced coenosteum (NND << 1); and well-developed minor septa (TNS-5 = 12–14, NMS-5 = 7–9). All photos, × 2. (**A**) Holotype of *Diploria strigosa* (Dana, 1846), USNM 00005, Recent, West Indies. (**B**) Figured specimen of *Diploria labyrinthiformis* (Linneaus, 1758), BM(NH) 1887.4.26.7, Recent, Nassau, Bahamas. (**C**) Figured specimen of *Diploria clivosa* (Ellis and Solander, 1786), BMNH 1928.3.1.25, Recent, Dry Tortugas.

Table 16.—Numbers of colonies and corallite valleys (parentheses) of three Recent species of *Diploria* used in quantitative analyses distinguishing species with meandroid colony forms (narrow valleys).

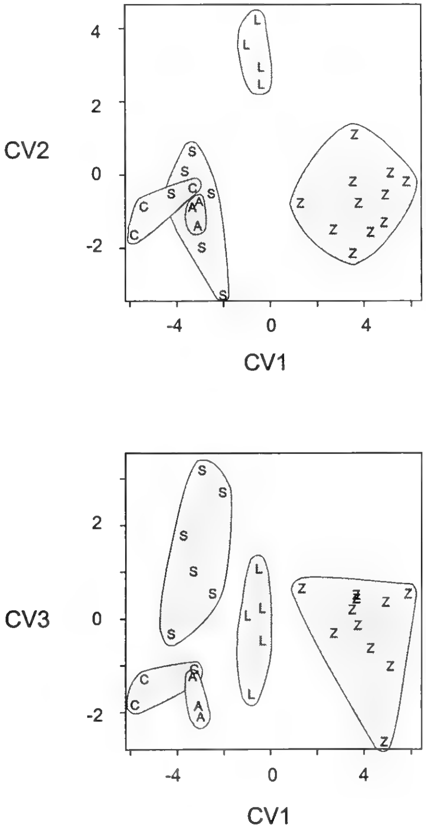
| Locality | *D. clivosa* | *D. labyrinthiformis* | *D. strigosa* |
|---|---|---|---|
| Belize | | | |
| 1. Backreef, Curlew Cay (8 m) | 1 (3) | 2 (7) | 2 (5) |
| 2. Reef crest, Carrie Bow Cay (1–2 m) | 2 (8) | — | 2 (7) |
| 3. Shallow forereef, Curlew Cay (8 m) | — | 1 (3) | 2 (6) |
| 4. Mid forereef (outer ridge), Carrie Bow Cay (15 m) | — | 1 (3) | — |
| Anguilla | | | |
| 1. Crocus Bay, rocky nearshore (1–3 m) | — | 1 (4) | — |
| Total | 3 (11) | 5 (17) | 6 (18) |

*ica,* for example, is morphologically similar in overall colony form to the Late Miocene to Recent meandrinid species, *Meandrina braziliensis* (Milne Edwards and Haime, 1849) (Text-fig. 19). On closer examination, however, *M. braziliensis* can be readily distinguished by its weakly developed lamellar columella, its more numerous septa, its reduced costae, and its broader and more solid coenosteum. It also lacks the septal lobes that are characteristic of species of *Manicina* (Text-fig. 20).

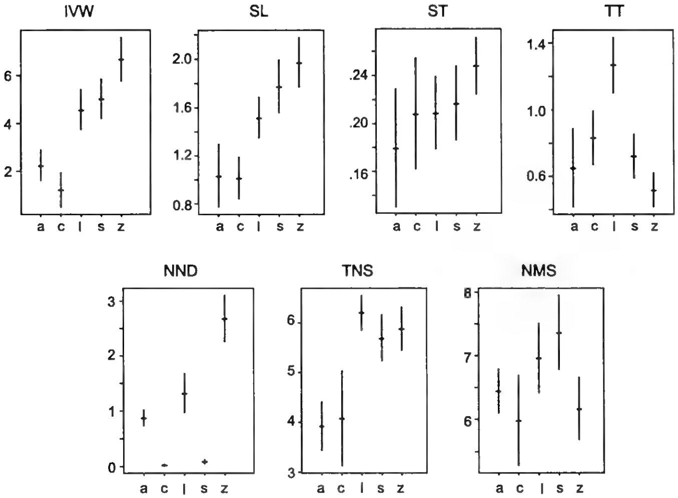
In summary, on the basis of the preceding statistical analyses and morphologic comparisons, we recognize a total of 17 species of the family Faviidae with intramural budding in the NMB collections from the Neogene of the northern Dominican Republic.



Text-figure 16.—Schematic diagram of a transverse thin section made on meandroid colony forms with narrow valley widths (shaded areas = skeleton, unshaded areas = void space). The diagram depicts two valleys (center left, and top to bottom right) separated by coenosteum (intervening pores). Five measurements were made: IVW, valley width; SL, major septum length; ST, major septum thickness; TT, theca thickness; and NND, distance between adjacent valleys. In addition to these five measurements, two distances (mm) extending across 10 septa were measured and the results were converted to numbers of septa per 5 mm: total number of septa (TNS-5) and number of major septa (NMS-5). "Major septa" are septa that extend completely to the columella.



Text-figure 17.—Plots of scores on the first three canonical variables in the final canonical discriminant analysis distinguishing species of meandroid colony forms (narrow valleys). Each point represents one colony. The polygons enclose clusters of colonies belonging to the following species: *A* = *Favia maoadentrensis*, *C* = *Diploria clivosa*, *L* = *Diploria labyrinthiformis*, *S* = *Diploria strigosa*, and *Z* = *Diploria zambensis*.



Text-figure 18.—Plots showing means and 95% confidence intervals for seven measurements made on species with meandroid colony forms (narrow valleys): *a* = *Favia maoadentrensis*, *c* = *Diploria clivosa*, *l* = *Diploria labyrinthiformis*, *s* = *Diploria strigosa*, and *z* = *Diploria zambensis*.

## GENUS RECOGNITION

The genera to which the 17 species in this monograph belong were determined by study of the results of a phylogenetic analysis of 40 species of all reported Cenozoic Caribbean members of the family Faviidae with intramural budding (Johnson, 1998). In addition to the 17 species treated herein, the analysis included: five primarily Eocene species (*Favia favoides* [sp. 1], *F. gregoryi* [sp. 2], *F. weisbordi* [sp. 3], *Colpophyllia duncani* [sp. 4], *C. elegans* [sp. 5]), one Eo-Oligocene species (*C. willoughbiensis* [sp. 6]), five primarily Oligocene species (*F. macdonaldi* [sp. 7], *Diploria antiguensis* [sp. 8], *D. dumblei* [sp. 9], *D. portoricensis* [sp. 10], *C. mexicanum* [sp. 11]), one Mio-Pliocene species (*D. bowersi* [sp. 12]), one Pliocene species (*D. sarasotana* [sp. 13]), and 10 Quaternary to Recent species (*F. fragum* [sp. 14], *F. gravida* [sp. 15], *F. leptophylla* [sp. 16], *D. clivosa* [sp. 17], *D. labyrinthiformis* [sp. 18], *D. strigosa* [sp. 19], *C. amaranthus* [sp. 20], *C. breviserialis* [sp. 21], *Manicina areolata* [sp. 22], *M. mayori* [sp. 23]). These taxa and their spatial and temporal distributions are described in Johnson (1998).

The analysis was performed using 22 multistate morphologic characters (Table 19) with a total of 65 states (see Johnson, 1998, for additional details concerning the definition of characters, their states and ordering, and selection of the outgroup). As many independent characters as possible were selected in order to completely encompass all morphologic differences

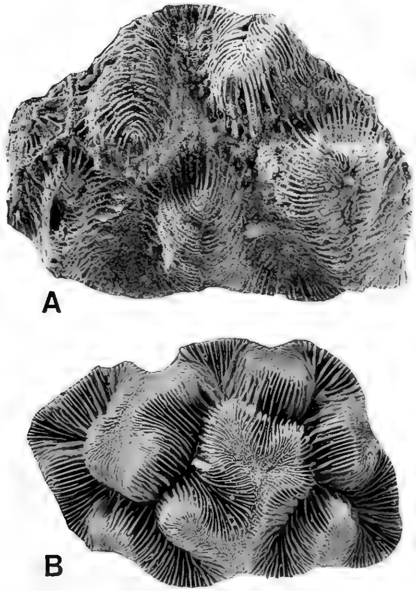
Table 17.—Pearson's correlations among the original variables and canonical variables (CV) in the final canonical discriminant analysis distinguishing species with meandroid colony forms (narrow valleys).

| Original variable | CV1 | CV2 | CV3 | CV4 |
|---|---|---|---|---|
| Valley width (IVW) | 0.699* | −0.023 | 0.488* | −0.157 |
| Major septum length (SL) | 0.610* | −0.098 | 0.545* | 0.064 |
| Major septum thickness (ST) | 0.473 | −0.083 | 0.234 | 0.467* |
| Theca thickness (TT) | −0.381 | 0.859* | 0.013 | 0.182 |
| Distance bet. adjacent corallites (NND) | 0.923* | 0.060 | −0.230 | −0.122 |
| Total no. of septa per 5 mm (TNS-5) | 0.520 | 0.385 | 0.649* | 0.070 |
| No. of major septa per 5 mm (NMS-5) | −0.254 | 0.187 | 0.510* | −0.518* |
| % variance explained | 78.0 | 14.4 | 6.6 | 0.01 |

* Heavily weighted characters.

Table 18.—Means and standard errors (parentheses) for characters in species with meandroid colony forms (narrow valleys), and results of Duncan's Multiple Comparisons Test. N, number of colonies measured; n, total number of valleys measured.

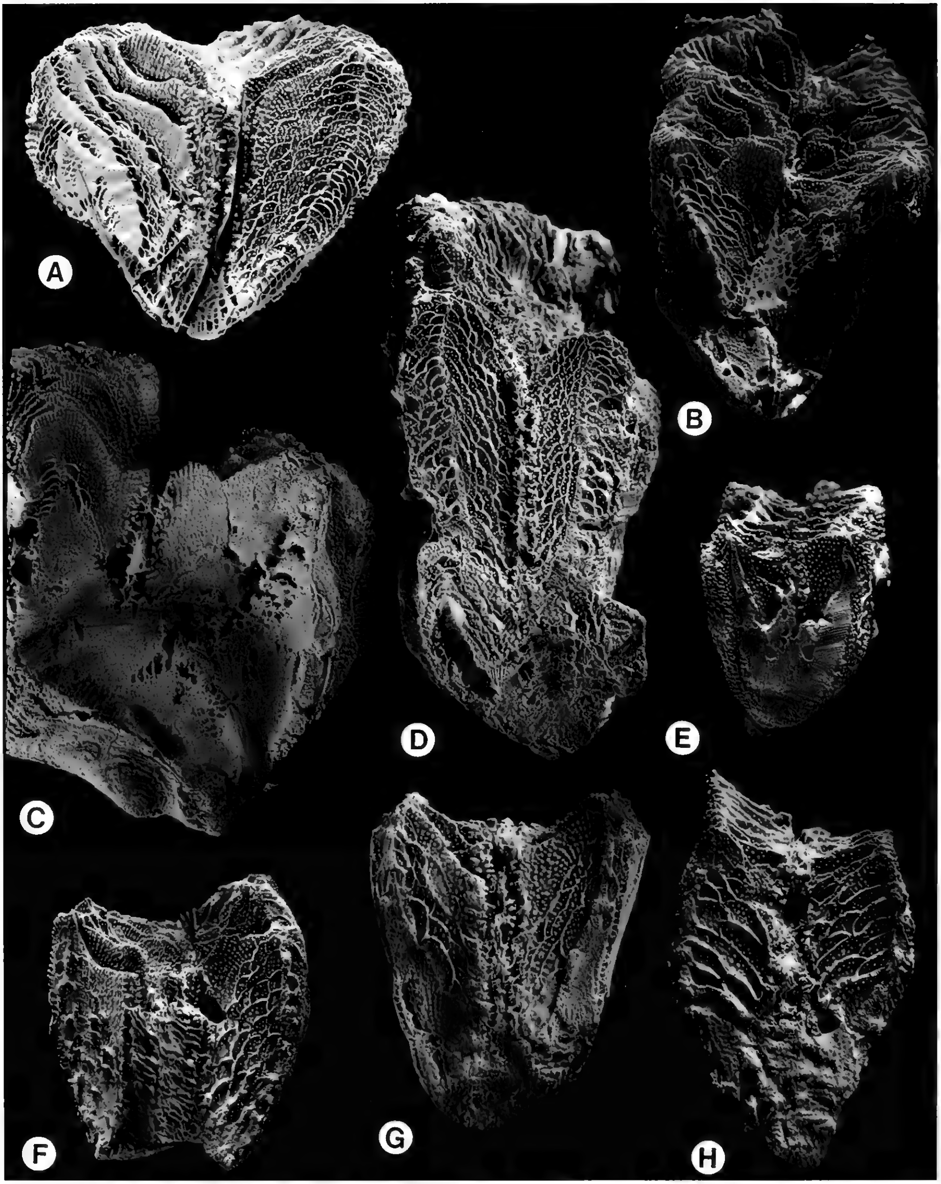
| Character | *D. clivosa*<br>N = 3, n = 11 | *D. labyrinthiformis*<br>N = 5, n = 17 | *D. strigosa*<br>N = 6, n = 18 | *F. maoadentrensis*<br>(NMB group #2)<br>N = 3, n = 6 | *D. zambensis*<br>(NMB group #1)<br>N = 11, n = 25 |
|---|---|---|---|---|---|
| Valley width (IVW) | 2.61 (0.17) | 4.30 (0.20) | 4.52 (0.20) | 3.13 (0.13) | 5.34 (0.22) |
| Major septum length (SL) | 1.02 (0.08) | 1.52 (0.08) | 1.78 (0.10) | 1.04 (0.10) | 1.98 (0.10) |
| Major septum thickness (ST) | 0.209 (0.021) | 0.209 (0.014) | 0.217 (0.015) | 0.18 (0.019) | 0.248 (0.011) |
| Theca thickness (TT) | 0.832 (0.074) | 1.270 (0.079) | 0.721 (0.093) | 0.651 (0.064) | 0.517 (0.051) |
| Distance bet. adjacent corallites (NND) | 0.026 (0.009) | 1.320 (0.170) | 0.085 (0.021) | 0.876 (0.059) | 2.680 (0.209) |
| Total no. of septa per 5 mm (TNS-5) | 4.09 (0.43) | 6.22 (0.17) | 5.71 (0.22) | 3.93 (0.19) | 5.90 (0.21) |
| No. of major septa per 5 mm (NMS-5) | 5.99 (0.32) | 6.97 (0.26) | 7.37 (0.28) | 6.45 (0.14) | 6.17 (0.24) |



Text-figure 19.—Calical surfaces of two species (*Manicina pliocenica, Meandrina braziliensis*) in different scleractinian families, with similar meandroid colony forms and corallite architectures. *M. pliocenica* has acute septal teeth, well-developed septal lobes, and a spongy columella, whereas *M. braziliensis* has minute septal teeth, reduced costae, and a lamellar columella. All photos, × 1. **(A)** Figured specimen of *Manicina pliocenica* Gane, 1895, family Faviidae, NMB D6164 (CCD 2050), Upper Miocene, locality NMB 16822, Río Cana, Gurabo Formation, Dominican Republic. **(B)** Figured specimen of *Meandrina braziliensis* (Milne Edwards and Haime, 1849), family Meandrinidae, NMB D6251 (CCD 1136), Upper Miocene, locality NMB 16852, Río Cana, Cercado Formation, Dominican Republic.

among the taxa. The characters involve many different components of whole colony and corallite architecture. Five continuous characters were closely related to the measurements and counts given in Table 6 including: character #7, calice or valley width (similar to CD-MIN, CD-MAX, IVW); character #10, coenosteum development (similar to NND); characters #13 and 14, number of septal cycles and septal spacing (similar to TNS and NMS); character #22, colony size (similar to CL-HT, CL-MIN, CL-MAX). Septal (ST) and thecal (TT) thickness were not included because they showed little differences among taxa in the analysis.

Eleven less easily measured characters (Table 19) were selected because they are often cited as diagnostic of faviid genera (*e.g.*, Table 13): (1) characters #2, 3 and 4, meander series sinuosity, wall development between buds (related to valley length), and symmetry of bud geometry (three characters related to budding and overall colony form); (2) characters #11 and 19, development of exothecal and endothecal dissepiments; (3) characters #16 and 17, columella width and continuity; (4) characters #18 and 19, development of septal and paliform lobes; and (5) characters #21 and 22, wall structure and double or single wall. Six characters that are sometimes useful in distinguishing morphologically similar taxa in different families (*e.g.*, Table 5) were also selected: (1) characters #5 and 6, calice platform shape and relief; (2) character #8, epitheca development; (3) characters #9 and 15, relative costae and septa thickness; and (4) character #12, continuity of costae (related to colony integration). Finally, two more ecologically controlled characters were selected: (1) character #1, attachment of skeleton, and (2) character #23, colony size. The portion of the character matrix for the 17 species treated herein is given in Table 20.



Text-figure 20.—Vertical breaks through valleys showing characters that can be used to distinguish *Hadrophyllia*, *Thysanus*, and *Manicina*. *Hadrophyllia* has neither paliform nor septal lobes, but is characterized by abundant endothecal and exothecal dissepiments. *Thysanus* is distinguished by reduced or absent endothecal and exothecal dissepiments and the presence of paliform lobes. *Manicina* is distinguished by the presence of septal lobes and well-developed endothecal and exothecal dissepiments. All photos, × 2. **(A)** Paratype of *Hadrophyllia saundersi*, NMB D6240 (CCD 2062), Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. **(B)** Paratype

A cladogram was constructed for the character matrix (40 taxa × 65 character states) using a heuristic search in PAUP version 3.1.1 of Swofford, 1993 (see Johnson, 1998, for methodological details). After an inital set of 78 equally parsimonious trees was found, the tree was rooted with *Caulastraea portoricensis* as the outgroup, and a strict consensus tree with length 175 was constructed (Text-fig. 21). Clade stability was assessed using a modified jackknife procedure in which a series of cladograms was constructed for subsets of taxa with each taxon removed.

Examination of the resulting cladogram (Text-fig. 21) suggests that: (1) the genera *Favia* and *Diploria* are paraphyletic as traditionally defined; (2) the genus *Colpophyllia* (node 38) is well-supported and is defined by four unambiguous apomorphies [sinuous meander series (character #2), low numbers of septal cycles (character #13), equal major and minor septa (character #15), and discontinuous columellae (character #17)]; (3) species that have previously been assigned to *Manicina, Teleiophyllia,* and *Thysanus* (node 50) form a large well-supported group defined by five unambiguous apomorphies (free-living skeletons [character #1], lack of wall development between buds [character #3], bi- or unidirectional budding [character #4], little or no coenosteum [character #10], small colony size [character #23]). No groups containing more than two species can be detected among the species previously assigned to "*Diploria.*" One species in the present monograph (*D. zambensis*) lies isolated in this unresolved part of the cladogram, and therefore is tentatively assigned to *Diploria* until a more complete revision of the genus is accomplished. In contrast, another species in the present monograph that is relatively isolated on the cladogram (*Colpophyllia natans*) clearly lies within the well-supported genus *Colpophyllia* (node 38) and is therefore assigned without doubt to this genus.

Four species in the present monograph appear to belong to groups of taxa that have previously been called "*Favia*" (Text-fig. 21). Of these four, two species, *Favia dominicensis* and *F.* n. sp. aff. *dominicensis,* belong to a group (node 2) defined by two unambiguous apomorphies (continuous costae [character #12], moderate development of endothecal dissepiments [character #20]). Two other species, *F. vokesae* and *F. maoadentrensis,* belong to a distinctly different group (node 13) defined by two unambiguous apomorphies (high numbers of septal cycles [character #13] and absent paliform lobes [character #19]). These two groups of *Favia* most likely represent different genera or subgenera, but are left together in the same genus at the present time until a more throrough revision of the genus is accomplished.

The remaining ten species in the monograph all lie on the cladogram (Text-fig. 21) within the larger group (node 50) containing species that have previously been assigned to *Manicina,* "*Teleiophyllia,*" and *Thysanus.* The topology of the cladogram suggests that this group can be broken up into three possible subgroups: (1) containing only *Hadrophyllia saundersi* (node 51), (2) containing *Thysanus corbicula, T. excentricus,* and *T. navicula* (node 53), and (3) containing *Manicina geisteri, M. grandis, M. jungi, M. puntagordensis, M. pliocenica,* and *M.* n. sp. aff. *mayori* (node 57). Node 51 (*Hadrophyllia,* n. gen.) is supported by two unambiguous apomorphies (large valley width [character #7], widely spaced septa [character #14]). The genus contains only one species which is newly described in this monograph (*H. saundersi*), and it is therefore previously unknown and described here as new. Node 53 (*Thysanus*) is supported by three unambiguous apomorphies (no exothecal dissepiments [character #11], paliform lobes [character #19], few or absent endothecal dissepiments [character #20]). As shown on the cladogram, it contains two species previously assigned to *Thysanus* (*Thysanus corbicula, T. excentricus*) and one previously assigned to *Teleiophyllia* (*T. navicula*). Node 57 (*Manicina*) is supported by two unambiguous apomorphies (well-developed epitheca [character #8], septal lobes [character #18]). It contains species with both bidirectional flabelloid and meandroid colony forms, and includes one species that was previously assigned to *Teleiophyllia* (*M. grandis*), one species that was previously assigned to *Manicina* (*M. puntagordensis*), and four species that are newly recognized herein (*M. geisteri, M. jungi, M. pliocenica, M.* n. sp. aff. *mayori*).

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of *Manicina geisteri,* NMB D6171 (CCD 2067), Upper Miocene, locality NMB 16824, Río Cana, Gurabo Formation, Dominican Republic. **(C)** Figured specimen of *Manicina pliocenica,* NMB D6164 (CCD 2050), Upper Miocene, locality NMB 16822, Río Cana, Gurabo Formation, Dominican Republic. **(D)** Figured specimen of *Manicina grandis,* NMB D6208 (CCD 2127), Lower Pliocene, locality NMB 16858, Río Cana, Gurabo Formation, Dominican Republic. **(E)** Figured specimen of *Thysanus excentricus,* SUI 90997 (AB94–11/1), Upper Pliocene AB94–11, Bowden Shell Beds, Bowden Formation, Jamaica. **(F)** Figured specimen of *Manicina grandis,* NMB D6204 (CCD 2121), Upper Miocene, locality NMB 16844, Río Cana, Cercado Formation, Dominican Republic. **(G)** Figured specimen of *Manicina jungi,* NMB D6249 (CCD 2161), Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. **(H)** Figured specimen of *Thysanus navicula,* NMB D6234 (CCD 2181), Upper Miocene, locality NMB 16810, Río Gurabo, Gurabo Formation, Dominican Republic.

Table 19.—Characters used in the phylogenetic analysis of 40 Cenozoic Caribbean species of Faviidae with intramural budding (after Johnson, 1998).

| Character | Number of states | States | Character type | Order |
|---|---|---|---|---|
| 1. Attachment of skeleton | 2 | free-living, attached | discontinuous | unordered |
| 2. Meander series sinuosity | 3 | straight, gently curved, sinuous | discontinuous | unordered |
| 3. Frequency of wall development between buds | 4 | always, most, few, never | continuous | ordered |
| 4. Symmetry of bud geometry | 3 | unidirectional, bidirectional, multidirectional | discontinuous | unordered |
| 5. Calicular platform shape | 2 | v-shaped (sloping), U-shaped (steep-sided) | discontinuous | unordered |
| 6. Calice relief | 4 | low (<2 mm), medium (2–4 mm), high (4–10 mm), very high (>10 mm) | continuous | ordered |
| 7. Calice or valley width | 4 | small (<5 mm), medium (5–10 mm), large (10–15 mm), very large (>15 mm) | continuous | ordered |
| 8. Epitheca | 3 | absent, reduced, well-developed | discontinuous | ordered |
| 9. Relative costae thickness | 2 | equal, unequal | discontinuous | unordered |
| 10. Coenosteum development | 5 | absent, fused walls, narrow (<CD-MIN or IVW), medium (=CD-MIN or IVW), wide (>CD-MIN or IVW) | continuous | unordered |
| 11. Exothecal dissepiments | 2 | absent, present | discontinuous | ordered |
| 12. Continuity of costae | 2 | discontinuous, continuous | discontinuous | unordered |
| 13. Number of septal cycles | 4 | 3, >3, <4, >4 | continuous | ordered |
| 14. Septal spacing (per 5 mm) | 3 | <6, 6–12, >12 | continuous | ordered |
| 15. Relative septal thickness | 2 | equal, unequal | discontinuous | unordered |
| 16. Columella width | 3 | ≤¼, ⅓, ½ | continuous | ordered |
| 17. Columella continuity | 2 | continuous, discontinuous | discontinuous | unordered |
| 18. Septal lobes | 2 | absent, present | discontinuous | unordered |
| 19. Paliform lobes | 2 | absent, present | discontinuous | unordered |
| 20. Endothecal dissepiments | 4 | absent, few, medium, abundant | continuous | ordered |
| 21. Wall structure | 2 | septothecal, parathecal | discontinuous | unordered |
| 22. Double or single wall | 2 | single, double | discontinuous | unordered |
| 23. Colony size | 3 | small (<10 cm), medium (10–30 cm), large (>30 cm) | continuous | unordered |

This subdivision of node 50 (containing meandroid and flabelloid forms with wide valleys and continuous spongy columellae) differs substantially from that proposed by Vaughan (1919), who placed all flabelloid members of the group in one genus (*Thysanus* [= *Teleiophyllia*]) and all meandroid members in a different genus ("*Maeandra*"). Although Wells (1936) originally used the development of dissepiments and septal and paliform lobes to define genera within this group, Wells (1956) followed Vaughan's (1919) use of growth form to define genera within the group, subdividing unidirectional flabelloid forms (*Thysanus*) from bidirectional flabelloid forms (*Teleiophyllia*) and from meandroid forms (*Manicina*). As proposed here, species of *Thysanus* include both unidirectional and bidirectional flabelloid forms, and are distinguished by the reduced or absent endothecal and exothecal dissepiments and the presence of paliform lobes. Species of *Manicina* include both flabelloid and meandroid forms, and are distinguished by the presence of septal lobes and well-developed endothecal and exothecal dissepiments. *Hadrophyllia saundersi* has neither paliform nor septal lobes, but is characterized by abundant endothecal and exothecal dissepiments (Text-fig. 20).

