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Neogene Paleontology in the northern Dominican Republic

11. The Family Faviidae (Anthozoa: Scleractinia)

Part I. The Genera *Montastraea* and *Solenastrea*

by

Ann F. Budd

Paleontological Research Institution
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by

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ABSTRACT

Multivariate statistical analyses are used to distinguish species in the genera *Montastraea* and *Solenastrea* through a continuous Neogene sequence (five Ma time interval) in the Cibao Valley of the northern Dominican Republic. Some older (by approximately 10 Ma) material from the same region also is included in the analyses. The material consists of approximately 280 colonies of *Montastraea* (74 of which are measured) from a total of 59 localities, and 66 colonies of *Solenastrea* (15 of which are measured) from a total of 37 localities. Twelve additional colonies of *Montastraea* from the Vokes' collections of the same localities are also measured, and added to the data set. The material is first sorted into the two genera on the basis of qualitative examination of septal structure, the structure of the columella and associated paliform lobes, and the texture of the coenosteum. Sixteen characters consisting of linear distances and counts are measured in transverse thin-sections of ten corallites per colony in *Montastraea*; ten similar characters are measured on the upper surface of ten calices per colony in *Solenastrea*. The data are analyzed using cluster and canonical discriminant analysis to group the colonies into clusters representing species. Seven species are so defined in *Montastraea* and two in *Solenastrea*. These groupings are then used statistically to reclassify type specimens for 12 of the 17 described species of *Montastraea* and four of the seven described species of *Solenastrea*.

Three of the 12 species are synonymized in *Montastraea*, and two of the four species are synonymized in *Solenastrea*. Further qualitative study of the remaining types suggests that nine species of *Montastraea* and two species of *Solenastrea* existed altogether in the Caribbean during the Neogene. The stratigraphic range of two of the seven Dominican Republic species of *Montastraea* is shown to extend back to the Oligocene. Another of the Dominican Republic species is found to exist today, and is widely distributed throughout the Caribbean. Of the nine Neogene Caribbean species, only this species survived the Plio-Pleistocene extinction event. Only one species of *Montastraea* is found to be endemic to the Dominican Republic. One of the remaining three species of *Montastraea* also has a limited stratigraphic distribution and appears confined to the southern Caribbean. Both species of *Solenastrea* appear to range from the Early Neogene to the Recent, and are widely distributed throughout the Caribbean.

Trends within each species of *Montastraea* are analyzed through the sequence using nonparametric statistical procedures. Significant changes are detected upsection for at least four of the seven species in character complexes related to corallite size, septal development, and coenosteum development; however, significant correlations with species diversity suggest that these trends may be environmental in origin. Occurrence data suggest that two of the seven species of *Montastraea* may be indicative of shallow, nearshore conditions, whereas another two may be confined to muddy, and presumably deeper, patch reef localities. When data spanning the Oligocene to Recent are analyzed, significant directional trends are detected in one of the three longer-ranging Dominican Republic species; however, the amount of change does not exceed that observed within modern species. This suggests that, despite an apparent zigzag pattern, net stasis may be the rule in *Montastraea*.

This study represents 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.

RESUMEN

Se utilizan análises estadísticos para distinguir especies en los géneros *Montastraea* y *Solenastrea* a travéz de una secuencia Neogena continua (intervalo de tiempo de cinco milliones de años) en el Valle Cibao en el norte de la República Dominicana. Se incluyen también en los análises algunos materiales más antiguos (de aproximadamente 10 milliones de años) de la misma región. Los materiales consisten en aproximadamente 280 colonias de *Montastraea* (74 de las cuales se miden) de un total de 59 localidades, y 66 colonias de *Solenastrea* (15 de las cuales se miden) de un total de 37 localidades. También se miden y se agregan al conjunto de datos 12 colonias adicionales de *Montastraea* de las colecciones Vokes de las mismas localidades de la Universidad de Tulane. Primero se separá el material de dos géneros en base a exámenes cualitativos de la estructura del septo, la estructura del eje central y de los lóbulos paliformes asociados, y de la textura del coenosteum. Luego se miden 16 carácteres consistentes de distancias y cuentas lineares en secciones finas transversas de 10 coralitas por colonia en *Montastraea*; se miden 10 caracteres similares en la superficie superior de 10 cálices por colonia en *Solenastrea*. Se analizan los datos utilizando análises discriminativos canónicos y de grupos para agrupar las colonias en colecciones representativas de las especies. Se definen así siete especies en *Montastraea* y dos en *Solenastrea*. Luego se usan estadísticamente estas agrupaciones para reclasificar especimenes tipos de 12 de las 17 especies descriptas de *Montastraea* y cuatro de las siete especies descriptas de *Solenastrea*. Tres de las 12 especies en *Montastraea* y dos de las cuatro de las especies de *Solenastrea* son sinónimas. Mas estudios cualitativos de los tipos restantes sugieren que nueve especies de *Montastraea* y dos de *Solenastrea* existieron en el Caribe durante el Neógeno. Se ha demostrado que la zona estratigráfica de dos de las siete especies de *Montastraea* de la República Dominicana se remonta al Oligoceno. Un otro de las especies de la República Dominicana existe hoy y está ampliamente distribuida a travéz del Caribe. De las nueve especies Neógenas del Caribe, solo esta especie sobrevive la extinción del Plio-Pleistoceno. Se ha encontrado que solo una especie de *Montastraea* es endemica de la República Dominicana. Uno de las tres otras especies restantes de *Montastraea* tambien tiene una distribucion estratigráfica limitada, y parece estar confinada al sur del Caribe. Ambas especies de *Solenastrea* aparentemente extenden desde el Neógeno temprano al Reciente, y están ampliamente distribuidas a travéz del Caribe.

Se analizan tendencias dentro de cada especie de *Montastraea* a travéz de la secuencia usando procedimientos estadísticos no paramétricos. Se detectan cambios importantes en una direccion arriba en la sección en á lo menos cuatro de las siete complejidades de carácteres relacionados con el tamaño de las coralitas, el desarrollo del septo, y el desarrollo del coenosteum; sin embargo, correlaciones importantes con la diversidad de especies sugieren que estas tendencias pueden ser debidas, en origen, al medio ambiente. Los datos de ocurrencia sugieren que dos de las siete especies de *Montastraea* pueden ser indicativa de la existencia de condiciones someras, y cerca de la costa; mientras que dos pueden estar confinadas a localidades barrosas de arrecifes isoladas, que estan presumiblemente mas hondas. Cuando se analizan datos que abarcan del Oligoceno al Reciente, se detectan tendencias direccionales significativas en solo uno de las especies Dominicanas de gran extension temporal; sin embargo la cantidad de cambio no excede lo que esta observada en especies Recientes. Este sugiere que, a pesar de un modelo que parece zigzag, estasis neta puede ser la regla en las especies de *Montastraea*.

Este estudio representa parte de un proyecto multidisciplinario de la paleontología y estratigrafía del norte de la República Dominicana, coordinado por P. Jung y J. B. Saunders del Naturhistorisches Museum en Basel, Suiza.

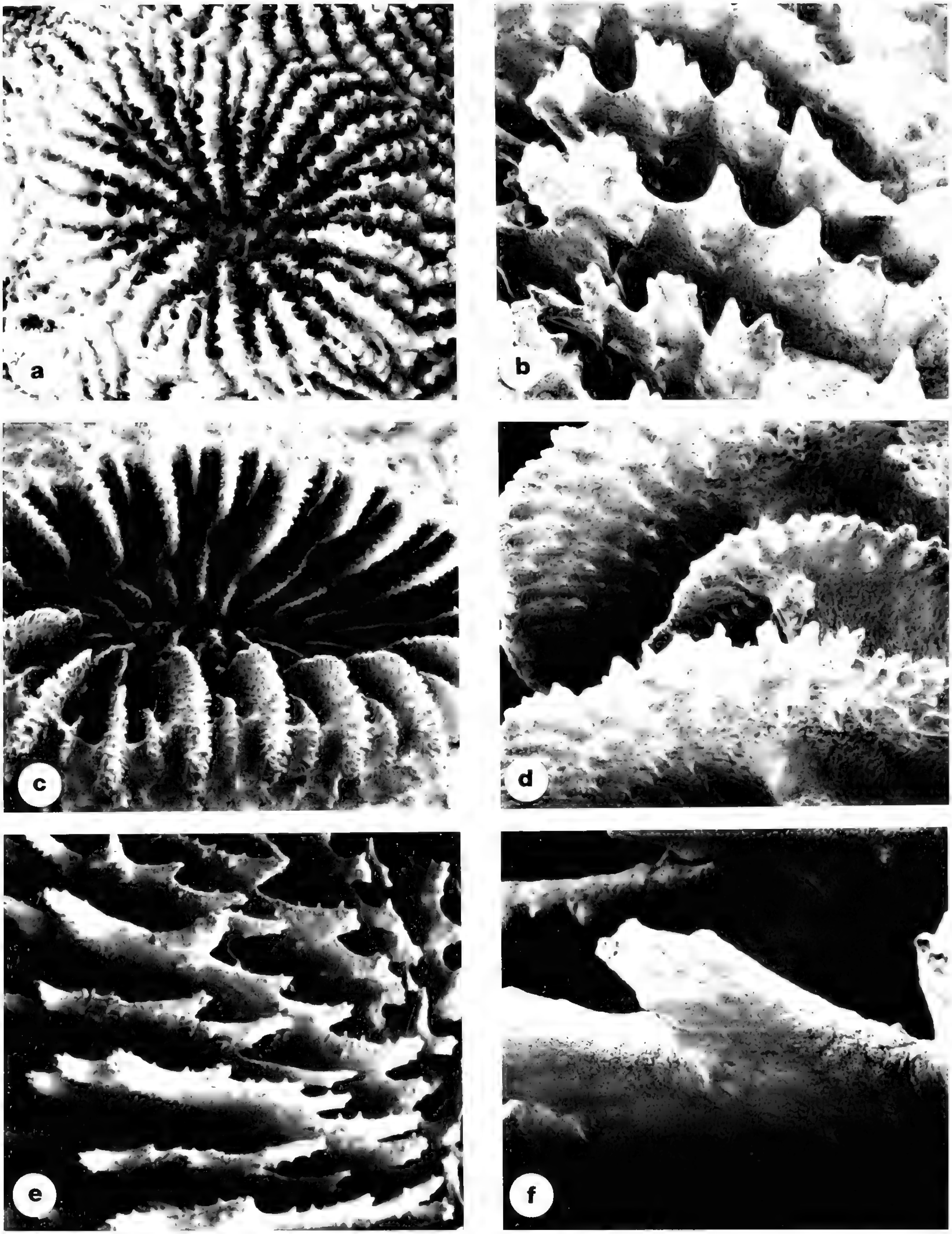
INTRODUCTION

This paper is the third in a series on the systematics and evolutionary history of the reef-corals from the middle Miocene to middle Pliocene of the northern Dominican Republic. It is the first of two papers on the family Faviidae Gregory, 1900, one of the most taxonomically diverse and abundant groups of corals throughout the sequence. Excluding the once-synonymized family Trachyphylliidae Verrill, 1901 (following Veron, Pichon, and Wijsman-Best, 1977), the family Faviidae is represented in the sequence by as many as nine genera and 20 species. Of these genera, two are currently extinct and five are currently restricted to the Caribbean. Similarly, only 12 species of the family Faviidae occur today in the Caribbean. Thus, the family was significantly more diverse in the Caribbean during the Neogene than it is today, and presumably experienced considerable extinction between late Pliocene and modern time. The purpose of the present study is morphometrically to redefine and formally to describe the taxa represented in the Caribbean Neogene using a well-documented sequence of fossil populations. The results are interpreted to ascertain which species became extinct and which have survived until modern time. The systematic revisions that constitute the basis of the present study will be used in the future to reconstruct the phylogeny of the family globally at the species level.

In general, the family Faviidae is characterized by septa composed of simple trabeculae, arranged in one or two laminar fan systems, which form smooth, acute teeth along the upper septal margins (Wells, 1956; Text-fig. 1). Within the family, genera are distinguished by colony form or, in other words, by degree of integration of corallites within colonies, a trait controlled by asexual budding of corallites during colony growth. Species are distinguished by the architecture of the individual corallites and, in particular, by features related to their size (Vaughan, 1901, 1907). Thus, formation of genera appears the result of changes in growth and development of colonies; whereas, formation of species (herein termed "speciation") involves changes in growth and development of individual corallites. Because of the large amount of material involved, the present treatment of the family has been subdivided into two parts. This first part focuses on species recognition within the two most abundant and presumably most speciose genera, *Montastraea* Blainville, 1830 and *Solenastrea* Milne Edwards and Haime, 1848. The second part, to follow later in the series, focuses on the recognition of seven less abundant and less diverse genera. The two genera in the present paper are strikingly similar morphologically. They both form massive, plocoid colonies by extratentacular budding; therefore, corallites within their colonies are relatively less well-integrated. Species within each of the two genera differ primarily in corallite size.

As in the two previous papers (Foster, 1986, 1987), the material on which this study is based 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 of the Cibao Valley region. All collecting localities are keyed into their detailed stratigraphic sections (Saunders *et al.*, 1982; Saunders,

Text-figure 1.—Scanning electron microscope photographs showing upper septal margins characteristic of three families within the suborder Faviina. (**A**, **B**) the family Faviidae, characterized by regularly well-developed septal teeth, SUI 54923, *Favia fragum* (Esper, 1795), Recent, La Parguera, Puerto Rico; (**C**, **D**) the family Meandrinidae, characterized by minute septal teeth, SUI 54925, *Dichocoenia stokesi* (Milne Edwards and Haime, 1848) Recent, Discovery Bay, Jamaica; (**E**, **F**) the family Mussidae, characterized by extremely long, wide teeth, SUI 54924, *Isophyllia sinuosa* (Ellis and Solander, 1786), Recent, Discovery Bay, Jamaica. **A**, **C**, **E**, ×10; **B**, **D**, **F**, ×39.


a
b
c
d
e
f

Jung, and Biju-Duval, 1986). The sequence is notable in that it is one of the longest, most continuous, and best-studied sections through Neogene coral deposits in the Caribbean. It is also distinctively well-preserved. The collections studied include all macrofossils extracted from the surface of the outcrop and all associated microfossils picked from bulk samples. The samples were taken at carefully selected, closely spaced stratigraphic intervals, and have been dated using microfossil occurrences. In total, the project involves as many as fifty specialists on a wide variety of taxonomic groups. The eventual aim is to assemble a data set of occurrences of different taxonomic groups through the sequence and to use this data set in interpreting environmental as well as evolutionary change.

The first major study of the Faviidae from the northern Dominican Republic was made by Duncan (1863, 1864, 1868) on the Heneken collection (Heneken, 1853), now deposited at the British Museum (Natural History) [BM(NH)]. In these publications, Duncan described 16 species (12 of which were new) belonging to the family Faviidae. Of these, nine (eight of which were new) belong to the genera *Montastraea* and *Solenastrea*. Most of Duncan's descriptions, however, were based on single specimens or fragments of specimens, which Vaughan (1919) later re-interpreted as representing a total of six species of *Montastraea* and *Solenastrea*, only four of which were new. Shortly after Duncan, Pourtalès (1875) listed ten species (three unidentified) of the family Faviidae in his list of corals, collected by W. B. Gabb (Gabb, 1873), and now deposited at the Museum of Comparative Zoology of Harvard University (MCZ) and at the Academy of Natural Sciences of Philadelphia (ANSP). None, however, were described as new. The ten species included four species of the genera *Montastraea* and *Solenastrea*.

Almost fifty years later, Vaughan (1919) described five species of the family Faviidae (including four in the genera *Montastraea* and *Solenastrea*) in the Maury collection [Maury, 1917; deposited at the United States National Museum (USNM)] from the Neogene of the Dominican Republic. None were described as new. Vaughan and Woodring (1921, pp. 134, 135) later added nine more faviids (including five *Montastraea* and *Solenastrea*) to the number, as part of a faunal list on their large, well-documented collections also deposited at the USNM. Again, however, no new species were formally described. Finally, Vaughan and Hoffmeister (1925) formally described two new species belonging to the family Faviidae, based on material in the Gabb collection. Neither new species belonged to *Montastraea* or *Solenastrea*. No further work has been done on the family Faviidae from the Neogene of the Dominican Republic.

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I am grateful to J. Geister (Bern, Switzerland), P. Jung [Naturhistorisches Museum Basel (NMB)], and J. B. Saunders (NMB) for collecting the material, providing locality information, and assisting in sorting and curating specimens. Emily and Harold Vokes, Tulane University (TU), also generously provided additional material. H. Klein of the University of Iowa (SUI) and R. Brickson (SUI) provided specimens of *Solenastrea* from the Pliocene of Florida. K. Müller (NMB) and T. Bahns (SUI) prepared the thin-sections; U. A. Dogan (SUI) assisted with scanning electron microscopy; and B. Fouke (SUI) measured the NMB *Solenastrea* colony surfaces. Points were digitized from *Solenastrea* thin-sections using image-analyzing equipment made available at the NSF-sponsored workshop on "Morphometrics in Systematic Biology" during May, 1988, at the University of Michigan. J. Geister provided x-radiographic equipment. Many of the whole colony photographs were prepared by the photography staff at the British Museum of Natural History [BM(NH)]. Photographs were also provided by W. Suter (NMB) and M. Serrete, Muséum national d'Histoire naturelle, Paris (MNHNP). H. Greenberg (SUI) and C. Brochu (SUI) assisted with preparation of plates; J. Kralick (SUI) with computer graphics; and R. Petrick (SUI) and G. Greiner (SUI) with typing.

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INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History, New York, NY, U. S. A.

ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, PA, U. S. A.

BM(NH): The Natural History Museum, London, England, U. K.

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, MA, U. S. A.

MNHNP: Muséum national d'Histoire naturelle Paris, Paris, France

NF: Nancy Foster coral collection specimen numbers (specimens reposited at USNM)

NMB: Naturhistorisches Museum Basel, Basel, Switzerland

NMS: Natur-museum Senckenberg, Frankfurt, Germany

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.

UCMP: University of California, Museum of Paleontology, Berkeley, CA, U. S. A.

UF: Florida State Museum, University of Florida, Gainesville, FL, U. S. A.

UI: University of Illinois, Department of Geology, Urbana, IL, U. S. A.

USGS: United States Geological Survey, Washington, DC, U. S. A.

USNM: United States National Museum of Natural History, Washington, DC, U.S.A.

WFIS: Wagner Free Institute of Science, Philadelphia, PA, U.S.A.

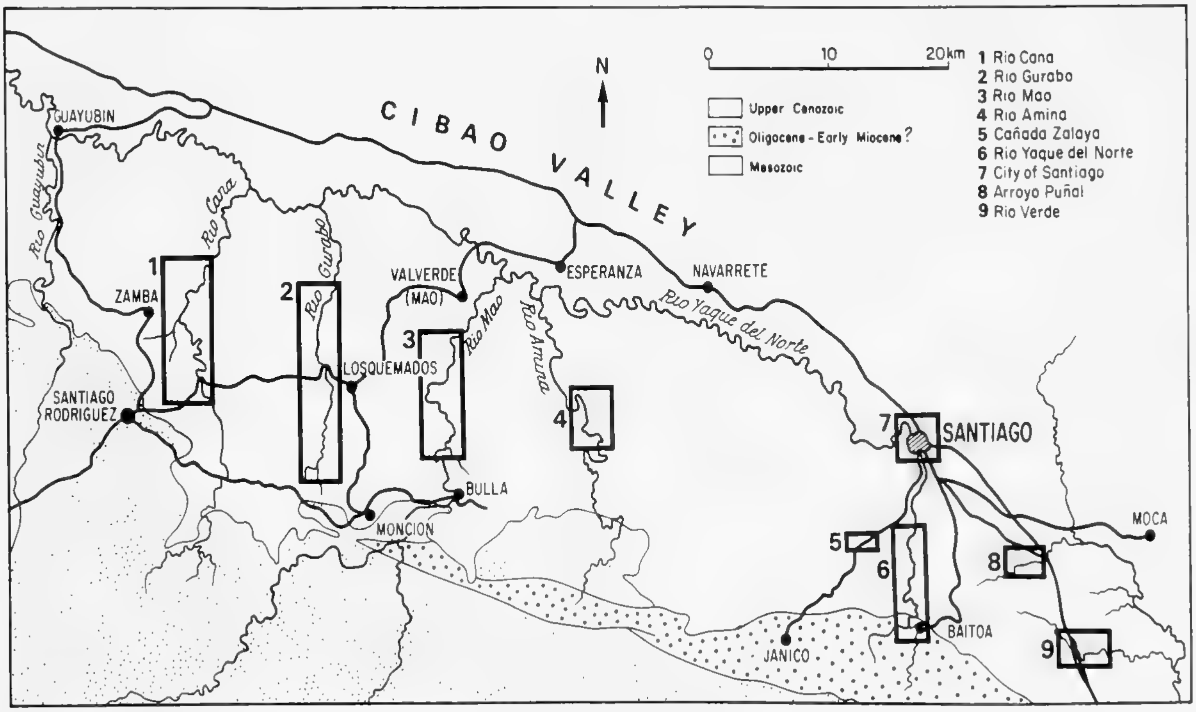
YPM: Yale Peabody Museum, New Haven, CT, U. S. A.

BIOSTRATIGRAPHY AND PALEOECOLOGY

Montastraea Blainville, 1830 and *Solenastrea* Milne Edwards and Haime, 1848 are abundant in four of the river sections (Río Cana, Río Gurabo, Río Mao, and Río Yaque del Norte) collected by Saunders, Jung, and Biju-Duval (1986) through the Neogene of the Cibao Valley (Text-fig. 2). They were not found elsewhere in the study area. Specimens of *Montastraea* were collected at a total of 59 localities, ranging in age from middle Miocene to middle Pliocene. Specimens of *Solenastrea* were collected at a total of 37 localities, ranging in age from late Oligocene to middle Pliocene.

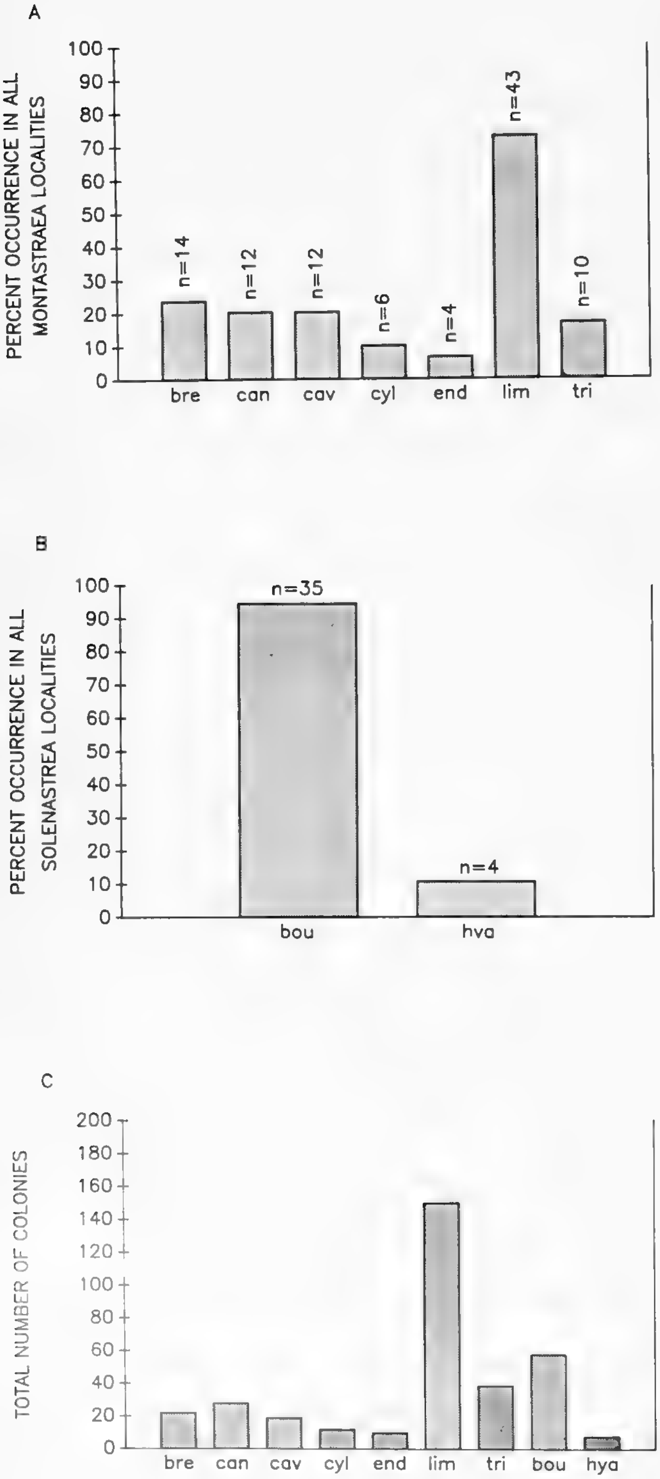
Two species, *M. limbata* (Duncan, 1863) and *S. bournoni* Milne Edwards and Haime, 1849 were especially common, occurring at more than 30 localities each (Text-fig. 3). *S. bournoni* was found throughout all four river sections, whereas *M. limbata* was restricted to late Miocene and younger portions of the four river sections (Text-fig. 4).