## DETERMINATION OF STRATIGRAPHIC RANGES

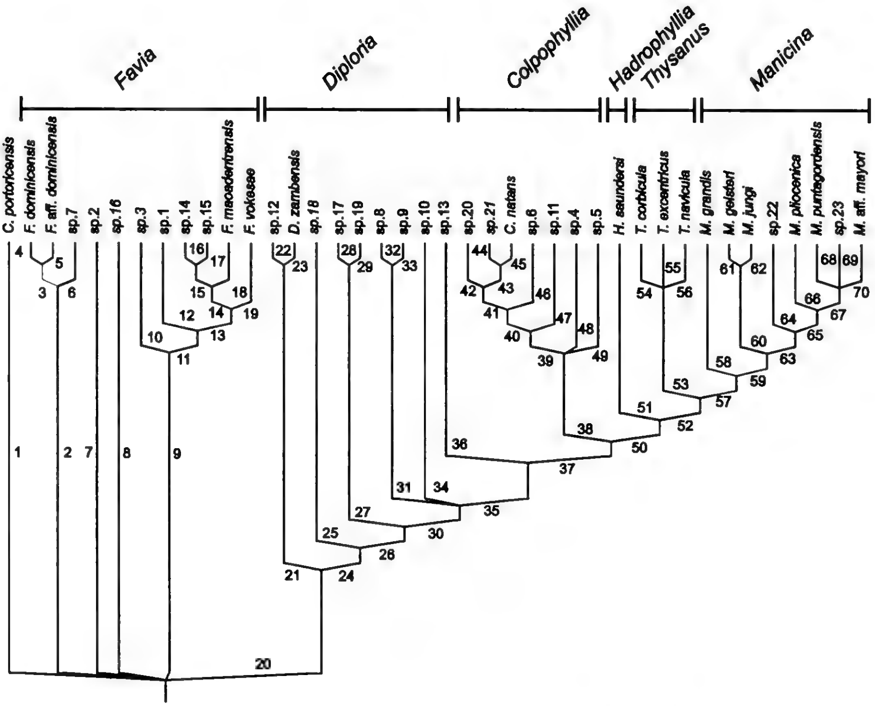
The 17 Dominican Republic species recognized in this monograph were compared qualitatively with species identified in well-documented collections from 39 other Neogene and Quaternary Caribbean localities (Table 4). These localities consist of all the localities entered in the 1995 version of the Cenozoic Coral Database (CCD), assembled by A. F. Budd, K. G. Johnson, and T. A. Stemann, different versions of which have served as the basis for the faunal analyses in Budd *et al.* (1994b); Johnson *et al.* (1995); and Budd

Table 20.—Character matrix for 17 species treated in the present monograph (after Johnson, 1998).

| Species | Attachment of skeleton | Meander series sinuosity | Wall development between buds | Symmetry of bud geometry | Calicular platform shape | Calice relief | Calice or valley width |
|---|---|---|---|---|---|---|---|
| *Caulastraea portoricensis* | attached | not meandroid | always | multidirectional | u-shaped | low | medium |
| *Favia dominicensis* | attached | not meandroid | always | multidirectional | u-shaped | low | medium |
| *Favia* n.sp. aff. *dominicensis* | attached | not meandroid | always | multidirectional | u-shaped | medium | medium |
| *Favia vokesae* | attached | not meandroid | always | multidirectional | u-shaped | medium | small |
| *Favia maoadentrensis* | free-living | gently curved | always | multidirectional | u-shaped | low | small |
| *Diploria zambensis* | attached | gently curved | most | multidirectional | u-shaped | medium | medium |
| *Thysanus corbicula* | free-living | straight | never | unidirectional | u-shaped | low | large |
| *Thysanus excentricus* | free-living | gently curved | never | unidirectional | v-shaped | medium | large |
| *Thysanus navicula* | free-living | straight | never | bidirectional | u-shaped | low | large |
| *Hadrophyllia saundersi* | free-living | gently curved | never | bidirectional | v-shaped | high | very large |
| *Manicina geisteri* | free-living | sinuous | never | bidirectional | v-shaped | high | very large |
| *Manicina grandis* | free-living | gently curved | never | bidirectional | u-shaped | medium | large |
| *Manicina jungi* | free-living | gently curved | never | bidirectional | u-shaped | medium | large |
| *Manicina pliocenica* | free-living | straight | never | bidirectional | u-shaped | very high | large |
| *Manicina puntagordensis* | free-living | straight | never | multidirectional | v-shaped | high | very large |
| *Manicina* n.sp. aff. *mayori* | attached | straight | never | multidirectional | v-shaped | very high | very large |
| *Colpophyllia natans* | attached | sinuous | few | multidirectional | v-shaped | high | very large |

| Species | Epitheca | Relative costae thickness | Coenosteum | Exothecal dissepiments | Continuity of costae | Number of septal cycles | Septal spacing (per 5 mm) | Relative septa thickness |
|---|---|---|---|---|---|---|---|---|
| *Caulastraea portoricensis* | absent | equal | absent | absent | not applicable | <4 | 6–12 | unequal |
| *Favia dominicensis* | unknown | equal | narrow | present | continuous | >3 | 6–12 | unequal |
| *Favia* n. sp. aff. *dominicensis* | unknown | equal | fused walls | present | continuous | >3 | 6–12 | unequal |
| *Favia vokesae* | reduced | equal | fused walls | present | continuous | >4 | >12 | unequal |
| *Favis maoadentrensis* | reduced | unequal | wide | present | discontinuous | >4 | >12 | unequal |
| *Diploria zambensis* | reduced | equal | wide | present | discontinuous | 3 | 6–12 | equal |
| *Thysanus corbicula* | absent | unequal | absent | absent | not applicable | >4 | >12 | unequal |
| *Thysanus excentricus* | absent | equal | absent | absent | not applicable | >3 | 6–12 | equal |
| *Thysanus navicula* | absent | equal | absent | absent | not applicable | >3 | 6–12 | equal |
| *Hadrophyllia saundersi* | absent | equal | absent | present | not applicable | >3 | <6 | equal |
| *Manicina geisteri* | reduced | unequal | absent | present | not applicable | <4 | 6–12 | unequal |
| *Manicina grandis* | well-developed | equal | absent | present | not applicable | >3 | 6–12 | equal |
| *Manicina jungi* | well-developed | unequal | absent | present | not applicable | >4 | >12 | unequal |
| *Manicina pliocenica* | well-developed | equal | narrow | present | continuous | >3 | 6–12 | unequal |
| *Manicina puntagordensis* | well-developed | equal | narrow | present | continuous | >3 | <6 | unequal |
| *Manicina* n. sp. aff. *mayori* | well-developed | equal | narrow | present | continuous | >3 | 6–12 | equal |
| *Colpophyllia natans* | absent | equal | narrow | present | discontinuous | >3 | <6 | equal |

| Species | Columella width | Columella continuity | Septal lobes | Paliform lobes | Endothecal dissepiments | Wall structure | Double or single wall | Colony size |
|---|---|---|---|---|---|---|---|---|
| *Caulastraea portoricensis* | ≤¼ | continuous | absent | absent | absent | septothecal | single | large |
| *Favia dominicensis* | ½ | continuous | absent | absent | medium | parathecal | single | medium |
| *Favia* n. sp. aff. *dominicensis* | ½ | continuous | absent | absent | medium | parathecal | single | small |
| *Favia vokesae* | ½ | continuous | absent | absent | absent | septothecal | single | small |
| *Favis maoadentrensis* | ½ | continuous | absent | absent | few | septothecal | single | small |
| *Diploria zambensis* | ½ | continuous | absent | absent | few | septothecal | single | medium |
| *Thysanus corbicula* | ≤¼ | continuous | absent | present | absent | parathecal | single | small |
| *Thysanus excentricus* | ≤¼ | continuous | absent | present | absent | parathecal | single | small |
| *Thysanus navicula* | ≤¼ | continuous | absent | present | few | parathecal | single | small |
| *Hadrophyllia saundersi* | ≤¼ | continuous | absent | absent | abundant | parathecal | single | small |
| *Manicina geisteri* | ≤¼ | continuous | present | absent | abundant | parathecal | single | small |
| *Manicina grandis* | ≤¼ | continuous | present | absent | abundant | parathecal | single | small |
| *Manicina jungi* | ≤¼ | continuous | absent | present | medium | parathecal | single | small |
| *Manicina pliocenica* | ⅓ | continuous | present | absent | abundant | parathecal | single | small |
| *Manicina puntagordensis* | ⅓ | continuous | present | absent | abundant | parathecal | double | medium |
| *Manicina* n. sp. aff. *mayori* | ≤¼ | continuous | present | absent | abundant | parathecal | double | medium |
| *Colpophyllia natans* | ≤¼ | discontinuous | absent | present | abundant | parathecal | double | large |

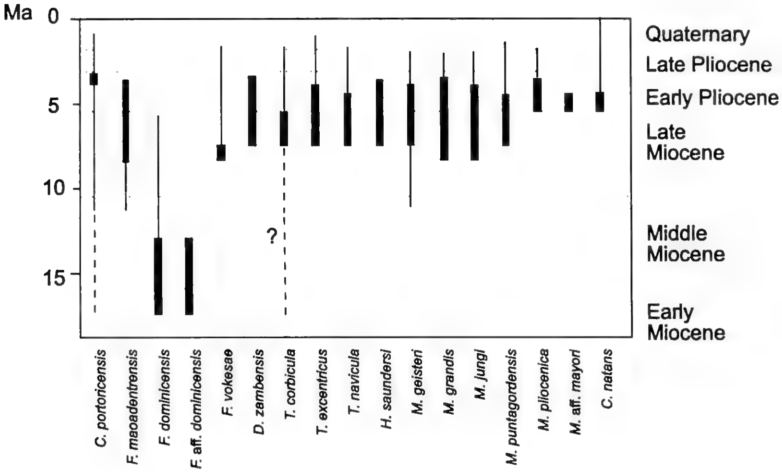


Text-figure 21.—Strict consensus tree calculated from 78 equally parsimonious trees (after Johnson, 1998) showing the groups of species that are recognized as genera. The cladogram was derived from a heuristic search of a character matrix consisting of 40 species and 65 character states. Names for the 17 species treated in this monograph are written above their corresponding branches on the cladogram. Species numbers (sp.#) are given for 23 other Cenozoic Caribbean species that also belong to the clade but do not occur in the sampled Dominican Republic sequence. Names for these species are given in the text. Branch nodes are also numbered near the base of their corresponding branches.

*et al.* (1996). They include: six Lower to Middle Miocene localities, seven Upper Miocene and Lower Pliocene localities, 17 Upper Pliocene localities, three Lower Pleistocene localities, and six Middle to Upper Pleistocene localities (Table 4). Species of the family Faviidae that bud intramurally were identified in these collections using the characters listed in Table 19, and they were compared with the Dominican Republic species using the character matrix given in Table 20.

Based on these comparisons and comparisons with Recent specimens described earlier in this section, occurrences of the 17 Dominican Republic species were interpreted for the Neogene and Quaternary of the Caribbean region as a whole, and oldest and youngest occurrences were used to estimate stratigraphic ranges (Text-fig. 22). Only four of the 17 Dominican Republic species (*Favia* n. sp. aff. *dominicensis, Diploria zambensis, Hadrophyllia saundersi, Manicina* n. sp. aff. *mayori*) are restricted to the northern Dominican Republic, and all four of these species are new. Two of the four new species are left in open nomenclature because they are represented by fewer than five specimens. Thus, most of the 17 species in this monograph appear to have been fairly widely distributed across the Caribbean region. Furthermore, these comparisons indicate that almost all of the intramurally budding faviids that are known from the Neogene of the Caribbean region are represented in the northern Dominican Republic. The two exceptions are: *Diploria bowersi* which occurs in the Upper Miocene of south-central California, and *Diploria sarasotana* which occurs in the Upper Pliocene of Florida.

Approximately 10 of the 13 more widely distributed species (all but *Caulastraea portoricensis, Favia maoadentrensis,* and *Manicina geisteri*) have first occurrences in the Dominican Republic sequence. One



Text-figure 22.—Stratigraphic ranges estimated for the 17 species in this monograph. The ranges were determined using youngest and oldest occurrences observed in the northern Dominican Republic (thick vertical lines), and in 39 other fossil Caribbean localities (Table 4) and the Recent (thin vertical lines). Many species have first occurrences in the Upper Miocene of the Dominican Republic, suggesting that origination rates were accelerated during the Late Miocene. Most species became extinct in the Plio-Pleistocene. Only one species (*C. natans*) still survives today.

(*F. dominicensis*) occurs first in the Upper Oligocene Tabera Group of the Río Yaque del Norte section. The others have first occurrences in the Upper Miocene to Lower Pliocene Cercado and Gurabo Formations. Therefore, origination rates were generally high in intramurally budding Caribbean faviids during Upper Miocene to Lower Pliocene time.

Only one of the 17 species in this monograph (*Colpophyllia natans*) still survives in the Caribbean today. At least nine of the 13 more widely distributed species have last occurrences at localities dated between 1.6–2 Ma. Most of these last occurrences are in the Bowden Formation and Old Pera Beds of southeast Jamaica. Only one of 13 more widely distributed species (*F. maoadentrensis*) has a last occurrence in the Dominican Republic. Therefore, extinction rates were generally high in intramurally budding Caribbean faviids during the Plio-Pleistocene.

## SYSTEMATIC PALEONTOLOGY

### INTRODUCTION

The formal systematic descriptions in this section are based strictly on the results presented in the section on "Taxonomic Methods." Unless otherwise indicated, synonymies are based on type material that was actually visually examined. In determining synonymies, all formally described species that were previously reported from the Early Miocene through Pliocene of the Caribbean region are considered. A list summarizing these species and their synonyms is given in Table 2. Detailed discussion of synonymies is provided in corresponding "Remarks" sections.

Formal diagnoses are provided only for genera and new species. A complete summary of diagnostic morphologic characters distinguishing the species treated herein is given in Table 20. Full descriptions are provided for all species, and detailed comparisons are given for morphologically similar species. Brief summaries of characters that can be used to distinguish selected genera are provided in Tables 5 and 13. If not indicated otherwise, morphologic terms are used as defined in Vaughan and Wells (1943) and Wells (1956). Abbreviations used for measurements are explained in Table 6.

The "Materials" sections give an approximate estimate of the number of specimens (= colonies) studied in the collections of: (1) Saunders *et al.* (1986), deposited at the NMB, and (2) Emily and Harold Vokes of Tulane University (TU), deposited at the USNM. Information on the specimens in these collections is available in the Cenozoic Coral Database (CCD) which can be obtained on request from the authors or from the Neogene Marine Biota of Tropical America (NMITA) site on the World Wide Web (http:

//porites.geology.uiowa.edu). CCD ID numbers for all specimens are given in "Materials" sections. Museum catalog numbers have been assigned only to type and figured specimens, and are not indicated in the "Materials" sections. A complete list of all NMB and TU specimens treated herein and their corresponding CCD and museum catalog numbers is given in the appendix.

Sections on "Occurrence" give detailed geographic and stratigraphic information within the studied areas of the Dominican Republic, whereas sections on "Distribution" give general information on all known occurrences throughout the Caribbean (Table 4). Assignment of formation names to individual localities in the northern Dominican Republic is based on Saunders *et al.* (1986), except along Río Mao where formation names are used as listed by Maury (1919).

### Family **FAVIIDAE** Gregory, 1900

The Faviidae are distinguished by exsert, laminar septa formed by one to two simple trabecular fan systems. Numerous acute teeth extend from the trabeculae along the upper margins of the septa. The columella is spongy and formed by trabecular extensions from the inner margins of the septa. Paliform lobes and/or reduced septal lobes are sometimes present. Corallite walls are septothecal or parathecal, and externally costate. When present, the coenosteum is usually well-developed and porous.

### Genus **CAULASTRAEA** Dana, 1846

*Caulastraea* Dana, 1846, p. 197–198.

*Type species.*—*Caulastraea furcata* Dana, 1846, p. 198–199 (by subsequent designation, Matthai, 1928, p. 272). Recent, Fiji Islands. (Syntype figured on Pl. 1, figs. 1, 2.)

*Diagnosis.*—Phaceloid colonies formed by intramural budding. Circular to elliptical corallites with one to three distinct centers. Costae well-developed. Septothecal corallite walls. Columella reduced, spongy, lacking paliform or septal lobes. Endotheca reduced. Epitheca absent.

*Remarks.*—The genus *Caulastraea* is widely distributed today across the Indo-Pacific region, and consists of approximately four species. It is confined primarily to the western portions of the Pacific Ocean, extending latitudinally from Japan and the Philippines across Indonesia to eastern Australia and the Great Barrier Reef. In the Indian Ocean, it is widespread, extending longitudinally from eastern Africa and the Red Sea to western Australia (Veron, 1993). The genus is first known from the Lower Oligocene Castelgomerto Limestone of the Vicentin area in northeastern Italy (Pfister, 1980). It has been reported in the Oligocene of the Caribbean and Indo-Pacific regions, the Mediterranean Miocene, and the Pliocene of the Caribbean and Indo-Pacific regions (Frost and Weiss, 1979; Chevalier, 1962; Budd *et al.*, 1994b).

### **Caulastraea portoricensis** (Coryell *in* Coryell and Ohlsen, 1929)

Plate 2, figures 1–10;
Text-figures 4, 6, 21, 22

*Calamophyllia portoricensis* Coryell *in* Coryell and Ohlsen, 1929, pp. 199–200, pl. 30, fig. 4.

*Description.*—Branched colony shape, permanently attached. Phaceloid colony form with intramural budding. Branches form in multiple directions, by unequal bifurcation. Calices with single centers, elliptical in shape, having a maximum diameter of 7–12 mm and a minimum diameter of 5–8 mm. Calicular platform steep-sided, with < 2 mm relief. Epitheca absent.

Costae well-developed, equal, continuing from the primary and secondary septa. Septa in more than three cycles, with a total number of septa per corallite of approximately 36–45 and an average total number of septa per 5 mm ranging from six to eight. Septa unequal in thickness, with thicker primary and secondary septa than tertiary and quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend three-fourths of the distance to the columella; quaternary septa are free and extend one-fourth of the distance to the columella. Columella spongy, consisting of a dense tangle approximately one-fourth of the width of the corallite. Paliform and septal lobes absent. Wall septothecal, greater in thickness than the primary septa. Endothecal dissepiments few, vesicular, thick. Coenosteum and exothecal dissepiments absent.

*Holotype.*—AMNH 23000 (Pl. 2, fig. 1).

*Measurements of the holotype.*—CD-MIN = 7.2, CD-MAX = 9.8, TNS = 50, NMS = 24, TNC-5 = 8, NND = 4.4, TT = 0.6, SL = 3.2–3.5, CL-HT = 140, CL-MAX = 80.

*Type locality.*—Arecibo to Ponce Road. Lares Formation, Puerto Rico. Upper Oligocene to Lower Miocene.

*Material.*—Two small NMB fragments (CCD 0057, CCD 2334).

*Remarks.*—The holotype (AMNH 23000) of *C. portoricensis* is poorly preserved, but appears to have higher total numbers of septa per corallite (often > 50) and higher numbers of costae per 5 mm (approximately eight) than the paratype (AMNH 23001). One of the two NMB specimens (NMB D6140 = CCD 0057) is very similar to the paratype, and so are at least nine of the eleven measured specimens (CCD

0141, 0423, 0770, 3429, 3423, 3435, 3443, 3445, 3456) collected in the Upper Pliocene to Lower Pleistocene Moín Formation of the Limón area in Costa Rica (Text-fig. 6). The second NMB specimen (NMB D6141 = CCD 2334) has smaller corallites (5 × 7 mm) and fewer total numbers of septa per corallite (approximately 26). Because this is the only specimen of its kind and it is a fragment, it is impossible to determine whether this specimen belongs to a separate species; however, preliminary statistical analyses (Text-fig. 6) suggest that it is an immature form of *C. portoricensis.*

*Comparison.*—*C. portoricensis* is morphologically similar to the only other species of *Caulastraea* that has been reported from the Oligocene to Recent of the Caribbean region, *C. dendroidea* (Coryell *in* Coryell and Ohlsen, 1929, p. 199, pl. 30, figs. 2, 3) from the Upper Oligocene Juana Draz Formation of southwest Puerto Rico (holotype and paratype figured on Pl. 1, figs. 7, 8). The two species have approximately the same corallite sizes and numbers of major septa per corallite. They differ mainly in total numbers of septa per corallite, numbers of costae per 5 mm, corallite spacing, and theca thickness. *C. dendroidea* is characterized by more septa per corallite (TNS > 60), more numerous costae (number of costae per 5 mm = 12–14), more narrowly spaced corallites (NND = 2.3), and slightly thicker, raised corallite walls (TT = 0.8). *C. dendroidea* strongly resembles *C. pseudoflabellum* (Catullo, 1852) from the Lower Oligocene of Italy (see Pfister, 1980). A more rigorous morphometric study based on larger sample sizes is needed to better understand the distinctions between *C. dendroidea* and *C. pseudoflabellum.*

*C. portoricensis* is also morphologically similar to the modern Indo-Pacific species *Caulastraea furcata* Dana, 1846 (syntype figured on Pl. 1, figs. 1, 2). It can be distinguished from *C. furcata* primarily by its more numerous, closely spaced septa.

*Occurrence.*—Río Gurabo: Mao Formation (locs. NMB 15822, 15834).

*Distribution.*—*C. portoricensis* ranges in age from Early Miocene to Early Pleistocene. Outside the Dominican Republic, it has been found in the following strata: (1) Lower Miocene, Lares Limestone of Puerto Rico; (2) Middle Miocene, Los Puertos and Ponce Formations of Puerto Rico; (3) Upper Miocene, Lirio Limestone of Isla de Mona, Puerto Rico; (4) Upper Pliocene, Unda and Clino cores (Bahamas Drilling Project); (5) Plio-Pleistocene, Manchioneal and Hope Gate Formations of Jamaica, and Moín Formation of Costa Rica.

### Genus **Favia** Oken, 1815

*Favia* Oken, 1815, p. 67.

*Type species.*—*Madrepora fragum* Esper, 1795, p. 79, pl. 64, figs. 1, 2. Recent, West Indies. (Holotype is lost [Scheer, 1990].)

*Diagnosis.*—Plocoid colonies formed by intra- and extramural budding. Circular, elliptical, and some polygonal corallites, with one to three (rarely four or five) distinct centers per corallite series. Costae usually well-developed. Corallite walls septothecal or parathecal. Columella well-developed, spongy, continuous, lacking paliform or septal lobes. Abundant vesicular endo- and exothecal dissepiments.

*Remarks.*—As shown in Text-figure 21, the genus *Favia* is paraphyletic and in need of revision. As currently defined, it is one of the more widely distributed of all zooxanthellate scleractinian genera. It occurs today throughout the Indo-Pacific, Atlantic and Caribbean regions, and consists of approximately 20 species. In the Indo-Pacific, it extends longitudinally from the Red Sea and eastern Africa through Indonesia to French Polynesia, and latitudinally from Japan to eastern Australia. It occurs throughout the Caribbean extending from Bermuda to Brazil, and across the Atlantic to western Africa (Veron, 1993). The genus is first known from the Cretaceous of Europe and the West Indies (Wells, 1933; Vaughan and Wells, 1943). It has been reported from the Tertiary in the Caribbean, Mediterranean, and Indo-Pacific regions (Budd *et al.*, 1992, 1994b; Pfister, 1980; Chevalier, 1962; Veron and Kelley, 1988).

### **Favia dominicensis** Vaughan *in* Vaughan and Hoffmeister, 1925

Plate 3, figures 5, 6; Plate 4, figures 3–6;
Text-figures 21, 22

*Favia dominicensis* Vaughan *in* Vaughan and Hoffmeister, 1925, p. 325, pl. 2, figs. 4, 6, 7; Frost and Langenheim, 1974, p. 242, pl. 84, figs. 1–4, pl. 85, figs. 2–4.

*Description.*—Massive hemispherical colony shape, permanently attached, intermediate in size (colony length = 9–10 cm, height = 5 cm). Plocoid colony form with infrequent, predominantly intramural budding. New buds form in multiple directions, by equal bifurcation. Calices with single centers, elliptical in shape, with a minimum diameter of 7–10 mm. Calicular platform steep-sided, with < 2 mm relief.

Costae well-developed, equal, continuous. Septa in more than three cycles, with the total number of septa per corallite reaching approximately 36 and the total number of septa per 5 mm ranging from six to seven. Septa unequal in thickness, with thicker primary and secondary septa than tertiary and quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free or fused and extend one-half to three-fourths of the distance to the columella; quaternary septa are free and extend one-fourth of the distance to the columella. Columella spongy, discontinuous; approximately one-third of the width of the corallite. Paliform and septal lobes absent. Wall parathecal, thinner than the primary septa. Endothecal dissepiments common, vesicular, thin; exothecal dissepiments abundant, vesicular, thick. Coenosteum porous, thin to intermediate in thickness. Distance between adjacent corallite walls 1–2 mm.

*Holotype.*—MCZ 103512 (Pl. 3, figs. 5, 6).

*Measurements of the holotype.*—(Median of five corallites) CD-MIN = 6.5, CD-MAX = 8.9, TNS-5 = 7, NMS-5 = 3, NND = 1.8, TT = 0.3, CL-HT = 4.3, CL-MIN = 5.2, CL-MAX = 7.0.

*Type locality.*—?Neogene, Dominican Republic.

*Material.*—Three NMB colonies (CCD 2045–2047); one TU colony (CCD 2366).

*Comparison.*—*F. dominicensis* is morphologically most similar to *F. leptophylla,* a Recent species from the Abrolhos reefs of Brazil. *F. dominicensis* is distinguished by its larger corallites and more numerous septa. In *F. leptophylla,* CD-MIN = 5–6 mm and TNS = 24–30. Many corallites in *F. leptophylla* have three centers and a distinctive thin raised wall, and they are separated by a more extensive coenosteum (NND = 2–4 mm).

*Occurrence.*—Río Yaque del Norte: ?Tabera Group (loc. TU 1362), Baitoa Formation (loc. NMB 17284).

*Distribution.*—*F. dominicensis* ranges in age from Late Oligocene to Late Miocene. Outside the Dominican Republic, it is known from the Upper Miocene Lirio Limestone of Isla de Mona, Puerto Rico and from the Lower Miocene of Isla de Providencia, Colombia.

### **Favia** n. sp. aff. **F. dominicensis** Vaughan *in* Vaughan and Hoffmeister, 1925

Plate 3, figures 3–4;
Text-figures 21, 22

*Description.*—Massive hemispherical colony shape, permanently attached, intermediate in size (colony length = 4–6 cm, height = 2–3 cm). Plocoid colony form with frequent new buds, formed in multiple directions, many extramurally. Intramural budding by equal bifurcation. Calices with single and in places double centers, polygonal in shape, with a minimum diameter of 5–7 mm. Calicular platform steep-sided, with 2–3 mm relief.

Costae well-developed, equal, continuous. Septa in more than three cycles, with the total number of septa per corallite reaching approximately 30, and the total number of septa per 5 mm ranging from six to seven. Septa unequal in thickness; with primary thicker than secondary septa, secondary thicker than tertiary septa, and tertiary thicker than quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free or fused and extend three-fourths of the distance to the columella. Columella spongy, discontinuous; approximately one-third of the width of the corallite. Paliform and septal lobes absent. Wall parathecal, thinner than the primary septa. Endothecal dissepiments common, vesicular, thin; and exothecal dissepiments abundant, vesicular, thick. Coenosteum porous, thin. Distance between adjacent corallite walls 0.1–0.2 mm.

*Material.*—One NMB specimen (CCD 2044 = NMB D6162; Pl. 3, figs. 3, 4).

*Remarks and comparison.*—This morphotype closely resembles *Favia dominicensis.* It differs primarily in its smaller, more closely spaced corallites, and its higher budding frequency. These differences appear to be significant enough to warrant distinguishing it as a separate species. This species is left in open nomenclature, however, because it is represented by only one specimen.

*Occurrence.*—Río Yaque del Norte: Baitoa Formation (loc. NMB 16943).

*Distribution.*—*Favia* n. sp. aff. *F. dominicensis* is known only from the Lower to Middle Miocene of the Dominican Republic.

### **Favia vokesae**, new species

Plate 5, figures 3–6;
Text-figures 5, 21, 22

*Diagnosis.*—Closely spaced, moderate-sized calices with one to two centers and four complete septal cycles.

*Description.*—Massive hemispherical colony shape, permanently attached, small in size (colony length = 2–3 cm, height = 1–2 cm). Plocoid colony form with predominantly intramural budding. New buds form in multiple directions, by equal bifurcation. Calices with single or double centers, elliptical or polygonal in shape, with a minimum diameter of 3.5–4 mm. Calicular platform steep-sided, with 2–3 mm relief.

Costae well-developed, equal, continuous. Septa in four cycles, with the total number of septa per corallite reaching approximately 48, and the total number of septa per 5 mm ranging from 12 to 14. Septa unequal in thickness; with primary thicker than secondary septa, secondary thicker than tertiary septa, and tertiary thicker than quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free or fused and extend three-fourths of the distance to the columella; quaternary septa are free and extend one-fourth of the distance to the columella. Columella spongy, discontinuous; approximately one-third of the width of the corallite. Paliform and septal lobes absent. Wall septothecal, thicker than the primary septa. Endothecal dissepiments rare, vesicular, thin; exothecal dissepiments abundant, vesicular, thick. Coenosteum porous, thin to intermediate in thickness. Distance between adjacent corallite walls 0.5–1.5 mm.

*Etymology.*—Named after Emily Vokes (Department of Geology, Tulane University), who collected several colonies of this species during her expeditions to the northern Dominican Republic.

*Holotype.*—NMB D6017 (Pl. 5, fig. 6).

*Paratypes.*—USNM 95212, 95251, 95278 (Pl. 5, figs. 3–5), 95319, 95325.

*Measurements of the holotype.*—(Median of five corallites) CD-MIN = 4.4, CD-MAX = 6.4, TNS-5 = 14, NMS-5 = 7, NND = 1.4, TT = 0.4, CL-HT = 1.5, CL-MIN = 2.2, CL-MAX = 2.7.

*Type locality.*—NMB loc. 16855, Río Cana, Cercado Formation, Dominican Republic. Upper Miocene.

*Material.*—One NMB colony (CCD 2043); four TU colonies (CCD 2367–2370).

*Comparison.*—*F. vokesae* is morphologically most similar to *F. fragum,* a Late Pliocene to Recent Caribbean species. *F. fragum* is distinguished by its smaller, more widely spaced corallites (CD-MIN = 2.5–3.5; NND = ~2), fewer septa (TNS = 36–40), thicker costae, and denser coenosteum.

*Occurrence.*—Río Cana: Cercado Formation (loc. NMB 16855). Guayubín: ?Mao Formation (loc. TU 1281).

*Distribution.*—*F. vokesae* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it is known from the Upper Pliocene Moín Formation of Limón, Costa Rica, and the Upper Pliocene of Unda core (Bahamas Drilling Project).

### **Favia maoadentrensis**, new species
Plate 6, figures 1–5; Plate 8, figures 1, 3, 5;
Text-figures 5, 17, 18, 21, 22

*Diagnosis.*—Meandroid colonies forming coralliths with thin, short, widely spaced valleys; low calical relief.

*Description.*—Massive spherical colony shape forming free-living coralliths, small to intermediate in size (colony diameter = 3–8 cm). Meandroid colony form, with series composed of 1–6 corallites. Intra- and extramural budding. Intramural budding predominantly bidirectional. Extramural budding unconstrained. Valleys separated by shallow ambulacra.

Valley width 3–4 mm. Calicular platform steep-sided, with < 2 mm relief. Epitheca well-developed. Costae well-developed, unequal, discontinuous. Septa in four cycles, with the total number of septa per 5 mm ranging from 13 to 14. Septa unequal in thickness, with the primary and secondary septa thicker than tertiary septa, and tertiary septa thicker than quaternary septa. Primary and secondary septa extend to the columella, tertiary septa are free and extend seven-eighths of the distance to the columella, quaternary septa are free and extend one-fourth of the distance to the columella. Columella spongy, continuous; approximately one-half of the width of the valley. Paliform and septal lobes absent. Wall septothecal, thicker than the primary septa. Endothecal dissepiments common, vesicular, thin; exothecal dissepiments abundant, vesicular, thick. Coenosteum porous, extensive. Distance between adjacent valley walls 3–4 mm.

*Etymology.*—Named after the Mao Adentro Limestone, the unit in which this species is most abundant.

*Holotype.*—NMB D6147 (16884/25) (Pl. 6, fig. 1; Pl. 8, fig. 3).

*Paratypes.*—NMB D6142 (Pl. 6, fig. 5), D6143, D6144, D6145 (Pl. 6, fig. 4; Pl. 8, fig. 5), D6146 (Pl. 6, fig. 3), D6148 (Pl. 8, fig. 1), D6149 (Pl. 6, fig. 2).

*Measurements of the holotype.*—IVW = 3.33, TNS-5 = 13, NMS-5 = 8, NND = 0.78, TT = 0.57, SL = 0.90, ST = 0.14, CL-HT = 5.7, CL-MIN, CL-MAX = 6.0.

*Type locality.*—Loc. NMB 16884, Lower Upper Pliocene, Río Cana, Mao Formation, Dominican Republic.

*Material.*—14 NMB colonies (CCD 2016–2028, 2042), three measured; one TU colony (CCD 2371).

*Comparison.*—*F. maoadentrensis* is morphologically most similar to *F. gravida,* a Recent species from the Abrolhos reefs of Brazil. *F. maoadentrensis* is distinguished by its free-living coralliths, its thick columella, and its widely spaced valleys separated by a distinctive ambulacral groove.

*Occurrence.*—Río Cana: Cercado Formation (loc. NMB 16855), Mao Formation (loc. NMB 16884). Río Gurabo: Gurabo Formation (loc. TU 1208).

*Distribution.*—*F. maoadentrensis* ranges in age from Late Miocene to Early Pliocene. Outside the Dominican Republic, it is known only from the Upper Miocene Lirio Limestone of Isla de Mona, Puerto Rico.

### Genus **Diploria** Milne Edwards and Haime, 1848

*Diploria* Milne Edwards and Haime, 1848, p. 493.

*Type species.*—*Meandrina cerebriformis* Lamarck, 1816, p. 246. Recent, West Indies (= *Madrepora labyrinthiformis* Linnaeus, 1758). (Following Matthai

[1928], the original description of *M. labyrinthiformis* was based on a protograph in Gualtieri [1742]. Lamarck's type of *Meandrina cerebriformis* is at the Muséum National d'Histoire Naturelle in Paris and is figured by Matthai [1928] on pl. 10, fig. 2.)

*Diagnosis.*—Meandroid colonies formed by multidirectional intra- and extramural budding. Long, shallow (< 6 mm), narrow (< 10 mm), and commonly sinuous series with indistinct centers. Multiple valley systems. Costae well-developed. Septothecal corallite walls. Columella well-developed, continuous, lacking paliform or septal lobes. Abundant vesicular endo- and exothecal dissepiments.

*Remarks.*—As shown in Text-figure 21, the genus *Diploria* is paraphyletic and in need of revision. As currently defined, it only occurs today in the Caribbean region and Bermuda (Veron, 1993), and consists of three species, *D. clivosa, D. labyrinthiformis, D. strigosa* (Table 3). Its oldest occurrences in the Caribbean are Late Miocene (Budd *et al.,* 1994b). *Diploria* has been reported from the Lower Oligocene (and possibly Upper Cretaceous) of Europe (Pfister, 1980; Vaughan and Wells, 1943), but the European forms have discontinuous columellae and therefore are distinctively different from those in the Caribbean.

### **Diploria zambensis**, new species

Plate 7, figures 1–6; Plate 8, figures 2, 4, 6;
Text-figures 4, 5, 17, 18, 21, 22

*Diagnosis.*—Meandroid colonies with continuous columellae, septothecal walls, and no septal lobes, moderate-sized valleys and numerous septa; relatively deep ambulacra separate valleys.

*Description.*—Massive hemispherical colony shape, permanently attached, intermediate to large in size (max. colony diameter = 15–20 cm, height = 7–8 cm). Meandroid colony form, with short to long sinuous series formed by intra- and extramural budding. Intramural budding predominantly bi- and tridirectional. Extramural budding unconstrained. Valleys separated by deep (2–3 mm) ambulacra. Valley width 4–6 mm. Calicular platform steep-sided, with 3–4 mm relief. Epitheca reduced.

Costae well-developed, equal, discontinuous. Septa in three cycles, with the total number of septa per 5 mm ranging from seven to eight. Septa equal in thickness. Primary and secondary septa extend to the columella; tertiary septa are free and extend four-fifths of the distance to the columella. Columella spongy, continuous; approximately one-third to one-fourth of the width of the valley. Paliform and septal lobes absent. Wall septothecal, thicker than the primary septa. Endothecal dissepiments common, vesicular, thin; exothecal dissepiments abundant, vesicular, thick. Coenosteum porous, intermediate in size. Distance between adjacent valley walls 2–3 mm.

*Etymology.*—Named after Cañada de Zamba, where this species is most abundant.

*Holotype.*—NMB D6018 (Pl. 7, figs. 1, 6; Pl. 8, fig. 6).

*Paratypes.*—NMB D5788 (Pl. 7, fig. 5; Pl. 8, fig. 2), D5790, D6150 (Pl. 7, fig. 3), D6151, D6152 (Pl. 7, fig. 2), D6153, D6154, D6155, D6156 (Pl. 7, fig. 4), D6157, D6158 (Pl. 8, fig. 4), D6159.

*Measurements of the holotype.*—IVW = 6.49, TNS-5 = 8, NMS-5 = 8, NND = 2.99, TT = 0.95, SL = 2.69, ST = 0.22, CL-HT = 5.8, CL-MIN = 6.5, CL-MAX = 8.5 (part of a larger colony).

*Type locality.*—Loc. NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Upper Miocene.

*Material.*—18 NMB colonies (CCD 2012–2015, 2029–2041, 2365), 10 measured.

*Comparison.*—*D. zambensis* is morphologically most similar to *D. labyrinthiformis,* a Late Pliocene to Recent Caribbean species. *D. labyrinthiformis* is distinguished by its slightly narrower valleys (IVW = 4.3), fewer septa (TNS-5 = 7.6), and its thicker wall (TT = 2.8).

*Occurrence.*—Río Gurabo: Gurabo Formation (loc. NMB 15808, 16921), Mao Formation (loc. NMB 15830). Río Cana: Gurabo Formation (loc. NMB 16815, 16817, 16881), Mao Formation (loc. NMB 16884, 16875, 16877).

*Distribution.*—*Diploria zambensis* is not known to occur outside the Upper Miocene to Lower Pliocene of the Dominican Republic.

### Genus **Thysanus** Duncan, 1863

*Thysanus* Duncan, 1863, pp. 439–440.

*Type species.*—*Thysanus excentricus* Duncan, 1863, pp. 439–440, pl. 16, figs. 3a–c (by subsequent designation, Vaughan, 1919, pp. 423–424). Upper Pliocene, Bowden Formation, Jamaica. (Holotype figured on Pl. 9, figs. 6, 7.)

*Diagnosis.*—Free-living, flabelloid colonies formed primarily by unidirectional intramural budding. Series commonly straight. Single valley system. Costae well-developed. Parathecal corallite walls. Columella weak, continuous, with occasional weak paliform lobes. Septal lobes absent. Rare or absent endo- and exothecal dissepiments. Epitheca absent.

*Remarks.*—The genus *Thysanus* occurs only in the Neogene (Lower Miocene to Lower Pleistocene) of the Caribbean region. It is currently extinct (Vaughan and Wells, 1943; Budd *et al.,* 1994b).

### **Thysanus corbicula** Duncan, 1863
Plate 9, figures 1, 4, 5, 8, 11, 12;
Plate 10, figures 2, 5, 6;
Text-figures 21, 22

*Thysanus corbicula* Duncan, 1863, p. 430, pl. 15, fig. 3a, b.

? *Thysanus vaughani* Weisbord, 1971, pp. 22–23, pl. 5, figs. 3–5.

*Thysanus floridanus* Weisbord, 1974, pp. 356–358, pl. 34, figs. 1–3.

*Description.*—Elongate flabelloid colony shape, free-living, small (max. colony length = 5.5–6 cm, width = 1.2–1.3 cm, height = 1–1.5 cm). Single straight series formed by unidirectional intramural budding. Valley width 10–11 mm. Calicular platform steep-sided, with < 2 mm relief. Epitheca absent or very reduced.

Costae well-developed, unequal, with thinner costae extending from quaternary septa. Septa in four cycles, with the total number of septa per 5 mm ranging from 13 to 14. Septa unequal in thickness, with primary, secondary, and tertiary septa thicker than quaternary septa. Primary, secondary, and tertiary septa extend to the columella; quaternary septa are free and extend one-fourth to one-third of the distance to the columella. Columella lamellar to spongy, continuous; approximately one-tenth of the width of the valley. Paliform lobes weakly developed. Septal lobes absent. Wall parathecal, equal in thickness to the primary septa. Endothecal dissepiments reduced or absent; exothecal dissepiments absent.

*Holotype.*—BM(NH) R28795 (Pl. 9, fig. 1).

*Measurements of the holotype.*—IVW = 7.5, OVW = 9.1, TNS-5 = 10, NMS-5 = 5, CL-HT = 0.5, CL-MAX = 1.2.

*Type locality.*—Neogene, Nivajé Shale, near Santiago, Dominican Republic.

*Material.*—One NMB colony (CCD 2198).

*Remarks.*—The holotype of *Thysanus corbicula* is only a fragment from the growing edge of an elongate colony, and it has a significantly narrower corallum width than the NMB specimen. Nevertheless, the two specimens are similar in the development of the quaternary septa and are therefore considered to represent the same species. The holotype of *T. floridanus* (USNM 79812) (Pl. 9, figs. 11, 12) has a very weakly developed columella that appears partially lamellar; however, the acute septal teeth and paliform lobes indicate that *T. floridanus* is clearly a member of the family Faviidae and the genus *Thysanus*. *T. floridanus* is similar in corallum size and septal development to the holotype of *T. corbicula* (Table 12), and is therefore synonymized. The holotype of *T. vaughani* (FMNH 8294) (Pl. 9, fig. 8) is a tiny, presumably immature specimen with well-developed quaternary septa, and is therefore only questionably synonymized with *T. corbicula.*

*Comparison.*—*T. corbicula* is closest morphologically to *T. excentricus,* from which it is distinguished by its relatively long series, low corallum height, low calical elevation, and unequal quaternary septa. *T. excentricus* has fewer septa per 5 mm, and its septa are equal.

*Occurrence.*—Río Mao: ?Gurabo Formation (loc. NMB 16910).

*Distribution.*—*Thysanus corbicula* ranges in age from Miocene to Late Pliocene. Outside the Upper Miocene of the Dominican Republic, it occurs: (1) possibly in the Lower to Middle Miocene Chipola Formation of Florida, and (2) in the Upper Pliocene Bowden Formation and Old Pera Beds of Jamaica and Caloosahatchee Formation of Florida.

### **Thysanus excentricus** Duncan, 1863
Plate 9, figures 2, 3, 6, 7, 9, 10, 13–17; Plate 10, figures 1, 3, 4;
Text-figures 4, 5, 21, 22

*Thysanus excentricus* Duncan, 1863, pp. 439–440, pl. 16, fig. 3a–c.
? *Thysanus elegans* Duncan *in* Duncan and Wall, 1865, p. 10, pl. 2, fig. 2a, b.
*Thysanus hayesi* Vaughan, 1919, p. 424, pl. 77, fig. 3a, b.

*Description.*—Flabelloid colony shape, free-living, short and small (max. colony length = 3–3.5 cm, width = 1–1.5 cm, height = 1.5–2 cm). Single straight series formed by unidirectional intramural budding. Valley width 10–12 mm. Calicular platform sloping, with 2–3 mm relief. Epitheca absent or very reduced.

Costae well-developed, equal, thick. Septa in three cycles or fewer, with the total number of septa per 5 mm ranging from six to seven. Septa equal in thickness. Primary and secondary septa extend to the columella; tertiary septa are free and extend three-fourths of the distance to the columella. Columella spongy, continuous; approximately one-eighth of the width of the valley. Paliform lobes weakly developed. Septal lobes absent. Wall parathecal, thinner than the primary septa. Endothecal dissepiments reduced or absent; exothecal dissepiments absent.

*Holotype.*—BM(NH) B.M. 46814 (Pl. 9, figs. 6–7).

*Measurements of the holotype.*—IVW = 8, OVW = 11.7, TNS-5 = 8–11, NMS-5 = 5–6, CL-HT = 15.3, CL-MAX = 36.8.

*Type locality.*—Upper Pliocene, Bowden Formation, Jamaica.

*Material.*—Seven NMB colonies (CCD 1171, 2192–2197).

*Remarks.*—Although the quaternary septa are partially developed in the holotype of *T. excentricus,* it resembles the seven NMB colonies in almost every other aspect (Tables 11, 12). The holotypes of *T. elegans* (BM(NH) R28918) (Pl. 9, figs. 9, 10) and *T. hayesi* (USNM 324994) (Pl. 9, figs. 2, 3) are even more similar to the NMB colonies, except that *T. elegans* has a slightly smaller corallum and *T. hayesi* has a slightly larger corallum (Table 12).

*Comparison.*—*T. excentricus* is closest morphologically to *T. corbicula,* from which it is distinguished by its relatively short series, high corallum elevation, high calical elevation, and lack of quaternary septa. *T. corbicula* has more septa per 5 mm, and its septa are unequal.

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16879, 17014). Río Gurabo: Gurabo Fomation (loc. NMB 15837, 15842, 16810).

*Distribution.*—*Thysanus excentricus* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, its occurrences are restricted to the Upper Pliocene and include the following strata: Pinecrest Sandstone, Florida; Bowden Formation and Old Pera Beds, Jamaica; La Cruz Marl and Matanzas, Cuba.

### **Thysanus navicula** (Duncan, 1864), new combination

Plate 11, figures 1–11;
Text-figures 4, 5, 9, 11, 12, 20–22

*Teleiophyllia navicula* Duncan, 1864, p. 36, pl. 4, fig. 1a, b.

*Description.*—Elongate flabelloid colony shape, free-living, intermediate in size (max. colony length = 6–8 cm, width = 1.2–1.5 cm, height = 2 cm). Straight series formed by bidirectional intramural budding. Valley width 10.5–12 mm. Calicular platform steep-sided, with 1–2 mm relief. Epitheca reduced.

Costae well-developed, equal. Septa in three complete cycles, the total number of septa per 5 mm ranging from five to nine. Septa unequal in thickness with primary and secondary septa thicker than tertiary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend nine-tenths of the distance to the columella. Columella spongy, continuous; approximately one-fifth of the width of the valley. Paliform lobes well-developed. Septal lobes absent or reduced. Wall parathecal, thicker than the primary septa. Endothecal dissepiments abundant, thin, vesicular; exothecal dissepiments absent.

*Holotype.*—BM(NH) R28766 (Pl. 11, figs. 1, 2).

*Measurements of the holotype.*—IVW = 9, OVW = 13.9, TNS-5 = 4, NMS-5 = 5–6, CL-HT = 15.3, CL-MAX = 36.8.

*Type locality.*—Neogene, Nivajé Shale, near Santiago, Dominican Republic.

*Material.*—14 NMB colonies, four measured (CCD 2178–2182, 2347, 2348, 2349[2], 2350, 2351[2], 2352, 2364).

*Remarks.*—Duncan (1864) originally designated this species as one of two "genosyntypes" of *Teleiophyllia*; Wells (1936), however, later selected the other "genosyntype," *Teleiophyllia grandis* Duncan, to be the "genolectotype" of *Teleiophyllia.* Although Vaughan (1919) had earlier synonymized Duncan's (1864) two genera *Teleiophyllia* and *Thysanus,* Wells (1936) believed them to be separate, because the two species assigned to *Thysanus* (*T. excentricus, T. corbicula*) had a distinctively broader edge-zone, absent exotheca, and a greatly reduced epitheca. Our work supports Wells' (1936) recognition of *Thysanus* as distinct; it shows, however, that "*Teleiophyllia*" *navicula* Duncan is morphologically and phylogenetically closer to species of *Thysanus* (Text-fig. 21) than to *Teleiophyllia* (= *Manicina*).

*Comparison.*—*T. navicula* differs from *T. corbicula* and *T. excentricus* in its bidirectional budding; however, it is similar to *T. corbicula* and *T. excentricus* in that it has a parathecal wall and lacks exothecal dissepiments. The four flabelloid species of *Manicina* described herein all have partially septothecal walls and exothecal dissepiments. Like *T. excentricus, T. navicula* has only three septal cycles; however, unlike *T. excentricus,* its septa are unequal.

*Occurrence.*—Río Cana: Cercado Formation (loc. NMB 16836), Gurabo Formation (loc. NMB 16831), Mao Formation (loc. NMB 16873). Río Gurabo: Gurabo Formation (loc. 15806, 15811, 15837, 16810).

*Distribution.*—*Thysanus navicula* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it is known only from Upper Pliocene Bowden Formation and Old Pera Beds of Jamaica.

### Genus **Hadrophyllia**, new genus

not *Hadrophyllum* Milne Edwards and Haime, 1850, p. lxvii.

*Type species.*—*Hadrophyllia saundersi,* n. sp. Upper Miocene, locality NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. (Holotype figured on Pl. 12, figs. 1, 2.)