Two species, *M. trinitatis* (Vaughan *in* Vaughan and Hoffmeister, 1926) and *S. hyades* (Dana, 1846) were more common lower in the sequence, especially in the lower to middle Miocene López section of the Río Yaque del Norte. In general, however, *S. hyades* was notably rare throughout the studied sequence. Three species, *M. brevis* (Duncan, 1864), *M. cylindrica* (Duncan, 1863), and *M. endothecata* (Duncan, 1863) were not found in the sections along the Río Yaque del Norte. They were common, instead, in exposures of



Text-figure 2.—Map indicating the location of the river sections sampled. *Montastraea* and *Solenastrea* were found in only four sections: (1) Río Cana, (2) Río Gurabo, (3) Río Mao, and (6) Río Yaque del Norte (map from Saunders, Jung, and Biju-Duval, 1986).

the late Miocene to earliest Pliocene Gurabo Formation along the Río Gurabo and the Río Cana. Of these three species, only *M. cylindrica* was found higher in the section in the early Pliocene Mao Formation reefs along Río Cana. The remaining two species, *M. canalis* (Vaughan, 1919) and *M. cavernosa* (Linnaeus, 1767), were found in moderate abundances throughout the four river sections.



To trace patterns of evolutionary and environmental change through the sequence within the nine species, morphologic variation was analyzed quantitatively across a composite of the Río Cana and Río Gurabo sections [constructed by correlating the two sections as in Foster (1986; 1987)], which spans a time interval of approximately five million years (Text-figs. 5, 6). The characters analyzed consisted of the most important character complexes (the so-called canonical variables calculated in the next section) distinguishing the Dominican Republic species within each genus. In *Montastraea*, three complexes were analyzed: (1) corallite size (canonical variable 1); (2) septal development (canonical variable 2); and (3) coenosteum development (canonical variable 3). In *Solenastrea*, only one character complex was studied, a complex related to the length of the tertiary septa and the development of the columella.

To determine if any changes in these complexes occurred upsection, the composite section was subdivided into twelve 100 m-thick intervals, and a Kruskal-Wallis rank-sum oneway analysis of variance (**PROC NPAR1WAY** of **SAS**) was performed to determine if any differences existed in means of colonies collected within each 100 m interval. In *Montastraea*, no significant differences could be detected in the three character complexes between stratigraphic intervals within any of the seven species. The one possible exception occurred in *M. cylindrica* in canonical variable 2 (Text-fig. 5). In *Solenastrea*, too few stratigraphic intervals were represented within each species to permit comparison (Text-fig. 6).

Further statistical tests performed by calculating Spearman rank correlation coefficients between canonical variable scores and stratigraphic elevation on the composite section for each colony (**PROC CORR**

←

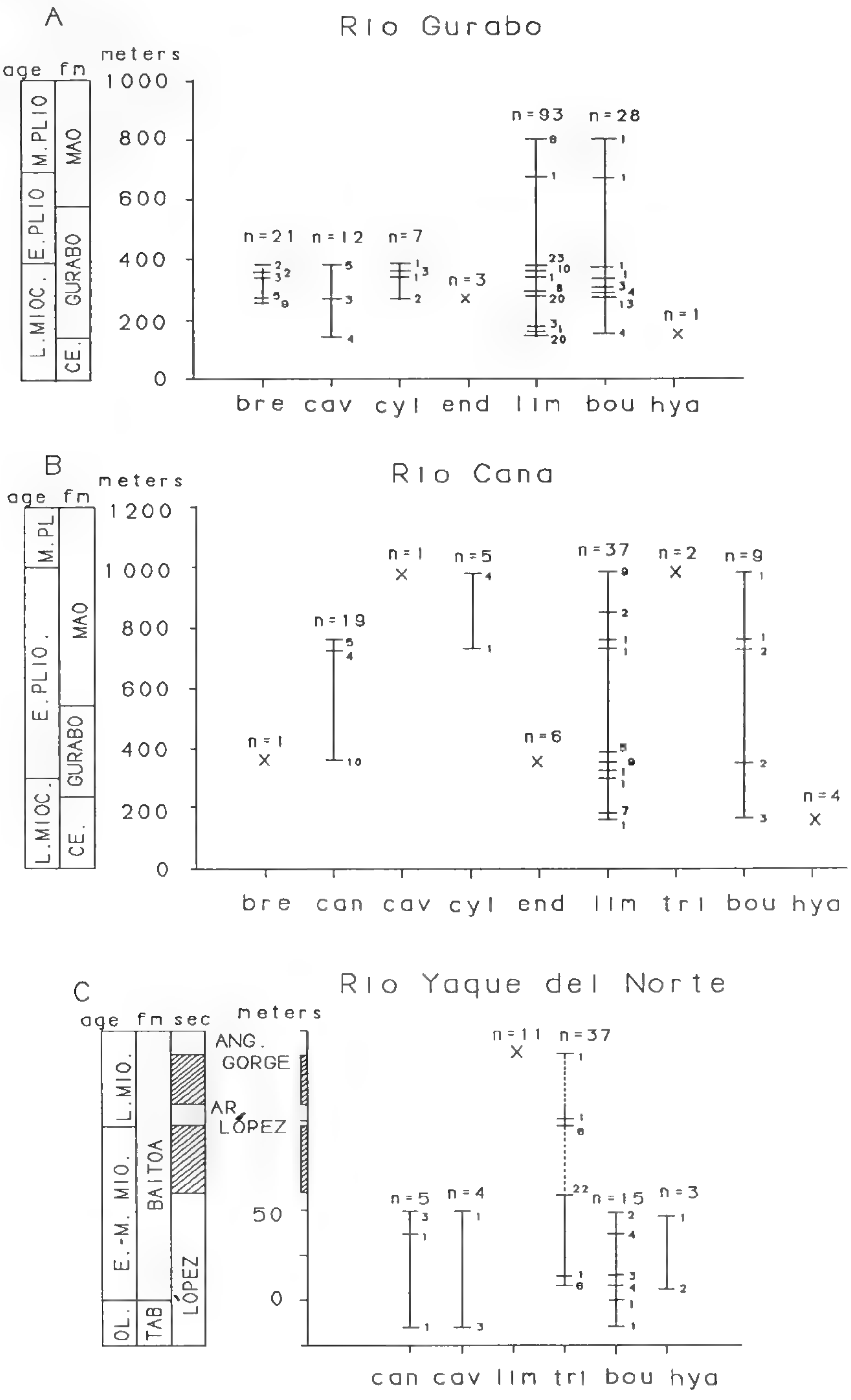
Text-figure 3.—Bar charts summarizing the quantity of material collected. (A) percentage of all *Montastraea* localities containing each species; (B) percentage of all *Solenastrea* localities containing each species; (C) total number of colonies collected of each species. "n" = total number of localities, "bre" = *M. brevis*, "can" = *M. canalis*, "cav" = *M. cavernosa*, "cyl" = *M. cylindrica*, "end" = *M. endothecata*, "lim" = *M. limbata*, "tri" = *M. trinitatis*, "bou" = *S. bournoni*, "hya" = *S. hyades*.

⟶

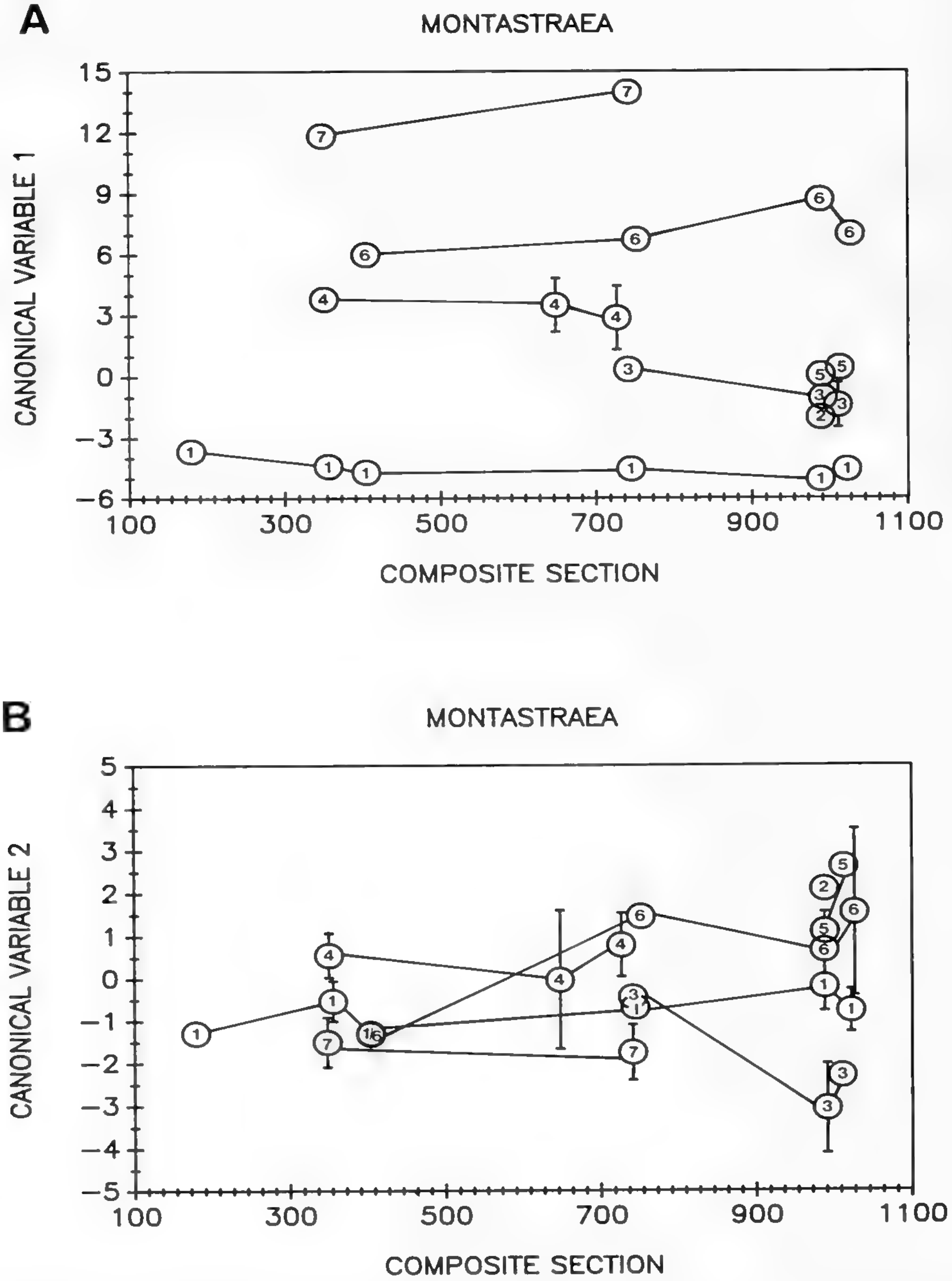
Text-figure 4.—Diagrams showing the distributions of species within selected river sections collected by Saunders, Jung, and Biju-Duval, 1986. Each vertical line within each plot represents one species. Ticks along each line represent stratigraphic positions (meters from the datum as measured by Saunders, Jung, and Biju-Duval, 1986) at which the species was found to occur. Numbers to the right of each tick mark indicate the number of localities represented by each point. "n" = total number of colonies containing each species, "bre" = *M. brevis*, "can" = *M. canalis*, "cav" = *M. cavernosa*, "cyl" = *M. cylindrica*, "end" = *M. endothecata*, "lim" = *M. limbata*, "tri" = *M. trinitatis*, "bou" = *S. bournoni*, "hya" = *S. hyades*. (A) Rio Gurabo, (B) Río Cana, (C) Río Yaque del Norte.

of SAS) suggest that slight directional change may have occurred upsection in *M. cylindrica* in canonical variable 2, and in *M. brevis* and *M. cavernosa* in canonical variable 3.

Because of the small sample sizes involved in these analyses, 12 colonies of *Montastraea* collected by Emily and Harold Vokes of Tulane University (Table 1) and 13 colonies collected by T. W. Vaughan [USNM 62728 (NF448), 66829 (NF458, 460, 461), 66831 (NF489), 66832 (NF485), 66833 (NF420, 421), 66867 (NF424, 425), 66899 (NF284), 66902 (NF289), 66904 (NF292)] were added to the data set, and the analyses were rerun using data for the first two canonical variables on each corallite. In this case, Kruskal-Wallis tests indicate that highly significant differences occur between statigraphic levels in all six species (Table 2),



with the exception of canonical variable 1 in *M. canalis*. Spearman rank correlation coefficients suggest that change within two of the five species (*M. brevis* and *M. cavernosa*) is directional in canonical variable 1, and that change within four of the six species (*M. limbata*, *M. brevis*, *M. canalis*, and *M. cavernosa*) is directional in canonical variable 2. In other words, corallite size is increasing upsection in *M. cavernosa*, and is decreasing upsection in *M. brevis*. Septal development is decreasing overall upsection in *M. cavernosa*, *M. canalis*, *M. brevis*, and *M. limbata*. These results suggest that significant change may be occurring within



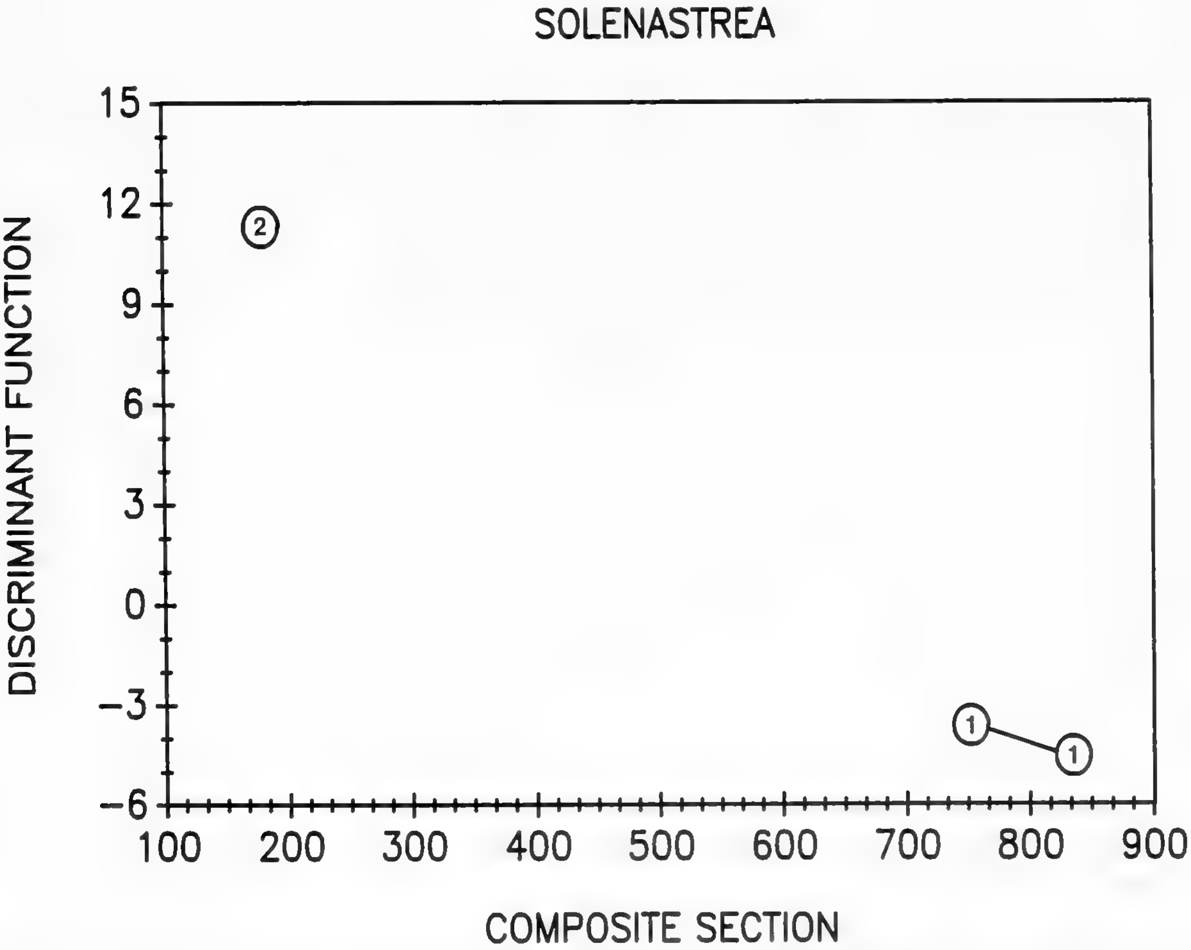
Text-figure 5.—*Montastraea*. Variation within species in two corallite character complexes through a composite stratigraphic section (constructed by correlating the two sections as in Foster, 1986, 1987). The points (labelled 1–7) represent means for every 100 m interval along the composite section. 1 = *M. limbata*, 2 = *M. trinitatis*, 3 = *M. brevis*, 4 = *M. canalis*, 5 = *M. cylindrica*, 6 = *M. cavernosa*, 7 = *M. endothecata*. Vertical lines on either side of each point are one-half standard deviation in length. (A) Canonical variable 1 of the *Montastraea* canonical discriminant analysis, which is most strongly related to corallite size. (B) Canonical variable 2 of the *Montastraea* canonical discriminant analysis, which is most strongly related to septal development. In canonical variable 1, significant directional change was detected upsection in species 3 (decrease) and species 6 (increase). In canonical variable 2, slight decreases were detected overall in species 1, 3, 4, and 6.

Table 1.—List of specimens of *Montastraea* collected by E. and H. Vokes, and measured and used in the statistical analyses. See Saunders, Jung, and Biju-Duval (1986) for detailed descriptions of localities.

catalogue number	*locality number*	*section*	*species*
USNM 86898	TU 1231	Río Gurabo	*M. endothecata*
USNM 86899	TU 1422	Río Cana (Arroyo Bellaco)	*M. canalis*
USNM 86900	TU 1354	Río Cana (Cañada de Zamba)	*M. limbata*
USNM 86901	TU 1344	Río Gurabo	*M. cylindrica*
USNM 86902	TU 1405	Río Yaque del Norte (Arroyo Babosico)	*M. endothecata*
USNM 86903	TU 1405	Río Yaque del Norte (Arroyo Babosico)	*M. limbata*
USNM 86904	TU 1215	Río Gurabo	*M. brevis*
USNM 86905	TU 1246	Río Gurabo	*M. brevis*
USNM 86906	TU 1278	Río Gurabo	*M. endothecata*
USNM 86907	TU 1208	Roadcut 4 km east of Los Quemados	*M. limbata*
USNM 86908	TU 1208	Roadcut 4 km east of Los Quemados	*M. trinitatis*
USNM 86909	TU 1208	Roadcut 4 km east of Los Quemados	*M. cavernosa*

lineages that appear static based on only the NMB material. To evaluate such change adequately, many more specimens of each species need to be collected and measured from the sequence using the NMB locality scheme.

With the data at hand, it is difficult to determine if the changes observed in the larger data set are environmental in origin. Although the Cibao Valley Neogene sequence is believed to have been deposited under gradually deepening conditions, some of the material



Text-figure 6.—*Solenastrea*. Variation within species in the corallite character complex distinguishing species through a composite stratigraphic section (constructed by correlating the two sections as in Foster, 1986, 1987). The points (labelled 1 and 2) represent means for every 100 m interval along the composite section. 1 = *S. hyades*, 2 = *S. bournoni*. In each case, standard deviations are smaller than the size of the dot representing the mean for each sample. Too few stratigraphic intervals are represented to permit analysis of directional change through the section.

Table 2.—Chi-square approximations resulting from the Kruskal-Wallis test and Spearman correlation coefficients between stratigraphic position within the Dominican Republic sequence, and the first two canonical variables (*CV1*, *CV2*) distinguishing species in each genus.

species	*number of corallites*	*stratigraphic range in DR (m)*	*number of 100 m intervals*	*CV1*		*CV2*	
				chi²	I_2	*chi²*	r_s
M. limbata (1)	304	847	6	49.02[a]	.022	29.65[a]	−.222[a]
M. brevis (3)	134	272	5	23.22[a]	−.361[a]	15.18[a]	−.277[a]
M. canalis (4)	55	382	3	5.36	−.372[a]	20.01[a]	−.437[a]
M. cylindrica (5)	83	365	4	35.25[a]	−.109	31.97[a]	.015
M. cavernosa (6)	57	622	4	14.56[a]	.370[a]	27.10[a]	−.684[a]
M. endothecata (7)	74	393	3	13.72[a]	.142	26.98[a]	−.071

[a] $p \leq 0.01$.

in the uppermost portions of the sequence (*e.g.*, the Mao Formation reefs along Río Cana) appears to have been transported from shallower water (Saunders, Jung, and Biju-Duval, 1986; Evans, 1986). Nevertheless, significant positive Spearman rank correlations between canonical variable 1 (corallite size) and counts of number of poritid species at each locality suggest that some of the trends may indeed be environmental in six species of *Montastraea* (all except *M. endothecata*). Significant negative correlations with number of poritid species also occur in canonical variable 2 (septal development) in *M. trinitatis* and *M. brevis*. Assuming that numbers of poritid species increase in shallow reefal environments, similar increases in corallite diameter and decreases in septal development have been observed on modern reefs extending from deeper forereef to shallower backreef environments (Foster, 1980; 1985). Thus, morphology may be responding to an increase in water energy and light.

The distribution patterns of occurrences of each species also appear to be environmentally controlled. For example, two of the three species of *Montastraea* that occur lower in the section (*M. cavernosa* and *M. trinitatis*) appear to be confined to the upper portions of the sequence (the Mao Formation) along Río Cana (Text-fig. 4), and may be indicative of more nearshore conditions. *M. brevis* and *M. endothecata*, on the other hand, appear to be confined to the muddy and presumably deeper patch reef localities in lower portions of the Gurabo Formation (Text-fig. 4). Occurrence data for more reef-coral species are needed to substantiate these hypotheses.

In contrast to the generally wide biogeographic distributions of both modern (Veron, 1986) and fossil (Foster, 1986) corals, two of the seven *Montastraea* species described herein (*M. brevis* and *M. cylindrica*) are restricted to a few isolated localities in the southern and central Caribbean, and may eventually prove indicative of a southern reef-coral biogeographic province or subprovince within the Caribbean during the Neogene (Budd, 1989). Data from more localities are needed to substantiate this hypothesis.

In conclusion, data on both morphological variation within species of *Montastraea* and associations of all reef-coral species through the sequence offer enormous potential in paleoenvironmental interpretation. However, in order to analyze such morphological variation within species, more samples need to be collected and measured from selected localities. *M. cavernosa* and to a lesser extent, *M. limbata*, appear the most useful in this regard, due to their high abundances and the more pronounced changes in morphology stratigraphically up the sequence. In order to analyze coral associations, more of the corals in the NMB collections need to be identified and tallied (see discussion in Foster, 1986).

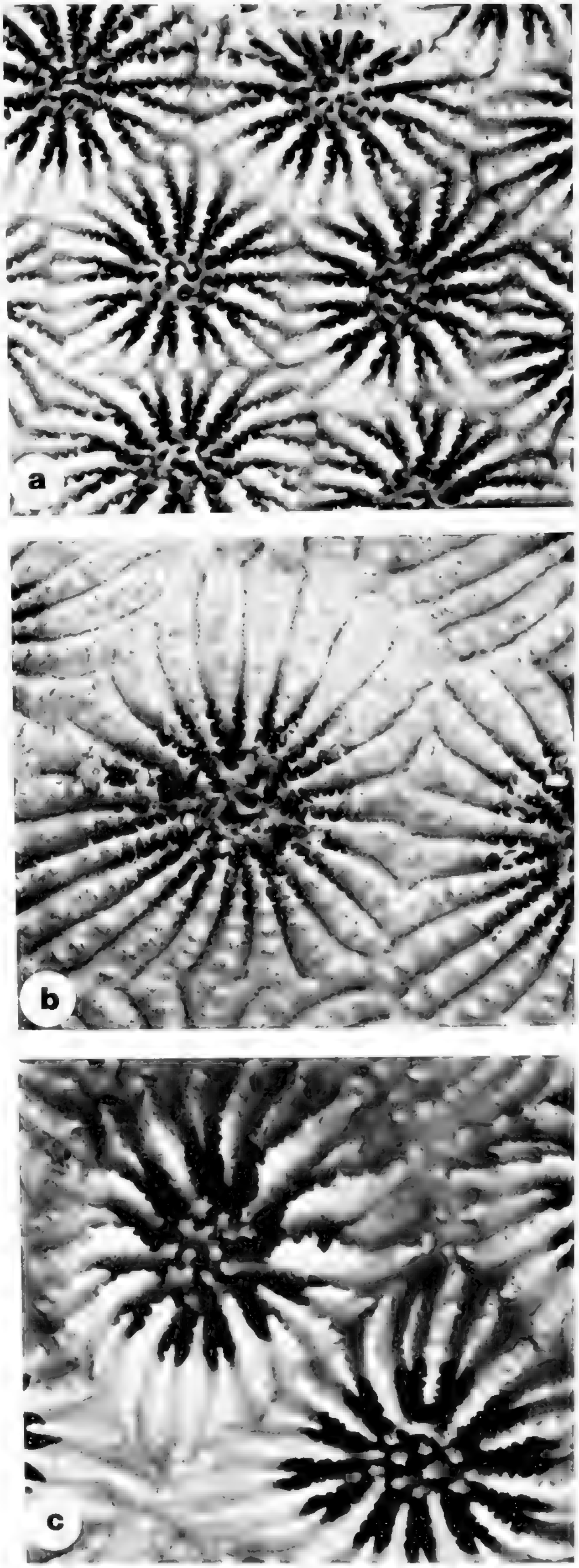
TAXONOMIC METHOD

PROBLEM

The major problem presented by the material studied in the present monograph is that of species recognition, and not recognition of higher categories. Although *Montastraea* Blainville, 1830 and *Solenastrea* Milne Edwards and Haime, 1848 have similar corallite sizes and spacing, and similar patterns of septal arrangement, they can be readily distinguished on the basis of texture of the coenosteum. Moreover, despite high levels of phenotypic plasticity and genetic variability within species, the two living Caribbean species of *Montastraea* also appear to form discrete morphologic units separated by a wide morphologic gap. This gap, however, is more likely the result of extinction of species with intermediate morphologies than of morphologic divergence during speciation or of phyletic evolution within lineages (Budd, 1990). Preliminary studies suggest that intermediate species of *Montastraea* may have been so numerous in the Caribbean during Neogene time as to form morphologic continua or species complexes (Budd, 1989; 1990). The lack of morphologically discrete species within these complexes appears the result of both high morphological variation within species and low morphological divergence during speciation (Budd, 1990). The problem may further be confounded by iterative evolution (Bell, 1988), in which similar morphologies evolve repeatedly over time from the same ancestral stock.

Although little work has been done to examine the influence of natural selection on morphological or genetic differentiation between living populations, morphological variation caused by phenotypic plasticity has been described quantitatively within the two living Caribbean species of *Montastraea* by Foster (1979, 1980, 1985). The results of this work suggest that no simple patterns of variation or relationships between skeletal morphology and the environment exist. The two living species differ not only in magnitude but also in pattern of morphological variation; therefore, results computed for one species cannot unequivocally be used to predict those in another species. Variation within colonies and populations is higher in *M. cavernosa* (Linnaeus, 1767); whereas variation between populations is higher in *M. annularis* (Ellis and Solander, 1786) (Foster, 1985; Budd, 1990). Thus, genetic variation is believed higher in *M. cavernosa*, and phenotypic plasticity higher in *M. annularis*. In both species, corallite diameter and corallite spacing increase, and theca thickness decreases in more protected, muddy habitats. However, in *M. annularis*, coenosteum density and septum thickness decrease in muddy habitats; whereas, in *M. cavernosa*, they remain the same or increase. Trends from shallow to deep water do not correspond with those from clear to muddy water. In *M. annularis*, deeper water colonies have smaller corallite diameters and more widely spaced corallites. Their coenosteum is denser, and theca thicker (Text-fig. 7). Similarly, trends across individual colonies from colony top to bottom do not always reflect those from clear to muddy water. In contrast to patterns between clear and muddy environments, coenosteum density and septum and theca thickness increase from colony top to bottom in *M. annularis*, and the theca thickness increases from colony top to bottom in *M. cavernosa* (Foster, 1985). Equally complex and unique patterns of morphologic variation have been described within four of the five living Australian species of *Montastraea* (Veron, Pichon, and Wijsman-Best, 1977).

The first comprehensive attempt to describe the full range of variation within species complexes of Tertiary Caribbean *Montastraea* was made by Vaughan (1919) who distinguished two major groups of species, one (four species) with three cycles of septa and the other



Text-figure 7.—Scanning electron microscope photographs of modern *Montastraea annularis* from different reef habitats near Discovery Bay, Jamaica. All photos, ×10. **(a)** SUI 45448, mid-forereef (20 m), **(b)** SUI 45794, deep forereef (50 m), **(c)** SUI 47056, backreef (1–2 m). Deeper-water colonies have smaller corallite diameters, more widely-spaced corallites, denser coenostea, and thicker thecae and septa.

(10 species) with four cycles. Within each group, he distinguished species primarily on the basis of (1) corallite size, (2) development of the costae, and (3) relative thicknesses and lengths of the septa. Within two species [*M. cavernosa* and *M. tampaensis* (Vaughan, 1919)], Vaughan (1919) named varieties, again based on corallite size and costae development. He described each variety as distinctive, but within the "ordinary" range of variation of the species. Nevertheless, Vaughan (1919) did change the status of some of his earlier varieties (*e.g.*, *Orbicella cavernosa brevis* Vaughan, 1901) by raising them to species status as new material became available for study. In general, Vaughan's treatment is particularly noteworthy in that he ranked the characters he used to distinguish species by studying variation within the living Caribbean species.

Another significant attempt at describing such Neogene species complexes in *Montastraea* was made by Chevalier (1954, 1961). In the Mediterranean Miocene alone, he distinguished five subgenera of *Montastraea* on the basis of wall structure and the development of the coenosteum. Within each subgenus, he distinguished a number of species (total: 28) on the basis of (1) development of the costae and (2) corallite size. Many of Chevalier's species, unlike Vaughan's, were based on fewer than three specimens, and Chevalier was unable to compare variability within living species with that he observed in the fossils.

Although *Solenastrea* is not reported to form such extensive species complexes, the problem of recognizing species is equally difficult, also due to widespread morphologic variation within species and morphologic overlap between species. This is especially the case in the two living Caribbean species, *S. hyades* (Dana, 1846) and *S. bournoni* Milne Edwards and Haime, 1849, which are distinguished primarily on the basis of highly variable characters such as fusion of the tertiary and secondary septa and corallite diameter (Vaughan, 1919). Although no attempts have been made to describe the variability among living representatives within these two species quantitatively, or to relate variability to specific environmental parameters, Vaughan (1919) does note extensive variation in corallite size and spacing and in coenosteum density.

Due to the above noted problems in species recognition, species in the present study have been discriminated phenetically using a morphometric approach similar to that of Foster (1984). The specimens were first qualitatively sorted into genera, and then quantitatively grouped into clusters using two multivariate statistical procedures: (1) cluster analysis based on distances between colonies; and (2) a series of canonical discriminant analyses in which the original clusters were combined and modified until the clusters proved maximally discrete. To facilitate final cluster definition, patterns of variation within each cluster were compared with variation observed among nearby, environmentally-distinct Jamaican populations of the two living Caribbean species. The final clusters, therefore, represent morphologic concentrations of specimens, herein recognized as "species", which can be traced through time and theoretically may overlap at the margins. Because of the limited amount of material in the NMB museum collections, the present study is only preliminary in nature. As more material is collected and analyzed, some specimens at the margins of clusters may prove misclassified. Thus, the present contribution serves mainly to identify the number of clusters and their centroids, and to estimate the variability within each cluster. Within this framework, all available type material from the Caribbean Neogene has been re-evaluated, and the evolutionary history of each cluster traced through Neogene time.

MATERIAL

The material studied consists of all specimens of *Montastraea* (280 colonies total) and *Solenastrea* (66 colonies total) collected in the Dominican Republic by J. Geister, P. Jung, J. B. Saunders, and other coworkers between 1978 and 1980 (Saunders, Jung, and Biju-Duval, 1986), and is currently deposited at the Naturhistorisches Museum in Basel. These coral collections from the Dominican Republic are termed "NMB" collections in the following discussion in order to distinguish them from other type and comparative material used in the analyses. Colonies of massive plocoid faviid corals with predominantly cylindrical corallites were first separated from the rest of the NMB coral collections and then sorted by genus. None of the material was found to have the synapticular wall structure characteristic of *Agathiphyllia* Reuss, 1864, the lamellar columella characteristic of *Tarbellastraea* Alloiteau, 1952 and *Antiguastrea* Vaughan, 1919, or well-developed, prominent pali characteristic of *Plesiastrea* Milne Edwards and Haime, 1848. *Solenastrea* was distinguished from *Montastraea* on the basis of the vesicular texture of the coenosteum, the reduced costae, and occasional reduced paliform lobes (Text-fig. 8). Of the 346 NMB specimens, 74 well-preserved colonies of *Montastraea* and 15 well-preserved colonies of *Solenastrea* were selected for measurement. These were chosen to represent a wide range of localities and corallite sizes. To increase the sample size, 11 colonies of *Montastraea* collected from the same stratigraphic sequence by Emily and Harold Vokes of Tulane University were also thin-sectioned, measured, and included in all statistical analyses (Table 1).

Measurements were also made on 33 type specimens (including topotypes, some primary types, and some nontype specimens identified by T. W. Vaughan) of 12

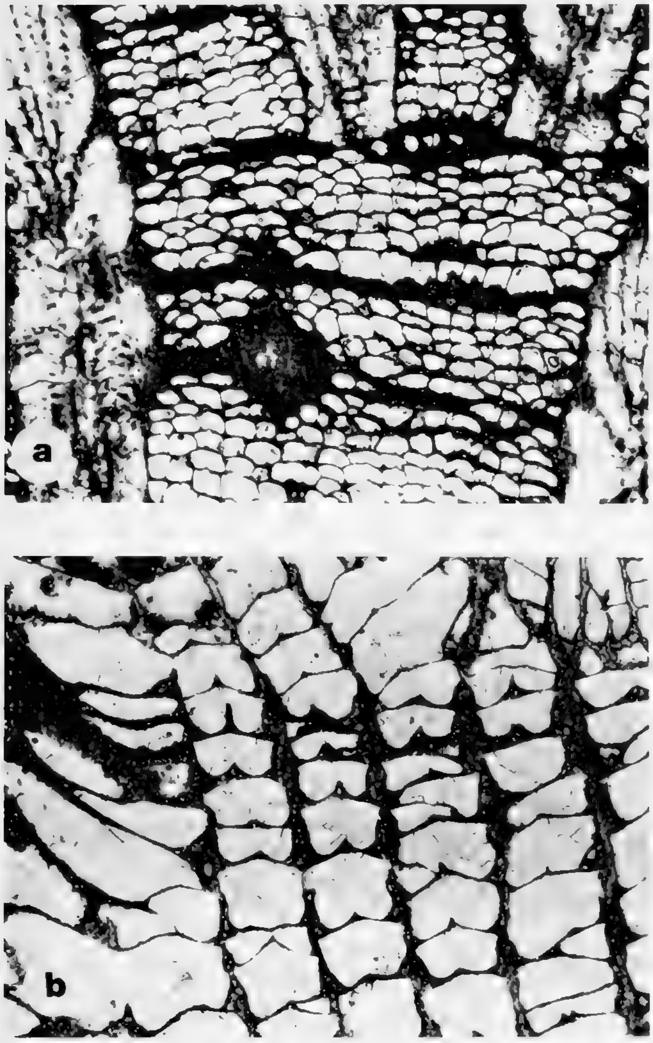
Table 3.—List of all formally described species of *Agathiphyllia, Montastraea,* and *Solenastrea* from the Miocene through lower Pliocene of the Caribbean region, showing their current taxonomic status.

Agathiphyllia:

- *Astraea antiguensis* Duncan, 1863[1]
- *Astraea tenuis* Duncan, 1863
- *Cyathomorpha anguillensis* Vaughan, 1919[2]

Montastraea:

- *Astraea brevis* Duncan, 1864
- *Astraea costata* Duncan, 1863 [= *Agathiphyllia antiguensis* (Duncan)]



Text-figure 8.—Longitudinal thin-sections showing the structure of the coenosteum in *Solenastrea* and *Montastraea*. **(a)** NMB D5794, *S. bournoni*, lower Pliocene, locality NMB 15822, Río Gurabo, Mao Formation, Dominican Republic, ×10; **(b)** NMB D5701, *M. endothecata*, upper Miocene, locality NMB 16911, Río Mao, ?Gurabo Formation, Dominican Republic, ×10. The coenosteum is more vesicular in *Solenastrea* due to the lack of costae extending across the coenosteum.

Table 3.—Continued.

- *Astraea cylindrica* Duncan, 1863
- *Astraea endothecata* Duncan, 1863
- *Astraea radiata* var. *intermedia* Duncan, 1863 [= ? *Montastraea imperatoris* (Vaughan)]
- *Cyathomorpha roxboroughi* Vaughan, 1919 [= *Montastraea endothecata* (Duncan)]
- *Heliastraea altissima* Duncan, 1868 [= ? *Montastraea trinitatis* (Vaughan)]
- *Heliastraea insignis* Duncan, 1868 [= ? *Montastraea canalis* (Vaughan)]
- *Madrepora annularis* Ellis and Solander, 1786
- *Madrepora cavernosa* Linnaeus, 1767
- *Montastrea davisina* Weisbord, 1973 [= *Solenastrea hyades* (Dana)]
- *Montastrea peninsularis* Weisbord, 1973 [= *Solenastrea hyades* (Dana)]
- *Orbicella bainbridgensis* Vaughan, 1919 [= *Montastraea endothecata* (Duncan)]
- *Orbicella canalis* Vaughan, 1919
- *Orbicella cavernosa* var. *cylindrica* Vaughan, 1919 [= *Montastraea cylindrica* (Duncan)]
- *Orbicella cavernosa* var. *endothecata* Vaughan, 1919 [= *Montastraea endothecata* (Duncan)]
- *Orbicella cumutensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926 [= ? *Montastraea trinitatis* (Vaughan)]
- *Orbicella gabbi* Vaughan, 1919 [= ? *Diploastrea*]
- *Orbicella imperatoris* Vaughan, 1919
- *Orbicella limbata* var. *pennyi* Vaughan *in* Vaughan and Hoffmeister, 1926 [= *Montastraea limbata* (Duncan)]
- *Orbicella tampäensis* Vaughan, 1919
- *Orbicella tampäensis* var. *silecensis* Vaughan, 1919 [= *Montastraea canalis* (Vaughan)]
- *Orbicella trinitatis* Vaughan *in* Vaughan and Hoffmeister, 1926
- *Plesiastraea ramea* Duncan, 1864 [= *Montastraea limbata* (Duncan)]
- *Phyllocoenia limbata* Duncan, 1863
- *Phyllocoenia sculpta* var. *tegula* Duncan, 1863 [= *Montastraea limbata* (Duncan)]

Solenastrea:

- *Astraea hyades* Dana, 1846
- *Cyphastrea tampae* Weisbord, 1973 [= *Solenastrea bournoni* Milne Edwards and Haime]
- *Plesiastraea distans* Duncan, 1864 [= *Solenastrea bournoni* Milne Edwards and Haime]
- *Plesiastraea globosa* Duncan, 1864 [= *Solenastrea bournoni* Milne Edwards and Haime]
- *Solenastrea bournoni* Milne Edwards and Haime, 1849
- *Solenastrea fairbanksi* var. *minor* Vaughan, 1917 [= ? *Solenastrea bournoni* Milne Edwards and Haime]
- *Solenastrea fairbanksi* var. *normalis* Vaughan, 1917 [= ? *Solenastrea bournoni* Milne Edwards and Haime]
- *Solenastraea verhelsti* Milne Edwards and Haime, 1857, of Duncan (1864) [=*Solenastrea bournoni* Milne Edwards and Haime]
- *Stephanocoenia fairbanksi* Vaughan, 1900 [= ? *Solenastrea bournoni* Milne Edwards and Haime]
- *Stephanocoenia fairbanksi* var. *columnaris* Vaughan, 1900 [= ? *Solenastrea bournoni* Milne Edwards and Haime]

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[1] Miocene specimens reported of this species (Vaughan, 1919) probably belong to *Montastraea endothecata* (Duncan)

[2] One specimen (USNM 325214; Pl. 1, fig. 5) originally assigned to this species belongs to *Agathiphyllia hilli* (Vaughan); all others are questionably assigned to *Montastraea*.

Table 4.—List of Neogene types identified by T. W. Vaughan and used in statistical analyses of *Montastraea*. Specimens in groups 16 and 17 consist of colonies of the two living species mentioned in the text.

Group 11:

1. USNM 66833 (NF 420), topotype, *Astraea brevis* Duncan, Dominican Republic
2. USNM 66883 (NF 421), topotype, *Astraea brevis* Duncan, Dominican Republic
3. USNM 66829 (NF 458), topotype, *Astraea brevis* Duncan, Dominican Republic
4. USNM 66829 (NF 460), topotype, *Astraea brevis* Duncan, Dominican Republic
5. USNM 66829 (NF 461), topotype, *Astraea brevis* Duncan, Dominican Republic
6. USNM 66831 (NF 489), topotype, *Astraea brevis* Duncan, Dominican Republic

Group 12:

7. USNM 66906 (NF 385), topotype, *Astraea cylindrica* Duncan, Dominican Republic
8. USNM 66880 (NF 68), Vaughan nontype, *Astraea cylindrica* Duncan, loc. USGS 8297, Trinidad

Group 13:

9. USNM 66867 (NF 424), topotype, *Astraea endothecata* Duncan, Dominican Republic

Table 4.—Continued.

10. USNM 66867 (NF425), topotype, *Astraea endothecata* Duncan, Dominican Republic

Group 14:

11. USNM 353656 (NF 65), hypotype, *Heliastraea altissima* Duncan, loc. USGS 8297, Trinidad
12. USNM 66832 (NF 485), Vaughan nontype, *Heliastraea altissima* Duncan, Dominican Republic

Group 15:

13. USNM 63432 (NF 276), Vaughan nontype, *Heliastraea insignis* Duncan, loc. USGS 8713, Dominican Republic

Group 18:

14. USNM 324881 (NF 192), holotype, *Orbicella bainbridgensis* Vaughan, loc. USGS 3383, Georgia
15. USNM 324882 (NF 209), topotype, *Orbicella bainbridgensis* Vaughan, loc. USGS 3383, Georgia

Group 19:

16. USNM 324867 (NF 261), topotype, *Orbicella canalis* Vaughan, loc. USGS 6016, Panama
17. USNM 324867 (NF 258), topotype, *Orbicella canalis* Vaughan, loc. USGS 6016, Panama
18. USNM 324867 (NF 260), topotype, *Orbicella canalis* Vaughan, loc. USGS 6016, Panama
19. USNM 324867 (NF 263), topotype, *Orbicella canalis* Vaughan, loc. USGS 6016, Panama

Group 21:

20. USNM 324890 (NF 238), topotype, *Orbicella imperatoris* Vaughan, loc. USGS 6015, Panama
21. USNM 324872 (NF 244), topotype, *Orbicella imperatoris* Vaughan, loc. USGS 6016, Panama
22. USNM 324875 (NF 246), topotype, *Orbicella imperatoris* Vaughan, loc. USGS 6016, Panama
23. USNM 324875 (NF 247), topotype, *Orbicella imperatoris* Vaughan, loc. USGS 6016, Panama

Group 22:

24. USNM 66878 (NF 61), Vaughan nontype, *Orbicella limbata* var. *pennyi* Vaughan, loc. USGS 9198, Trinidad

Group 23:

25. USNM 324891 (NF 172), topotpye, *Orbicella tampaensis* Vaughan, loc. USGS 4999, Florida
26. USNM 324890 (NF 176), topotype, *Orbicella tampaensis* Vaughan, loc. USGS 4999, Florida
27. USNM 324890 (NF177), topotype, *Orbicella tampaensis* Vaughan, loc. USGS 4999, Florida
28. USNM 324890 (NF 178), topotype, *Orbicella tampaensis* Vaughan, loc. USGS 4999, Florida

Group 24:

29. USNM 66852 (NF 492), Vaughan nontype, *Orbicella trinitatis* Vaughan, Dominican Republic

Group 25:

30. USNM 66899 (NF 284), topotype, *Phyllocoenia limbata* Duncan, loc. USGS 8545, Dominican Republic
31. USNM 66902 (NF 289), topotype, *Phyllocoenia limbata* Duncan, loc. USGS 8541, Dominican Republic
32. USNM 66904 (NF 292), topotype, *Phyllocoenia limbata* Duncan, loc. USGS 8738, Dominican Republic
33. USNM 62728 (NF 448), topotype, *Phyllocoenia limbata* Duncan, Dominican Republic

of the 17 described species of *Montastraea* from the Neogene of Caribbean region (Tables 3, 4). Two of the remaining six described species, *M. annularis* (Ellis and Solander, 1786) and *M. cavernosa* (Linnaeus, 1767), occur today in a range of reef environments across the Caribbean region, and were represented in the current analyses by measurements taken on 40 colonies of living *M. annularis* (group 16: SUI 45425–45464) and 32 colonies of living *M. cavernosa* (group 17: SUI 48748–48779), both collected from four environmentally-distinct reef habitats near Discovery Bay, Jamaica. Of the remaining four species, *M. cumutensis* (Hoffmeister *in* Vaughan and Hoffmeister, 1926) and *M. ramea* (Duncan, 1864) were each described on the basis of only one small specimen, the holotype, which could not be thin-sectioned due to museum restrictions. *M. radiata* var. *intermedia* (Duncan, 1863) also consists of one specimen, which could not be found.

In *Solenastrea*, measurements were made on the surface of six holotypes listed in Table 3 (*Plesiastraea distans* Duncan, 1864, *Plesiastraea globosa* Duncan, 1864, *Solenastrea bournoni* Milne Edwards and Haime, 1849, *Stephanocoenia fairbanksi* Vaughan, 1900, *Solenastrea fairbanksi minor* Vaughan, 1917, and *Solenastrea fairbanksi normalis* Vaughan, 1917). Holotypes for *Astraea hyades* Dana, 1846 and *Stephanocoenia fairbanksi columnaris* Vaughan, 1900 could not be found, and the surface of the holotype for *Cyphastrea tampae* Weisbord, 1973 is too poorly preserved for measurement. Therefore, to represent *Solenastrea hyades* in the statistical analyses, the holotype of *Astraea excelsa*

Table 5.—List and description of characters analyzed in *Montastraea*. Measurements in characters 1–6 were made at maximum to the nearest 0.10 mm, those in characters 7–12 to the nearest 0.05 mm, and those in characters 13–16 to the nearest 0.025 mm.

character	*abbreviation*	*description*
1. corallite diameter	**CD**	Linear measure between theca/corallite cavity margins; average of longest and shortest lengths (**CD** lines)
2. total number of septa	**NS**	Count
3. corallite spacing	**NND**	Linear measure between theca/corallite cavity margins of nearest neighboring corallites
4. coenosteum diameter	**CND**	Linear measure between theca/coenosteum margins of nearest neighboring corallites
5. coenosteum density	**CNNV**	Linear measure, parallel to the **CND** line, of non-void material across the coenosteum
6. coenosteum density	**CNP**	Linear measure, perpendicular to the **CND** line, of non-void material crossing a 1 cm line
7. columella width	**CLW**	Linear measure between outer columella/corallite cavity margins, average of longest and shortest lengths
8. columella density	**CLNV**	Linear measure, parallel to two **CD** lines, of non-void material across the columella; average
9. theca thickness	**TT**	Linear measure between theca/coenosteum margins; average at two **CD** lines
10. septum length (first cycle)	**SLP**	Linear measure between columella and theca margins; average at two **CD** lines
11. septum length (second cycle)	**SLS**	Linear measure similar to **SLP** on major septa adjacent to **SLP**; average
12. septum length (highest cycle)	**SLT**	Linear measure between septum tip and theca margin of septum between **SLS** and **SLP**; average
13. septum thickness (first cycle)	**STP**	Linear measure of thickness of septa at **SLP** at septum midpoint; average
14. septum thickness (second cycle)	**STS**	Linear measure of thickness of septa at **SLS** at septum midpoint; average
15. septum thickness (highest cycle)	**STT**	Linear measure of thickness of septa at **SLT** at septum midpoint; average
16. costa thickness (first cycle)	**CST**	Linear measure of costa thickness at **SLP**; ≈0.15 mm from corallite cavity; average

Dana, 1846 [= *S. hyades* in Vaughan (1919)] was measured. In addition, for comparison with other Neogene Caribbean faunas, five colonies of *S. hyades* and five colonies of *S. bournoni* from the lower Pliocene Tamiami Formation of south Florida (SUI 60785–60794), and eight colonies (topotypes) of *S. fairbanksi* from the lower Pliocene Imperial Formation of south-central California (SUI 45614, 45616–45618, 45625, 45627, 45628, 45631) were measured in thin-section.

Where possible, 10 mature corallites were measured in each colony. Maturity was judged by examination of the development of the highest septal cycle. These 10 consisted of two to five corallites in each of two to three transverse thin-sections, cut from approximately the top, middle, and base of each colony. Previous work on living Caribbean *Montastraea* (Foster, 1985) has indicated that this sampling scheme is adequate for estimating colony means and variances needed to discriminate species, and to make preliminary estimates of variation within species.