*Diagnosis.*—Free-living, flabelloid colonies formed by intramural budding. Series curved. Single valley system. Costae well-developed. Parathecal corallite walls. Columella narrow, spongy, continuous, lacking paliform and septal lobes. Abundant vesicular endo- and exothecal dissepiments. Epitheca absent.

*Etymology.*— From the Greek *hadros* (thick, bulky) plus *phyllo* (leaf). Gender: feminine.

*Remarks.*—As shown by phylogenetic analysis in the section on "Taxonomic Methods" (pp. 29–34), *Hadrophyllia* differs from *Manicina* by its lack of septal lobes and epitheca. It differs from *Thysanus* by its lack of paliform lobes and by having abundant endothecal and exothecal dissepiments. As shown on Text-figure 21, it forms its own separate branch on the cladogram, which is supported by two apomorphies: very large valley width and widely spaced septa. The genus contains only one species (*Hadrophyllia saundersi*) and occurs only in the Upper Miocene to Lower Pliocene of the Dominican Republic. It is currently extinct.

### **Hadrophyllia saundersi**, new species

Plate 9, figures 18, 19; Plate 12, figures 1–6;
Plate 13, figures 1, 3, 5;
Text-figures 4, 5, 9, 11, 12, 20–22

? *Thysanus crassicostatus* Vaughan *in* Vaughan and Hoffmeister, 1925, p. 326, pl. 3, figs. 5–8.

*Diagnosis.*—Bidirectional flabelloid forms with large valleys and well-developed exothecae; three widely spaced, equal septal cycles.

*Description.*—Elongate flabelloid colony shape, free-living, intermediate in size (max. colony length = 11–12 cm, width = 3–4.5 cm, height = 3–4 cm). Gently curving series formed by bidirectional intramural budding. Valley width 16–20 mm. Calicular platform sloping, with 5–8 mm relief. Epitheca reduced or absent.

Costae well-developed, equal. Septa in slightly more than three cycles, with the total number of septa per 5 mm ranging from five to six. Septa equal in thickness. Primary and secondary septa extend to the columella; tertiary septa are free or fused and extend nine-tenths of the distance to the columella. Well-developed teeth along septal margins. Columella spongy, continuous; approximately one-tenth of the width of the valley. Paliform lobes weak. Septal lobes absent. Wall parathecal, thicker than the primary septa. Endothecal dissepiments abundant, moderately thick, vesicular; exothecal dissepiments abundant, vesicular.

*Etymology.*—Named after John B. Saunders (Naturhistorisches Museum Basel), who collected and studied many of the microfossils in the Saunders *et al.* (1986) collections at the NMB.

*Holotype.*—NMB D6241 (Pl. 12, figs. 1, 2; Pl. 13, fig. 5).

*Paratypes.*—NMB D6237, D6238, D6239 (Pl. 12, figs. 3, 4; Pl. 13, fig. 3), D6240, D6242 (Pl. 12, figs. 5, 6; Pl. 13, fig. 1), D6243, D6244.

*Measurements of the holotype.*—IVW = 19.3, OVW = 42.8, TNS-5 = 4.5, NMS-5 = 4.5, CL-HT = 3.5, CL-MAX = 10.5.

*Type locality.*—Loc. NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. Upper Miocene.

*Material.*—10 NMB colonies, eight measured (CCD 0010, 2059–2065, 2069, 2359).

*Remarks.*—The holotype of "*T. crassicostatus*" (MCZ 9280) is generally similar to *H. saundersi* in corallum height and in septal development, but is only a partial fragment of one side of a valley, and its corallum (OVW) and valley (IVW) widths cannot be estimated with certainty. Therefore, it can only be questionably synonymized.

*Comparison.*—*Hadrophyllia saundersi* is unique among flabelloid members of the Faviidae in that it lacks paliform and septal lobes and possesses wide valleys, an extensive exotheca, and only three widely spaced, equal septal cycles.

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16827), Mao Formation (loc. NMB 16884). Río Gurabo: Gurabo Formation (loc. NMB 15837, 15846, 15847, 15858, 15859, 16883).

*Distribution.*—*Hadrophyllia saundersi* occurs only in the Upper Miocene to Lower Pliocene of the Dominican Republic.

## Genus **Manicina** Ehrenberg, 1834

*Manicina* Ehrenberg, 1834, p. 325.
? *Podiasteria* Ehrenberg, 1834, p. 326.
*Teleiophyllia* Duncan, 1864, p. 34.

*Type species.*—*Madrepora areolata* Linnaeus, 1758, p. 795 (by subsequent designation, Milne Edwards and Haime, 1848). Recent, West Indies. (Holotype = BM(NH) 28.3.1.32)

*Diagnosis.*—Free-living or attached flabelloid and meandroid colonies formed usually by bidirectional and/or multidirectional intramural budding, and less commonly by extramural budding. Wide (> 10 mm) and in places sinuous series with indistinct centers. Single or multiple valley systems. Costae well-developed. Parathecal or partially septothecal corallite walls. Columella moderately well-developed, continuous, in places with well-developed septal lobes. Abundant vesicular endo- and exothecal dissepiments. Epitheca well-developed.

*Remarks.*—The genus "*Teleiophyllia,*" previously characterized as possessing bidirectional flabelloid colony forms (Wells, 1956, p. F403), is synonymized with the genus *Manicina* based on results of the phylogenetic analysis (Text-fig. 21). As a result, we have expanded the diagnosis of *Manicina* to include both flabelloid and meandroid forms and place greater emphasis on the presence of endo- and exothecal dissepiments and well-developed septal lobes. *Manicina* differs from *Hadrophyllia* by having septal lobes and epitheca. It differs from *Thysanus* by having abundant endothecal and exothecal dissepiments.

The genus *Manicina* occurs today only in the Caribbean region (Veron, 1993) and consists of two species, *M. areolata* and *M. mayori* (Table 3). Throughout its duration, *Manicina* has been restricted to the Caribbean, and its oldest occurrences are in the Upper Miocene of the Dominican Republic (Budd *et al.*, 1994b).

### **Manicina geisteri**, new species

Plate 12, figures 7–11; Plate 13, figures 2, 4, 6;
Text-figures 4, 5, 9–12, 20–22

*Diagnosis.*—Bidirectional flabelloid forms with moderate-sized valleys and well-developed exothecae; four unequal septal cycles.

*Description.*—Triangular to elongate flabelloid colony shape, free-living, intermediate in size (max. colony length = 6–10 cm, width = 1.5–3 cm, height = 4–5.5 cm). Curved to tightly sinuous series formed by bidirectional intramural budding. Valley width 16–20 mm. Calicular platform sloping, with 5–6 mm relief. Epitheca reduced.

Costae well-developed, unequal, with thinner costae extending from quaternary septa. Septa in four cycles or slightly less, with the total number of septa per 5 mm ranging from eight to 12. Septa unequal in thickness with primary, secondary, and tertiary septa thicker than quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend nine-tenths of the distance to the columella; quaternary septa are free and extend less than one-tenth of the distance to the columella. Well-developed teeth along septal margins. Columella spongy, continuous; approximately one-fifth of the width of the valley. Paliform lobes weak. Septal lobes in places well-developed. Wall parathecal, thicker than the primary septa. Endothecal dissepiments abundant, moderately thick, vesicular; exothecal dissepiments abundant, vesicular.

*Etymology.*—Named after Jörn Geister (Geologisches Institut, Universität Bern), who collected many of the corals in the Saunders *et al.* (1986) collections at the NMB.

*Holotype.*—NMB D6173 (Pl. 12, figs. 10, 11; Pl. 13, fig. 2).

*Paratypes.*—NMB D6170, D6171, D6172, D6174 (Pl. 12, fig. 7), D6175 (Pl. 12, figs. 8, 9; Pl. 13, fig. 4), D6176, D6177 (Pl. 13, fig. 6).

*Measurements of the holotype.*—IVW = 19.2, OVW = 29.0, TNS-5 = 9, NMS-5 = 6, CL-HT = 4.8, CL-MAX = 9.0.

*Type locality.*—Loc. NMB 16844, Río Cana, Cercado Formation, Dominican Republic. Upper Miocene.

*Material.*—18 NMB colonies, six measured (CCD 2066–2068, 2070, 2071[5], 2072, 2073, 2184, 2185, 2187[2], 2188, 2189, 2362).

*Comparison.*—*Manicina geisteri* is most similar morphologically to *M. grandis*, but is distinguished by wider valleys and better developed quaternary septa. Unlike *M. grandis*, most specimens also contain well-developed septal lobes.

*Occurrence.*—Río Cana: Cercado Formation (loc. NMB 16835, 16842, 16844), Gurabo Formation (loc. NMB 16824, 16827, 16859, 16862). Río Gurabo: Gurabo Formation (loc. NMB 15844, 15850, 15872). Río Mao: ?Gurabo Formation: (loc. NMB 16910).

*Distribution.*—*Manicina geisteri* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it is known from the Upper Miocene Lirio Limestone of Isla de Mona, Puerto Rico, and from the Upper Pliocene Bowden Formation of Jamaica.

### **Manicina grandis** (Duncan, 1864), new combination

Plate 14, figures 1–7; Plate 15, figures 1–8;
Plate 17, figures 2, 4, 6;
Text-figures 4, 5, 9–13, 20–22

*Teleiophyllia grandis* Duncan, 1864, pp. 34–35, pl. 3, fig. 5a, b.

*Description.*—Triangular to elongate flabelloid colony shape, free-living, intermediate in size (max. colony length = 8–18 cm, width = 1.5–2 cm, height = 4–5.5 cm). Curved to straight series formed commonly by bidirectional and rarely by tridirectional intramural budding. Valley width 11.5–16 mm. Calicular platform steep-sided, with 3–6 mm relief. Epitheca well-developed.

Costae well-developed, equal. Septa in slightly more than three cycles, the total number of septa per 5 mm ranging from seven to nine. Septa unequal in thickness with primary and secondary septa thicker than tertiary septa, and tertiary septa thicker than quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend nine-tenths of the distance to the columella; quaternary septa are free and extend less than one-tenth of the distance to the columella. Columella spongy, continuous; approximately one-tenth of the width of the valley. Paliform lobes moderately well-developed. Septal lobes variably developed. Wall parathecal, thinner than the primary septa. Endothecal dissepiments abundant, moderately thick, vesicular; exothecal dissepiments abundant, thin, vesicular.

*Holotype.*—BM(NH) R28754 (Pl. 14, figs. 1–3).

*Measurements of the holotype.*—IVW = 18, OVW = 23, TNS-5 = 11, NMS-5 = 6, CL-HT = 12, CL-MAX = > 31.5.

*Type locality.*—Neogene, Nivajé Shale, near Santiago, Dominican Republic.

*Material.*— > 90 NMB colonies, 34 measured (CCD 2074–2077[2], 2078[2]–2079, 2081–2086[2], 2087–2094[> 10], 2095–2113[4], 2114–2115[2], 2116–2121[2], 2122–2136, 2191, 2353–2358, 2360–2361); one TU colony [CCD 2372]. 10 colonies figured (CCD 2081 [Pl. 17, figs. 2, 4], 2109 [Pl. 14, fig. 5], 2120 [Pl. 15, figs. 6, 7], 2121 [Text-fig. 20], 2122 [Pl. 15, fig. 3], 2126 [Pl. 15, figs. 1, 2, 4], 2127 [Text-fig. 20], 2130 [Pl. 14, figs. 6, 7], 2131 [Pl. 17, fig. 6], 2361 [Pl. 14, fig. 4; Pl. 15, fig. 8]).

*Comparison.*—*Manicina grandis* is distinguished in the statistical analyses from other species of flabelloid *Manicina* by having a relatively weak exotheca and three unequal septal cycles with poorly developed quaternary septa. The specimens in the NMB cluster for *M. grandis* consist of two morphotypes: (1) having long, narrow, straight valleys and reduced septal lobes, and (2) having short, wide, curved valleys and well-developed septal lobes. Study of more and better preserved material is needed in order to confirm the distinctiveness of these two morphotypes.

*Occurrence.*—Río Amina: Gurabo Formation (loc. NMB 16805). Río Cana: Cercado Formation (loc. NMB 16835, 16837, 16839, 16842, 16844, 16852, 16853, 16857), Gurabo Formation (loc. NMB 16813, 16815, 16817, 16818, 16819, 16827, 16828, 16830, 16831, 16858, 16859, 16865), Mao Formation (loc. NMB 16872). Río Gurabo: Cercado Formation (loc. NMB 15901), Gurabo Formation (loc. NMB 15809, 15814, 15815, 15837, 15838, 15851, 15855, 15866, 15867, 15868, 15870, 15883, 15885, 15887, 15888, 15891, 16808, 16810, 16921, 16934). Río Mao: ?Gurabo Formation (loc. NMB 16910, 16914; loc. TU 1293).

*Distribution.*—*Manicina grandis* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it is known only from the Upper Pliocene Bowden Formation of Jamaica.

### **Manicina jungi**, new species

Plate 16, figures 1–12; Plate 17, figures 1, 3, 5;
Text-figures 4, 5, 9–12, 20–22

*Diagnosis.*—Distinctively triangular, bidirectional flabelloid forms with narrow valleys; four closely spaced, unequal septal cycles.

*Description.*—Triangular flabelloid colony shape, free-living, small to intermediate in size (max. colony length = 8–10 cm, width = 1.2–1.7 cm, height = 4.5–6 cm). Slightly sinuous series formed by bidirectional intramural budding. Valley width 10.5–13 mm. Calicular platform steep-sided, with 3–5 mm relief. Epitheca extremely well-developed.

Costae well-developed, unequal, with thinner costae extending from quaternary septa. Septa in four complete cycles, with the total number of septa per 5 mm ranging from 12 to 15. Septa unequal in thickness with primary, secondary, and tertiary septa thicker than quaternary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend nine-tenths of the distance to the columella; quaternary septa are free and extend one-third of the distance to the columella. Columella spongy, continuous; approximately one-tenth of the width of the valley. Paliform lobes in places well-developed. Septal lobes absent or weak. Wall parathecal, equal in thickness to the primary septa. Endothecal dissepiments common, thin, vesicular; exothecal dissepiments thin, vesicular.

*Etymology.*—Named after Peter Jung (Naturhistorisches Museum Basel), who collected and studied the systematics of many of the macrofossils in the Saunders *et al.* (1986) collections at the NMB.

*Holotype.*—NMB D6220 (Pl. 16, figs. 1, 2).

*Paratypes.*—NMB D6020 (Pl. 16, figs. 3, 4), D6090, D6215 (Pl. 16, figs. 9, 10, 12), D6216–D6219, D6221 (Pl. 16, figs. 5, 6), D6222–D6227, D6228 (Pl. 17, figs. 1, 3), D6229, D6230 (Pl. 17, fig. 5), D6231 (Pl. 16, figs. 7, 8, 11).

*Measurements of the holotype.*—IVW = 14.4, OVW = 18.1, TNS-5 = 16, NMS-5 = 8, CL-HT = 4.7, CL-MAX = 7.9.

*Type locality.*—Loc. NMB 16821, Río Cana, Gurabo Formation, Dominican Republic. Upper Miocene.

*Material.*—49 NMB colonies, 16 measured (CCD 2137–2150, 2151[2], 2152–2177, 2186, 2342–2345[2], 2346).

*Comparison.*—*Manicina jungi* is most similar morphologically to *M. geisteri,* but is distinguished by its narrower valleys and better developed quaternary septa. Like *M. geisteri,* most specimens also contain well-developed internal lobes, but the internal lobes of *M. jungi* are smaller and paliform.

*Occurrence.*—Río Cana: Cercado Formation (loc. NMB 16842, 16844, 16852), Gurabo Formation (loc. NMB 16814, 16818, 16821, 16825, 16831, 16833, 16862). Río Gurabo: Gurabo Formation (loc. NMB 15814, 15850, 15863, 15866, 15889, 15964). Río Yaque del Norte: ?Gurabo Formation (loc. NMB 17268).

*Distribution.*—*Manicina jungi* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it occurs only in the Upper Pliocene Bowden Formation of Jamaica.

### **Manicina pliocenica** Gane, 1895

Plate 18, figure 4; Plate 19, figure 2;
Text-figures 5, 19–22

*Manicina pliocenica* Gane, 1895, p. 10.

*Description.*—Massive ellipsoidal colony shape, free-living, small to intermediate in size (colony length = 8–10 cm, width = 5–6 cm, height = 4–5 cm).

Meandroid colony form with a single valley system. Exclusively intramural budding, with bidirectional and tridirectional budding geometries. Valleys sinuous and separated by shallow ambulacra.

Valley width 10–12 mm. Calicular platform steep-sided, with 12–15 mm relief. Epitheca well-developed, thick. Costae well-developed, equal, continuous. Septa in three cycles, the total number of septa per 5 mm ranging from six to seven. Septa thin and slightly unequal in thickness; primary and secondary septa thicker than tertiary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend three-fourths of the distance to the columella. Columella spongy, continuous; approximately one-third to one-fourth of the width of the valley. Septal lobes well-developed. Paliform lobes weak. Wall parathecal, in places double, thinner than the primary septa. Endothecal dissepiments abundant, vesicular, intermediate in thickness; exothecal dissepiments abundant, vesicular, thin. Coenosteum porous, moderately wide. Distance between adjacent valley walls 5–8 mm.

*Neotype (herein selected).*—NMB D6165 (Pl. 19, fig. 2).

*Measurements of the neotype.*—IVW = 10.0, TNS-5 = 7, NMS-5 = 5, NND = 6.4, TT = 0.7.

*Neotype locality.*—Loc. NMB 16822, Río Cana, Gurabo Formation, Dominican Republic. Upper Miocene.

*Material.*—Four NMB colonies, one measured (NMB D6163 = CCD 2048 [Pl. 18, fig. 4], NMB D6164 = CCD 2050 [Text-fig. 20], CCD 2058).

*Remarks.*—The original description of *M. pliocenica* Gane, 1895 states that, like the four NMB colonies, *M. pliocenica* has slightly wider valleys and fewer septa per 5 mm than *M. areolata.* No exact dimensions are given in this description, the holotype is lost (T. Coffer, written commun., 1996), and no photographs have been published of the holotype: therefore, we designate a neotype for this species from the NMB Dominican Republic collections. Gane's (1895) original specimen was from the Late Pliocene Caloosahatchee Formation of Florida.

*Comparison.*—*M. pliocenica* is most similar morphologically to *M. areolata,* but is distinguished by its fewer numbers of major septa and total septa per 5 mm and its more widely spaced valleys. It is similar to *M. areolata* in its small, free-living colonies with deep sinuous valleys united in a single valley system.

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16817, 16822), Mao Formation (loc. NMB 16884).

*Distribution.*—*M. pliocenica* ranges in age from Early to Late Pliocene. Outside the Dominican Republic, it occurs in the Upper Pliocene Bowden Formation and Old Pera Beds of Jamaica and the Caloosahatchee Formation of Florida.

### **Manicina puntagordensis** Weisbord, 1968, new rank

Plate 20, figures 1–6;
Text-figures 5, 21, 22

*Manicina areolata puntagordensis* Weisbord, 1968, p. 51–57, pl. 4, fig. 5; pl. 5, figs. 1–5; pl. 12, fig. 4.

*Description.*—Massive ellipsoidal colony shape, free-living, intermediate to large in size (colony length = 20–22 cm, width = 10–11 cm, height = 6–7 cm). Meandroid colony form with highly regular single valley system. Exclusively intramural budding, with bidirectional and tridirectional budding geometries. Valleys straight and separated by narrow ambulacra.

Valley width 13–17 mm. Calicular platform sloping, with 8–9 mm relief. Epitheca well-developed, thick. Costae well-developed, equal, continuous. Septa in three cycles, the total number of septa per 5 mm ranging from five to seven. Septa thin and slightly unequal in thickness, with primary and secondary septa thicker than tertiary septa. Primary and secondary septa extend to the columella; tertiary septa are free and extend nine-tenths of the distance to the columella. Columella spongy, continuous, in places appearing almost lamellar; approximately one-fourth to one-fifth of the width of the valley. Septal and paliform lobes moderately well-developed. Wall parathecal, in places double, thinner than the primary septa. Endothecal dissepiments abundant, vesicular, intermediate in thickness; exothecal dissepiments thick. Coenosteum porous, narrow. Distance between adjacent valley walls 1.5–3.5 mm.

*Holotype.*—PRI 27560 (Pl. 20, figs. 1, 2).

*Measurements of the holotype.*—IVW = 15.2, TNS-5 = 7, NMS-5 = 5, NND = 1.7–2, TT = 0.3, CL-HT = 5.3, CL-MIN = 8.9, CL-MAX = 11.

*Type locality.*—Punta Gorda anticline (W-23), Playa Grande Formation, Venezuela. Lower Pliocene.

*Material.*—Seven NMB colonies, three measured (CCD 2049, 2052–2054, 2056, 2057, 2363).

*Remarks.*—*M. puntagordensis* may actually represent a complex of two or more species, but more material is needed to confirm the distinctiveness of species within the complex. Two morphotypes can be recognized in the NMB material: (1) with large valleys (IVW 15 mm), convex septa, and more numerous septa per 5 mm (TNS-5 7) [CCD 2056]; and (2) with small valleys (IVW 15 mm), concave septa, and fewer septa per 5 mm (TNS-5 7) [CCD 2049, 2052–2054, 2057, 2363). The holotype is more similar to the first morphotype.

*Comparison.*—*M. puntagordensis* is most similar morphologically to *M. areolata,* but is distinguished by its slightly larger colonies, fewer septa per 5 mm, lamellar-like columella, and its more regular, less sinuous, larger valleys. It is similar to *M. areolata* in that it forms ellipsoidal free-living colonies, whose valleys are united in a single valley system.

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16819, 16827, 16858, 16859).

*Distribution.*—*M. puntagordensis* ranges in age from Late Miocene to Late Pliocene. Outside the Dominican Republic, it occurs in the Lower Pliocene Playa Grande Formation of Venezuela and Río Banano Formation of Costa Rica; and the Upper Pliocene Pinecrest Sandstone, Bowden Formation and Old Pera Beds of Jamaica, Moín Formation of Costa Rica, and Caloosahatchee Formation of Florida.

### **Manicina** n. sp. aff. **mayori** Wells, 1936

Plate 18, figures 3, 5; Plate 19, figure 1;
Text-figures 5, 21, 22

*Description.*—Massive hemispherical colony shape, attached, intermediate to large in size (colony diameter = 10–12 cm). Meandroid colony form with multiple valley systems. Budding, predominantly intramural, with bidirectional and tridirectional budding geometries. Valleys sinuous and separated by narrow ambulacra.

Valley width 18–19 mm. Calicular platform sloping, with 12–15 mm relief. Epitheca moderately well-developed, thick. Costae well-developed, equal, continuous. Septa in three cycles, with the total number of septa per 5 mm ranging from 6 to 7. Septa thin and equal in thickness. Primary and secondary septa extend to the columella; tertiary septa are free and extend three-fourths of the distance to the columella. Columella spongy, continuous; approximately one-fifth of the width of the valley. Paliform lobes well-developed. Wall parathecal, in places double, thinner than the primary septa. Endothecal dissepiments abundant, vesicular, intermediate in thickness; exothecal dissepiments thick. Coenosteum porous, narrow. Distance between adjacent valley walls 1–2 mm.

*Material.*—One NMB colony, one measured (NMB D6166 = CCD 2055 [Pl. 18, figs. 3, 5; Pl. 19, fig. 1]).

*Remarks and Comparison.*—*M.* n. sp. aff. *mayori* is most similar morphologically to *M. mayori* (Pl. 18, fig. 6; Pl. 19, figs. 3, 5), but is distinguished by its wider, more closely spaced valleys and thicker theca. It is similar to *M. mayori* in its large, attached colonies composed of multiple sinuous valleys. This species is left in open nomenclature because it is represented by only one specimen.

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16859).

*Distribution.*—*M.* n. sp. aff. *mayori* is known only from the Lower Pliocene of the Dominican Republic.

### Genus **Colpophyllia** Milne Edwards and Haime, 1848

*Colpophyllia* Milne Edwards and Haime, 1848, p. 492.

*Type species.*—*Meandrina gyrosa* Lamarck, 1816, p. 247. Recent, West Indies (= *Madrepora natans* Houttuyn, 1772). (Holotype is lost [Matthai, 1928; Wells, 1936].)

*Diagnosis.*—Attached meandroid colonies formed usually by bidirectional and/or multidirectional intra- and extramural budding. Wide (usually > 10 mm) and in places deep (> 10 mm) series with distinct centers. Multiple valley systems. Septa widely spaced, thin. Parathecal, double corallite walls. Columella spongy and discontinuous, with lamellar linkage and in places with small paliform lobes. Abundant thin vesicular endothecal dissepiments. Epitheca absent or reduced.

*Remarks.*—As shown in Text-figure 21, the genus *Colpophyllia* is a well-supported clade that is restricted today to the Caribbean region (Veron, 1993), and it consists of three or more species (Table 3). Its oldest occurrences are in the Middle Eocene of Jamaica (Budd *et al.,* 1992). Through the Tertiary, it was especially abundant in the Mediterranean during the Oligocene (Pfister, 1980) and Miocene (Chevalier, 1962), and in the Caribbean during the Oligocene (Vaughan, 1919; Frost and Langenheim, 1974). It has never been found as a fossil in the Indo-Pacific region (Vaughan and Wells, 1943).

### **Colpophyllia natans** (Houttuyn, 1772)

Plate 21, figures 1, 2, 4, 6;
Text-figures 5, 14, 21, 22

*Madrepora natans* Houttuyn, 1772, p. 124; Esper, 1795, pp. 140–143, pl. 23 (figured in Matthai, 1928, pl. 67, figs. 1–2) (not seen).