CHARACTERS

The characters analyzed consist of linear measurements and counts on 16 corallite features in transverse thin-sections of *Montastraea* Blainville, 1830 (Table 5; Text-fig. 9a) and on 10 calice features on colony surfaces of *Solenastrea* Milne Edwards and Haime, 1848 (Table 6). In addition, for comparison with other Caribbean faunas, six features were measured in transverse thin-sections of *Solenastrea*. Linear distances calculated in this third data set were based on points digitized in two dimensions (Table 6; Text-fig. 9b). In general, measurements made on thin-sections are preferred over those made on calical surfaces in studies of fossil massive colonial corals, because colony surfaces are often worn. Therefore, many more characters can be measured with greater accuracy and consistency in thin-section. However, in *Solenastrea*, measurements were made on colony surfaces, due to the importance of surficial paliform lobes in distinguishing species. Throughout the present study, all thin-sections were prepared from chips cut within 5 mm of the colony surface and ground to a thickness of 40 μm.

The characters were selected to include all diagnostic features traditionally used to distinguish species of *Montastraea* and *Solenastrea* (Vaughan, 1919). Although colony shape is described qualitatively herein in the section on systematic paleontology, no attempt has been made to quantify colony shape, or to use it as a character in discriminating species, because of the fragmentary nature of much of the material. In general, the characters analyzed can be grouped into five interrelated categories: (1) corallite size and spacing; (2) septal number and length; (3) columella (and associated paliform lobes) width and porosity; (4) septum, theca, and costa thickness; and (5) development of the coenosteum.

1. *Corallite size and spacing.*—Because of their plocoid colony form and strong hexagonal symmetry, corallites are almost invariably circular in both *Montastraea* and *Solenastrea*; therefore, an average of the longest and shortest corallite diameter (**CD**) was used to describe the size of each corallite. However, in the

Table 6.—List and description of characters analyzed in *Solenastrea.* Measurements in characters 1, 2, 4, 5, 9, and 10 were made at maximum to the nearest 0.05 mm; those in characters 6–8 to the nearest 0.033 mm.

character	*abbreviation*	*description*
at colony surface:		
1. corallite diameter	**CD**	Linear measure across corallite center between theca/corallite cavity margins; mean of greatest and smallest lengths
2. corallite spacing	**NND**	Linear measure between theca/corallite cavity margins of nearest neighboring corallites
3. total number of septa	**NS**	Count of all major and minor septa
4. paliform crown width	**PA**	Linear measure through corallite center across paliform crown; mean of the greatest and shortest distances
5. columella width	**CLW**	Linear measure through corallite center across columellar complex; mean of the greatest and smallest lengths
6. theca thickness	**TT**	Linear measure across theca between theca/corallite cavity and theca/coenosteum margins
7. costa thickness	**CST**	Linear measure across primary costa along theca
8. septum thickness	**ST**	Linear measure across major septum at septum midpoint; mean of thickest and thinnest septum
9. tertiary septum length	**SLT**	Linear measure from septum tip to inner thecal margin; mean of longest and shortest septa
10. calice elevation	**CA**	Vertical distance from columella to uppermost thecal margin
in transverse thin-section:		
1. chord length	**CH**	Linear measure between margins of every other primary septa; mean of six lengths
2. columella width	**CLW**	Linear measure through corallite center across columellar complex; mean of three lengths
3. secondary septum length	**SLS**	Linear measure from septum tip to inner thecal margin; mean of three lengths
4. tertiary septum length	**SLT**	Linear measure from septum tip to inner thecal margin; mean of six lengths
5. angle between secondary and tertiary septa	**AT**	Cosine of angle formed by points at the outer and inner tertiary septum margins and at the outer secondary septum margin; mean of three angles
6. theca thickness	**TT**	Linear measure across theca from outer secondary septum margin to coenosteal cavity; mean of three lengths

Solenastrea thin-sections, the average distance between points at the thecal margins of every other primary septum (**CH**) was used as a measure of corallite size. Calice elevation (**CA**) was estimated only in *Solenastrea*, by measuring surface relief within calices. In both genera, each mature corallite is surrounded by five to seven mature neighboring corallites, which are separated by highly variable amounts of coenosteum. Spacing between corallites was therefore estimated in *Montastraea* and on *Solenastrea* surfaces by measuring the distance to the nearest neighboring mature corallite (**NND**).

2. *Septal number and length.*—Septal number (**NS**) was determined by counting all major and minor septa within each corallite. In general, in *Montastraea* and *Solenastrea*, the six primary and usually the six secondary septa extend completely from the theca to the columella. If present, the 12 tertiary and 24 quaternary septa usually extend only partially from the theca to the columella, and often are directed toward and may even fuse with the next higher cycle. In the present study, the lengths of the primary (**SLP**), secondary (**SLS**), and highest septal cycle (**SLT**) were measured in *Montastraea*, and the lengths of the secondary (**SLS**) and tertiary (**SLT**) septa were measured in *Solenastrea*. In the *Solenastrea* thin-sections, the angle between the secondary and tertiary septa (**AT**) was also approximated.

3. *Columella width and porosity.*—In both *Montastraea* and *Solenastrea*, the columella consists of a spongy, upward-spiralling network of trabeculae extending from the inner edges of the septa. In the present study, the width of this columellar complex (**CLW**) and its porosity (**CLNV**) were estimated. Although separate, discrete structures formed by septal substitution, termed "pali" (Vaughan and Wells, 1943; Wells, 1956), do not occur, paliform lobes do develop along the upper surface of the septa, forming a crown that encircles the columella, especially in *Solenastrea*. On *Solenastrea* surfaces, the width of this palar crown (**PA**) was also measured.

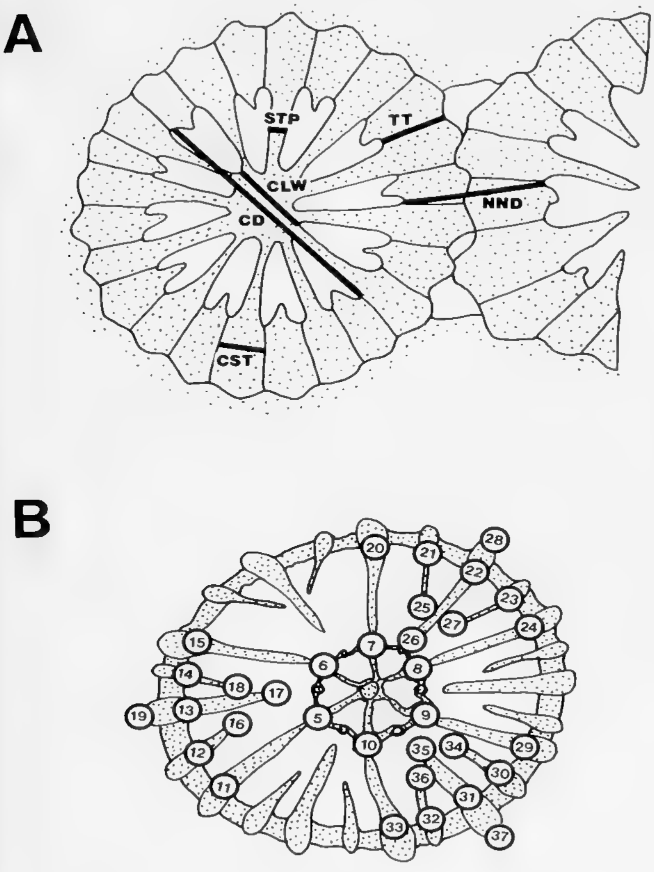
4. *Septum, theca, and costa thickness.*—In *Montastraea*, the theca is septothecal (*i.e.*, formed by thickening of the septa); whereas, in *Solenastrea*, it is septothecal or parathecal (*i.e.*, formed by dissepiments). The costa represent prolongations of the septa beyond the theca, which form strong planar vertical partitions within the coenosteum. In the present study, the thicknesses of three of these elements were measured and compared [*i.e.*, the theca (**TT**), the septa (**ST**, **STP**, **STS**, **STT**), and the costa (**CST**)].

5. *Development of the coenosteum.*—The volume

(**CND**) and density (**CNNV**, **CNP**) of the coenosteum were measured only in *Montastraea*. Here, the coenosteal voids are rectangular in shape due to the influence of the costae in coenosteal construction. In contrast, the costae are weak in *Solenastrea*, and the coenosteum is vesicular in structure.

STATISTICAL PROCEDURES

Discrimination of species using the NMB material.—Species were distinguished within each of the two genera in the present study following a three-step procedure (*cf.* Foster, 1984; Budd, 1988): (1) Mahalanobis' distances were calculated between all NMB and TU colonies within each genus (**PROC CANDISC** of **SAS**); (2) these distances were used to group colonies into clusters by average linkage cluster analysis (**UPGMA**) (**PROC CLUSTER** of **SAS**); and (3) a series of canonical discriminant analyses (**SPSS-X** discriminant procedure) were run on the clusters, and on combinations and modifications thereof, until the clusters were distinct at $p<0.0001$. The resulting clusters or "groups" represent the species described in this paper. The use of Mahalanobis' distances in cluster analysis (step 1) most heavily weights those characters that best distinguish among colonies. Canonical discriminant analysis (step 3) further refines the clusters, and thereby alleviates some of the ambiguities associated with choice of clustering level. Due to the small sample size and short length of geologic time represented (<10 Ma), no attempt was made to sort the colonies by time interval before running the analyses (*cf.* Budd, 1988) in order to prevent artifically inducing stasis. As found by Cheetham (1986) in trial runs on hypothetical data sets, such use of discriminant analysis in species recognition does not mask gradual changes within characters. All analyses in the present study have been run using **SAS** version 5 (SAS Institute, Cary, NC) and **SPSS-X** release 3.0 (SPSS Inc., Chicago, IL) on the University of Iowa IBM 4381 mainframe computer.



Text-figure 9.—Drawings showing some of the characters measured and points digitized on thin-sections. (**a**) *Montastraea*: **CD**, corallite diameter; **CLW**, columella width; **CST**, costa thickness; **NND**, corallite spacing; **STP**, septum thickness; **TT**, theca thickness. (**b**) *Solenastrea*: **CH**, chord length = average of distances from points 11 to 20, 20 to 29, 11 to 29, 15 to 24, 24 to 33, and 15 to 33; **CLW**, columella width = average of distances from points 5 to 8, 6 to 9, and 7 to 10; **SLS**, secondary septum length = average of distances from points 13 to 17, 22 to 26, and 31 to 35; **SLT**, tertiary septum length = average of distances from points 12 to 16, 14 to 18, 21 to 25, 23 to 27, 30 to 34, and 32 to 36; **TT**, theca thickness = average of distances from points 13 to 19, 22 to 28, and 31 to 37.

In *Montastraea*, all 16 characters were used to calculate the Mahalanobis' distances between all pairwise combinations of the 84 measured NMB and TU colonies. The results of cluster analysis performed on these distances are shown in the dendrogram in Text-figure 10. Using a cutpoint of approximately 0.38 for colonies with smaller corallites and 0.55 for colonies with larger corallites, 14 groups were formed based on qualitative study of the dendrogram (Text-fig. 10). Cutpoints are higher for groups with larger corallites due to the fact that amounts of variability within species are strongly correlated with size (Foster, 1985). These groups were then re-analyzed by performing a series of stepwise discriminant analyses on means of the 16 characters for each colony. In this procedure, groups were combined if F-values derived from Mahalanobis' distances had significance levels of greater than 0.0001. Group assignments for misclassified colonies were modified by trial and error to obtain the highest percentage of correctly classified corallites. The final results yielded seven groups among the NMB specimens in *Montastraea* (Text-fig. 11; Table 7). The validity of these groups was further tested by subdividing each colony into two halves and performing average linkage cluster analysis as above using the colony half data. The positions of the two halves for each colony were then examined on the dendrogram to ensure that no two halves of the same colony were assigned to different groups.

In *Solenastrea*, all ten colony surface characters were used to calculate the Mahalanobis' distances between all pairwise combinations of 12 of the 15 measured colonies. The three remaining colonies had to be de-

Table 7.—Weighting of characters in the *Montastraea* stepwise discriminant analysis. Total-sample correlations between the canonical variables (**CV1–CV3**) and the original variables (**COR**), and standardized canonical coefficients (**SCC**). Only values with high magnitudes are given. Abbreviations for characters are explained in Table 5.

	CV1 (86.1%)		CV2 (5.2%)		CV3 (4.4%)	
original variable	**COR**	**SCC**	**COR**	**SCC**	**COR**	**SCC**
CD	.703*	—	.155	—	—	1.22
NS	—	—	.329*	—	—	—
NND	—	0.31	—	−3.06	−.631	−3.18*
CND	—	—	—	3.97*	−.707*	2.07
CNNV	—	−0.88*	—	—	−.553	—
CNP	—	—	—	—	.318	—
CLW	.649	0.26	.182	—	—	−1.15
CLNV	—	0.50	—	—	—	—
TT	—	0.25	—	1.52	—	1.67
SLP	.666	—	.153	—	—	—
SLS	.640	0.67	—	—	—	—
SLT	—	—	−.336*	—	—	—
STP	—	—	—	—	—	—
STS	—	—	.166	1.16	—	—
STT	—	—	−.125	—	—	—
CST	.243	−0.31	.121	—	—	—

* Most important variables.

leted at this stage of the analysis because of missing values caused by poor preservation. The cluster analysis results are shown in Text-figure 12. Using a cut-point of 0.85, two groups were formed based on qualitative study of the dendrogram. Canonical discriminant analysis performed on means of the ten characters for each colony confirmed that the two groups were discrete, and was used to assign the remaining colonies to one of the two groups (Text-fig. 13; Table 8).

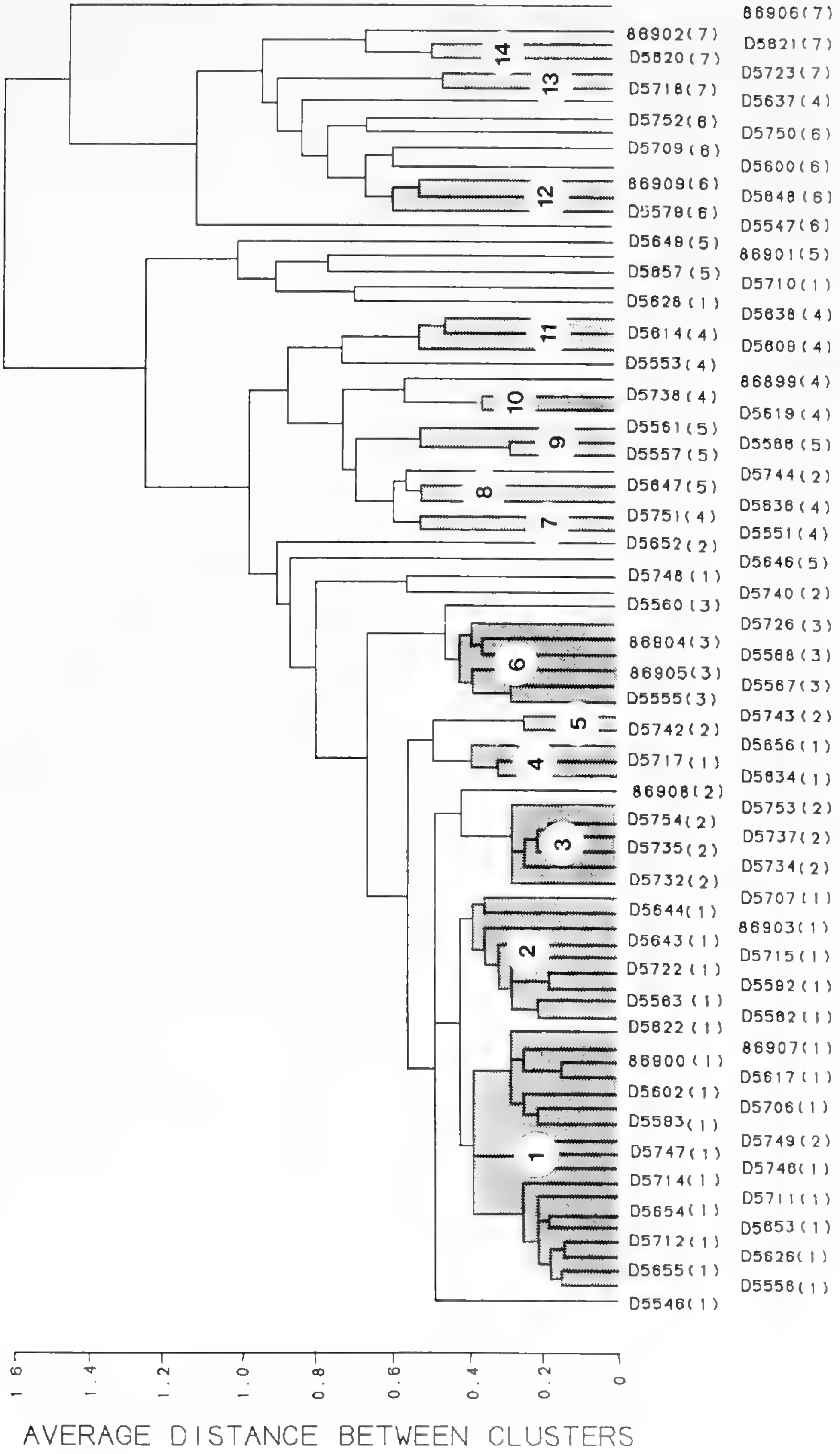
Finally, to identify the NMB species, two further canonical discriminant analyses were performed using the NMB clusters and the measured types: (1) Mahalanobis' distances were calculated between every pairwise combination of the NMB *Montastraea* clusters and types in each of the groups representing the previously-described *Montastraea* species in Table 4; and (2) the final canonical discriminant analyses distinguishing the *Montastraea* and the *Solenastrea* NMB species were rerun adding the types and leaving them unclassified. Results for *Montastraea* are given in Table 9 and Text-figure 11b; and for *Solenastrea* in Table 10. Both sets of results reveal a very complicated relationship between the types and the NMB species. Therefore, to interpret these relationships further, comparisons with other Caribbean faunas reported in the next section were also used in determining final synonymies.

Means and standard deviations of all single characters are given for each species in Appendix I. Characters revealing highly significant differences between species are plotted for *Montastraea* in Text-figure 14, and for *Solenastrea* in Text-figure 15. In all text-figures, tables, and appendices, the data used in *Montastraea* represent colony means, whereas in *Solenastrea*, they represent individual corallites.

RESULTS AND INTERPRETATIONS

In the final canonical discriminant analysis of *Montastraea*, seven groups were distinguished with 100% of all colonies correctly classified. Although minor overlap occurs between groups (Text-fig. 11a), F-statistics derived from pairwise Mahalanobis' distances between groups reveal highly significant differences (in all cases, $p \ll 0.0001$). Four significant canonical discriminant functions (**CV1–CV4**) were calculated, with **CV1** accounting for 86.1% of the variation, **CV2** for 5.2%, **CV3** for 4.4%, and **CV4** for 2.7%. The stepwise variable selection procedure showed that all 16 measured characters were needed to distinguish maximally among groups in the final analysis. In descending order, the four most important characters were: **CD**, **CND**, **SLT**, and **CNNV**. The first canonical variable (**CV1**) distinguished six of the seven groups, and appears to be most strongly related to corallite size. It weighted coenosteum density (**CNNV**) most heavily, and it is most strongly correlated with corallite diameter (**CD**) (Table 7). The second canonical variable (**CV2**) pri-

Text-figure 10.—Cluster analysis of colonies of *Montastraea* in the NMB collections. Dendrogram calculated by average linkage cluster analysis on Mahalanobis' distances among colonies. Each terminal branch represents one colony and is labelled using museum catalog numbers (numbers preceded by "D" = NMB; others = USNM). Parentheses indicate the species to which the colony was eventually assigned: 1 = *M. limbata*, 2 = *M. trinitatis*, 3 = *M. brevis*, 4 = *M. canalis*, 5 = *M. cylindrica*, 6 = *M. cavernosa*, 7 = *M. endothecata*. Shaded areas on the dendrogram delineate the initial 14 groups described in the text.


86906(7)
86902(7)
14
D5821(7)
D5820(7)
13
D5723(7)
D5718(7)
D5637(4)
D5752(6)
D5750(6)
D5709(6)
D5600(6)
86909(6)
12
D5848(6)
D5579(6)
D5547(6)
D5649(5)
86901(5)
D5857(5)
D5710(1)
D5628(1)
D5838(4)
11
D5614(4)
D5809(4)
D5553(4)
86899(4)
10
D5738(4)
D5619(4)
D5561(5)
9
D5588(5)
D5557(5)
D5744(2)
8
D5647(5)
D5636(4)
7
D5751(4)
D5551(4)
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86908(2)
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D5754(2)
D5737(2)
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D5734(2)
D5732(2)
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D5644(1)
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D5582(1)
D5822(1)
86907(1)
86800(1)
D5617(1)
D5602(1)
D5706(1)
D5583(1)
D5749(2)
1
D5747(1)
D5746(1)
D5714(1)
D5711(1)
D5654(1)
D5653(1)
D5712(1)
D5626(1)
D5655(1)
D5558(1)
D5546(1)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
AVERAGE DISTANCE BETWEEN CLUSTERS

marily distinguished groups 3 and 5, and appears to be most strongly related to septal development. It weighted coenosteum density (**CND**) most heavily, and it is most strongly correlated with number of septa (**NS**) and the inverse of the length of the highest septal cycle (−**SLT**). **CND** was also most heavily weighted on **CV3**,

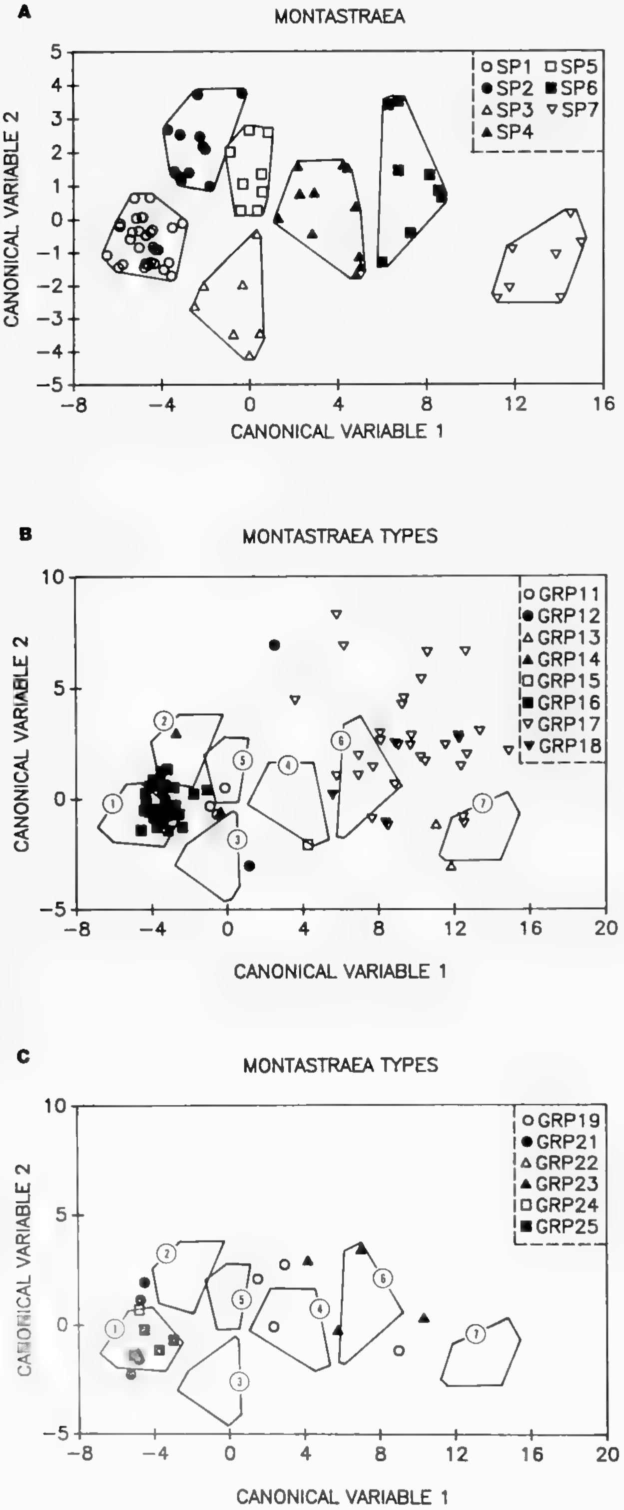
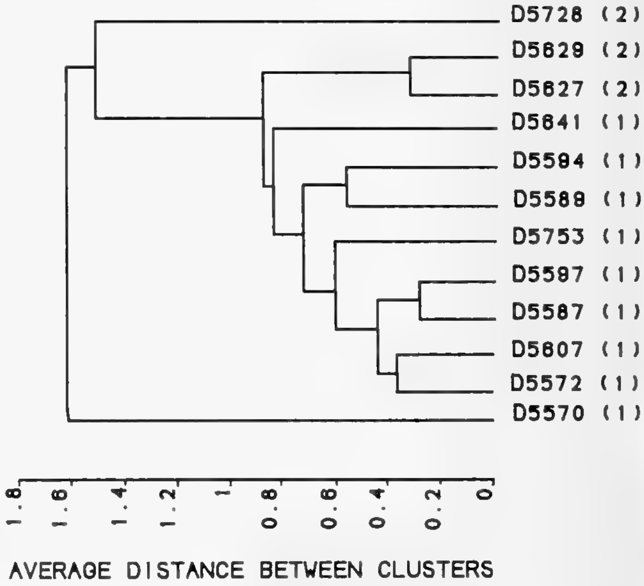


Table 8.—Weighting of characters in the *Solenastrea* stepwise discriminant analysis. Total-sample correlations between the canonical variable and the original variables (**COR**), and standardized canonical coefficients (**SCC**). Abbreviations for characters are explained in Table 6. NU = characters not used by stepwise procedure.

original variable	COR	SCC
CD	.189	NU
NND	−.023	0.87
NS	−.154	NU
PA	.195	−2.53
CLW	.214	4.66*
TT	.242	NU
CST	.116	−3.29
ST	−.054	−1.75
SLT	.289*	2.78
CA	−.194	NU

* Most important variables.