*Description.*—Massive hemispherical colony shape, attached, large in size (colony diameter >> 10 cm). Meandroid colony form with multiple valley systems. Intra- and extramural budding, with bidirectional and tridirectional budding geometries. Long, sinuous, mostly continuous valleys separated by narrow ambulacra.

Valley width 15–20 mm. Calicular platform sloping, with 4–10 mm relief. Costae well-developed, equal, discontinuous. Septa in three cycles, the total number of septa per 5 mm ranging from four to five. Septa very thin and equal in thickness. Primary and secondary septa extend to the columella; tertiary septa are free and extend three-fourths of the distance to the columella. Columella spongy, discontinuous with lamellar linkage; approximately one-fifth of the width of the valley. Paliform lobes weak. Wall parathecal, in places double, thinner than the primary septa. Endothecal dissepiments abundant, vesicular, thin; exothecal dissepiments intermediate in thickness. Coenosteum porous, narrow. Distance between adjacent valley walls 3–5 mm.

*Holotype.*—This specimen has long been lost (Matthai, 1928).

*Neotype* (designated by Matthai, 1928).—*Madrepora natans* Esper, 1795, pp. 140–143, pl. 23 (figured in Matthai, 1928, pl. 67, figs. 1–2). This specimen is also currently lost (Scheer, 1990).

*Measurements of a figured specimen* (USNM 83111, Pl. 21, fig. 1).—IVW = 15–22, TNS-5 = 5, NMS-5 = 3, CL-HT = 60, CL-MIN = 140, CL-MAX = 210. Center-to-center distance between corallites within a series = 10–15 mm. Calice height = 15–20 mm.

*Type locality.*—Unknown.

*Material.*—One NMB colony (NMB D6022 = CCD2011 [Pl. 21, figs. 2, 4, 6]).

*Remarks.*—The Recent species of *Colpophyllia* are greatly in need of revision. Currently two species (*C. natans* [Houttuyn, 1772] and *C. breviserialis* Milne Edwards and Haime, 1849 [Pl. 21, fig. 3]) are widely recognized in the Caribbean (Wells, 1973), and a third species *C. amaranthus* (Houttuyn, 1772) (Pl. 21, fig. 5) is accepted by some authors (*e.g.*, Matthai, 1928). Our own ongoing studies of collections from the Plio-Pleistocene Moín Formation near Limón, Costa Rica, suggests that *C. natans* may consist of at least two morphotypes, one with wide valleys (IVW > 15) and the other with narrow valleys (IVW < 15). The wide-valley form most closely resembles *C. natans* as it is most commonly distinguished (see Matthai, 1928), whereas the narrow-valley form resembles *C. fissa* (Ehrenberg, 1834) figured by Matthai (1928) on plate 65, figure 5. More detailed molecular and morphometric studies are needed to determine whether these two morphotypes indeed represent distinct species.

*Comparison.*—As indicated in Table 14, other than *C. fissa, C. natans* is closest morphologically to *C. amaranthus.* Unlike *C. natans,* however, *C. amaranthus* has discontinuous, shorter, deeper valleys and more septa. The Upper Oligocene species *C. willoughbiensis* (Vaughan, 1919) is similar in valley size and shape to *C. fissa,* but differs markedly from it and all other described Neogene species in having unusually high numbers of septa (19–22 septa per cm).

*Occurrence.*—Río Cana: Gurabo Formation (loc. NMB 16818).

*Distribution.*—*C. natans* ranges in age from Early Pliocene to Recent. Outside the Lower Pliocene of the Dominican Republic, it occurs in the Lower Pliocene Río Banano Formation of Costa Rica; the Upper Pliocene Pinecrest Sands of Florida, Hope Gate Formation and Old Pera Beds of Jamaica, and Moín Formation of Costa Rica; the Lower Pleistocene Manchioneal Formation of Jamaica; the Upper Pleistocene Key Largo Formation of Florida and Falmouth Formation of Jamaica and Upper Pleistocene coastal terraces near Santo Domingo, Dominican Republic, and on San Andrés, Colombia; and the Recent of the Caribbean region. It also possibly occurs in the Miocene of San Andrés, Colombia.

Appendix.—List of all NMB specimens from the Dominican Republic that belong to the family Faviidae and are treated in this monograph.

| CCD # | NMB catalog # | Type status | Genus | Species | NMB locality # | River |
|---|---|---|---|---|---|---|
| 0057 | NMB D6140 | figured | *Caulastraea* | *portorcensis* | 15834 | Río Gurabo |
| 2334 | NMB D6141 | figured | *Caulastraea* | *portoricensis* | 15822 | Río Gurabo |
| 2011 | NMB D6022 | figured | *Colpophyllia* | *natans* | 16818 | Río Cana |
| 2012 | — | — | *Diploria* | *zambensis* | 16875 | Río Cana |
| 2013 | — | — | *Diploria* | *zambensis* | 16875 | Río Cana |
| 2014 | NMB D6150 | paratype | *Diploria* | *zambensis* | 15808 | Río Gurabo |
| 2015 | NMB D6151 | paratype | *Diploria* | *zambensis* | 16881 | Río Cana |
| 2029 | NMB D6152 | paratype | *Diploria* | *zambensis* | 15830 | Río Gurabo |
| 2030 | NMB D6153 | paratype | *Diploria* | *zambensis* | 16815 | Río Cana |
| 2031 | NMB D6018 | holotype | *Diploria* | *zambensis* | 16817 | Río Cana |
| 2032 | NMB D6154 | paratype | *Diploria* | *zambensis* | 16817 | Río Cana |
| 2033 | NMB D5788 | paratype | *Diploria* | *zambensis* | 16817 | Río Cana |
| 2034 | — | — | *Diploria* | *zambensis* | 16877 | Río Cana |
| 2035 | NMB D5790=57 | paratype | *Diploria* | *zambensis* | 16881 | Río Cana |
| 2036 | NMB D6155 | paratype | *Diploria* | *zambensis* | 16881 | Río Cana |
| 2037 | NMB D6156 | paratype | *Diploria* | *zambensis* | 16881 | Río Cana |
| 2038 | — | — | *Diploria* | *zambensis* | 16884 | Río Cana |
| 2039 | NMB D6157 | paratype | *Diploria* | *zambensis* | 16921 | Río Gurabo |
| 2040 | NMB D6158 | paratype | *Diploria* | *zambensis* | 16921 | Río Gurabo |
| 2041 | NMB D6159 | paratype | *Diploria* | *zambensis* | 16921 | Río Gurabo |
| 2365 | — | — | *Diploria* | *zambensis* | 16881 | Río Cana |
| 2016 | — | — | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2017 | — | — | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2018 | — | — | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2019 | NMB D6142 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2020 | NMB D6143 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2021 | NMB D6144 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2022 | — | — | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2023 | NMB D6145 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2024 | NMB D6146 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2025 | — | — | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2026 | NMB D6147 | holotype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2027 | NMB D6148 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2028 | NMB D6149 | paratype | *Favia* | *maoadentrensis* | 16884 | Río Cana |
| 2042 | — | — | *Favia* | *maoadentrensis* | 16855 | Río Cana |
| 2044 | NMB D6162 | figured | *Favia* | aff. *dominicensis* | 16943 | Río Yaque del Norte |
| 2045 | NMB D6160 | figured | *Favia* | *dominicensis* | 17284 | Río Yaque del Norte |
| 2046 | NMB D6161 | — | *Favia* | *dominicensis* | 17284 | Río Yaque del Norte |
| 2047 | — | — | *Favia* | *dominicensis* | 17284 | Río Yaque del Norte |
| 2043 | NMB D6017 | figured | *Favia* | *vokesae* | 16855 | Río Cana |
| 2048 | NMB D6163 | figured | *Manicina* | *pliocenica* | 16817 | Río Cana |
| 2050 | NMB D6164 | figured | *Manicina* | *pliocenica* | 16822 | Río Cana |
| 2051 | NMB D6165 | figured | *Manicina* | *pliocenica* | 16822 | Río Cana |
| 2058 | — | — | *Manicina* | *pliocenica* | 16884 | Río Cana |
| 2055 | NMB D6166 | figured | *Manicina* | aff. *mayori* | 16859 | Río Cana |
| 2049 | NMB D6167 | — | *Manicina* | *puntagordensis* | 16819 | Río Cana |
| 2052 | NMB D6168 | figured | *Manicina* | *puntagordensis* | 16827 | Río Cana |
| 2053 | — | — | *Manicina* | *puntagordensis* | 16858 | Río Cana |
| 2054 | — | — | *Manicina* | *puntagordensis* | 16859 | Río Cana |
| 2056 | NMB D6169 | — | *Manicina* | *puntagordensis* | 16859 | Río Cana |
| 2057 | NMB D6019 | figured | *Manicina* | *puntagordensis* | 16859 | Río Cana |
| 2363 | NMB D6107 | — | *Manicina* | *puntagordensis* | 16858 | Río Cana |
| 2066 | NMB D6170 | paratype | *Manicina* | *geisteri* | 15872 | Río Gurabo |
| 2067 | NMB D6171 | paratype | *Manicina* | *geisteri* | 16824 | Río Cana |
| 2068 | — | — | *Manicina* | *geisteri* | 16827 | Río Cana |
| 2070 | NMB D6172 | paratype | *Manicina* | *geisteri* | 16827 | Río Cana |
| 2071 | — | — | *Manicina* | *geisteri* | 16835 | Río Cana |
| 2072 | — | — | *Manicina* | *geisteri* | 16842 | Río Cana |
| 2073 | NMB D6173 | holotype | *Manicina* | *geisteri* | 16844 | Río Cana |
| 2184 | NMB D6174 | paratype | *Manicina* | *geisteri* | 15844 | Río Gurabo |

Appendix.—Continued.

| CCD # | NMB catalog # | Type status | Genus | Species | NMB locality # | River |
|---|---|---|---|---|---|---|
| 2185 | NMB D6175 | paratype | *Manicina* | *geisteri* | 15850 | Río Gurabo |
| 2187 | NMB D6176 | paratype | *Manicina* | *geisteri* | 16859 | Río Cana |
| 2188 | NMB D6177 | paratype | *Manicina* | *geisteri* | 16862 | Río Cana |
| 2189 | — | — | *Manicina* | *geisteri* | 16910 | Río Mao |
| 2362 | NMB D6105 | — | *Manicina* | *geisteri* | 16827 | Río Cana |
| 2074 | — | — | *Manicina* | *grandis* | 15809 | Río Gurabo |
| 2075 | NMB D6178 | — | *Manicina* | *grandis* | 15809 | Río Gurabo |
| 2076 | NMB D6179 | — | *Manicina* | *grandis* | 15814 | Río Gurabo |
| 2077 | NMB D6180 | — | *Manicina* | *grandis* | 15815 | Río Gurabo |
| 2078 | — | — | *Manicina* | *grandis* | 15837 | Río Gurabo |
| 2079 | — | — | *Manicina* | *grandis* | 15838 | Río Gurabo |
| 2081 | NMB D6181 | figured | *Manicina* | *grandis* | 15855 | Río Gurabo |
| 2082 | — | — | *Manicina* | *grandis* | 15855 | Río Gurabo |
| 2083 | — | — | *Manicina* | *grandis* | 15866 | Río Gurabo |
| 2084 | NMB D6182 | — | *Manicina* | *grandis* | 15867 | Río Gurabo |
| 2085 | NMB D6183 | — | *Manicina* | *grandis* | 15868 | Río Gurabo |
| 2086 | NMB D6184 | — | *Manicina* | *grandis* | 15868 | Río Gurabo |
| 2087 | — | — | *Manicina* | *grandis* | 15870 | Río Gurabo |
| 2088 | — | — | *Manicina* | *grandis* | 15883 | Río Gurabo |
| 2089 | NMB D6185 | — | *Manicina* | *grandis* | 15885 | Río Gurabo |
| 2090 | NMB D6186 | — | *Manicina* | *grandis* | 15887 | Río Gurabo |
| 2091 | — | — | *Manicina* | *grandis* | 15888 | Río Gurabo |
| 2092 | NMB D6187 | — | *Manicina* | *grandis* | 15901 | Río Gurabo |
| 2093 | NMB D6188 | — | *Manicina* | *grandis* | 16805 | Río Gurabo |
| 2094 | — | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2095 | — | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2096 | NMB D6189 | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2097 | NMB D6190 | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2098 | NMB D6191 | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2099 | NMB D6192 | — | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2100 | NMB D6193 | — | *Manicina* | *grandis* | 16810 | Río Gurabo |
| 2101 | — | — | *Manicina* | *grandis* | 16813 | Río Cana |
| 2102 | — | — | *Manicina* | *grandis* | 16815 | Río Cana |
| 2103 | NMB D6194 | — | *Manicina* | *grandis* | 16817 | Río Cana |
| 2104 | NMB D6195 | — | *Manicina* | *grandis* | 16818 | Río Cana |
| 2105 | NMB D6196 | — | *Manicina* | *grandis* | 16819 | Río Cana |
| 2106 | — | — | *Manicina* | *grandis* | 16827 | Río Cana |
| 2107 | — | — | *Manicina* | *grandis* | 16827 | Río Cana |
| 2108 | NMB D6197 | — | *Manicina* | *grandis* | 16827 | Río Cana |
| 2109 | NMB D6198 | figured | *Manicina* | *grandis* | 16827 | Río Cana |
| 2110 | — | — | *Manicina* | *grandis* | 16828 | Río Cana |
| 2111 | — | — | *Manicina* | *grandis* | 16830 | Río Cana |
| 2112 | — | — | *Manicina* | *grandis* | 16831 | Río Cana |
| 2113 | — | — | *Manicina* | *grandis* | 16835 | Río Cana |
| 2114 | — | — | *Manicina* | *grandis* | 16837 | Río Cana |
| 2115 | NMB D6199 | — | *Manicina* | *grandis* | 16839 | Río Cana |
| 2116 | NMB D6200 | — | *Manicina* | *grandis* | 16842 | Río Cana |
| 2117 | — | — | *Manicina* | *grandis* | 16842 | Río Cana |
| 2118 | NMB D6201 | — | *Manicina* | *grandis* | 16842 | Río Cana |
| 2119 | NMB D6202 | — | *Manicina* | *grandis* | 16842 | Río Cana |
| 2120 | NMB D6203 | figured | *Manicina* | *grandis* | 16844 | Río Cana |
| 2121 | NMB D6204 | figured | *Manicina* | *grandis* | 16844 | Río Cana |
| 2122 | NMB D6205 | figured | *Manicina* | *grandis* | 16852 | Río Cana |
| 2123 | NMB D6206 | — | *Manicina* | *grandis* | 16852 | Río Cana |
| 2124 | — | — | *Manicina* | *grandis* | 16853 | Río Cana |
| 2125 | — | — | *Manicina* | *grandis* | 16857 | Río Cana |
| 2126 | NMB D6207 | figured | *Manicina* | *grandis* | 16857 | Río Cana |
| 2127 | NMB D6208 | figured | *Manicina* | *grandis* | 16858 | Río Cana |
| 2128 | NMB D6209 | — | *Manicina* | *grandis* | 16859 | Río Cana |
| 2129 | — | — | *Manicina* | *grandis* | 16872 | Río Cana |

Appendix.—Continued.

| CCD # | NMB catalog # | Type status | Genus | Species | NMB locality # | River |
|---|---|---|---|---|---|---|
| 2130 | NMB D6210 | figured | *Manicina* | *grandis* | 16910 | Río Mao |
| 2131 | NMB D6211 | figured | *Manicina* | *grandis* | 16910 | Río Mao |
| 2132 | NMB D6212 | — | *Manicina* | *grandis* | 16910 | Río Mao |
| 2133 | — | — | *Manicina* | *grandis* | 16914 | Río Mao |
| 2134 | — | — | *Manicina* | *grandis* | 16921 | Río Gurabo |
| 2135 | — | — | *Manicina* | *grandis* | 16921 | Río Gurabo |
| 2136 | NMB D6213 | — | *Manicina* | *grandis* | 16934 | Río Gurabo |
| 2191 | — | — | *Manicina* | *grandis* | 16865 | Río Cana |
| 2353 | — | — | *Manicina* | *grandis* | 15885 | Río Gurabo |
| 2354 | — | — | *Manicina* | *grandis* | 16910 | Río Mao |
| 2355 | — | — | *Manicina* | *grandis* | 16842 | Río Cana |
| 2356 |  | — | *Manicina* | *grandis* | 15891 | Río Gurabo |
| 2357 | — | — | *Manicina* | *grandis* | 16819 | Río Cana |
| 2358 | — | — | *Manicina* | *grandis* | 16859 | Río Cana |
| 2360 | — | — | *Manicina* | *grandis* | 15851 | Río Gurabo |
| 2361 | NMB D6214 | figured | *Manicina* | *grandis* | 16808 | Río Gurabo |
| 2137 | — | — | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2138 |  | — | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2139 | — | — | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2140 | NMB D6215 | Paratype | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2141 | NMB D6216 | paratype | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2142 | — | — | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2143 | NMB D6217 | paratype | *Manicina* | *jungi* | 15863 | Río Gurabo |
| 2144 | — | — | *Manicina* | *jungi* | 15866 | Río Gurabo |
| 2145 | NMB D6218 | paratype | *Manicina* | *jungi* | 16814 | Río Cana |
| 2146 | — | — | *Manicina* | *jungi* | 16818 | Río Cana |
| 2147 | NMB D6219 | paratype | *Manicina* | *jungi* | 16818 | Río Cana |
| 2148 | NMB D6220 | holotype | *Manicina* | *jungi* | 16821 | Río Cana |
| 2149 | NMB D6221 | paratype | *Manicina* | *jungi* | 16821 | Río Cana |
| 2150 | NMB D6222 | paratype | *Manicina* | *jungi* | 16821 | Río Cana |
| 2151 | — | — | *Manicina* | *jungi* | 16821 | Río Cana |
| 2152 | NMB D6223 | paratype | *Manicina* | *jungi* | 16821 | Río Cana |
| 2153 | — | — | *Manicina* | *jungi* | 16825 | Río Cana |
| 2154 | NMB D6224 | paratype | *Manicina* | *jungi* | 16831 | Río Cana |
| 2155 | — | — | *Manicina* | *jungi* | 16831 | Río Cana |
| 2156 | — | — | *Manicina* | *jungi* | 16831 | Río Cana |
| 2157 | — | — | *Manicina* | *jungi* | 16831 | Río Cana |
| 2158 | — | — | *Manicina* | *jungi* | 16833 | Río Cana |
| 2159 | — | — | *Manicina* | *jungi* | 16842 | Río Cana |
| 2160 | — | — | *Manicina* | *jungi* | 16852 | Río Cana |
| 2161 | NMB D6249 | figured | *Manicina* | *jungi* | 16862 | Río Cana |
| 2162 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2163 | NMB D6225 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2164 | NMB D6226 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2165 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2166 | NMB D6227 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2167 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2168 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2169 | NMB D6228 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2170 | NMB D6229 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2171 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2172 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2173 | NMB D6230 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2174 | NMB D6231 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2175 | NMB D6020 | paratype | *Manicina* | *jungi* | 16862 | Río Cana |
| 2176 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |
| 2177 | — | — | *Manicina* | *jungi* | 17268 | Río Yaque del Norte |
| 2186 | NMB D6090 | paratype | *Manicina* | *jungi* | 15850 | Río Gurabo |
| 2342 | — | — | *Manicina* | *jungi* | 16844 | Río Cana |
| 2343 | — | — | *Manicina* | *jungi* | 16862 | Río Cana |

Appendix.—Continued.

| CCD # | NMB catalog # | Type status | Genus | Species | NMB locality # | River |
|---|---|---|---|---|---|---|
| 2344 | — | — | *Manicina* | *jungi* | 15814 | Río Gurabo |
| 2345 | — | — | *Manicina* | *jungi* | 15889 | Río Gurabo |
| 2346 | — | — | *Manicina* | *jungi* | 15964 | Río Gurabo |
| 0010 | — | — | *Hadrophyllia* | *saundersi* | 16884 | Río Cana |
| 2059 | NMB D6237 | paratype | *Hadrophyllia* | *saundersi* | 15837 | Río Gurabo |
| 2060 | NMB D6238 | paratype | *Hadrophyllia* | *saundersi* | 15837 | Río Gurabo |
| 2061 | NMB D6239 | paratype | *Hadrophyllia* | *saundersi* | 15846 | Río Gurabo |
| 2062 | NMB D6240 | paratype | *Hadrophyllia* | *saundersi* | 15847 | Río Gurabo |
| 2063 | NMB D6241 | holotype | *Hadrophyllia* | *saundersi* | 15858 | Río Gurabo |
| 2064 | NMB D6242 | paratype | *Hadrophyllia* | *saundersi* | 15859 | Río Gurabo |
| 2065 | NMB D6243 | paratype | *Hadrophyllia* | *saundersi* | 16883 | Río Gurabo |
| 2069 | NMB D6244 | paratype | *Hadrophyllia* | *saundersi* | 16827 | Río Cana |
| 2359 | — | — | *Hadrophyllia* | *saundersi* | 15837 | Río Gurabo |
| 2198 | NMB D6021 | figured | *Thysanus* | *corbicula* | 16910 | Río Mao |
| 1171 | — | — | *Thysanus* | *excentricus* | 16879 | Río Cana |
| 2192 | — | — | *Thysanus* | *excentricus* | 15837 | Río Gurabo |
| 2193 | NMB D6245 | — | *Thysanus* | *excentricus* | 15837 | Río Gurabo |
| 2194 | NMB D6246 | figured | *Thysanus* | *excentricus* | 15842 | Río Gurabo |
| 2195 | — | — | *Thysanus* | *excentricus* | 15842 | Río Gurabo |
| 2196 | — | — | *Thysanus* | *excentricus* | 16810 | Río Gurabo |
| 2197 | — | — | *Thysanus* | *excentricus* | 17014 | Río Cana |
| 2178 | NMB D6232 | — | *Thysanus* | *navicula* | 15806 | Río Gurabo |
| 2179 | NMB D6233 | figured | *Thysanus* | *navicula* | 15811 | Río Gurabo |
| 2180 | — | — | *Thysanus* | *navicula* | 16810 | Río Gurabo |
| 2181 | NMB D6234 | figured | *Thysanus* | *navicula* | 16810 | Río Gurabo |
| 2182 | NMB D6235 | figured | *Thysanus* | *navicula* | 16810 | Río Gurabo |
| 2347 | — | — | *Thysanus* | *navicula* | 16831 | Río Cana |
| 2348 | — | — | *Thysanus* | *navicula* | 16836 | Río Cana |
| 2349 | — | — | *Thysanus* | *navicula* | 16873 | Río Cana |
| 2350 | NMB D6236 | figured | *Thysanus* | *navicula* | 15837 | Río Gurabo |
| 2351 | — | — | *Thysanus* | *navicula* | 15837 | Río Gurabo |
| 2352 | — | — | *Thysanus* | *navicula* | 15837 | Río Gurabo |
| 2364 | NMB D6110 | — | *Thysanus* | *navicula* | 16873 | Río Cana |

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## EXPLANATION OF PLATE 1

*Caulastraea* and two morphologically similar Neogene Caribbean genera (*Mussismilia, Eusmilia*) that are phaceloid and bud intramurally but do not belong to the family Faviidae. The genus *Caulastraea* is distinguished by its acute septal teeth, numerous equal-sized costae, septothecal wall structure, reduced endotheca, and absent epitheca.

Figure Page

1, 2. ***Caulastraea furcata*** Dana (Type species of *Caulastraea* Dana, 1846) . . . . . . . . . . 16, 38
    1. Syntype. USNM 80. Recent, Fiji. Side view of colony, ×1.
    2. Syntype. USNM 80. Same specimen as figure 1. Calical surface, ×1.

3, 6. ***Mussismilia hartti*** (Verrill) (Type species of *Mussismilia* Ortmann, 1890) . . . . . . . . . . 16
    3. Figured specimen. USNM 5344. Recent, Abrolhos Reefs, Brazil. Calical surface, ×1.
    6. Figured specimen (*Mussismilia* sp. aff. *M. hartti* [Verrill]). USNM 94768 (CCD 13414), Upper Pliocene, locality PPP 01332 (AB93–22), Avenida Barracuda, Limón area, Costa Rica. Calical surface, ×2.

4, 5. ***Eusmilia fastigiata*** (Pallas) (Type species of *Eusmilia* Milne Edwards and Haime, 1848) . . . . . . . . . . 16
    4. Figured specimen. USNM 47736. Recent, Carrie Bow Cay, Belize. Calical surface, ×1.
    5. Figured specimen. USNM 94764 (CCD 13463), Upper Pliocene, locality PPP 02010 (JW93–11), Lomas del Mar, Limón area, Costa Rica. Calical surface, ×2.

7, 8. ***Caulastraea dendroidea*** (Coryell) . . . . . . . . . . 39
    7. Holotype. AMNH 23003. Upper Oligocene, Guayanilla, Puerto Rico. Side view of colony, ×0.75.
    8. Paratype. AMNH 23004. Upper Oligocene, Guayanilla, Puerto Rico. Side view of colony, ×2.

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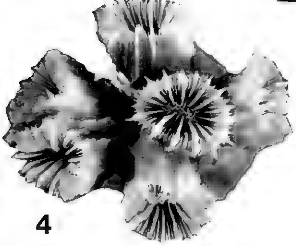

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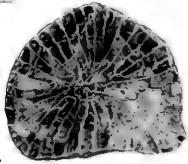

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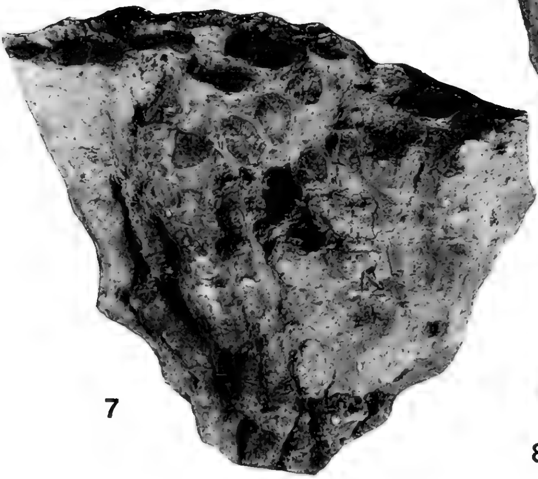

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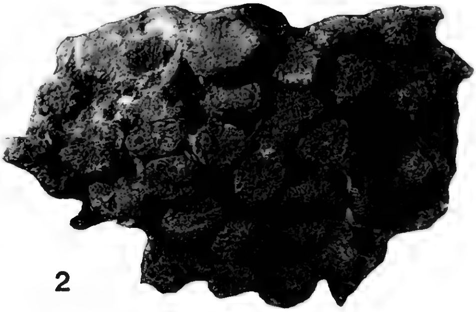
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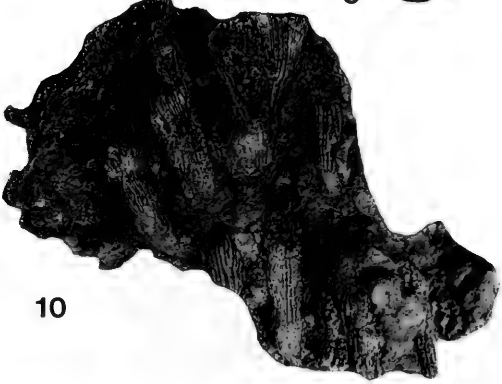
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## EXPLANATION OF PLATE 2

| Figure | | Page |
|---|---|---|
| 1–10. | ***Caulastraea portoricensis*** (Coryell) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . | 38 |

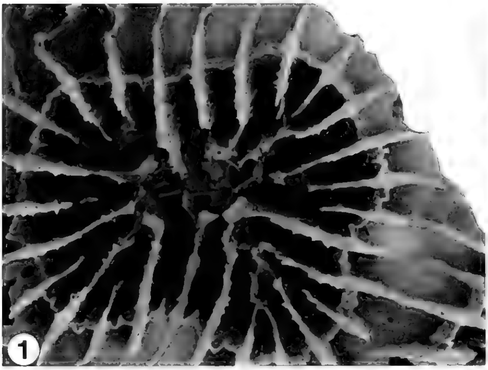
Whole colony and calical surfaces. *C. portoricensis* is distinguished by reduced numbers of septa (36–45 per corallite), elevated costae, and thin wall.

1. Holotype. AMNH 23000. Upper Oligocene to Lower Miocene, Lares, Puerto Rico. Side view of colony, ×0.75.
2. Paratype. AMNH 23001. Upper Oligocene, Guánica, Puerto Rico. Calical surface, ×1.
3. Figured specimen. NMB D6141 (CCD 2334). Lower Upper Pliocene, locality NMB 15822, Río Gurabo, Mao Formation, Dominican Republic. Side view of colony, ×1.
4. Figured specimen. NMB D6140 (CCD 0057). Lower Upper Pliocene, locality NMB 15834, Río Gurabo, Mao Formation, Dominican Republic. Side view of colony, ×1.
5. Figured specimen. NMB D6140 (CCD 0057). Same specimen as figure 4. Calical surface, ×2.
6. Figured specimen. USNM 94767a (CCD 10423). Upper Pliocene, locality PPP 00719 (TS-CR-8), Pueblo Nuevo, Limón area, Costa Rica. Side view of colony, ×1.
7. Figured specimen. USNM 94767b (CCD 10423). Upper Pliocene, locality PPP 00719 (TS-CR-8), Pueblo Nuevo, Limón area, Costa Rica. Side view of colony, ×1.
8. Figured specimen. USNM 94767c (CCD 10423). Upper Pliocene, locality PPP 00719 (TS-CR-8), Pueblo Nuevo, Limón area, Costa Rica. Side view of colony, ×1.
9. Figured specimen. USNM 94767d (CCD 10423). Upper Pliocene, locality PPP 00719 (TS-CR-8), Pueblo Nuevo, Limón area, Costa Rica. Side view of colony, ×1.
10. Figured specimen. USNM 94766 (CCD 10141). Upper Pliocene, locality PPP 01126 (KJ-P1), Portete, Limón area, Costa Rica. Side view of colony, ×0.75.

## EXPLANATION OF PLATE 3

*Favia dominicensis* Vaughan and other morphologically similar Neogene and Recent species. *F. dominicensis* and other *Favia* with large corallites generally have thinner septa and walls than *Favia* with small corallites. They also have distinctive parathecal walls.

| Figure | Page |
|---|---|
| 1, 2. ***Favia leptophylla*** Verrill . . . . . . . . . . | 18, 40 |
| 1. Holotype. YPM 517. Recent, Abrolhos Reefs, Brazil. Scanning electron micrograph of calical surface, ×10. | |
| 2. Holotype. YPM 517. Same specimen as figure 1. Scanning electron micrograph of longitudinal break through a corallite showing the columella (*c*), an endothecal dissepiment (*d*), and the wall (*w*), ×10. | |
| 3, 4. ***Favia*** n. sp. aff. *dominicensis* Vaughan . . . . . . . . . . | 40 |
| 3. Figured specimen. NMB D6162 (CCD 2044). Lower to Middle Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Calical surface, ×5. | |
| 4. Figured specimen. NMB D6162 (CCD 2044). Same specimen as figure 3. Colony surface, ×1. | |
| 5, 6. ***Favia dominicensis*** Vaughan . . . . . . . . . . | 39 |
| 5. Holotype. MCZ 103512. Neogene, Gabb collection, Dominican Republic. Colony surface, ×1.5. | |
| 6. Holotype. MCZ 103512. Same specimen as figure 5. Calical surface, ×6.3. | |



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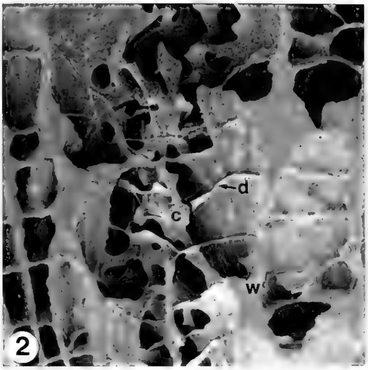

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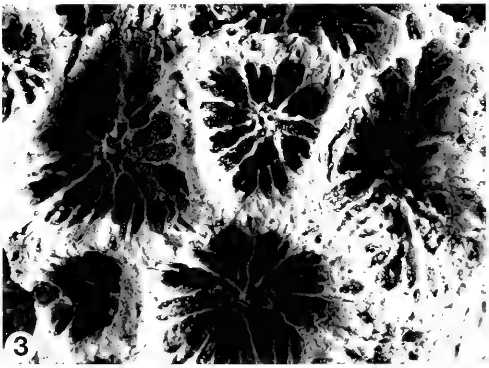

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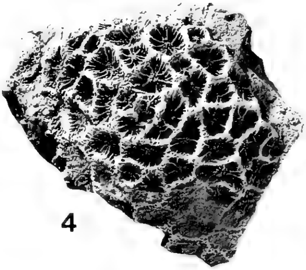

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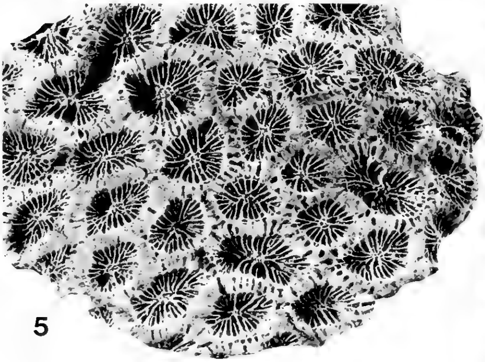

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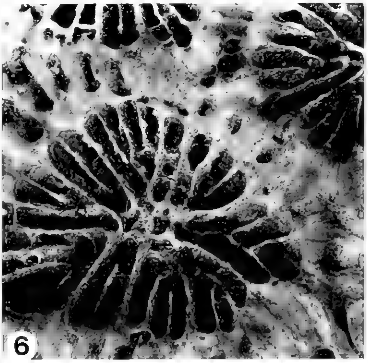

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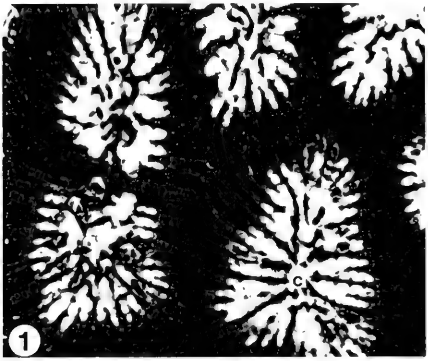
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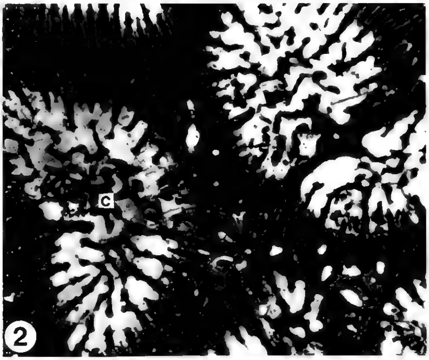
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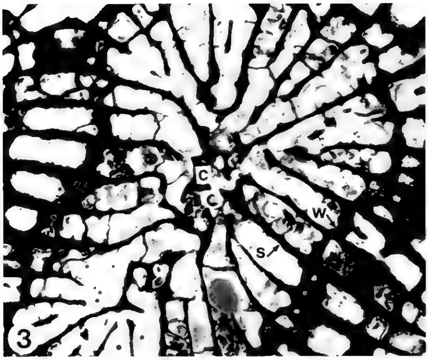
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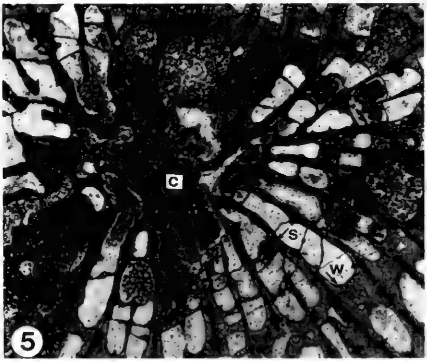
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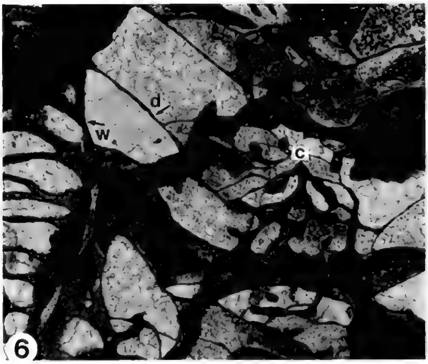
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## EXPLANATION OF PLATE 4

*Favia dominicensis* Vaughan, with Recent specimens of *Favia fragum* (Esper) for comparison. Thin section photographs. In addition to larger corallites, *F. dominicensis* has a thin parathecal wall and better developed endothecal dissepiments than *F. fragum*. *c* = columella, *d* = endothecal dissepiment, *s* = primary septum, *w* = wall.

Figure Page

1, 2. ***Favia fragum*** (Esper) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18, 41

1. Figured specimen. SUI 84994A (LP201-A1). Recent, La Parguera, Puerto Rico. Transverse section of corallites, ×10. The corallite pair on the left is dividing.
2. Figured specimen. SUI 84990B (LP201-B2). Recent, La Parguera, Puerto Rico. Transverse section of corallites, ×10.

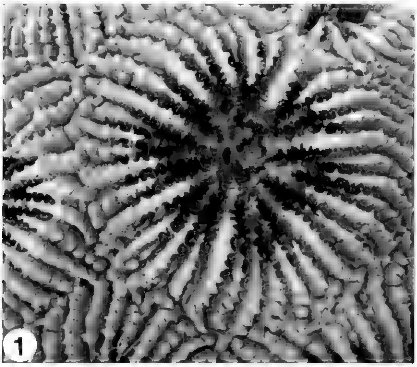
3–6. ***Favia dominicensis*** Vaughan . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 39

3. Figured specimen. USNM 95266. ?Upper Oligocene, locality TU 1362, Río Yaque del Norte, ?Tabera Group, Dominican Republic. Transverse thin section of a corallite, ×8.
4. Figured specimen. USNM 95266. Same specimen as figure 3. Longitudinal thin section of a corallite, ×8.
5. Figured specimen. NMB D6160 (CCD 2045). Lower to Middle Miocene, locality NMB 17284, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Transverse thin section of a corallite, ×8.
6. Figured specimen. NMB D6160 (CCD 2045). Same specimen as figure 5. Longitudinal section of a corallite, ×8.

## EXPLANATION OF PLATE 5

*Favia vokesae*, n. sp., with Recent specimens of *Favia fragum* (Esper) for comparison. Scanning electron micrographs and calical surfaces. *F. vokesae* has larger, more closely spaced corallites, and more septa per corallite than *F. fragum*.

| Figure | Page |
|---|---|
| 1, 2. ***Favia fragum*** (Esper) | 18, 41 |
| 1. Figured specimen. SUI 84992 (LP202). Recent, La Parguera, Puerto Rico. Scanning electron micrograph of calical surface, ×10. | |
| 2. Figured specimen. SUI 84991 (LP201). Recent, La Parguera, Puerto Rico. Scanning electron micrograph of calical surface, ×10. | |
| 3–6. ***Favia vokesae,*** n. sp. | 40 |
| 3. Paratype. USNM 95278. ?Upper Pliocene, locality TU 1281, Guayubín, Dominican Republic. Scanning electron micrograph of calical surface, ×10. | |
| 4. Paratype. USNM 95278. Same specimen as figure 3. Scanning electron micrograph of calical surface showing the walls of three corallites (*w*) and the intercorallite area, ×15. | |
| 5. Paratype. USNM 95278. Same specimen as figure 3. Scanning electron micrograph of calical surface, ×10. | |
| 6. Holotype. NMB D6017 (CCD 2043). Upper Miocene, locality NMB 16855, Río Cana, Cercado Formation, Dominican Republic. Calical surface, ×5. | |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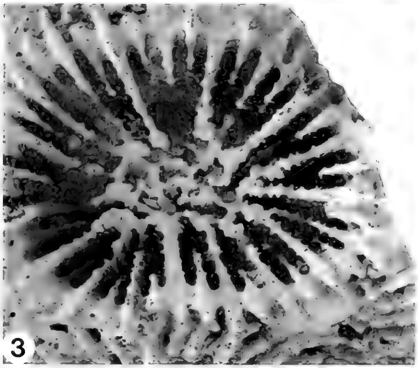
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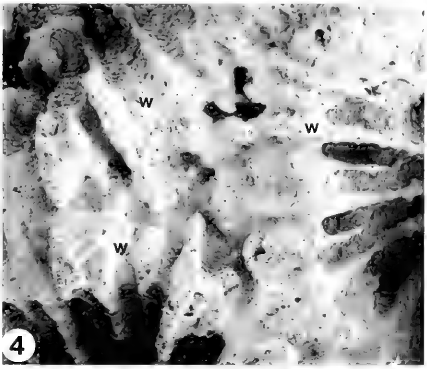

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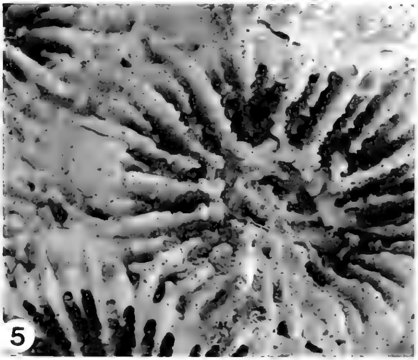
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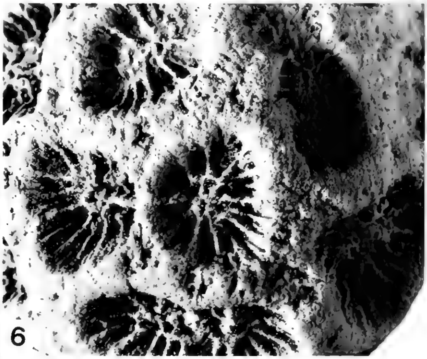
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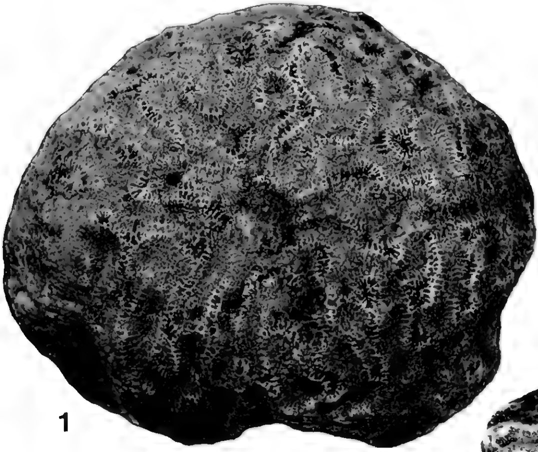
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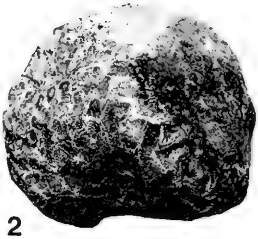
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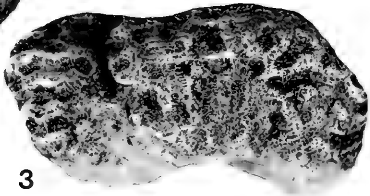
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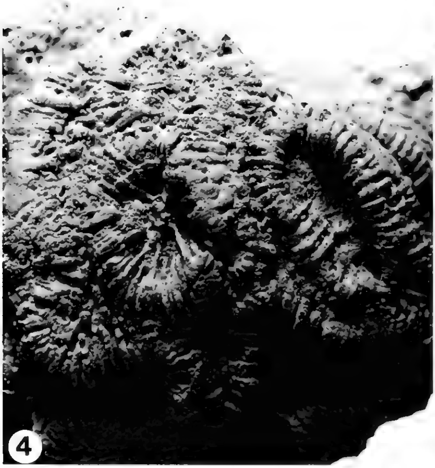
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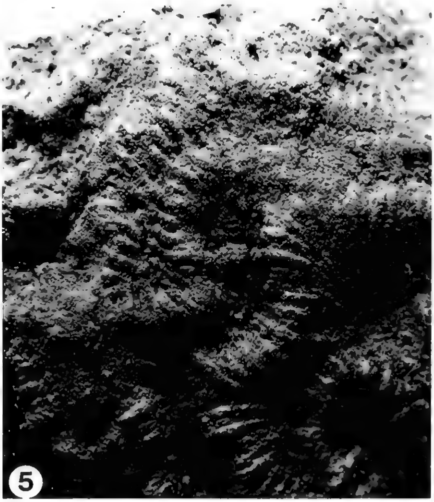
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## EXPLANATION OF PLATE 6

| Figure | | Page |
|---|---|---|
| 1–5. | ***Favia maoadentrensis,*** n. sp. | 41 |

Colony and calical surfaces. *F. maoadentrensis* forms coralliths and has series composed of one to six corallites. Its valleys are widely spaced and separated by distinctive ambulacral grooves.

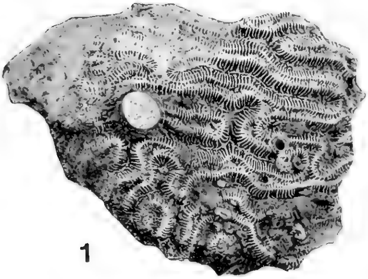
1. Holotype. NMB D6147 (CCD 2026). Lower Upper Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Colony surface, ×2.
2. Paratype. NMB D6149 (CCD 2028). Lower Upper Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Colony surface, ×0.75.
3. Paratype. NMB D6146 (CCD 2024). Lower Upper Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Colony surface, ×1.
4. Paratype. NMB D6145 (CCD 2023). Lower Upper Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Calical surface, ×5.
5. Paratype. NMB D6142 (CCD 2019). Lower Upper Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Calical surface, ×5.

## EXPLANATION OF PLATE 7

| Figure | | Page |
|---|---|---|
| 1–6. | ***Diploria zambensis,*** n. sp. | 42 |

Colony and calical surfaces. *D. zambensis* is distinguished by its relatively large, widely spaced valleys.

1. Holotype. NMB D6018 (CCD 2031). Upper Miocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
2. Paratype. NMB D6152 (CCD 2029). Lower Upper Pliocene, locality NMB 15830, Río Gurabo, Mao Formation, Dominican Republic, ×1.
3. Paratype. NMB D6150 (CCD 2014). Upper Miocene, locality NMB 15808, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×0.75.
4. Paratype. NMB D6156 (CCD 2037). Lower Pliocene, locality NMB 16881, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×0.75.
5. Paratype. NMB D5788 (CCD 2033). Upper Miocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Calical surface, ×5.
6. Holotype. NMB D6018 (CCD 2031). Same specimen as figure 1. Calical surface, ×5.



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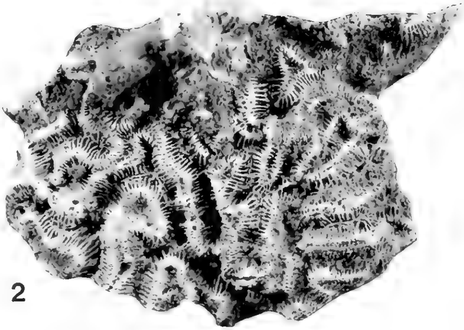

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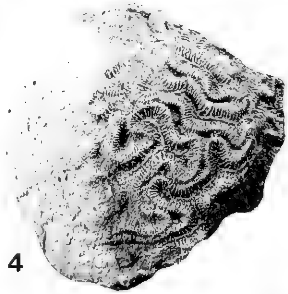

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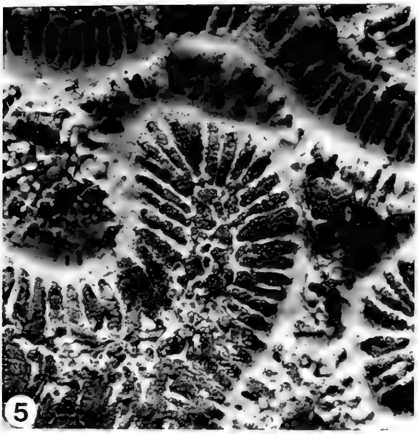

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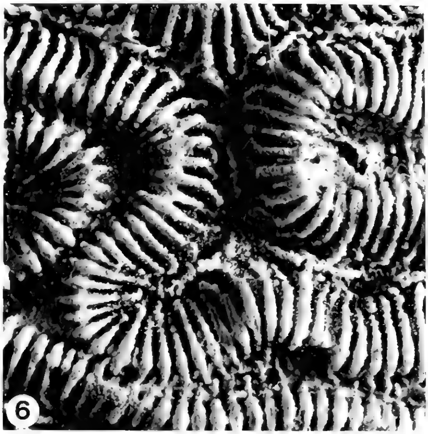

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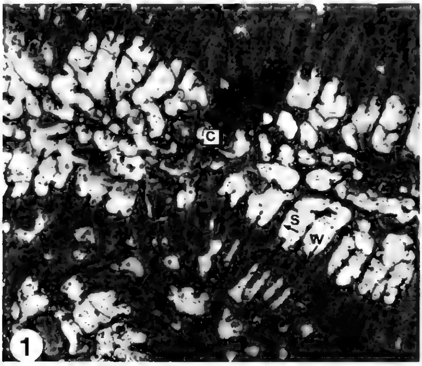
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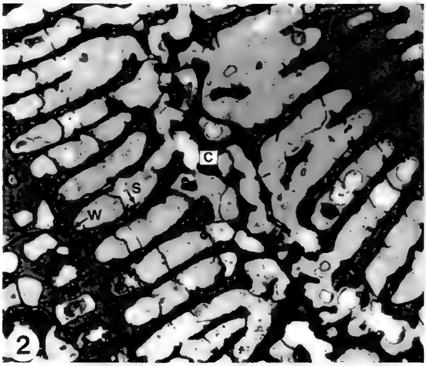
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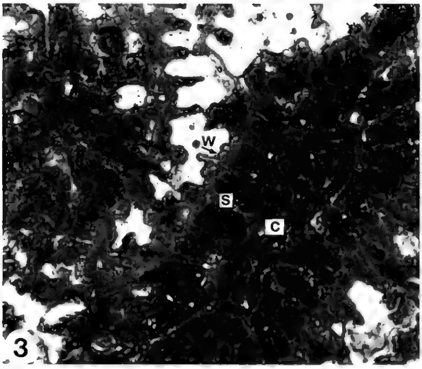
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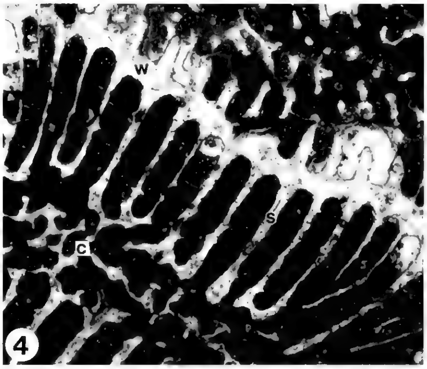
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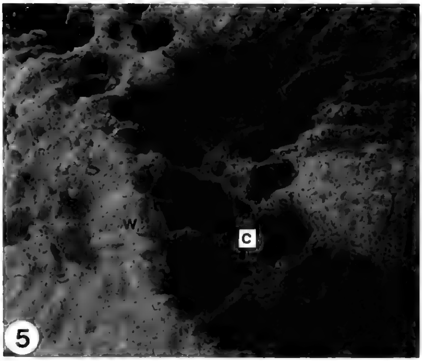
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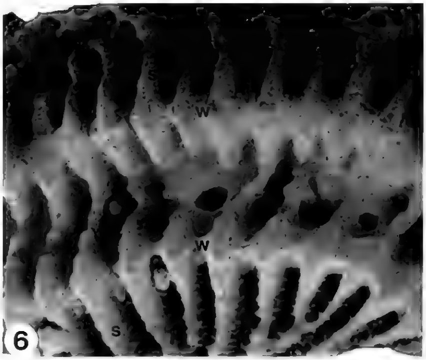
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## EXPLANATION OF PLATE 8

*Favia maoadentrensis,* n. sp., and *Diploria zambensis,* n. sp. Thin section and scanning electron micrographs. *F. maoadentrensis* is distinguished by four cycles of septa and a thick wall, whereas *D. zambensis* only has three cycles. The genus *Diploria* tends to form longer series that lack paliform lobes. *c* = columella, *s* = primary septum, *w* = wall.

| Figure | | Page |
|---|---|---|
| 1, 3, 5. | ***Favia maoadentrensis,*** n. sp. | 41 |
| | 1. Paratype. NMB D6148 (CCD 2027). Lower Upper Pliocene locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Transverse thin section of a corallite series, ×10. | |
| | 3. Holotype. NMB D6147 (CCD 2026). Same specimen as Plate 6, figure 1. Transverse thin section of two corallite series, ×10. | |
| | 5. Paratype. NMB D6145 (CCD 2023). Same specimen as Plate 6, figure 4. Scanning electron micrograph of calical surface showing a corallite series, ×10. | |
| 2, 4, 6. | ***Diploria zambensis,*** n. sp. | 42 |
| | 2. Paratype. NMB D5788 (CCD 2033). Same specimen as Plate 7, figure 5. Transverse thin section of a corallite series, ×10. | |
| | 4. Paratype. NMB D6158 (CCD 2040). Upper Miocene, locality NMB 16921, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin section of a corallite series, ×10. | |
| | 6. Holotype. NMB D6018 (CCD 2031). Same specimen as Plate 7, figure 1. Scanning electron micrograph of calical surface showing the intercorallite area, ×10. | |

## EXPLANATION OF PLATE 9

*Thysanus.* Whole colony photographs. The genus *Thysanus* is generally characterized by parathecal walls, weak paliform lobes, rare or absent endothecal and exothecal dissepiments, and no epitheca.