Text-figure 12.—Cluster analysis of colonies of *Solenastrea* in the NMB collections. Dendrogram calculated by average linkage cluster analysis on Mahalanobis' distances among colonies. Each terminal branch represents one colony and is labelled using NMB catalog numbers. Parentheses indicate the two groups or clusters evaluated using canonical discriminant analysis.

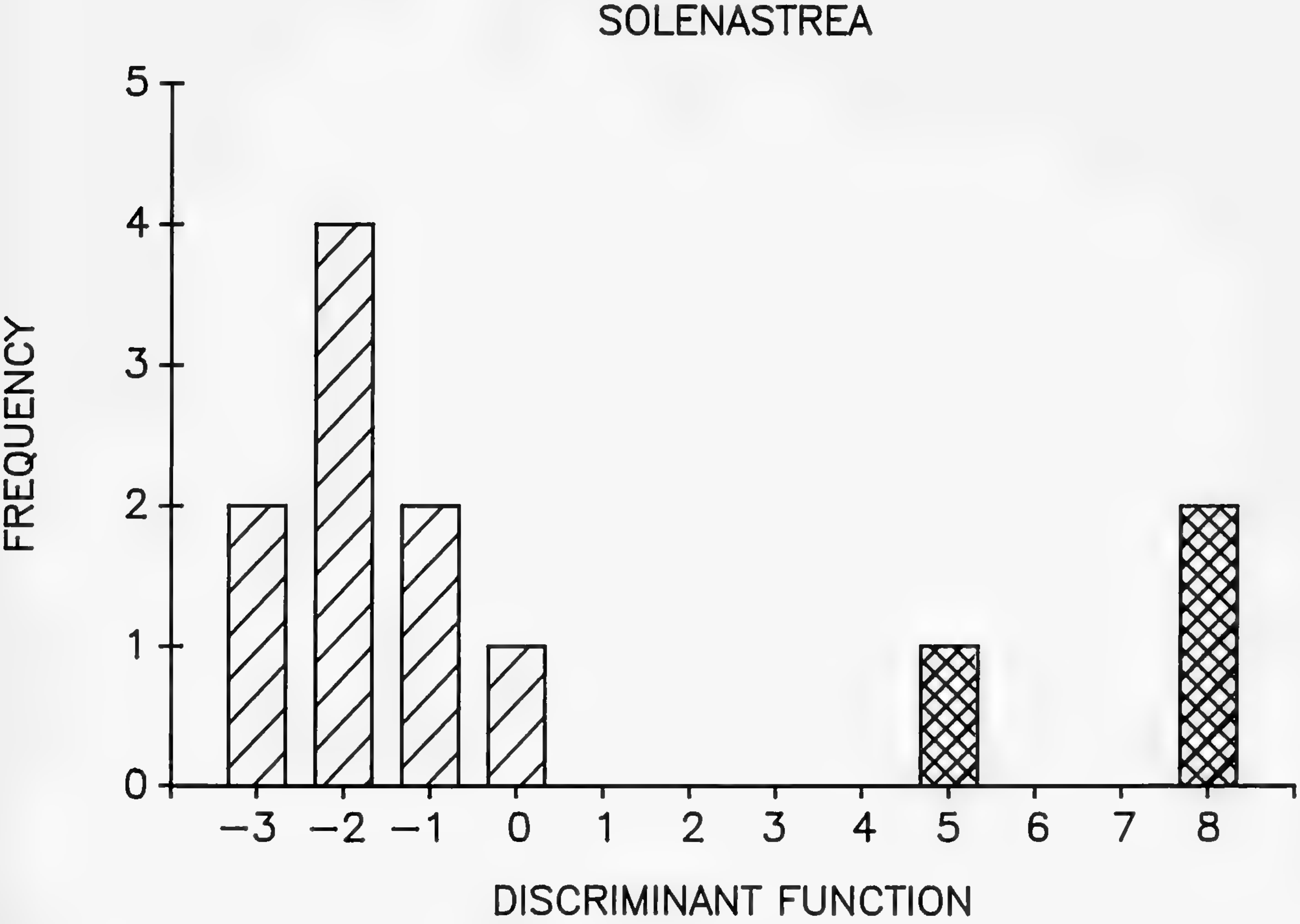
←

Text-figure 11.—*Montastraea*. Canonical discriminant analysis of the NMB collections. (**a**) Plot of scores on the first two canonical variables showing polygons outlining the range of variation between colonies in the seven species. Species 1 = *M. limbata*; species 2 = *M. trinitatis*; species 3 = *M. brevis*; species 4 = *M. canalis*; species 5 = *M. cylindrica*; species 6 = *M. cavernosa*; species 7 = *M. endothecata*. (**b**), (**c**) Plots of scores showing polygons around the NMB species [labelled with circled numbers as given in (**a**)] and points indicating the measured types listed in Table 4. Based on these results, groups 22 and 25 were synonymized with species 1; groups 14 and 24 with species 2; group 11 with species 3; groups 15 and 19 with species 4; group 12 with species 5; group 17 with species 6; and group 13 with species 7. Group 23 was later synonymized with species 4 and group 18 with species 7. Groups 16 and 21 were left unsynonymized at this stage.

Table 9.—*Montastraea.* F-statistics (and their significance levels) for Mahalanobis' distances between the seven NMB clusters (columns labelled 1–7), groups based on Neogene types (rows labelled 11–25) as listed in Table 4, and populations of two modern species. Because of differences in sample sizes, values were compared only between columns within rows.

species (group)	*number of colonies*	1 *n = 32*	2 *n = 13*	3 *n = 7*	4 *n = 11*	5 *n = 8*	6 *n = 8*	7 *n = 7*
A brevis (11)	6	7.06 (.00)	3.46 (.00)	1.75 (.04)*	5.16 (.00)	5.99 (.00)	11.45 (.00)	22.26 (.00)
A. cylindrica (12)	2	6.07 (.00)	3.76 (.00)	2.76 (.00)	2.76 (.00)	2.11 (.01)*	3.10 (.00)	8.68 (.00)
A. endothecata (13)	2	19.53 (.00)	14.74 (.00)	10.51 (.00)	6.79 (.00)	10.27 (.00)	3.41 (.00)	2.48 (.00)*
H. altissima (14)	2	1.71 (.05)	0.98 (.48)*	1.83 (.03)	2.17 (.00)	2.05 (.01)	5.36 (.00)	12.37 (.00)
H. insignis (15)	1	4.52 (.00)	4.49 (.00)	3.95 (.00)	1.98 (.02)*	3.01 (.00)	2.98 (.00)	4.75 (.00)
O. bainbridgensis (18)	2	19.94 (.00)	15.91 (.00)	12.86 (.00)	11.22 (.00)	20.76 (.00)	8.82 (.00)	9.16 (.00)*
O. canalis (19)	4	13.34 (.00)	7.99 (.00)	8.11 (.00)	2.30 (.01)*	5.59 (.00)	3.99 (.00)	9.42 (.00)
O. imperatoris (21)	4	7.90 (.00)	8.86 (.00)	9.60 (.00)	11.66 (.00)	10.68 (.00)	19.19 (.00)	31.21 (.00)
O. limbata var. *pennyi* (22)	1	0.45 (.96)*	1.11 (.34)	1.40 (.15)	2.92 (.00)	2.82 (.00)	5.79 (.00)	10.67 (.00)
O. tampaensis (23)	4	30.76 (.00)	22.39 (.00)	19.07 (.00)	12.26 (.00)*	14.70 (.00)	9.79 (.00)	12.82 (.00)
O. trinitatis (24)	1	0.45 (.96)	0.45 (.96)*	1.50 (.11)	2.48 (.00)	2.43 (.00)	5.39 (.00)	10.08 (.00)
P. limbata (25)	4	0.34 (.99)*	2.31 (.00)	2.70 (.00)	6.20 (.00)	4.69 (.00)	13.81 (.00)	26.04 (.00)
M. annularis (16)	40	18.14 (.00)	12.14 (.00)	13.22 (.00)	25.82 (.00)	31.02 (.00)	40.68 (.00)	63.24 (.00)
M. cavernosa (17)	32	127.34 (.00)	55.08 (.00)	38.05 (.00)	24.86 (.00)	11.13 (.00)	18.72 (.00)*	19.38 (.00)

* Synonymized in species descriptions.



Text-figure 13.—*Solenastrea.* Canonical discriminant analysis of the NMB collections. Histogram of frequencies of mean colony scores on the discriminant function. Left angle stripes = *S. bournoni*; crosshatch = *S.hyades*.

Table 10.—*Solenastrea.* Differences in canonical discriminant scores between means of the two NMB clusters (columns labelled 1, 2) and holotypes for Caribbean Neogene species.

species	*museum catalogue number*	*number of variables used in analysis*	1	2
Astraea excelsa Dana (= *hyades*)	YPM 1727	7	4.367	3.218*
Plesiastraea distans Duncan	BMNH R28758	7	7.026*	14.612
Plesiastraea globosa Duncan	BMNH R28871	7	1.425*	9.011
Solenastrea bournoni Milne Edwards and Haime	MNHNP 794	6	0.557*	5.628
Stephanocoenia fairbanksi Vaughan	USNM 157516	3	3.019	0.077
Solenastrea fairbanksi var. *minor* Vaughan	USNM 68284	3	3.520	0.577
Solenastrea fairbanksi var. *normalis* Vaughan	USNM 68283	3	3.520	1.577

* Synonymized in species descriptions.

which appears most strongly related to corallite spacing and the structure of the coenosteum. A number of characters including **CD**, **CND**, **CLW**, and **STS** were most heavily weighted on **CV4**, which appears to be most strongly related to septal thickness.

Univariate analyses of variance further show differences among the seven clusters in all 16 measured characters. The greatest differences among clusters occur in four characters related to corallite size: corallite diameter (**CD**); primary septum length (**SLP**); columella width (**CLW**); and secondary septum length (**SLS**) (Text-fig. 14).

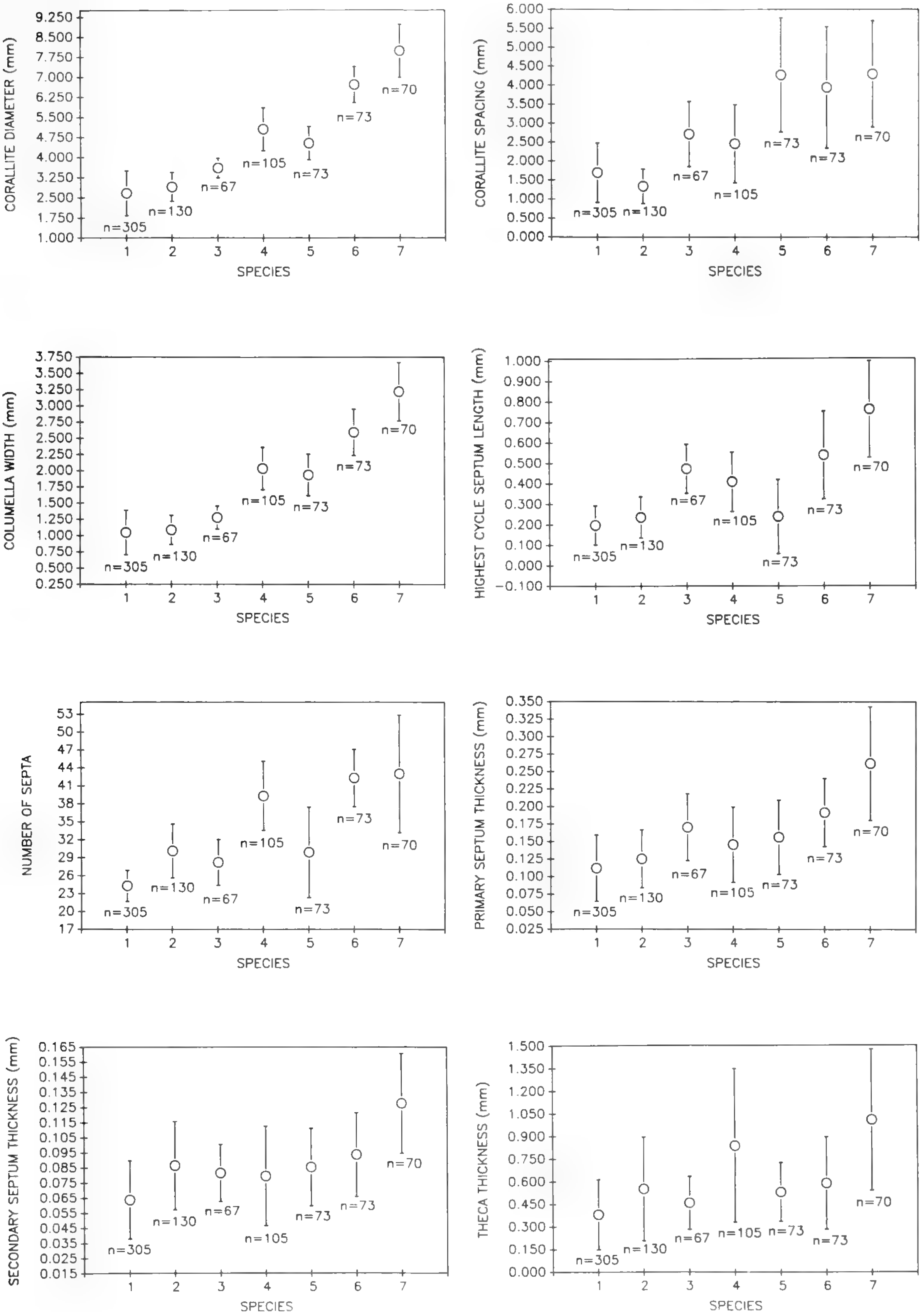
Comparisons between the NMB *Montastraea* clusters and groups based on the *Montastraea* types (Table 4) reveal a highly complicated relationship between the two data sets. The results of the canonical discriminant analysis in which the types were left unclassified (Text-figs. 11b, c) show that none of the 14 groups of types falls clearly within any of the NMB clusters. Instead, the groups lie at the margins of clusters or equally near two adjacent clusters. However, Mahalanobis' distances between the NMB clusters and groups based on the types (Table 9) do clearly suggest some synonymies. Using a significance level of 0.01, groups 25 and 22 appear to be the same as NMB cluster 1, groups 14 and 24 appear to be the same as NMB cluster 2, group 11 appears to be the same as NMB cluster 3, groups 15 and 19 appear to be the same as NMB cluster 4, and group 12 appears to be the same as NMB cluster 5. A relatively short distance also occurs between group 13 and NMB cluster 7. In addition, as discussed in the next section, modern populations of *M. cavernosa* appear temporally continuous with NMB cluster 6. This reduces the 12 groups listed in Table 4 to a total of 10 species, one of which belongs to one of the two modern species. As noted in the section on systematic paleontology, together with results of comparisons with other Caribbean faunas and qualitative study of the primary types of 14 of the 17 *Montastraea* species [*i.e.*, not including primary types of *M. radiata* var. *intermedia*, *M. altissima*, or *M. insignis* that could not be found (Table 3)], these results suggest that the total number of Neogene species of *Montastraea* can be reduced to nine.

In the final canonical discriminant analysis of *Solenastrea*, two groups were distinguished with 100% of all colonies correctly classified. The F-statistic (F=10.417 with six and four degrees of freedom) derived from the Mahalanobis' distance between the two groups has a significance of p=0.02, which further indicates that the two groups are discrete. One canonical discriminant function was calculated which had a Wilks' lambda value of 0.06015 and a corresponding chi-square value of 16.866, with four degrees of freedom and a p-value of 0.0098. The stepwise variable selection procedure showed that only six of the 10 measured characters were needed in the final analysis. They included in descending order of importance: **SLT**, **ST**, **CLW**, **CST**, **NND**, and **PA**. The canonical discriminant function weighted columella width most heavily, and is most strongly correlated with length of the tertiary septa (Table 8).

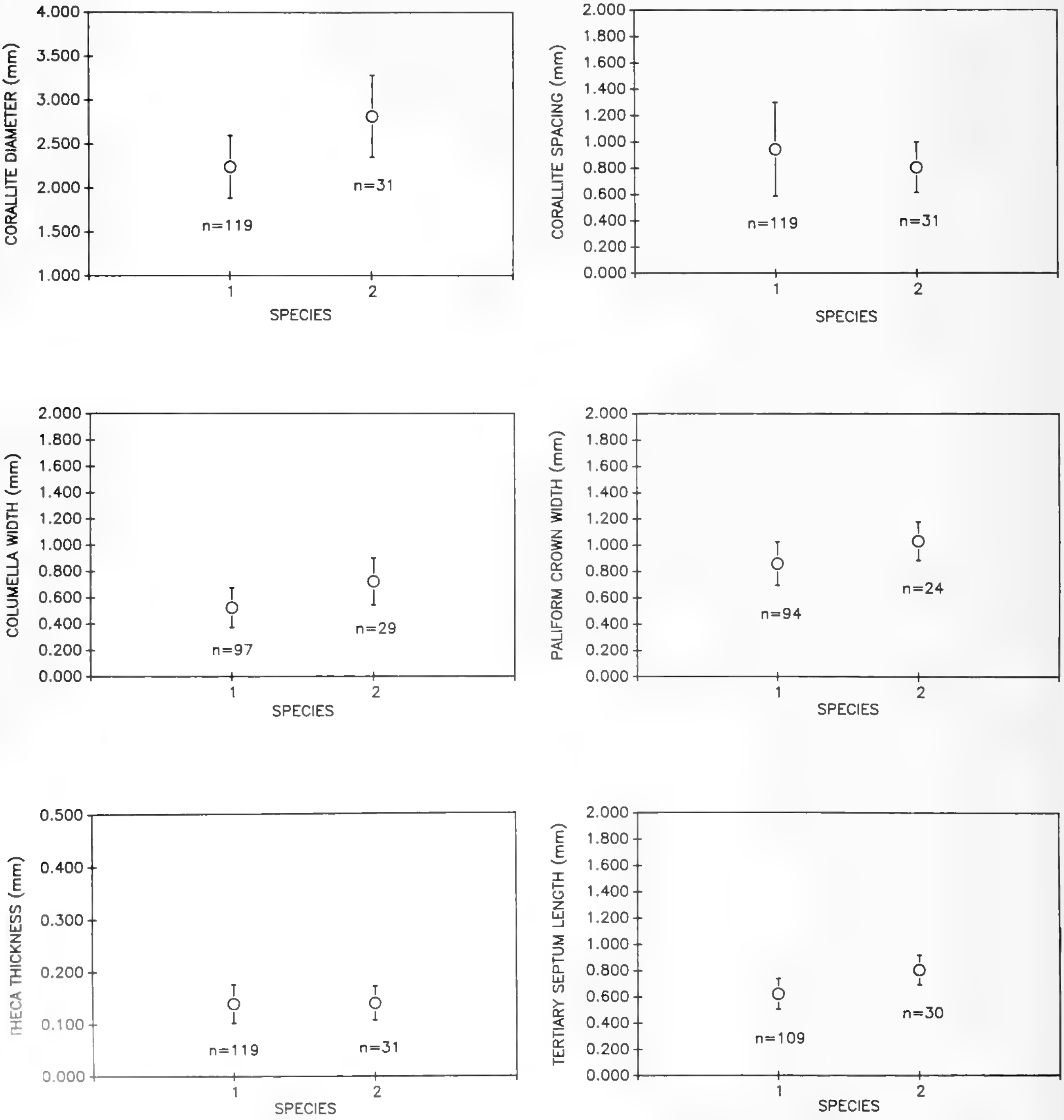
Univariate analyses of variance show that seven of the 10 measured characters differ between the two *Solenastrea* clusters. In descending order of significance, these include: tertiary septum length (**SLT**); corallite diameter (**CD**); columella width (**CLW**); paliform crown width (**PA**); and total number of septa (**NS**) (Text-fig. 15). Differences between clusters could not be detected in theca thickness (**TT**), septum thickness (**ST**), or costa thickness (**CST**).

The results of canonical discriminant analyses in which the six *Solenastrea* holotypes were left unclassified (Table 10) suggest that holotypes for three species (*Plesiastraea distans* Duncan, *Plesiastraea globosa* Duncan,

Text-figure 14.—Means and standard deviations for eight characters in the seven *Montastraea* species (Appendix Ia). The midpoint of each vertical line represents the mean, and the length of the line on either side of the midpoint is one standard deviation. Nonparametric analysis of variance (**PROC NPAR1WAY** of **SAS**) shows that the species differ significantly in each case. "n" = number of colonies measured. Species 1 = *M. limbata*; species 2 = *M. trinitatis*; species 3 = *M. brevis*; species 4 = *M. canalis*; species 5 = *M. cylindrica*; species 6 = *M. cavernosa*; species 7 = *M. endothecata*.


CORALLITE DIAMETER (mm)
9.250
8.500
7.750
7.000
6.250
5.500
4.750
4.000
3.250
2.500
1.750
1.000
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
1
2
3
4
5
6
7
CORALLITE SPACING (mm)
6.000
5.500
5.000
4.500
4.000
3.500
3.000
2.500
2.000
1.500
1.000
0.500
0.000
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
COLUMELLA WIDTH (mm)
3.750
3.500
3.250
3.000
2.750
2.500
2.250
2.000
1.750
1.500
1.250
1.000
0.750
0.500
0.250
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
HIGHEST CYCLE SEPTUM LENGTH (mm)
1.000
0.900
0.800
0.700
0.600
0.500
0.400
0.300
0.200
0.100
0.000
-0.100
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
NUMBER OF SEPTA
53
50
47
44
41
38
35
32
29
26
23
20
17
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
PRIMARY SEPTUM THICKNESS (mm)
0.350
0.325
0.300
0.275
0.250
0.225
0.200
0.175
0.150
0.125
0.100
0.075
0.050
0.025
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
SECONDARY SEPTUM THICKNESS (mm)
0.165
0.155
0.145
0.135
0.125
0.115
0.105
0.095
0.085
0.075
0.065
0.055
0.045
0.035
0.025
0.015
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES
THECA THICKNESS (mm)
1.500
1.350
1.200
1.050
0.900
0.750
0.600
0.450
0.300
0.150
0.000
n=305
n=130
n=67
n=105
n=73
n=73
n=70
SPECIES

can, and *Solenastrea bournoni* Milne Edwards and Haime) clearly belong to NMB cluster 1. The holotype for *Astraea excelsa* (= *S. hyades*) appears closer to NMB cluster 2. Holotypes for *Stephanocoenia fairbanksi* Vaughan and its varieties appear closer to NMB cluster 2; however, as discussed in the next section, study of thin-section measurements made on topotypes and comparisons with other Neogene Caribbean faunas suggest that *S. fairbanksi* actually may be intermediate between the two NMB clusters and may therefore represent a separate species. More material belonging to NMB cluster 2 is needed to evaluate this



Text-figure 15.—Means and standard deviations for six characters in the two *Solenastrea* species (Appendix Ib). The midpoint of each vertical line represents the mean, and the length of the line on either side of the midpoint is one standard deviation. Nonparametric analysis of variance (**PROC NPAR1WAY** of **SAS**) shows that the species differ significantly in each case. "n" = number of corallites measured. Species 1 = *S. bournoni*; species 2 = *S. hyades*.

Table 11.—Localities and number of colonies measured in each of five time intervals.

age	*locality*	*number of colonies*	*repository*
1. late Oligocene	Anahuac Formation, Texas	9	SUI
	Juana Diaz Formation, Puerto Rico	12	SUI
	Brownstown Formation, Jamaica	5	SUI
2. early Miocene	Tampa Formation, Florida	8	USNM
	Chattahoochee formation, Georgia	11	USNM
	Larés Formation, Puerto Rico	7	SUI
	Santa Ana and Río Lajas formations, Chiapas, Mexico	24	UI
3. middle Miocene	Anguilla Formation, Anguilla	23	USNM
	La Boca Formation, Panama	27	USNM
	Baitoa Formation, Dominican Republic	9	NMB
4. late Miocene/early Pliocene	Cercado, Gurabo, and Mao formations, Dominican Republic	90	NMB
5. Recent	Discovery Bay, Jamaica	72	SUI

possibility.