Figure Page

1, 4, 5, 8, 11, 12. ***Thysanus corbicula*** Duncan . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 43

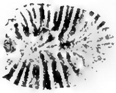
1. Holotype. BM(NH) R28795. Neogene, Nivajé Shale, near Santiago, Dominican Republic. Colony surface, ×2.
4. Figured specimen. NMB D6021 (CCD 2198). Upper Miocene, locality NMB 16910, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
5. Figured specimen. NMB D6201 (CCD 2198). Same specimen as figure 4. Colony side, ×1.
8. Holotype of *Thysanus vaughani* Weisbord. FMNH 8294. Possible synonym. Lower Miocene, Chipola 01 (CA001), Chipola Formation, Florida. Colony surface, ×2.5.
11. Holotype of *Thysanus floridanus* Weisbord. USNM 79812. Synonym. Upper Pliocene, locality USGS 3300, Shell Creek, Caloosahatchee Formation, Florida. Colony surface, ×2.5.
12. Holotype of *Thysanus floridanus* Weisbord. USNM 79812. Synonym. Same specimen as figure 11. Colony bottom, ×2.5.

2, 3, 6, 7, 9, 10, 13–17. ***Thysanus excentricus*** Duncan . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 43

2. Holotype of *Thysanus hayesi* Vaughan. USNM MO324994. Synonym. Upper Pliocene, locality USGS 3461, Matanzas, Cuba. Colony surface, ×2.
3. Holotype of *Thysanus hayesi* Vaughan. USNM MO324994. Synonym. Same specimen as figure 2. Colony side, ×2.
6. Holotype. BM(NH) 48614. Upper Pliocene, Bowden Shell Beds, Bowden Formation, Jamaica. Colony surface, ×2.
7. Holotype. BM(NH) 48614. Same specimen as figure 6. Colony side, ×2.
9. Holotype of *Thysanus elegans* Duncan. BM(NH) R28918. Possible synonym. Upper Pliocene, Bowden Shell Beds, Bowden Formation, Jamaica. Colony surface, ×2.
10. Holotype of *Thysanus elegans* Duncan. BM(NH) R28918. Possible synonym. Same specimen as figure 9. Colony side, ×2.
13. Figured specimen. NMB D6246 (CCD 2194). Upper Miocene, locality NMB 15842, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×2.
14. Figured specimen. SUI 90997 (AB94–11/1). Upper Pliocene, AB94–11, Bowden Shell Beds, Bowden Formation, Jamaica. Colony surface, ×2.
15. Figured specimen. SUI 90997 (AB94–11/1). Same specimen as figure 14. Colony side, ×2.
16. Figured specimen. SUI 90998 (AB94–11/3). Upper Pliocene, AB94–11, Bowden Shell Beds, Bowden Formation, Jamaica. Colony surface, ×2.
17. Figured specimen. SUI 90998 (AB94–11/3). Same specimen as figure 16. Colony side, ×2.

18–19. ***Hadrophyllia saundersi*** . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 45

18. Holotype of *Thysanus crassicostatus* Vaughan. MCZ 9280. Possible synonym. Neogene, Gabb collection, Dominican Republic. Longitudinal break through colony, ×1.6.
19. Holotype of *Thysanus crassicostatus* Vaughan. MCZ 9280. Possible synonym. Same specimen as igure 18. Colony side, ×1.6.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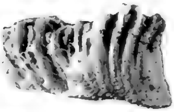
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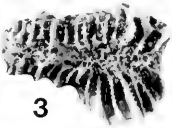
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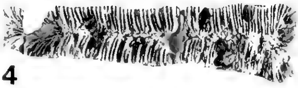
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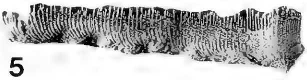
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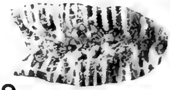
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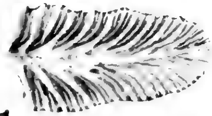
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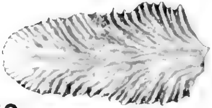
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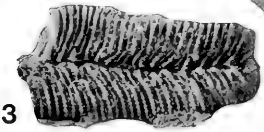
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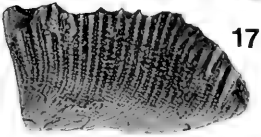
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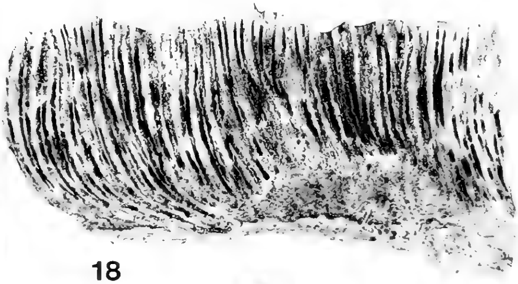
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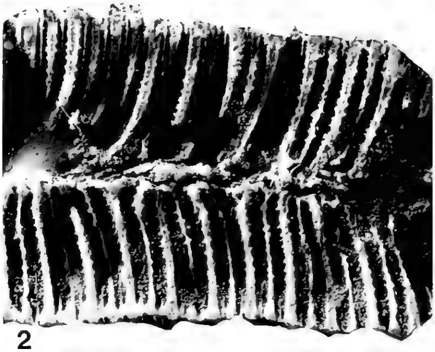

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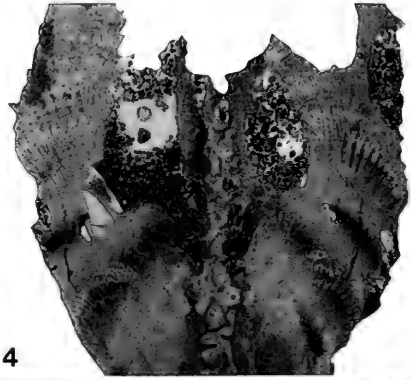

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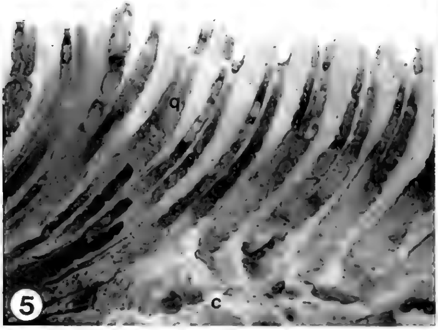

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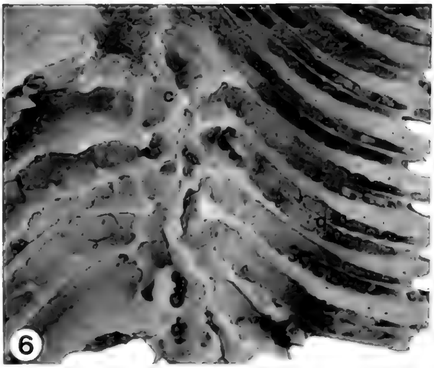

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## EXPLANATION OF PLATE 10

*Thysanus*. Calical surface, thin section, and scanning electron micrographs. *T. corbicula* has well-developed quaternary septa which are absent in *T. excentricus*.

| Figure | | Page |
|---|---|---|
| 1, 3, 4. | ***Thysanus excentricus*** Duncan | 43 |

1. Figured specimen. NMB D6246 (CCD 2194). Same specimen as Plate 9, figure 13. Calical surface, ×5.
3. Figured specimen. USNM 95240. Upper Pliocene, locality TU 705, Bowden Shell Beds, Bowden Formation, Jamaica. Transverse thin section, ×8.
4. Figured specimen. USNM 95240. Upper Pliocene, locality TU 705, Bowden Shell Beds, Bowden Formation, Jamaica. Longitudinal thin section, ×8.

| Figure | | Page |
|---|---|---|
| 2, 5, 6. | ***Thysanus corbicula*** Duncan | 43 |

2. Figured specimen. NMB D6201 (CCD 2198). Same specimen as Plate 9, figure 4. Calical surface, ×5.
5. Figured specimen. NMB D6201 (CCD 2198). Same specimen as Plate 9, figure 4. Scanning electron micrograph showing the columella (*c*) and a quaternary septum (*q*), ×10.
6. Figured specimen. NMB D6201 (CCD 2198). Same specimen as Plate 9, figure 4. Scanning electron micrograph of columella showing the columella (*c*) and a quaternary septum (*q*), ×10.

# EXPLANATION OF PLATE 11

Figure Page

1–11. ***Thysanus navicula*** (Duncan) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 44

Whole colony and colony surface photographs. Although *T. navicula* forms bidirectional flabelloid colonies, it is placed in the genus *Thysanus* because it lacks exothecal dissepiments and epitheca. Its walls are also distinctively parathecal.

1. Holotype. BM(NH) R28766. Neogene, Nivajé Shale, near Santiago, Domincan Republic. Colony surface, ×2.
2. Holotype. BM(NH) R28766. Same specimen as figure 1. Colony side, ×2.
3. Figured Specimen. NMB D6234 (CCD 2181). Upper Miocene, locality NMB 16810, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
4. Figured specimen. NMB D6234 (CCD 2181). Same specimen as figure 3. Colony side, ×1.
5. Figured specimen. NMB D6233 (CCD 2179). Lower Pliocene, locality NMB 15811, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
6. Figured specimen. NMB D6233 (CCD 2179). Same specimen as figure 5. Colony side, ×1.
7. Figured specimen. NMB D6236 (CCD 2350). Upper Miocene, locality NMB 15837, Río Gurabo, Gurabo Formation, Dominican Republic. Sample containing numerous colonies, ×0.75.
8. Figured specimen. NMB D6235 (CCD 2182). Upper Miocene, locality NMB 16810, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
9. Figured specimen. NMB D6235 (CCD 2182). Same specimen as figure 8. Colony side, ×1.
10. Figured specimen. NMB D6233 (CCD 2179). Same specimen as figure 5. Calical surface, ×5.
11. Figured specimen. NMB D6234 (CCD 2181). Same specimen as figure 3. Calical surface, ×5.


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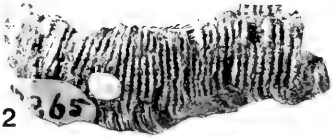
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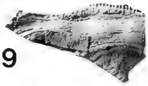
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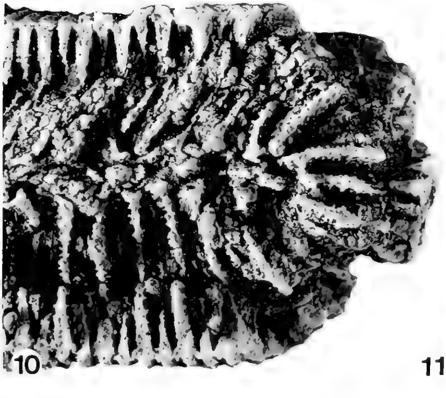
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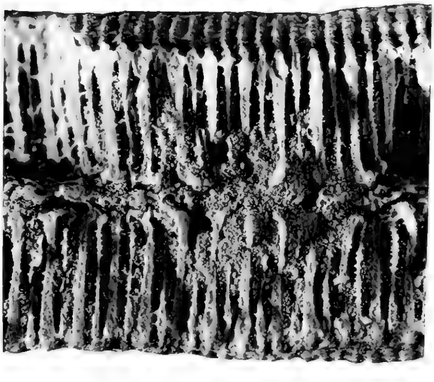
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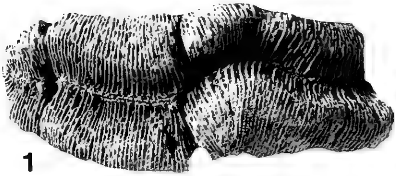
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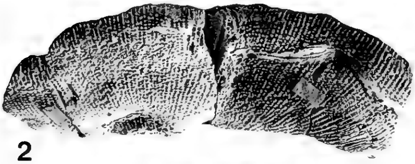
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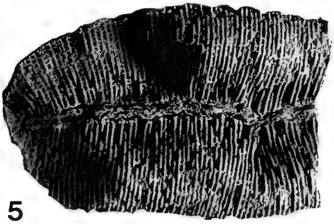
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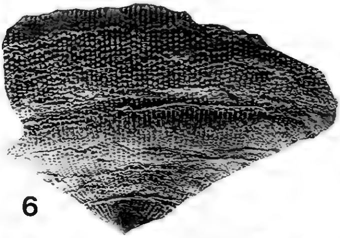
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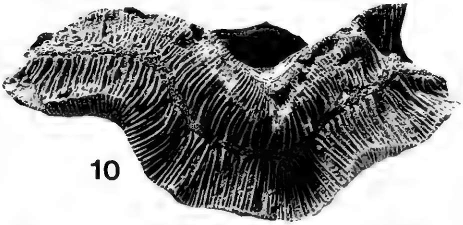
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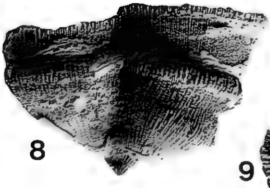
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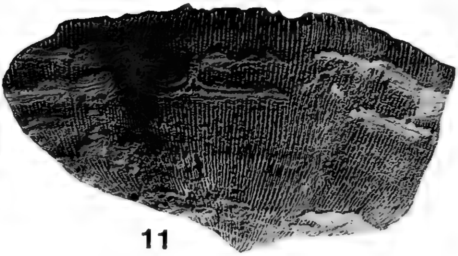
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## EXPLANATION OF PLATE 12

*Hadrophyllia saundersi,* n. sp., and *Manicina geisteri,* n. sp. Whole colony photographs. *H. saundersi* lacks septal and paliform lobes and has fewer septal cycles than *M. geisteri. M. geisteri* commonly has prominent well-developed septal lobes.

Figure | Page

1–6. ***Hadrophyllia saundersi,*** n. sp. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 45

1. Holotype. NMB D6241 (CCD 2063). Upper Miocene, locality NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×0.75.
2. Holotype. NMB D6241 (CCD 2063). Same specimen as figure 1. Colony side, ×0.75.
3. Paratype. NMB D6239 (CCD 2061). Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×0.75.
4. Paratype. NMB D6239 (CCD 2061). Same specimen as figure 3. Colony side, ×0.75.
5. Paratype. NMB D6242 (CCD 2064). Upper Miocene, locality NMB 15859, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
6. Paratype. NMB D6242 (CCD 2064). Same specimen as figure 5. Colony side, ×1.

7–11. ***Manicina geisteri,*** n. sp. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 46

7. Paratype. NMB D6174 (CCD 2184). Upper Miocene, locality NMB 15844, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
8. Paratype. NMB D6175 (CCD 2185). Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Colony side, ×1.
9. Paratype. NMB D6175 (CCD 2185). Same specimen as figure 8. Colony surface, ×1.
10. Holotype. NMB D6173 (CCD 2073). Upper Miocene, locality NMB 16844, Río Cana, Cercado Formation, Dominican Republic. Colony surface, ×1.
11. Holotype. NMB D6173 (CCD 2073). Same specimen as figure 10. Colony side, ×1.

## EXPLANATION OF PLATE 13

*Hadrophyllia saundersi,* n. sp., and *Manicina geisteri,* n. sp. Calical surface, thin section, and scanning electron micrographs. Both *H. saundersi* and *M. geisteri* have abundant endothecal dissepiments and a narrow spongy columella.

| Figure | | Page |
|---|---|---|
| 1, 3, 5. | ***Hadrophyllia saundersi,*** n. sp. | 45 |
| | 1. Paratype. NMB D6242 (CCD 2064). Same specimen as Plate 12, figure 5. Calical surface, ×5.<br>3. Paratype. NMB D6239 (CCD 2061). Same specimen as Plate 12, figure 3. Calical surface, ×5.<br>5. Holotype. NMB D6241 (CCD 2063). Same specimen as Plate 12, figure 1. Scanning electron micrograph of a septal face along upper interior margin showing endothecal dissepiments, ×10. | |
| 2, 4, 6. | ***Manicina geisteri,*** n. sp. | 46 |
| | 2. Holotype. NMB D6173 (CCD 2073). Same specimen as Plate 12, figure 10. Calical surface, ×5.<br>4. Paratype. NMB D6175 (CCD 2185). Same specimen as Plate 12, figure 8. Calical surface, ×5.<br>6. Paratype. NMB D6177 (CCD 2188). Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. Transverse thin section showing the columella (*c*), an endothecal dissepiment (*d*), and a primary septum (*s*), ×8. | |


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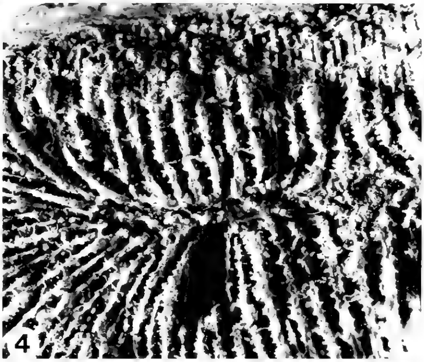
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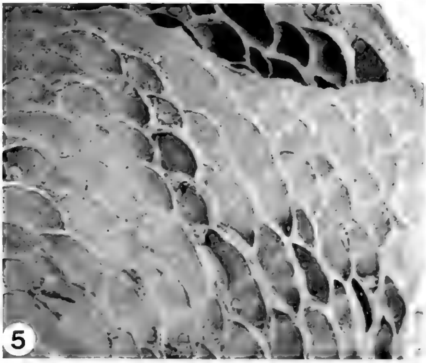
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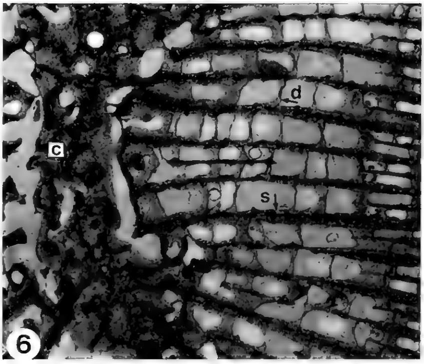
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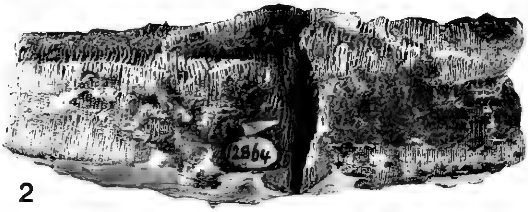

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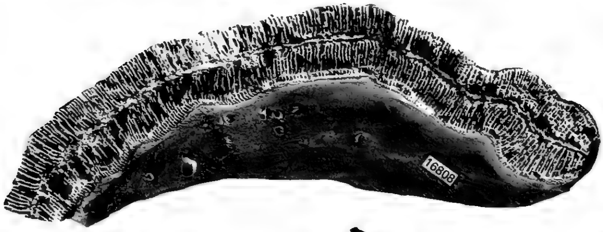

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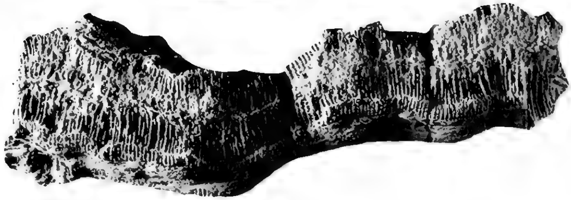

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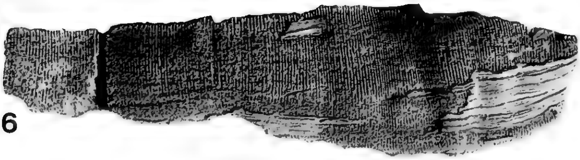

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## EXPLANATION OF PLATE 14

Figure Page

1–7. ***Manicina grandis*** Duncan . . . . . . . . . . 46

Whole colony photographs. Some colonies of *M. grandis* have long, narrow straight valleys and reduced septal lobes.

1. Holotype. BM(NH) R28754. Neogene, Nivajé Shale, near Santiago, Domincan Republic. Colony surface, ×1.
2. Holotype. BM(NH) R28754. Same specimen as figure 1. Colony side, ×1.
3. Holotype. BM(NH) R28754. Same specimen as figure 1. Longitudinal break, ×2.
4. Figured specimen. NMB D6214 (CCD 2361). Upper Miocene, locality NMB 16808, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×0.75.
5. Figured specimen. NMB D6198 (CCD 2109). Lower Upper Pliocene, locality NMB 16827, Río Cana, Mao Formation, Dominican Republic. Colony surface, ×1.
6. Figured specimen. NMB D6210 (CCD 2130). ? Upper Miocene, locality NMB 16910, Río Mao, Gurabo Formation, Domincan Republic. Colony side, ×0.75.
7. Figured specimen. NMB D6210 (CCD 2130). Same specimen as figure 6. Colony surface, ×0.75.

## EXPLANATION OF PLATE 15

| Figure | Page |
|---|---|
| 1–8. ***Manicina grandis*** Duncan | 46 |

Whole colony and calical surface photographs. Many colonies of *M. grandis* are triangular in shape and have short, wide, curved valleys and well-developed septal lobes. The species is generally characterized by a weak exotheca and three unequal septal cycles.

1. Figured specimen. NMB D6207 (CCD 2126). Upper Miocene, locality NMB 16857, Río Cana, Cercado Formation, Dominican Republic. Colony surface, ×1.
2. Figured specimen. NMB D6207 (CCD 2126). Same specimen as figure 1. Colony side, ×1.
3. Figured specimen. NMB D6205 (CCD 2122). Upper Miocene, locality NMB 16852, Río Cana, Cercado Formation, Dominican Republic. Colony surface, ×1.
4. Figured specimen. NMB D6205 (CCD 2126). Same specimen as figure 3. Colony side, ×1.
5. Figured specimen. NMB D6203 (CCD 2120). Upper Miocene, locality NMB 16844, Río Cana, Cercado Formation, Dominican Republic. Colony surface, ×1.
6. Figured specimen. NMB D6203 (CCD 2120). Same specimen as figure 5. Colony side, ×1.
7. Figured specimen. NMB D6207 (CCD 2126). Same specimen as figure 1. Colony surface, ×5.
8. Figured specimen. NMB D6214 (CCD 2361). Same specimen as Plate 14, figure 4. Colony surface, ×5.


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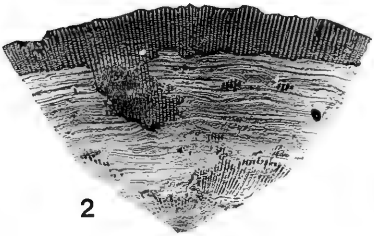
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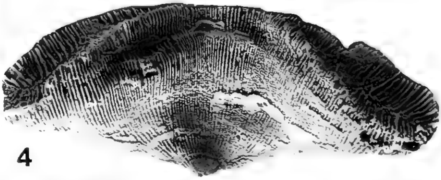
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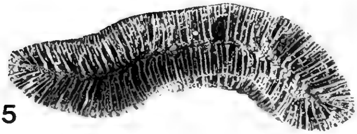
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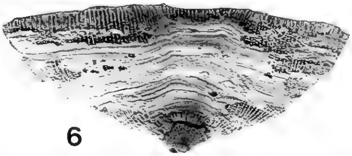
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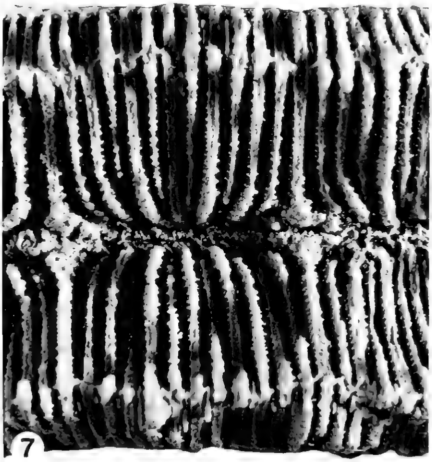
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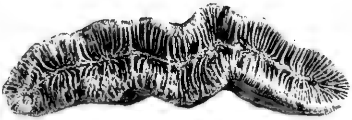
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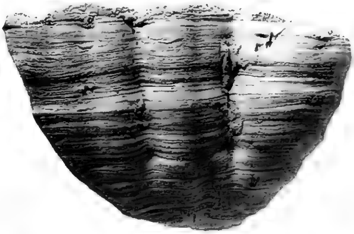
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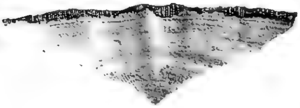
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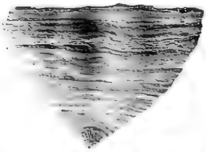
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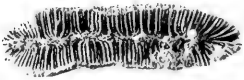
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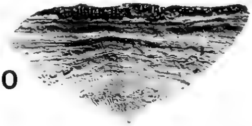
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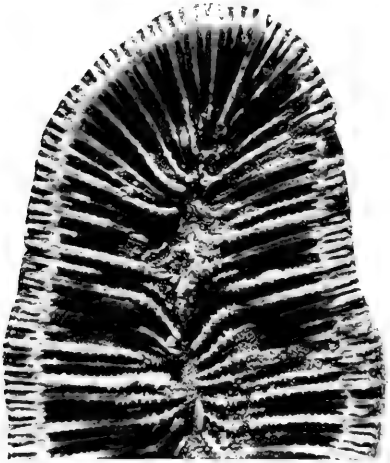
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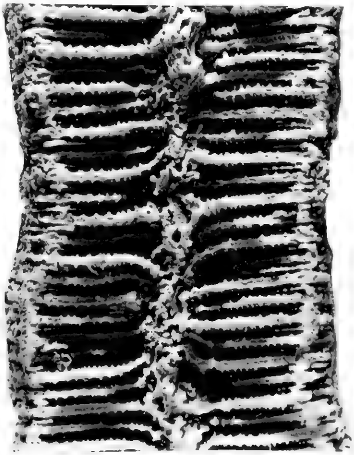
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## EXPLANATION OF PLATE 16

Figure Page

1–12. ***Manicina jungi,*** n. sp. . . . . . . . . . . 47

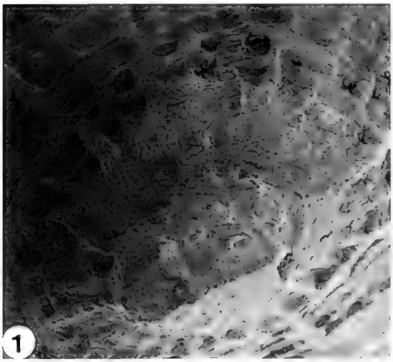
Whole colony and colony surface photographs. *M. jungi* forms distinctive triangular colonies with well-developed epitheca. It has small paliform lobes, narrow valleys, and well-developed quaternary septa.

1. Holotype. NMB D6220 (CCD 2148). Upper Miocene, locality NMB 16821, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
2. Holotype. NMB D6220 (CCD 2148). Same specimen as figure 1. Colony side, ×1.
3. Paratype. NMB D6020 (CCD 2175). Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
4. Paratype. NMB D6020 (CCD 2175). Same specimen as figure 3. Colony side, ×1.
5. Paratype. NMB D6221 (CCD 2149). Upper Miocene, locality NMB 16821, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
6. Paratype. NMB D6221 (CCD 2149). Same specimen as figure 5. Colony side, ×1.
7. Paratype. NMB D6231 (CCD 2174). Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
8. Paratype. NMB D6231 (CCD 2174). Same specimen as figure 7. Colony side, ×1.
9. Paratype. NMB D6215 (CCD 2140). Lower Pliocene, locality NMB 15814, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
10. Paratype. NMB D6215 (CCD 2140). Same specimen as figure 9. Colony side, ×1.
11. Paratype. NMB D6231 (CCD 2174). Same specimen as figure 7. Calical surface, ×5.
12. Paratype. NMB D6215 (CCD 2140). Same specimen as figure 9. Calical surface, ×5.

## EXPLANATION OF PLATE 17

*Manicina jungi*, n. sp., and *Manicina grandis* Duncan. Thin section and scanning electron micrographs. The ornamentation on the septa and costae is better developed in *M. grandis* than in *M. jungi*. The endotheca is also better developed in *M. grandis*. *c* = columella, *d* = endothecal dissepiment, *s* = primary septum, *w* = wall.

| Figure | | Page |
|---|---|---|
| 1, 3, 5. | ***Manicina jungi***, n. sp. | 47 |
| | 1. Paratype. NMB D6228 (CCD 2169). Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. Scanning electron micrograph of colony base, ×20. | |
| | 3. Paratype. NMB D6228 (CCD 2169). Same specimen as figure 1. Scanning electron micrograph of a septal face through the corallite wall showing endothecal dissepiments and the wall, ×10. | |
| | 5. Paratype. NMB D6230 (CCD 2173). Lower Pliocene, locality NMB 16862, Río Cana, Gurabo Formation, Dominican Republic. Transverse thin section showing the columella and a primary septum, ×8. Endothecal dissepiments are scarce. | |
| 2, 4, 6. | ***Manicina grandis*** Duncan | 46 |
| | 2. Figured specimen. NMB D6181 (CCD 2081). Upper Miocene, locality NMB 15855, Río Gurabo, Gurabo Formation, Dominican Republic. Costae along colony side, ×20. | |
| | 4. Figured specimen. NMB D6181 (CCD 2081). Same specimen as figure 2. Scanning electron micrograph of a longitudinal break through a colony, showing endothecal dissepiments and the wall, ×10. | |
| | 6. Figured specimen. NMB D6211 (CCD 2131). ? Upper Miocene, locality NMB 16910, Río Mao, Gurabo Formation, Dominican Republic. Transverse thin section showing the columella, an endothecal dissepiment, and a primary septum, ×8. | |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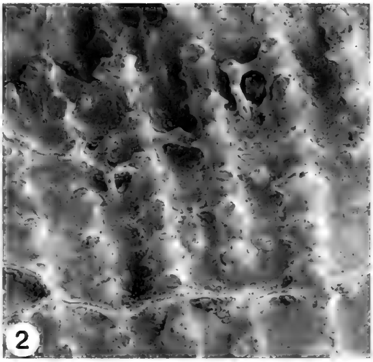
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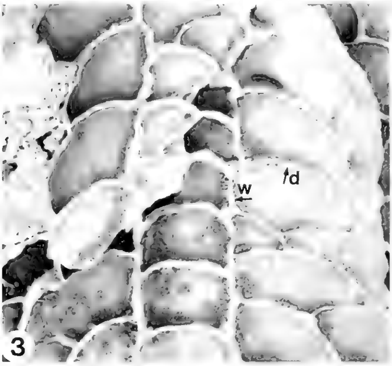
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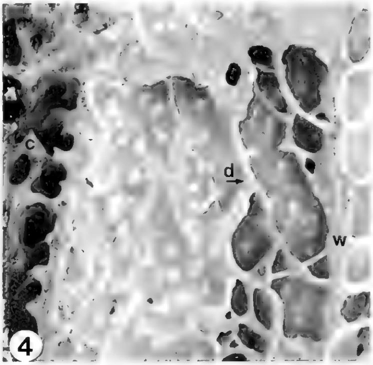
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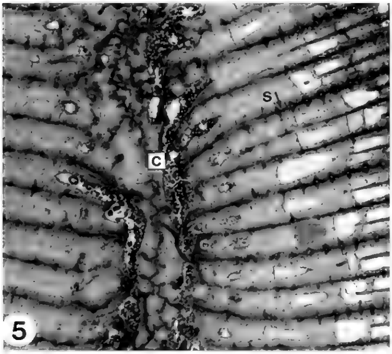
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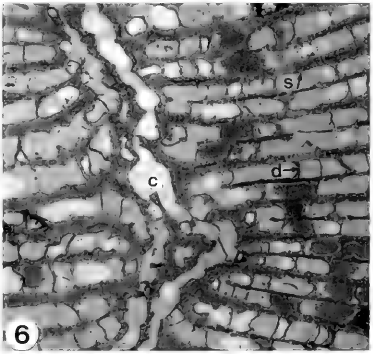
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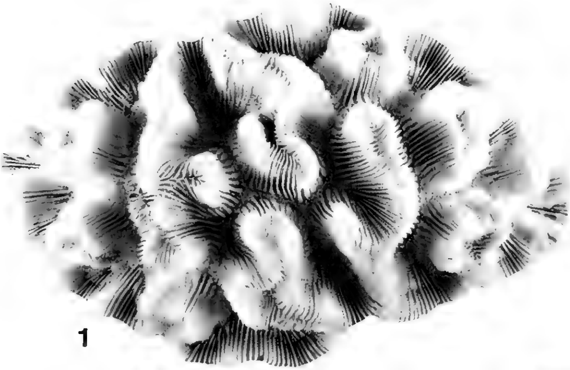
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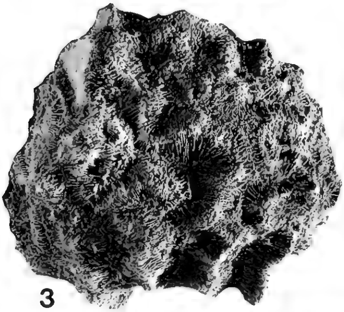
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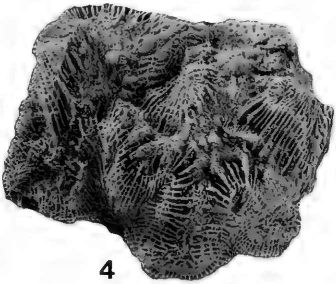
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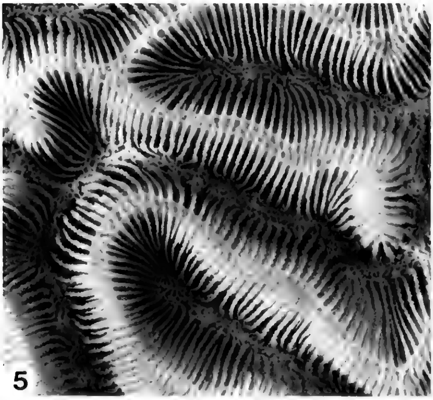
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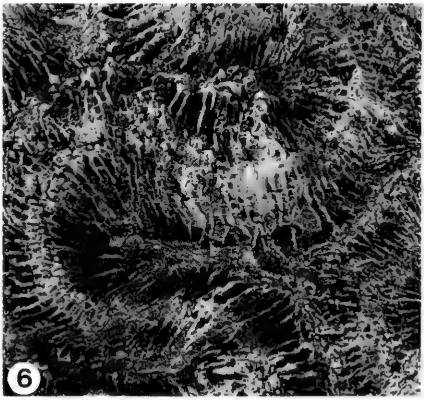
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## EXPLANATION OF PLATE 18

*Manicina.* Whole colony and colony surface photographs. Both *M. pliocenica* and *M.* n. sp. aff. *mayori* have wider valleys than their modern counterparts, *M. areolata* and *M. mayori. M. pliocenica* has more widely spaced valleys than *M. areolata,* whereas *M.* n. sp. aff. *mayori* has more narrowly spaced valleys than *M. mayori.*

Figure Page

1, 2. ***Manicina areolata*** (Linnaeus) . . . . . . . . . . 24, 46
  1. Figured specimen. SUI 80507 (KJ 370). Recent, locality KJ-88P3, Buena Ventura, Panama. Colony surface, ×1.
  2. Figured specimen. SUI 80495 (KJ B316). Recent, locality KJ-88B3, Blue Ground Range, Belize. Colony surface, ×1.

4. ***Manicina pliocenica*** Gane . . . . . . . . . . 47
  Figured specimen. NMB D6163 (CCD 2048). Upper Miocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.

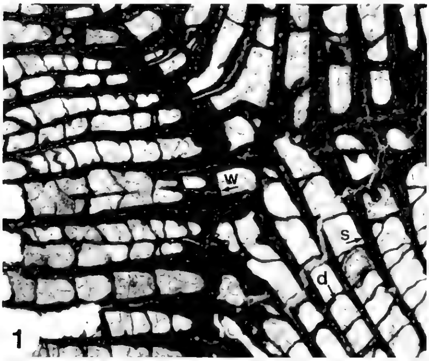
3, 5. ***Manicina*** n. sp. aff. *mayori* Wells . . . . . . . . . . 49
  3. Figured specimen. NMB D6166 (CCD 2055). Lower Pliocene, locality NMB 16859, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×0.5.
  5. Figured specimen. NMB D6166 (CCD 2055). Same specimen as figure 3. Calical surface, ×2.

6. ***Manicina mayori*** Wells . . . . . . . . . . 24, 49
  Figured specimen. BM(NH) 1928.3.136. Recent, Dry Tortugas. Calical surface, ×2.

## EXPLANATION OF PLATE 19

*Manicina.* Thin section and scanning electron micrographs. The genus *Manicina* is generally characterized by acute septal teeth, parathecal walls, and well-developed endotheca. $c$ = columella, $d$ = endothecal dissepiment, $s$ = primary septum, $w$ = wall.

| Figure | | Page |
|---|---|---|
| 1. | ***Manicina*** n. sp. aff. *mayori* Wells | 49 |
| | 1. Figured specimen. NMB D6166 (CCD 2055). Same specimen as Plate 18, figure 3. Transverse thin section showing the walls of three adjacent corallite series, ×8. | |
| 2. | ***Manicina pliocenica*** Gane | 47 |
| | 2. Neotype. NMB D6165 (CCD 2051). Upper Miocene, locality NMB 16822, Río Cana, Gurabo Formation, Dominican Republic. Transverse thin section of the end of a corallite series, ×8. | |
| 3, 5. | ***Manicina mayori*** Wells | 24, 49 |
| | 3. Figured specimen. SUI 84989. Recent, Florida. Scanning electron micrograph of the wall between two adjacent corallite series, ×10. | |
| | 5. Figured specimen. SUI 84989. Same specimen as figure 3. Scanning electron micrograph of septal margins, ×20. | |
| 4, 6. | ***Manicina areolata*** (Linnaeus) | 24, 46 |
| | 4. Figured specimen. USNM 96241 (NF497). Recent, Florida Keys. Scanning electron micrograph of wall, ×12. | |
| | 6. Figured specimen. USNM 96241 (NF497). Same specimen as figure 4. Scanning electron micrograph of septal margins, ×20. | |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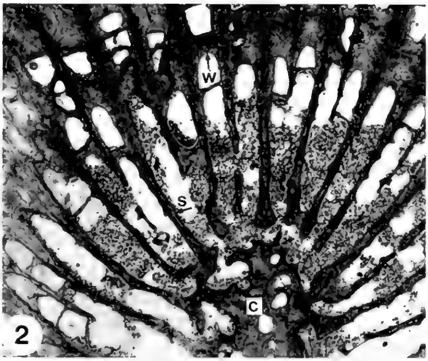
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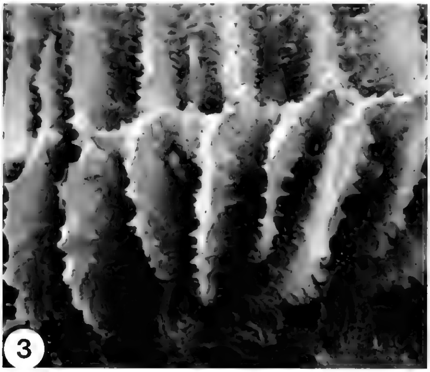
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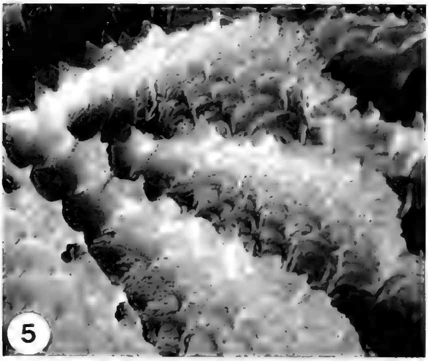
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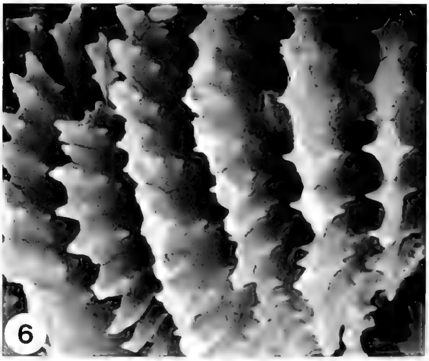
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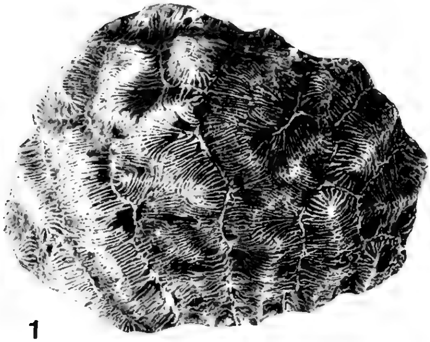
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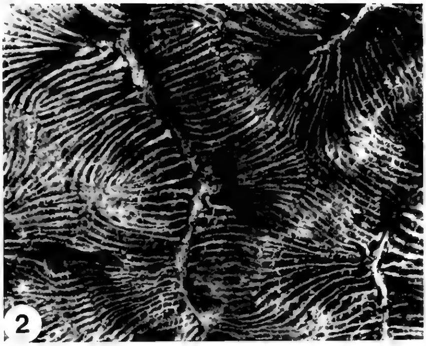
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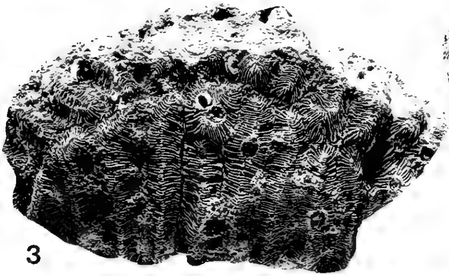
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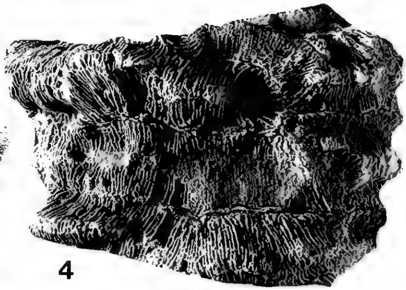
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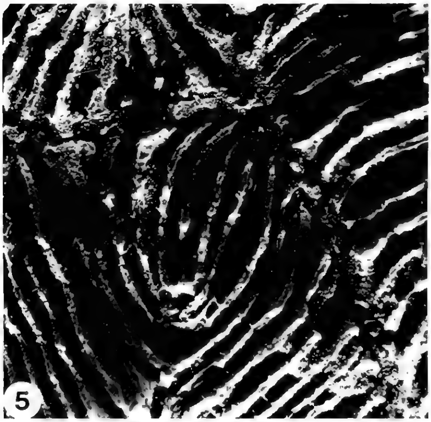
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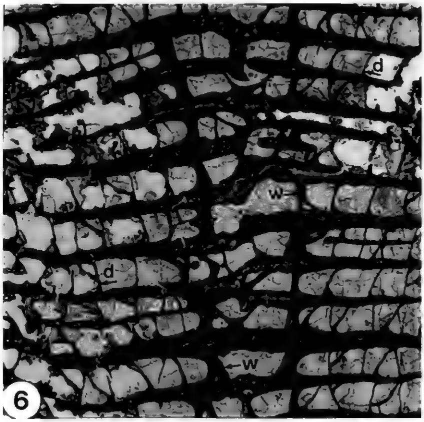

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## EXPLANATION OF PLATE 20

| Figure | Page |
|---|---|
| 1-6. ***Manicina puntagordensis*** Weisbord | 48 |

Whole colony, calical surface, and thin section photographs. *M. puntagordensis* is distinguished by ellipsoidal free-living colonies, regular straight valleys, reduced numbers of septa, and lamellar-like columella. *d* = endothecal dissepiment, *w* = wall.

1. Holotype. PRI 27560. Lower Pliocene, Punta Gorda anticline (W-23), Playa Grande Formation, Venezuela. Colony surface, ×0.75.
2. Holotype. PRI 27560. Same specimen as figure 1. Calical surface, ×2.
3. Figured specimen. NMB D6168 (CCD 2052). Upper Miocene, locality NMB 16827, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×0.5.
4. Figured specimen. NMB D6019 (CCD 2057). Lower Pliocene, locality NMB 16859, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1.
5. Figured specimen. NMB D6168 (CCD 2052). Same specimen as figure 3. Calical surface, ×5.
6. Figured specimen. NMB D6019 (CCD 2057). Same specimen as figure 4. Transverse thin section showing a double wall between two adjacent corallite series, ×8.

## EXPLANATION OF PLATE 21

*Colpophyllia*. Colony surfaces and transverse thin section. The genus *Colpophyllia* is distinguished by discontinuous lamellar columellae, thin septa, and double parathecal walls. *c* = columella, *d* = endothecal dissepiment, *s* = primary septum.

| Figure | | Page |
|---|---|---|
| 1, 2, 4, 6. | ***Colpophyllia natans*** (Houttuyn) | 49 |
| | 1. Figured specimen. USNM 83111. Recent, Curacao. Colony surface, ×2. | |
| | 2. Figured specimen. NMB D6022 (CCD 2011). Lower Pliocene, locality NMB 16818, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, ×1. | |
| | 4. Figured specimen. NMB D6022 (CCD 2011). Same specimen as figure 2. Calical surface, ×5. | |
| | 6. Figured specimen. NMB D6022 (CCD 2011). Same specimen as figure 2. Transverse thin section through a corallite center, ×8. | |
| 3. | ***Colpophyllia breviserialis*** Milne Edwards & Haime | 50 |
| | 3. Holotype. BM(NH) 1840.5.29.6. Colony surface, ×2. | |
| 5. | ***Colpophyllia amaranthus*** (Houttuyn) | 50 |
| | 5. Figured specimen. BM(NH) 1928.3.1.69. Colony surface, ×2. | |


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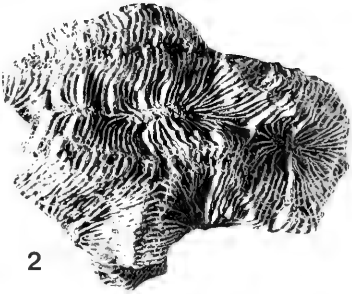
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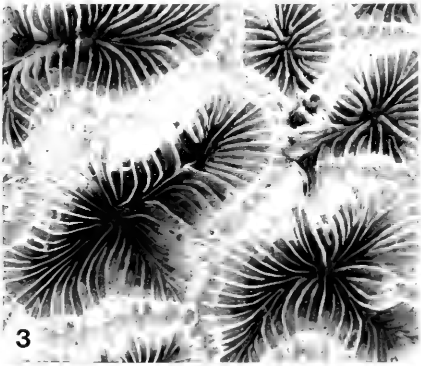
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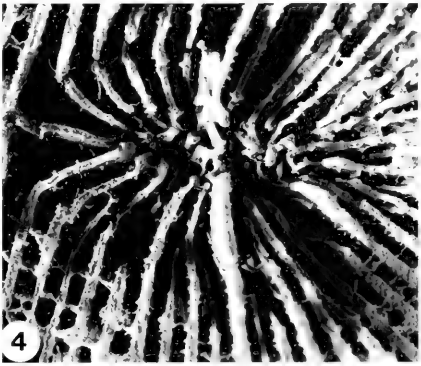
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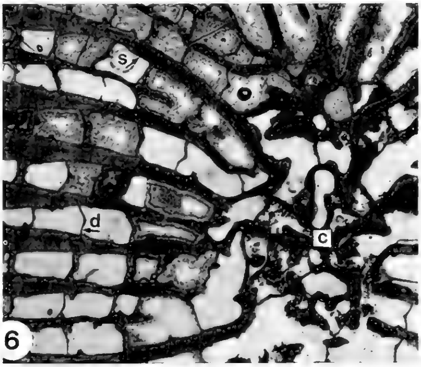

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Note: Page numbers for descriptions of genera and species are shown in **bold** type