In summary, the results for *Montastraea* are as follows.

(1) Seven slightly overlapping groups exist. The most overlap occurs between species 4 and 6 and between species 3 and 5. The amount of overlap, however, is far less than that found in species of *Porites* from the same sequence in the Dominican Republic.

(2) All 16 characters contribute to distinguishing the seven groups. The most important character complex is related to corallite size. Other character complexes are related to corallite spacing and the density of the coenosteum and to the thickness and length of the highest septal cycle.

(3) Analyses of type material for 12 Neogene species and of populations of the two modern Caribbean species suggest that two described species belong to NMB cluster 1 (*M. limbata*), two belong to NMB cluster 2 (*M. trinitatis*), and possibly two belong to NMB cluster 4 (*M. canalis*). One described species belongs to NMB cluster 3 (*M. brevis*), one belongs to NMB cluster 5 (*M. cylindrica*), and one belongs to NMB cluster 7 (*M. endothecata*). This results in a reduction in the number of Neogene species from 12 to 10. Together with the results presented in the next section, this suggests that a total of nine species of *Montastraea* existed in the central Caribbean during the Neogene.

In summary, the results for *Solenastrea* are as follows.

(1) Two groups exist. Too few specimens were collected of the second group, however, to examine possible overlap between groups.

(2) Only six of the 10 measured characters were needed to distinguish the two groups. The characters most important in distinguishing species are the length of the tertiary septa (**SLT**) and several features, such as columella width, which were found to be directly correlated with corallite size.

(3) Comparisons with primary types suggest that either two or three species of *Solenastrea* may have occurred in the Caribbean during the Neogene.

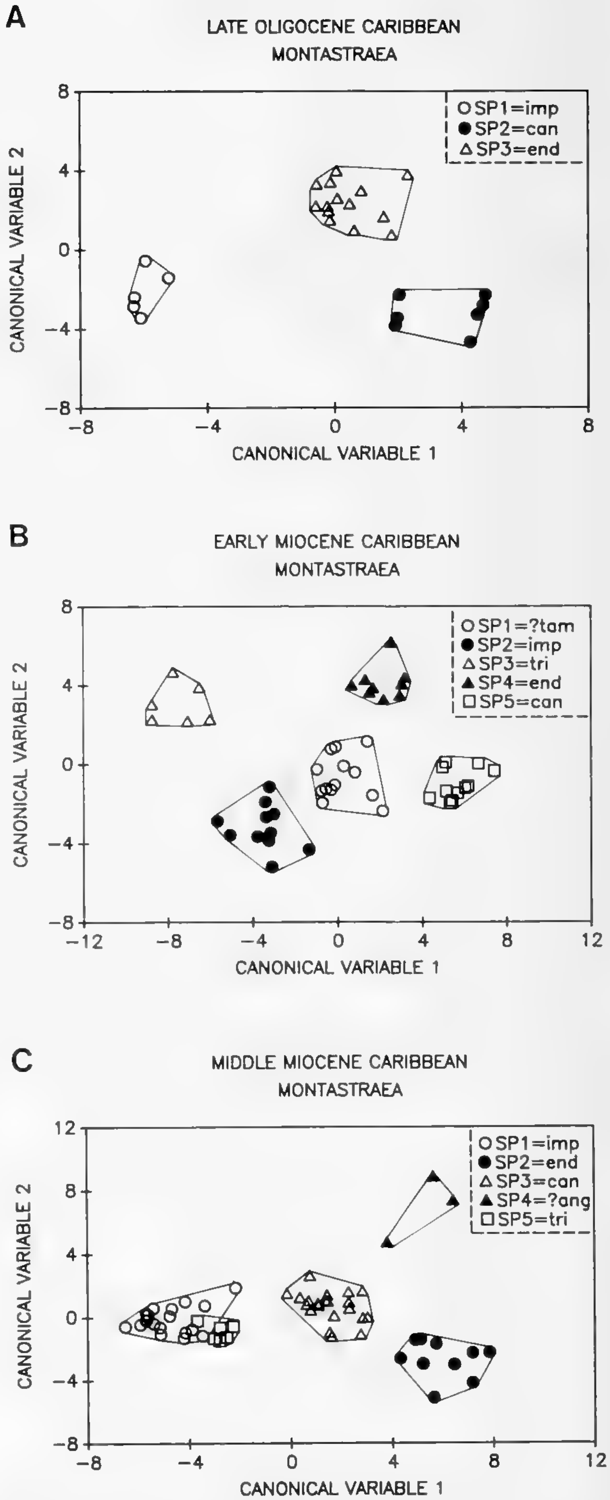
COMPARISONS WITH OTHER CARIBBEAN FAUNAS

To determine the total duration and geographic range of the species described herein, morphological measurements for each species have been compared with measurements made on colonies from a number of other Tertiary and modern Caribbean localities. In *Montastraea* Blainville, 1830, these localities occur in 10 widely scattered formations of late Oligocene and early to middle Miocene age (Table 11), in addition to the previously described modern reef environments near Discovery Bay, Jamaica. The measurements analyzed are identical to those described earlier for the NMB material (Table 5; Text-fig. 9). Measurements for all the NMB material were included in the analyses. In *Solenastrea* Milne Edwards and Haime, 1848, due to the general paucity of abundant older material, the material analyzed consisted of 10 colonies from the lower Pliocene Tamiami Formation of south Florida and eight colonies from the lower Pliocene Imperial Formation of south-central California, as described previously in the section on material. Unlike the previous statistical analyses, the measurements were derived from points digitized on thin-sections, as described previously in the section describing the characters (Table 6; Text-fig. 9). Measurements for only eight NMB colonies were included in the analyses: four from Río Gurabo (D5584, D5603, D5724, D5794), one from Río Cana (D5627), and three from the Miocene section along Río Yaque del Sur (D5670, D5675, D5690).

To analyze the *Montastraea* data, the material was sorted into five time intervals as shown on Table 11, and species were statistically discriminated within each time interval using cluster analysis and canonical discriminant analysis as described in the previous section on statistical techniques. In addition to the two modern Caribbean species, a total of 20 fossil species were distinguished altogether (13 of which are shown on Text-fig. 16). These species were then linked into lineages representing single species lines using Mahalanobis' distances among all 21 species (following the methods of Budd, 1988). In this procedure, distances between species in successive time intervals were compared with distances between species within time intervals (Text-fig. 17). Species in successive time intervals were linked if the distance between them was less than the minimum distance between species in each of the two intervals. In three cases, linkages appear ambiguous: (1) in *M. imperatoris* (Vaughan, 1919) from the Oligocene to early Miocene; (2) in *M. trinitatis* (Vaughan *in* Vaughan and Hoffmeister, 1926) from the middle Miocene to late Miocene/early Pliocene; and (3) in *M. cavernosa* (Linnaeus, 1767) from the late Miocene/early Pliocene to Recent. In such cases where more than one possible linkage appears viable, Mahalanobis' distances calculated using only the adjacent pair of intervals were used to establish linkage.

Linkage reduced the 22 species to eleven (Text-fig. 17). These results suggest that two of the early Miocene types listed in Table 4 (*i.e.*, groups 18 and 23) may be synonymous with Dominican Republic species. Group 18, which includes the holotype of *Orbicella bainbridgensis* Vaughan, 1919, appears linked with *M. endothecata* (Duncan, 1863). Group 23, which includes topotypes but not the holotype of *Orbicella tampaensis* Vaughan, 1919, appears linked with *M. canalis* (Vaughan, 1919).

The results provide preliminary estimates of patterns of speciation and extinction within Caribbean *Montastraea* as well as amounts of directional phyletic evolution within each *Montastraea* species. However, due to small sample sizes, some estimates of species durations may be reduced. The patterns found suggest that all three Oligocene species (*M. endothecata*, *M. imperatoris*, and *M. canalis*) survived the late Oligocene extinction event (Frost, 1977), and two (*M. endothecata* and *M. canalis*) may have been abundant for more than twenty million years. During the early Miocene, two new species (*M. tampaensis* and *M. trinitatis*) arose, one of which (*M. tampaensis*) became extinct shortly thereafter. During the middle Miocene, only one new species [*M.* ? *anguillensis* (Vaughan, 1919)] arose, but it soon became extinct. Within the late Miocene to early Pliocene (covered herein), four new species [*M. limbata*, *M. brevis*, *M. cylindrica* (Duncan, 1863), and *M. cavernosa*] arose, and three



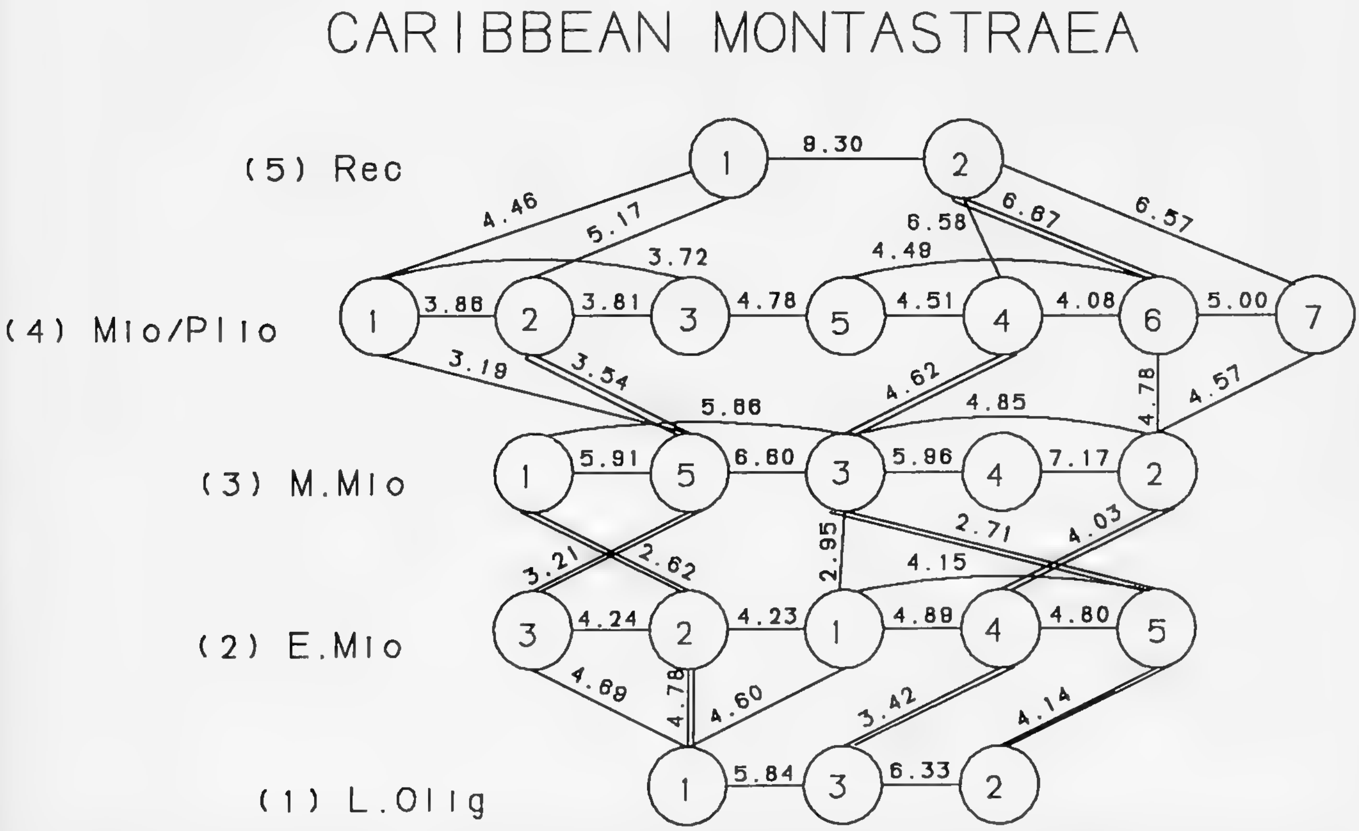
Text-figure 16.—*Montastraea*. Canonical discriminant analyses distinguishing three Oligocene and nine Neogene Caribbean species. Plots of scores on the first two canonical variables showing polygons outlining the range of variation among colonies within each species. Oligocene species 3, early Miocene species 4, and middle Miocene species 2 were subsequently linked with NMB species 7 (= *M. endothecata*). Oligocene species 2, early Miocene species 5, and middle Miocene species 3 were subsequently linked with NMB species 4 (= *M. canalis*). Early Miocene species 3 and middle Miocene species 5 were subsequently linked with NMB species 2 (= *M. trinitatis*). "imp" = *M. imperatoris*; "can" = *M. canalis*; "end" = *M. endothecata*; "tam" = *M. tampaensis*; "tri" = *M. trinitatis*; "ang" = *M. anguillensis*.

(*M. limbata*, *M. brevis*, and *M. cylindrica*) became extinct shortly thereafter. Furthermore, two longer-ranging species (*M. canalis* and *M. trinitatis*) also became extinct at the end of the Neogene time interval represented in the northern Dominican Republic. Only one new species [*M. annularis* (Ellis and Solander, 1786)] arose after the Pliocene.

Thus, rapid periods of species diversification (adaptive radiations) appear to have been rare in Caribbean *Montastraea*. Unlike *Porites* (see Foster, 1986), a few species were capable of surviving extinction episodes during the late Oligocene and Plio–Pleistocene. Some species had long durations (maximum = 20 Ma) with limited speciation and extinction within each interval. Maximum diversity occurred during the late Miocene/early Pliocene.

To test whether gradual directional change occurred within any of the longer-ranging species lines, canonical discriminant analysis was performed among the 11 unlinked species. The scores for the first two canonical variables were then analyzed for non-random change through time in the four longer ranging lineages (Text-fig. 18). In this case, characters related to corallite size (*e.g.*, **CD**, **CLW**, **SLP**, **SLS**) are most strongly correlated with canonical variable 1, and characters related to skeletal texture (*e.g.*, **CNP**, **STS**, **CST**) are most strongly correlated with canonical variable 2. Results of Duncan's multiple range test indicate that directional changes occur in these two variables through the sequence in *M. imperatoris* and in *M. canalis*, but not in *M. trinitatis* or *M. endothecata*. Mahalanobis' distances between pairs of nearby populations of the two living Caribbean species were compared between earliest and latest occurrences for these two species, following the methods of Stanley and Yang (1987). These results indicate that the observed temporal change is less than or equal to environmental variation within the two species. Therefore, stasis prevailed.

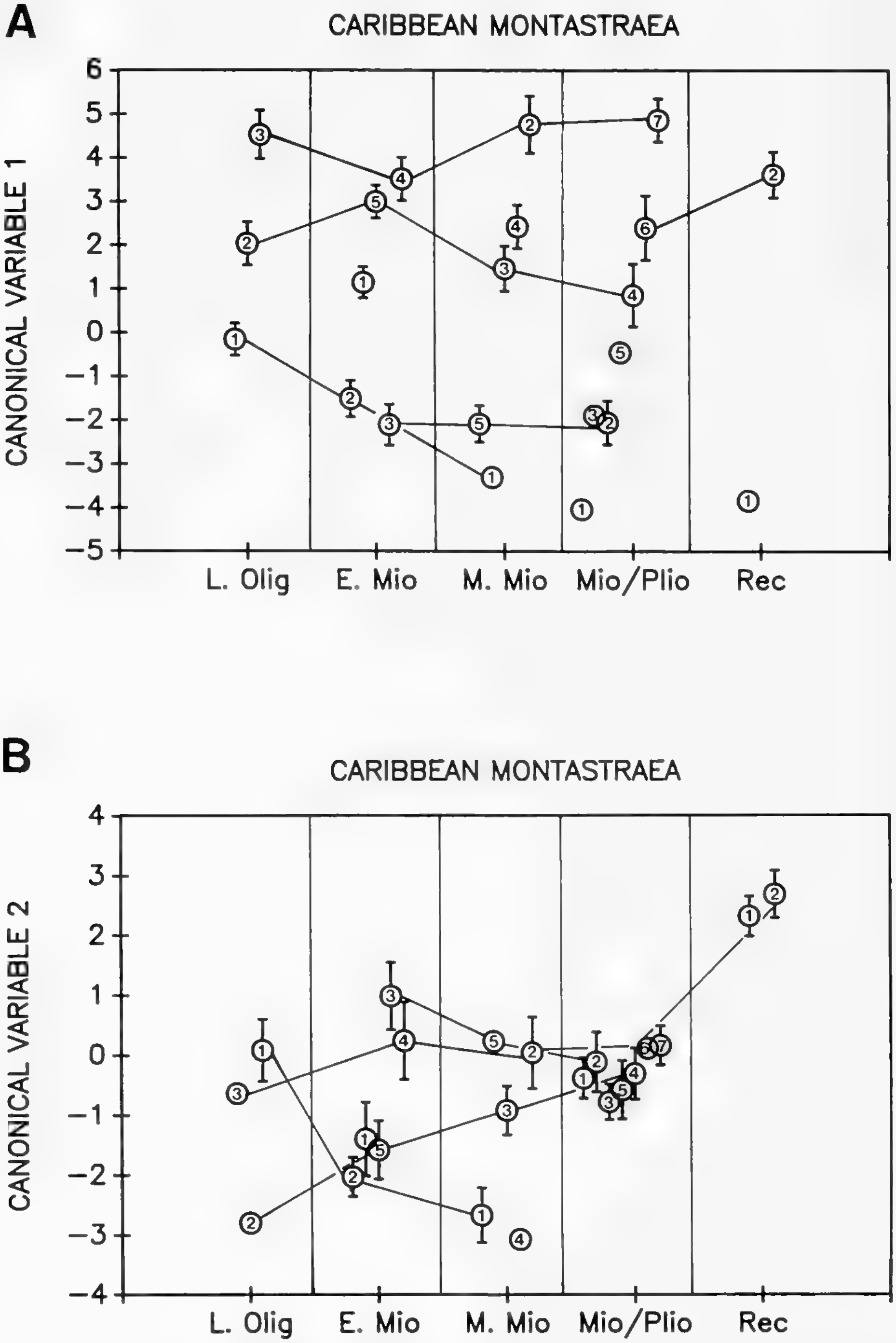
In *Solenastrea*, the material was sorted by locality, and species were first discriminated within each locality region (Dominican Republic; Tamiami Formation of Florida; Imperial Formation of California) using cluster analysis and canonical discriminant analysis as described in previous statistical techniques. The clusters from each locality were combined with those from other localities using Mahalanobis' distances, and a final series of canonical discriminant analyses were run on the combined clusters. The final results are



Text-figure 17.—*Montastraea*. Network of shortest Mahalanobis' distances between Caribbean species within stratigraphic levels and between adjacent levels. Double lines indicate species linked between levels. Numbers for each species are identification numbers previously used for that interval (see Text-fig. 16).

shown in Text-figure 19. Two discrete species were found, and the characters **SLS** and **−SLT** were most heavily weighted on the discriminant function distinguishing the two species. One species (*S. bournoni*) occurred in all three locality regions. The other was found only in the Tamiami Formation.

Mahalanobis' distances were then calculated between localities in which the species co-occurred. The results show that distances were insignificant between populations from the Imperial Formation and Florida.



Text-figure 18.—*Montastraea*. Variation within Caribbean species in corallite characters through the Cenozoic. Variation through five levels of Cenozoic time (see Table 11) in the first two canonical variables distinguishing the eleven species. The five time intervals are blocked off along the horizontal axis. Means and one standard deviation for each species within each interval are indicated by vertical bars. Numbers for each bar refer to the species identification number within that interval (see Text-fig. 16). Solid lines between bars indicate linkages. Statistically significant directional change could be detected in canonical variable 1 and 2 in the lineage extending from late Oligocene species 1 to middle Miocene species 1 (= *M. imperatoris*) and in the lineage extending from late Oligocene species 2 to Mio-Pliocene species 4 (= *M. canalis*).

However, the distance between the Imperial Formation and the Dominican Republic was found to be statistically significant. The results imply that Neogene populations of *Solenastrea* in the northern Caribbean and Gulf of California are more closely related to each other than they are to populations from the central Caribbean. This pattern resembles that found in *Porites* but not in *Siderastrea* (see Budd, 1989), suggesting that each genus has had a unique biogeographic history.

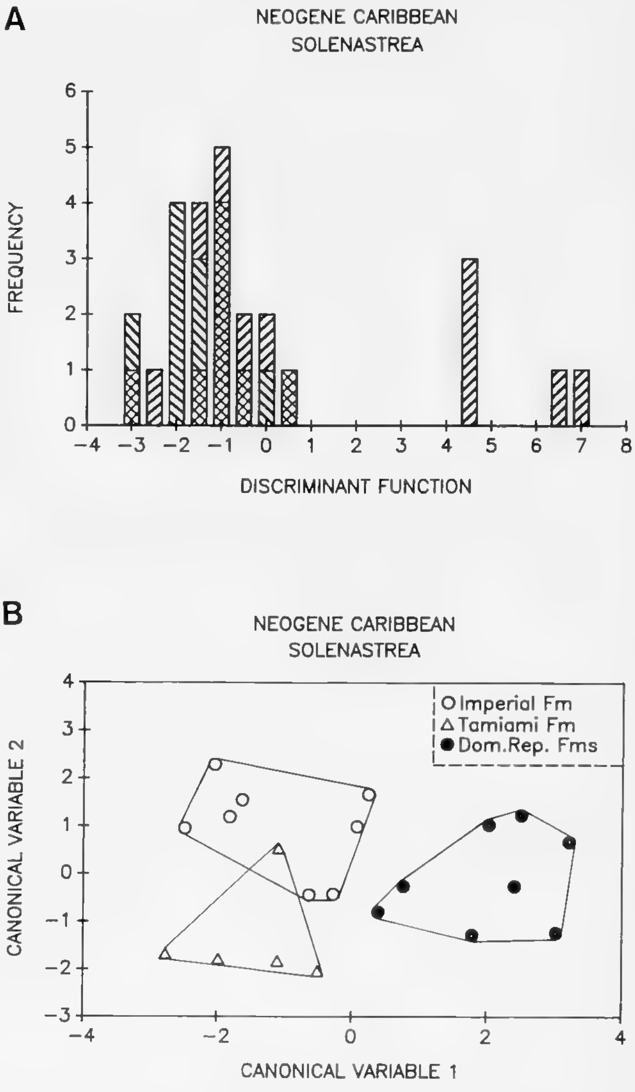
SYSTEMATIC PALEONTOLOGY

INTRODUCTION

The formal systematic descriptions in this section are based strictly on the statistical analyses given in the previous section. Since the present monograph describes only a small subset of the family Faviidae (the two plocoid genera represented in the NMB collections), classification of higher categories has not been re-evaluated, and diagnosis of higher categories strictly follows the system of Chevalier (1971) and Veron, Pichon, and Wijsman-Best (1977). Unless otherwise indicated, the synonymies are based on type material actually measured and statistically analyzed. The term "not seen" indicates that type material could not be located for examination. A list summarizing the synonymies is given in Table 3. As explained in Table 3, emphasis is given to Miocene through lower Pliocene material described from the Caribbean region. The synonymies provide a guide to the ensuing "Remarks" section, and therefore include not only forms in synonymy but forms definitely not in synonymy. As in Foster (1986), the term "Diagnosis" is used only to describe higher categories such as genera, whereas the term "Description" is reserved for complete descriptions of species, which, as described in the previous section, herein merely represent morphologic clusters of specimens. The terminology used in the "Description" sections is defined and described in the previous section entitled "Characters". It follows the usage of Vaughan and Wells (1943) and Wells (1956).

Unless otherwise indicated, all measurements are given in mm, and abbreviations used for measurements are explained in Tables 5 and 6. Holotypes have not been sectioned; therefore, the characters listed as holotype measurements were measured on the colony surface and are not as accurate as many thin-section measurements given in the descriptions of species of *Montastraea*. These holotype measurements cannot be directly compared with the thin-section measurements of *Montastraea* used in the statistical analyses, and given in Text-figure 14 and in Appendix Ia. In *Solenastrea*, however, measurements used in statistical analyses were made on colony surfaces just as those made for holotypes; therefore, *Solenastrea* holotype measurements can be directly compared with values given in species descriptions and used in statistical analyses (Text-fig. 15, Appendix Ib).

The "Materials" sections give an approximate estimate of the amount of material in the collection of Saunders, Jung, and Biju-Duval (1986), and the number of specimens in that collection that were statistically analyzed. A few additional specimens collected in the same sections by Emily and Harold Vokes, and



Text-figure 19.—*Solenastrea*. Comparisons with the Tamiami Formation of south Florida, formations in the Dominican Republic, and the Imperial Formation of south-central California. (**a**) Histogram of frequencies of mean colony scores on the first discriminant function distinguishing species. The peak on the left represents *S. bournoni*, and on the right *S. hyades*. Crosshatch = colonies from the Imperial Formation; left slant = colonies from the Dominican Republic; right slant = colonies from the Tamiami Formation. (**b**) Plot of scores for each colony on the two canonical variables distinguishing populations of *S. bournoni*. Polygons outline the maximum variation within each population. Populations from the Imperial and Tamiami formations overlap and are discrete from populations in the Dominican Republic formations.

currently reposited at the USNM, were added to this material to perform the statistical analyses. Species definitions are based on both the Saunders, Jung, and Biju-Duval (1986) and the Vokes' specimens (listed in part in Table 1). Catalogue numbers have been assigned to all figured and measured material. A unique number was given to each colony.

The "Remarks" sections explain synonymies and additional museum material used to estimate distribution patterns. Separate sections entitled "Variability" describe the variation within each cluster. Sections entitled "Occurrence" give detailed geographic and stratigraphic information within the studied areas of the Dominican Republic, whereas those entitled "Distribution" give general information on all known occurrences throughout the world. Unless otherwise indicated, the locality numbers belong to the Naturhistorisches Museum Basel (NMB), and the material is deposited at the NMB. Assignment of formation names to individual localities is based on Saunders, Jung, and Biju-Duval (1986) (especially text-figs. 4, 6, 15, 16), except along Río Mao where formation names are used as listed by Maury (1919). Ages for Caribbean localities mentioned outside the Dominican Republic are based on the following sources: Anguilla, Bold (1970); Antigua, Bold (1966); Cuba, Bold (1975); Jamaica, Robinson (1969); Puerto Rico, Frost *et al.* (1983); Chiapas, Mexico, Frost and Langenheim (1974); Florida and Georgia, Puri and Vernon (1964); Panama, Woodring (1957, 1964); Trinidad, J. B. Saunders (oral commun., 1985).

Family **FAVIIDAE** Gregory, 1900

The Faviidae are defined as colonial and hermatypic. Colonies may be formed by intra- or extratentacular budding. With the exception of a few phaceloid (*e.g.*, *Caulastraea* Dana, 1846) and branching (*e.g.*, *Hydnophora* Fischer, 1807) genera, colonies are generally massive or thickly encrusting plocoid, cerioid, or meandroid. The wall structure is septothecate or parathecate, rarely partially synapticulothecate. Septa are formed by one fan system of mostly simple trabeculae, and are regularly dentate. Paliform lobes are commonly developed by the inner fan system. The columella is trabecular or laminar.

The Faviidae converge in colony form with other common colonial hermatypic Neogene to Recent families of the suborder Faviina Vaughan and Wells, 1943, including, for example, the families Meandrinidae Gray, 1847, and Mussidae Ortmann, 1890. The most important character distinguishing families in these cases is septal structure (Text-fig. 1). Septa are composed of simple trabeculae, arranged in one or two laminar fan systems. Smooth acute teeth project from the trabeculae along the upper septal margins (Wells, 1956).

Genus **MONTASTRAEA** Blainville, 1830

Montastraea Blainville, 1830, p. 339.
Orbicella Dana, 1846, p. 205.
Phyllocoenia Milne Edwards and Haime, 1848, p. 469.
Heliastraea Milne Edwards and Haime, 1857, p. 456.

Type species.—*Astrea guettardi* Defrance, 1826, p. 379

Diagnosis.—Colonies massive, encrusting or subfoliaceous: plocoid, formed predominantly by extratentacular budding. Costae well-developed. Wall structure septothecate with dentate septal margins. Trabecular columella. (Chevalier, 1971).

Remarks.—The genus *Montastraea* is widely distributed today across the Indo-Pacific (Red Sea to west Pacific) and tropical Atlantic and Caribbean regions. It consists of approximately eight Recent species (three Caribbean, five or more Indo-Pacific). It is abundant in all reef zones ranging from shallow nearshore areas across the reef crest to the deep forereef (Goreau, 1959). It dominates shallow backreef and forereef zones as well as deeper parts of the forereef down to 30–40 m (Geister, 1983). The genus reportedly arose during the Upper Jurassic/Lower Cretaceous; however, it did not become abundant in the Mediterranean (Chevalier, 1961; Pfister, 1980) or in the Caribbean until the Miocene (Frost and Weiss, 1979).

Seventeen valid Neogene species of *Montastraea* have been described from the Caribbean region (Table 3). This tally does not include four additional species herein reassigned to other genera including *Astraea costata* Duncan, 1863 (= *Agathiphyllia* Reuss, 1864); *Orbicella gabbi* Vaughan, 1919 (= ?*Diploastrea* Matthai, 1914), *Montastrea davisina* Weisbord, 1973 (= *Solenastrea* Milne Edwards and Haime, 1848); and *Montastrea peninsularis* Weisbord, 1973 (= *Solenastrea*). Based on the synonymies shown in Table 3, as many as 10 species of *Montastraea* may have existed in the Caribbean Neogene, three of which (*M. intermedia* = *M. imperatoris*, *M.* ? *anguillensis*, and *M. tampaensis* s.s.) did not occur in the Dominican Republic but were common in Panama and Anguilla during the middle Miocene.

In previous systematic studies of the Caribbean and Mediterranean Neogene Faviidae, the following plocoid genera have been confused.

(1) *Montastraea* Blainville, 1830 (Mediterranean, Atlantic, Caribbean, to Indo-Pacific; ?Late Jurassic to Recent): septothecate, strong costae, trabecular columella, usually no pali or paliform lobes.

(2) *Solenastrea* Milne Edwards and Haime, 1848 (Mediterranean and Caribbean; Oligocene to Recent): septothecate, extremely weak costae, trabecular colu-

mella, no pali, reduced or absent paliform lobes.

(3) *Plesiastrea* Milne Edwards and Haime, 1848 (Mediterranean to Indo-Pacific; Eocene to Recent): septothecate, strong costae, trabecular columella, true pali.

(4) *Agathiphyllia* Reuss, 1864 (Mediterranean and Caribbean; Oligocene to Miocene): synapticulothecate, strong costae, trabecular columella, internal septal lobes, wide paliform lobes.

(5) *Tarbellastraea* Alloiteau, 1952 (Mediterranean; Oligocene to Miocene): parathecal wall structure, weak costae, a lamellar (to sublamellar) columella, no pali or paliform lobes.

(6) *Antiguastrea* Vaughan, 1919 (Mediterranean and Caribbean; Eocene to Oligocene): usually subcerioid, parathecal wall structure, weak costae, a lamellar columella, no pali or paliform lobes.

In the current study, the most problematic pair of these genera is *Agathiphyllia* and *Montastraea*. One common species, *A. antiguensis* (Duncan, 1863) [Pl. 1, figs. 2, 3], has corallite morphologies strikingly convergent with *Montastraea endothecata* (Duncan, 1863). The two genera under consideration in the present study (*Montastraea* and *Solenastrea*) are readily distinguished by the texture of the coenosteum (Text-fig. 7).

The spelling ***Montastraea*** used herein directly follows the original spelling of Blainville (1830), and not the more commonly used spelling ***Montastrea*** of Vaughan and Wells (1943) and Wells (1956).

Montastraea brevis (Duncan, 1864)

Plate 2, figures 1–6; Plate 3, figures 1–6;
Plate 4, figures 1–6;
Text-figures 3, 4, 5, 10, 11, 14, 17

Astraea brevis Duncan, 1864, p. 37, pl. 4, figs. 3a, 3b.

Description.—Colony small, regular, discoidal (maximum colony diameter 5.0 cm, height 3.6 cm) to ellipsoidal (maximum colony length 5.0 cm, width 4.2 cm, height 2.3 cm) in shape, weakly attached if at all. Colony surface smooth, well-rounded. Growth bands faint, at 2–4 mm intervals. Epitheca well-developed with growth ridges at 0.5 to 1.0 mm intervals.

Calices circular, intermediate in size (3.3 to 4.0 mm), moderately deep (1.5 to 2.0 mm), and moderately to widely spaced (nearest neighbor distance of 2.3 to 3.8 mm). Corallite wall thin (0.3 to 0.6 mm), projecting moderately (maximum 3 mm) above the colony surface.

Costae prominent, usually equal in thickness but not in length, discontinuous, elongate, intermediate in thickness (0.35 to 0.48 mm) and finely dentate to beaded. Septa in three to four cycles, ranging from 26 to 40 in number, with the first and second cycles extending to the columella. First cycle intermediate in thickness (0.14 to 0.22 mm), and thicker than the second cycle. Third cycle three-fourths as long as the second cycle and fusing with it. Fourth cycle free, thin, one-half as long as the second cycle. Columella trabecular, papillate, small (1.13 to 1.52 mm) and whorled, formed by the inner margins of the primary and secondary septa.

Endothecal dissepiments well-developed (0.02 to 0.04 mm thick) at 0.6 mm intervals. Exothecal dissepiments thin (0.1 mm) at 0.5 mm intervals. Exothecal voids vesicular to wide (1.2 mm), rectangular.

Holotype.—BM(NH) R28767 (refigured here: Pl. 2, fig. 5).

Measurements of the holotype.—Means of seven calices: **CD**, 5.08; **NS**, 28.6; **NND**, 2.73; **CLW**, 1.85; **TT**, 0.40; **SLP**, 1.58; **SLS**, 1.58; **SLT**, 0.39; **STP**, 0.26; **STS**, 0.16; **STT**, 0.10; **CST**, 0.61; calice elevation, 1.99; colony length, 39; colony width, 30; colony height, 25.

Type locality.—"Nivajé Shale" of Heneken (1853), Dominican Republic. Neogene.

Material.—Twenty-two colonies from 14 localities. Six specimens thin-sectioned and measured.

Remarks.—Vaughan (1901, pp. 31–32) initially believed *M. brevis* to be synonymous with *M. cavernosa*, but later (Vaughan, 1919) described it as a separate species due to its smaller calices and subequal costae. In the later description, he suggested that *M. brevis* may be synonymous with *M. tampaensis* (herein partially synonymized with *M. canalis*). However, *M. brevis*' smaller calices and less developed columella, in addition to its distinctive colony shape, suggest that it is a separate species.

Variability.—*Montastraea brevis* is one of the least variable of the species studied, especially in corallite diameter and theca thickness. Trends across colonies are not pronounced. Near the colony margin, calices appear more exsert and costae less developed. The calices also appear slightly larger and more widely spaced.

Comparison.—Study of Mahalanobis' distances between species shows that *M. brevis* is closest morphologically to *M. cylindrica* and *M. trinitatis*. It is distinguished by its small colonies; its small to intermediate-sized and moderately spaced corallites; its thin, elevated wall; its few septa; its thick primary septa and prominent equal costae; and its narrow, whorled columella.

Occurrence.—Río Cana: Gurabo Formation (loc. NMB 16881). Río Gurabo: Gurabo Formation (locs. NMB 15807, 15837, 15838, 15839, 15841, 15846, 15847, 15850, 15851, 15858, 16883, 16921, 16934); locs. TU 1215, 1246; loc. USGS 7780).

Distribution.—This species is known to occur only in the lower Pliocene of the Dominican Republic. Specimens of this species reported from the lower Miocene Nariva Formation of Trinidad (Vaughan and Hoffmeister, 1926) belong to *M. canalis*.

Montastraea canalis (Vaughan, 1919)

Plate 5, figures 1–8; Plate 6, figures 1–6;
Plate 7, figures 1–6;
Plate 8, figure 2; Plate 9, figure 2; Plate 14, figure 2;
Text-figures 3, 4, 5, 10, 11, 14, 17

?*Heliastraea insignis* Duncan, 1868, p. 19, pl. 1, fig. 4 (not seen).
Orbicella tampaensis Vaughan, 1919, p. 390, pl. 95, figs. 1, 3, 3a; *not* pl. 95, figs. 2, 2a.
Orbicella tampaensis var. *silecensis* Vaughan, 1919, pp. 390–391, pl. 96.
Orbicella canalis Vaughan, 1919, pp. 389–390, pl. 94, figs. 1, 1a, 3, 3a; *not* pl. 94, figs. 2, 2a; *not* pl. 97, figs. 4, 4a.
not *Montastraea costata* (Duncan). Chevalier, 1954, p. 166, pl. 6, fig. 4.
Montastrea tampaensis (Vaughan). Frost and Langenheim, 1974, pp. 253–258, pl. 91, figs. 1, 2; pl. 92, figs. 1, 2, 4, 6; pl. 93, figs. 1, 2; ?pl. 91, fig. 2 (not seen); ?pl. 92, figs. 3, 5 (not seen).
Montastrea cf. *M. costata* (Duncan). Weisbord, 1971, p. 31, pl. 7, figs. 1–4.
not *Montastrea tampaensis* (Vaughan). Weisbord, 1973, pp. 48–50, pl. 20, fig. 6; pl. 21, fig. 1.
Montastrea cf. *M. tampaensis silecensis* (Vaughan). Weisbord, 1973, pp. 50–51, pl. 22, figs. 1, 2; pl. 23, fig. 1.

Description.—Colony irregular, intermediate-sized (minimum diameter 5.5 cm, maximum diameter 14.0 cm), hemispherical mounds. Colony surface smooth, well-rounded. Growth bands at 4–6 mm intervals. Epitheca moderately developed with growth ridges irregular, at approximately 1 mm intervals.

Calices circular, intermediate to large in size (4.2 to 6.6 mm), moderately deep (1.0 to 1.5 mm), with variable and intermediate spacing (nearest neighbor distance of 6.5 to 10 mm). Corallite wall thick (0.4 to 1.5 mm), projecting high (maximum 4 mm) above the colony surface.

Costae prominent, roughly equal, discontinuous, elongate, intermediate to thick in size (0.38 to 0.62 mm) and moderately dentate. Septa in three to four cycles, ranging from 26 to 44 in number, with the first and second cycles extending to the columella. First cycle relatively thin (0.09 to 0.21 mm), thicker than the second. Third cycle free, about three-fourths as long as the second cycle. Fourth cycle free, thin, one-fourth to one-eighth as long as the second cycle. Columella trabecular, papillate, intermediate in thickness (1.64 to 2.56 mm), strong, formed by the inner margins of the primary and secondary septa.

Endothecal dissepiments weak (0.02 to 0.03 mm thick), irregular, at 0.6 mm intervals. Exothecal disspeiments well-developed (0.2 mm) at 0.7 mm intervals. Exothecal voids wide (1.6 mm), rectangular.

Holotype.—USNM 324862 (refigured here: Pl. 5, fig. 2; Pl. 6, fig. 1).

Measurements of the holotype.—Means of six calices: **CD**, 4.93; **NS**, 27.7; **NND**, 2.42; **CLW**, 1.82; **TT**, 0.42; **SLT**, 0.62; **STP**, 0.30; **STS**, 0.16; **CST**, 0.73; colony length, 44; colony width, 37; colony height, 35.

Type locality.—Locality USGS 6016, Empire Quarry, Emperador Limestone of the La Boca Formation of Panama. Middle Miocene.

Material.—Twenty-eight colonies from 12 localities. Ten specimens sectioned and measured.

Remarks.—*Montastraea canalis* appears to intergrade with *M. cavernosa* from which it differs by having smaller calices, a thicker wall, and equal costae. Vaughan (1919) even included specimens of *M. endothecata* (Vaughan, 1919, pl. 94, figs. 2, 2a, pl. 97, figs. 4, 4a) amongst his paratypes for *O. canalis* Vaughan, 1919. However, canonical discriminant analysis of the Dominican Republic material shows the clusters for *M. canalis*, *M. cavernosa*, and *M. endothecata* to be discrete.

Much like *M. canalis*, Vaughan (1919) describes "*Orbicella intermedia* (Duncan)" as having four cycles of septa, intermediate-sized calices, and subequal costae. On examination, however, the holotype of *Astraea radiata intermedia* Duncan, 1863 [BM(NH) R28725, illustrated by Vaughan (1919) on pl. 97, fig. 2] more clearly falls within Vaughan's (1919) description of *M. imperatoris*, which is distinguished by three cycles of septa and intermediate-sized calices. *M. intermedia* is therefore believed synonymous with *M. imperatoris*.

The holotype of *Heliastraea insignis* Duncan, 1868 is currently lost; however, in addition to Duncan's (1868, pl. 1, fig. 4) original figure, it is also figured by Vaughan (1919, pl. 98, fig. 1). Due to its extensive, porous coenosteum, it and another specimen figured by Vaughan (USNM 324883; pl. 98, figs. 2, 2a; refigured herein on Pl. 14, fig. 2) surficially resemble *M. endothecata*. However, the results of canonical discriminant analysis show that it clearly falls within the *M. canalis* cluster.

The results of canonical discriminant analysis show that one of Vaughan's (1919) hypotypes of "*O. costata* (Duncan)" [USNM 324838 (NF234); pl. 92, fig. 2] also belongs to the *M. canalis* cluster. Similarly, Weisbord's (1971) specimen of *Montastrea* cf. *M. costata* (UF 8931) strongly resembles *M. canalis* in corallite size and septal arrangement as described herein.

The holotype of *Orbicella tampaensis* Vaughan, 1919 (USNM 324900, refigured here on Pl. 8, fig. 2) is distinct from the paratype (USNM 324901, refigured here on Pl. 8, fig. 3) as well as measured topotypic material. It is also distinct from the holotype (WFIS 893) and paratype (USNM 324896, refigured here on Pl. 9, fig. 2) of *Orbicella tampaensis* var. *silecensis* Vaughan 1919. Not only does it have a small colony size, but it also has highly elevated and widely spaced calices with prominent, numerous septa and a high frequency of juvenile calices. In fact, it more closely resembles *Orbicella irradians* (Milne Edwards and Haime) of Vaughan, 1919 (pp. 394–395; pl. 97, figs. 3, 3a) from the Oligocene of Castel Gomerto, Italy. Similarly, Weisbord's (1973) specimens of "*Montastrea* cf. *M. tampaensis silecensis* (Vaughan)" (UF 8954, 8974, 12254) belong to *M. canalis*.

Results of canonical discriminant analyses described in the section on Comparisons with other Caribbean faunas show that Frost and Langenheim's (1974) lower Miocene specimens of *M. tampaensis* belong to four lower Miocene (Text-fig. 16) clusters: (1) *M. canalis* (UI X-3676, X-3695, X-3696); (2) *M. endothecata* (UI X-3674, X-3687, X-3692, X-3694); (3) *M. imperatoris* (UI X-3682, X-3686); (4) *M. tampaensis* (UI X-3671, X-3673, X-3691). However, Frost and Langenheim's (1974) figured material of *M. tampaensis* all clearly belongs to *M. canalis* as described herein. Three figured specimens (UCMP 10358, 10359; UI X-3675) were not seen, because they could not be located at either the University of Illinois or the University of California at Berkeley.

The holotype of *Orbicella tampaensis* Vaughan, 1919 also resembles photographs of *Cyathomorpha anguillensis* Vaughan, 1919 (Vaughan, 1919, pp. 460–461; pl. 127, figs. 1–5). These types could not be found on recent request at the University of Uppsala. However, subjective study of thin-sections of topotypes (SUI 60795–60800) suggests strong similarities among the two species.

Variability.—Variability within *Montastraea canalis* is low in corallite spacing, but high in theca and septum thickness. Trends across colonies are not pronounced. The corallites appear larger, more exsert and more widely spaced toward the colony edge, and the costae appear thinner.

Comparison.—Study of Mahalanobis' distances between species suggests that *M. canalis* is closest morphologically to *M. cavernosa*. It is distinguished from *M. cavernosa* by its relatively thicker corallite wall; its smaller, more closely spaced calices; and its prominent, equal costae.

Occurrence.—Río Cana: Baitoa Formation (loc. TU 1422), Gurabo Formation (locs. NMB 16814, 16815, 16817, 16881) and Mao Formation (locs. NMB 16875, 16876, 16877). Río Gurabo: Mao Formation (loc. NMB 15830). Río Yaque del Norte: Baitoa Formation (locs. NMB 16943, 16944, 17279, 17289).

Distribution.—*M. canalis* ranges in age from late Oligocene to Pliocene and has been found widely distributed across the central and northern Caribbean. The occurrences in the Dominican Republic are among the youngest reported for the species. It has been found outside the Dominican Republic in the following strata: (1) the upper Oligocene Anahuac Formation of Texas, and Juana Diaz Formation of Puerto Rico; (2) the lower Miocene Tampa Formation of Florida, and the Santa Ana and Río Lajas formations of Chiapas, Mexico; and (3) the middle Miocene La Boca Formation of Panama, Chipola Formation of Florida, and Anguilla Formation of Anguilla.

Montastraea cavernosa (Linnaeus, 1767)

Plate 8, figures 1, 4, 6, 7; Plate 9, figures 1, 3–6;
Plate 10, figures 1–6;
Text-figures 3, 4, 5, 10, 11, 14, 17, 19

Madrepora cavernosa Linnaeus, 1767, p. 1276 (not seen).

Description.—Colony irregular, small (colony diameter, 4.5 cm; height, 4.5 cm) to large (colony diameter, 18 cm; height, 14 cm) hemispherical mounds. Colony surface smooth, well-rounded. Growth bands at 4–6 mm intervals. Epitheca moderately developed with growth ridges irregular at approximately 1 mm intervals.

Calices circular, variably large in size (6.0 to 7.1 mm), moderately deep (0.5 to 1.0 mm) with variable, intermediate spacing (nearest neighbor distance of 6 to 10 mm). Corallite wall thin to intermediate in thickness (0.3 to 0.9 mm) projecting variably (usually 1 to 2 mm high) above the colony surface.

Costa moderately well-developed, relatively thin (0.46–0.66 mm), subequal (the first, second, and third cycles are equal and greater than the fourth), discontinuous, elongate, and finely dentate. Septa in four cycles with a fifth cycle weakly developed, 48 to 56 in number. The first, second, and uncommonly the third cycles extend to the columella. First cycle intermediate to high in thickness (0.16–0.27 mm) and rarely thicker than the second. Third cycle usually free; three-fourths as long or equal to the second. Fourth cycle free; one-half to one-fourth as long as the second. Fifth cycle short, thin, free. Columella trabecular, papillate, intermediate to high in thickness (2.05–2.80 mm) and slightly whorled, formed by the inner margins of the primary and secondary septa.

Endothecal dissepiments thin (0.03–0.05 mm thick) at 0.6 mm intervals. Exothecal dissepiments thin to intermediate (0.15 mm), at 0.7 mm intervals. Exothecal voids wide (1.6 mm), rectangular.

Holotype.—The holotype is a specimen illustrated by Seba (1758, pl. 112). This specimen cannot be located, but Seba's original drawing of it is refigured here in Text-figure 20. A presumed specimen of Esper (1795) (NMS catalogue number unknown) belonging to the same species was studied, and is refigured here on Plate 8, figure 6, and on Plate 9, figure 1.

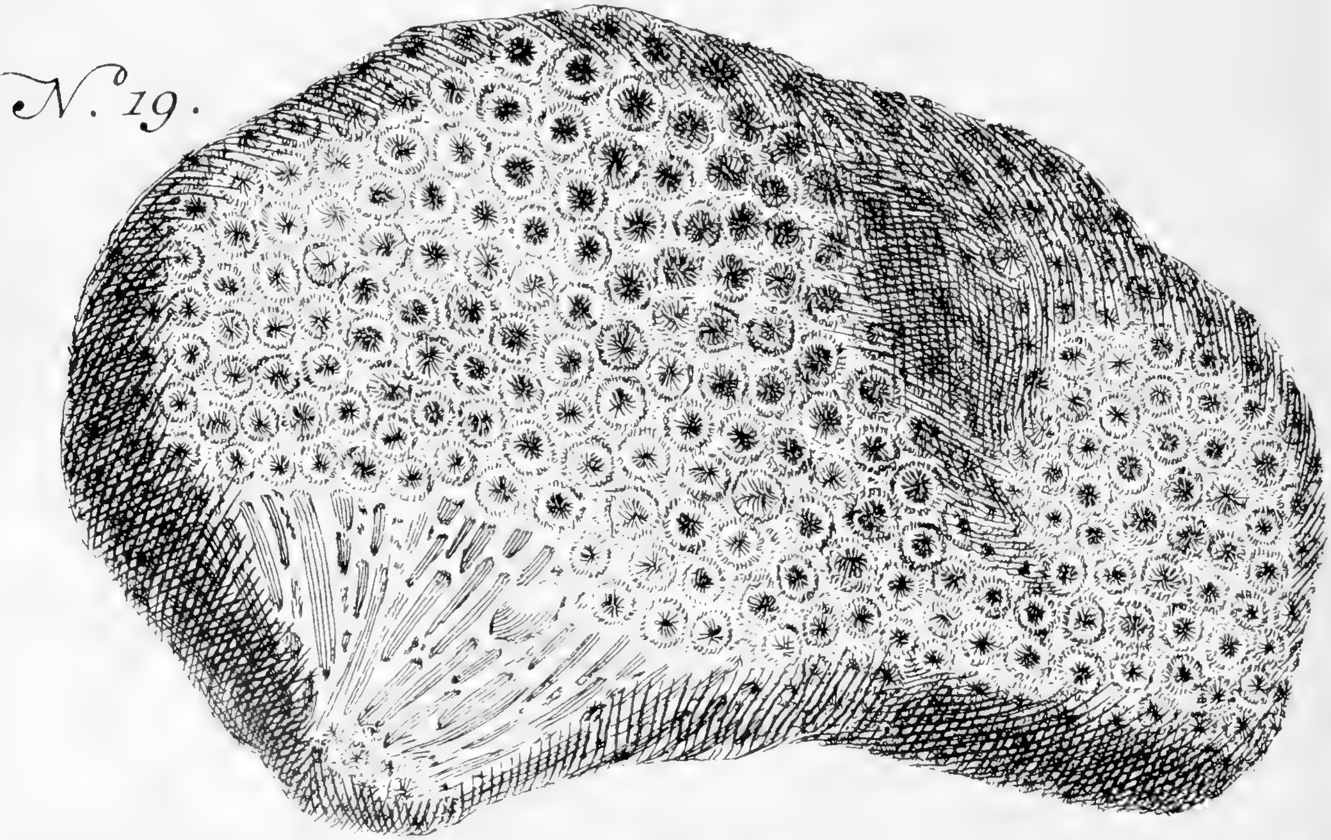
Measurements of topotypes.—Means of ten corallites in each of 32 modern colonies from four reef habitats near Discovery Bay, Jamaica (SUI 48748–48779): **CD**, 6.43; **NND**, 2.96; **CLW**, 2.67; **SLP**, 1.82; **SLS**, 1.78; **SLT**, 0.40; **STP**, 0.141; **STS**, 0.114; **STT**, 0.065; **NS**, 39.2; **CNNV**, 0.308; **CNP**, 5.022; **CLNV**, 1.405; **CND**, 1.282; **CST**, 0.389.

Type locality.—"Habitat in O. Americano." Recent.

Material.—Nineteen colonies from 12 localities. Seven specimens sectioned and measured.

Remarks.—Vaughan (1919) described four Neogene species and one variety of "*Orbicella*" as having four cycles of septa and mean corallite diameters within the range of 6.5 to 7 mm: (1) *M. cavernosa*; (2) *M. bainbridgensis*; (3) *M. canalis*; (4) *M. tampaensis*; and (5) *M. tampaensis silecensis*. The five differ primarily in the development of the costae and paliform lobes: (1) *M. cavernosa* is described as having subequal costae corresponding to all septa, and paliform lobes; (2) *M. bainbridgensis* is described as having low, equal costae corresponding to all septa, and paliform lobes; (3) *M. canalis* is described as having subequal costae corresponding to all septa, prominent primary septa, and paliform lobes; (4) *M. tampaensis* is described as having elevated calices, prominent costae in all but the last septal cycle, and no paliform lobes; and (5) *M. tampaensis silecensis* is described as having prominent equal costae corresponding to all septa, and no paliform lobes. Many of the differences described between these species, however, may be preservational and are not apparent in thin-section. Canonical variable polygons of topotypes of the four species clearly overlap (Text-fig. 11) suggesting that these specimens could belong to either *M. canalis*, *M. cavernosa*, or *M. endothecata*. Further study of the distributions of these species through the Neogene Caribbean stratigraphic sequence and comparisons of Mahalanobis' distances between species in adjacent stratigraphic levels suggests that: (1) *M. cavernosa* may indeed be distinct from the other four species; (2) *M. bainbridgensis* may be synonymous with *endothecata*; and (3) *M. canalis*, *M. tampaensis*, and *M. tampaensis silecensis* may be synonymous. Unlike the paratypes, the holotype of *Orbicella tampaensis* Vaughan 1919 is, however, distinctive, and the name is therefore retained. The holotype of *Madrepora cavernosa* Linnaeus, 1767, itself, is lost; therefore, its relationship to the Dominican Republic material is based on the study of the 32 previously mentioned specimens from Discovery Bay, Jamaica (SUI 48748–48779).

Variability.—*Montastraea cavernosa* is among the most variable of the species studied, especially in cor-



Text-figure 20.—Drawing on which the original description of *Montastraea cavernosa* was based (from Seba, 1758, vol. 3, t. 112, fig. 19).

allite spacing. Within colonies, variation is pronounced with the corallites becoming more exsert, larger, and more widely spaced toward the colony margin.

Comparison.—Study of Mahalanobis' distances shows that *M. cavernosa* morphologically is closest to *M. canalis* and, to a lesser extent, to *M. endothecata*. These three species are readily distinguished on the basis of corallite diameter, with *M. canalis* having the smallest diameter, *M. cavernosa* having the intermediate diameter, and *M. endothecata* having the largest diameter. Nevertheless, number of septa are roughly similar in the three species. The theca is thicker in *M. canalis* and *M. endothecata*, and corallite spacing is reduced in *M. canalis*. Costae are equal in *M. canalis* and subequal in *M. cavernosa* and *M. endothecata*.

Occurrence.—Río Cana: Mao Formation (loc. NMB 16884). Río Gurabo: Gurabo Formation (locs. NMB 15808, 15836, 15847, 15858, 15893, 16184, 16921; loc. TU 1208). Río Mao: Cercado Formation (loc. NMB 16908) and ?Gurabo Formation (loc. NMB 16911). Río Yaque del Norte: Baitoa Formation (locs. NMB 16944, 17279).

Distribution.—*M. cavernosa* ranges in age from Pliocene to Recent. The occurrences in the Dominican Republic are among the oldest known for the species. It has been found outside the Dominican Republic in the following strata: (1) the upper Pliocene Tamiami Formation of Florida; and (2) Pleistocene to Recent reefs ranging south and southwestward from Bermuda across the Caribbean and Texas coast to Brazil. Today, *M. cavernosa* possibly occurs also in the Gulf of Guinea on the west coast of Africa.

Montastraea cylindrica (Duncan, 1863)

Plate 11, figures 1–7; Plate 12, figures 1–6;
Plate 13, figures 1–6;
Text-figures 3, 4, 5, 10, 11, 14, 17

Astraea cylindrica Duncan, 1863, p. 434, pl. 15, fig. 8.
Orbicella cavernosa var. *cylindrica* Vaughan, 1919, p. 385–386, pl. 89, fig. 2.

Description.—Colony intermediate to large in size (maximum colony diameter, 26 cm; height, 9 cm) forming thick plates to low mounds, which have often experienced periods of partial mortality (up to one-half of the colony) with subsequent overgrowth. Colony surface smooth, generally flat. Growth bands faint, at 3–6 mm intervals. Epitheca relatively weak, with growth ridges at approximately 1 mm intervals.

Calices circular, intermediate in size (3.9–5.2 mm), intermediate in depth (approximately 0.5 mm), evenly widely spaced (nearest neighbor distance, 9–11 mm), and strongly exsert (maximum 4–5 mm). Corallite wall thin (0.2–0.7 mm).

Costae exsert, subequal (the first and second cycles are equal and slightly thicker than the third, which is thicker than the fourth), discontinuous, elongate, relatively thin (0.37–0.74 mm), and finely to coarsely dentate. Septa in three cycles with a fourth cycle weakly developed, 26 to 36 in number. The first, second, and sometimes third cycles extend to the columella. First cycle relatively thin (0.09–0.22 mm) and slightly thicker than the second. Third cycle free; almost as long, if not equal to the second. Fourth cycle free, short, thin. Columella trabecular, relatively wide (1.56–2.19 mm), strongly exsert; formed by the inner margins of the primary, secondary, and some tertiary septa.

Endothecal dissepiments thin (0.03 mm thick), irregular, at 0.6 mm intervals. Exothecal dissepiments thin (0.01 mm), almost vesicular, at 0.7 mm intervals. Exothecal voids wide (1.6 mm).

Holotype.—BM(NH) R28790 (refigured here: Pl. 12, figs. 1, 2).

Measurements of the holotype.—Means of five calices: **CD**, 5.96; **NS**, 38.0; **NND**, 5.84; **CLW**, 2.74; **TT**, 1.18; **SLP**, 1.58; **SLS**, 1.40; **SLT**, 0.12; **STP**, 0.23; **STS**, 0.12; **STT**, 0.05; **CST**, 0.62; calice elevation, 11.55; colony length, 38; colony width, 18; colony height, 43.

Type locality.—"The tuffaceous limestone" of Heneken (1853), Dominican Republic. Neogene.

Material.—Twelve colonies from six localities. Seven specimens sectioned and measured.

Remarks.—Vaughan (1901, 1919) described *M. cylindrica* as a variety of *M. cavernosa* having smaller calices and lacking a fifth cycle of costae. Study of the Dominican Republic material shows that *M. cylindrica* forms a discrete cluster clearly distinct from *M. cavernosa*; therefore, Duncan's name is reinstated.

Variability.—Variability in *M. cylindrica* is reduced in corallite diameter, but highly variable in number of septa and costa thickness. Trends across colonies are not pronounced. Corallites appear larger, more widely spaced, and more exsert towards colony margins.

Comparison.—Study of Mahalanobis' distances between species shows that *M. cylindrica* is close morphologically only to *M. brevis*. It is distinguished by its large, often plate-shaped colonies, and its larger, more widely spaced and more elevated calices. Like *M. brevis*, septa are few in number, but unlike *M. brevis*, the septa are shorter and the columella wider.

Occurrence.—Río Cana: Mao Formation (locs. NMB 16876, 16884). Río Gurabo: Gurabo Formation (locs. NMB 15838, 15841, 15846, 16921; loc. TU 1344).

Distribution.—*M. cylindrica* ranges in age from late Miocene to late Pliocene. Outside the Dominican Republic, it occurs only in the upper Pliocene Moín Formation of Costa Rica.

Montastraea endothecata (Duncan, 1863)

Plate 1, figure 4; Plate 5, figure 7; Plate 8, figure 5;
Plate 14, figures 1, 3–5; Plate 15, figures 1–4;
Plate 16, figures 1–6; Plate 17, figures 1–6;
Text-figures 3, 4, 5, 7, 10, 11, 14, 17

Astraea endothecata Duncan, 1863, pp. 419, 434, pl. 14, fig. 9, pl. 15, figs. 7a, b.

not *Astraea antiguensis* Duncan, 1863, p. 419, pl. 13, fig. 8.

not *Astraea costata* Duncan, 1863, p. 422 (not seen).

Orbicella cavernosa var. *endothecata* Vaughan, 1919, pp. 384–385, pl. 89, figs. 1, 1a.

Orbicella bainbridgensis Vaughan, 1919, pp. 386–387, pl. 90, figs. 1, 1a–c.

Orbicella costata (Duncan). Vaughan, 1919, pp. 387–389, pl. 92, figs. 1, 3, and pl. 93, figs. 1, 1a; *not* pl. 91, figs. 1, 1a, 2, 3, 3a; *not* pl. 92, fig. 2.

Orbicella canalis Vaughan, 1919, pp. 389–390, pl. 94, figs. 2, 2a; pl. 97, figs. 4, 4a; *not* pl. 94, figs. 1, 1a, 3, 3a.

Cyathomorpha roxboroughi Vaughan, 1919, pp. 461–463, pl. 129, figs. 1, 1a, 1b.

Orbicella cavernosa (Linnaeus). Coryell and Ohlsen, 1929, pp. 195–196, pl. 29, fig. 1.

?*Orbicella costata* (Duncan). Coryell and Ohlsen, 1929, pp. 196–197, pl. 29, fig. 2 (not seen).

?*Orbicella tampaensis* Vaughan. Coryell and Ohlsen, 1929, pp. 197–198, pl. 30, fig. 1 (not seen).

not *Montastraea costata* (Duncan). Chevalier, 1954, p. 166, pl. 6, fig. 4.

Montastrea cavernosa (Linnaeus). Weisbord, 1971, pp. 23–30, pl. 6, figs. 4–9.

?*Montastrea bainbridgensis* (Vaughan). Frost and Langenheim, 1974, pp. 259–261, pl. 95, figs. 1–5 (not seen).

?*Agathiphyllia roxboroughi* (Vaughan). Frost and Langenheim, 1974, p. 279, pl. 105, figs. 1–5 (not seen); pl. 106, figs. 1, 2 (not seen).

Description.—Colony hemispherical, generally large in size (maximum colony diameter, roughly 20 cm; height, 20 cm). Colony surface smooth, well-rounded. Growth bands at 4–7 mm intervals. Epitheca weakly developed, with growth ridges irregular at approximately 1 mm intervals.

Calices circular to elliptical, very large in size (7.0–9.3 mm), moderately deep (0.5–1 mm) with variable, intermediate spacing (nearest neighbor distance, 9–13 mm). Corallite wall intermediate to high in thickness (0.7–1.5 mm) projecting slightly (1–2 mm) above the colony surface.

Costae prominent, alternating in thickness, discontinuous, elongate, intermediate to thick in size (0.51–0.77 mm), moderately dentate. Septa in four cycles, commonly with a fifth cycle weakly developed, 48 to 52 in number. The first, second, and commonly the third cycles extend to the columella. The first and second cycles are relatively intermediate and equal in thickness (0.16–0.35 mm), and thicker than the third cycle, which commonly is equal in length to the second. Fourth cycle free, one-fourth to one-half as long as the second, thin. Columella trabecular, papillate, wide (2.80–3.79 mm) and strongly whorled, formed by the inner margins of the first, second, and third septal cycles.

Endothecal dissepiments thick (0.08 mm), irregular, at 0.8–1.4 mm intervals. Exothecal dissepiments intermediate in thickness (0.15 mm), at 0.8 mm intervals. Exothecal voids wide (1.7 mm), rectangular.

Holotype.—BM(NH) R28791 (refigured here: Pl. 14, fig 4; Pl. 16, fig. 1; Pl. 17, fig. 5).

Measurements of the holotype.—Means of seven calices: **CD**, 10.02; **NS**, 53.4; **NND**, 3.91; **CLW**, 4.04; **TT**, 0.71; **SLT**, 1.86; **STP**, 1.33; **CST**, 0.62; calice elevation, 5.93; colony length, 101; colony width, 43; colony height, 135.

Type locality.—"Nivajé Shale" of Heneken (1853), Dominican Republic. Neogene.

Material.—Ten colonies from four localities. Four specimens sectioned and measured.

Remarks.—Vaughan (1900, 1919) described *M. endothecata* as a variety of *M. cavernosa* having larger calices with subequal costae and a long, well-developed fourth septal cycle. Study of the Dominican Republic material shows *M. endothecata* to form a discrete cluster, clearly distinct from *M. cavernosa*; therefore, Duncan's name is reinstated.

The holotype of *Astraea costata* Duncan, 1863 cannot be located at the BM(NH); however, Duncan's figure (pl. 13, fig. 9) as well as another specimen in his original material [BM(NH) R365, refigured herein in Pl. 1, fig. 2] have calice sizes and distributions and synapticulae characteristic of *Agathiphyllia antiguensis* (Duncan) (Table 2). On the other hand, some of Vaughan's (1919) hypotypes of "*O. costata* (Duncan)" (USNM 324837, pl. 92, fig. 1; USNM 324841, pl. 92, fig. 3; USNM 324840, pl. 93, figs. 1, 1a), as well as the holotype and paratype of *Cyathomorpha roxboroughi* Vaughan, 1919 (USNM 325220, pl. 129, figs. 1, 1a, 1b, and USNM 325248, respectively), have calice sizes and distributions, whorled columellae, and costae that strongly resemble *M. endothecata*, and these hypotypes are therefore synonymized with it.

Although Vaughan's (1919) holotype of *Orbicella bainbridgensis* Vaughan, 1919 (USNM 324881, refigured here on Pl. 8, fig. 5) lies close to the *M. cavernosa* cluster (Text-fig. 11b), statistical study of it together with other topotypes suggests that two clusters exist within Vaughan's material, one of which may belong to *M. tampaensis* and the other (including the holotype) to *M. endothecata*. Additional material is needed in order further to understand the relationships among these taxa.

One of Coryell's and Ohlsen's (1929) specimens [AMNH 23066 = "*O. cavernosa* (Linnaeus)"] clearly belongs to *M. endothecata* as described herein. Photographs of two other Coryell and Ohlsen (1929) specimens ["*O. costata* (Duncan)" and "*O. tampaensis*

Vaughan"], which could not be located at the AMNH, also strongly resemble *M. endothecata*.

Chevalier's (1954) specimen of "*M. costata* (Duncan)" appears to belong to *Agathiphyllia antiguensis*; whereas Weisbord's (1971) specimens of "*M. cavernosa* (Linnaeus)" closely resemble *M. endothecata* as described herein.

Frost and Langenheim's (1974) specimens of "*M. bainbridgensis* (Vaughan)" (UI X-3723–X-3728) and three specimens of "*A. roxboroughi* (Vaughan)" (UI X-3825, X-3768; UCMP 10275) could not be located at the University of Illinois or at the University of California at Berkeley; however, Frost and Langenheim's (1974) figures also closely resemble *M. endothecata* as described herein.

Variability.—Variability within *Montastraea endothecata* is generally high; however, trends across colonies are not pronounced. Toward colony margins, corallites are larger, more widely spaced, and less exsert, and they have thicker walls and costae.

Comparison.—As stated previously, *M. endothecata* is closest morphologically to *M. cavernosa*. It is distinguished by its larger calices, its thick corallite wall, strong costae, and its prominent, strongly whorled columella.

Occurrence.—Río Cana: Gurabo Formation (locs. NMB 16817, 16818). Río Gurabo: Gurabo Formation (loc. NMB 16933; locs. TU 1231, 1278; locs. USGS 8538, 8539). Río Mao: ?Gurabo Formation (loc. NMB 16911). Río Yaque del Norte: Arroyo Babosico (loc. TU 1405).

Distribution.—*M. endothecata* ranges in age from Oligocene to late Pliocene, and is common across the central Caribbean throughout that time interval. It has been found outside the Dominican Republic in the following strata: (1) the upper Oligocene Anahuac Formation of Texas, Juana Diaz Formation of Puerto Rico, and Brownstown Formation of Jamaica; (2) the lower Miocene Chattahoochee Formation of Georgia, Larés Formation of Puerto Rico, and Santa Ana and Río Lajas formations of Chiapas, Mexico; (3) the Middle Miocene Chipola Formation of Florida, La Boca Formation of Panama, and Anguilla Formation of Anguilla; and (4) upper Pliocene Moín Formation of Costa Rica.

Montastraea limbata (Duncan, 1863)

Plate 18, figures 1–7, 9; Plate 19, figures 1–6;
Plate 20, figures 1, 2, 4–6; Plate 21, figures 1–6;
Plate 24, figure 4; Text-figures 3, 4, 5, 10, 11, 14, 17

not *Astrea sculpta* Michelin, 1846, p. 300, pl. 71, fig. 3 (not seen).
Phyllocoenia sculpta var. *tegula* Duncan, 1863, p. 432.
Phyllocoenia limbata Duncan, 1863, p. 433.
Plesiastraea ramea Duncan, 1864, p. 39, pl. 5, figs. 1a, b.
Orbicella limbata var. *pennyi* Vaughan *in* Vaughan and Hoffmeister, 1926, pp. 120–121, pl. 3, figs. 1, 1a, b.
not *Orbicella limbata* (Duncan). Coryell and Ohlsen, 1929, p. 197, pl. 29, fig. 3.
not *Montastrea limbata* (Duncan). Frost and Langenheim, 1974, pp. 258–259, pl. 93, figs. 3–6; pl. 94, fig. 1.

Description.—Colony columnar (1.4–4.5 cm wide, up to 20 cm high) to hemispherical (maximum diameter, 15 cm), with skirted to irregularly encrusting margins which may form plates (0.5–2 cm thick). Columns commonly anastomose to form thickets, and rarely branch. Colony surface generally smooth with occasional lumps or protuberances. Growth bands well-developed at 4–12 mm intervals. Epitheca reduced to absent, with irregular growth ridges at 0.5–1.0 mm intervals. In platelike shapes, the undersurface is formed by prominent elongate costae, paralleling the direction of growth.

Calices circular, generally small in size (1.9–2.9 mm), shallow (less than 0.5 mm depth) and widely spaced (nearest neighbor distance, 4–6 mm) at roughly even intervals. Corallite wall thin (0.1–0.7 mm), projecting slightly (less than 0.5 mm) above the colony surface.

Costae usually equal, discontinuous, elongate (1–2 mm), relatively thick (0.19–0.46 mm) and dentate to beaded. Septa in three cycles, always 24 in number, with the first and second cycles extending to the columella. First cycle relatively thick (0.05–0.18 mm) and commonly thicker than the second. Third cycle free, short, and thin. Columella relatively thick (0.75–1.23 mm) but porous, formed by the inner margins of usually the primary septa. Small paliform lobes form irregularly in front of the primary and secondary septa.

Endothecal dissepiments well-developed (0.03–0.05 mm), at 0.4–0.6 mm intervals. Exothecal dissepiments well-developed (0.18 mm), at 0.7 mm intervals. Exothecal voids wide (1.2 mm), rectangular.

Holotype.—BM(NH) R28780 (refigured here: Pl. 18, fig. 1; Pl. 20, fig. 1).

Measurements of the holotype.—Means of eight calices: **CD**, 2.81; **NS**, 23.9; **NND**, 1.75; **CLW**, 1.14; **TT**, 0.88; **SLT**, 0.34; **STP**, 0.22; **STS**, 0.15; **CST**, 0.51; calice elevation, 0.56; colony height, 82; branch thickness, 26.

Type locality.—The "Yellow Shale" of Heneken (1853), Dominican Republic, Neogene.

Material.—One-hundred-fifty colonies from 43 localities. Twenty-eight specimens sectioned and measured.

Remarks.—Following Vaughan (1919, pp. 376–377), cursory examination of colony surfaces of holotypes of *Phyllocoenia limbata* Duncan, 1863 [BM(NH) R28780, refigured herein on Pl. 18, fig. 1 and Pl. 20, fig. 1], *Plesiastraea ramea* Duncan, 1864 [BM(NH) R28755, refigured herein on Pl. 20, fig. 2], and *Phyl-*

locoenia sculpta var. *tegula* Duncan, 1863 [BM(NH) R28781, refigured herein on Pl. 18, fig. 9] suggest that these three described species clearly lie within the range of variability observed within the Dominican Republic *M. limbata* cluster. Despite the relatively large size of its calices, canonical discriminant analysis also shows that the holotype of *Orbicella limbata* var. *pennyi* Vaughan *in* Vaughan and Hoffmeister, 1926 (USNM 353654, refigured herein on Pl. 18, fig. 5 and Pl. 24, fig. 4) lies within the *M. limbata* cluster. Vaughan (1919) further suggested that *M. limbata* was synonymous with the Recent species *M. annularis* (Pl. 22, fig. 5); however, the present study shows *M. annularis* to be discrete from *M. limbata* and closer in morphology to *M. trinitatis*.

As explained under *M. trinitatis*, Coryell and Ohlsen's (1929) specimen of "*Orbicella limbata* (Duncan)" (AMNH FI23069) is closer to *M. trinitatis*. Similarly, much of the material described by Frost and Langenheim (1974) as "*Montastrea limbata* (Duncan)" was found statistically to belong to *M. trinitatis*.

Results of canonical discriminant analyses described in the section on Comparisons with other Caribbean faunas show that Frost and Langenheim's (1974) lower Miocene specimens of *M. limbata* belong to two lower Miocene clusters (Text-fig. 16): (1) *M. imperatoris* (UI X-3700, X-3701, X-3712, X-3713, X-3714, X-3720, X-3721; and (2) *M. tampaensis* (UI X-3704). Furthermore, subjective study suggests that all of Frost and Langenheim's (1974) figured material of *M. limbata* belongs to *M. imperatoris*. Two figured specimens (UCMP 10360, 10361) were not seen because they could not be found at the University of California at Berkeley.

Variability.—Although variability in colony shape is high in *Montastraea limbata*, variability in corallite architecture is relatively reduced, especially in corallite diameter. Trends across colonies are not pronounced. From colony top to bottom, corallites appear larger, more widely spaced and less exsert, and costae are less prominent.

Comparison.—Study of Mahalanobis' distances between species shows that *M. limbata* is closest morphologically to *M. trinitatis* and, to a lesser extent, to *M. brevis*. It is distinguished, however, by its irregular, encrusting, and often columnar colony shape; and its smaller, widely-spaced calices; fewer septa; and thin corallite walls. *M. limbata* is distinguished from the common Recent species *M. annularis* by its thick primary septa and paliform lobes.

Occurrence.—Río Cana: Cercado Formation (locs. NMB 16853, 16855, 16856), Gurabo Formation (locs. NMB 16814, 16815, 16817, 16818, 16819, 16823, 16826, 16861, 16863, 16881; loc. TU 1354), and Mao Formation (locs. NMB 16874, 16875, 16877, 16884). Río Gurabo: Gurabo Formation (locs. NMB 15808, 15837, 15838, 15841, 15846, 15847, 15850, 15852, 15853, 15855, 15858, 15878, 15885, 15892, 15893, 16184, 16811, 16883, 16921, 16933, 16934; locs. TU 1208, 1215; locs. USGS 7775, 8540), and Mao Formation (locs. NMB 15822, 15830, 15834). Río Mao: ?Gurabo Formation (loc. NMB 16911). Río Yaque del Norte: Baitoa Formation (loc. NMB 17277), Arroyo Babosico (loc. TU 1405).

Distribution.—*M. limbata* ranges in age from early Miocene to late Pliocene. It becomes abundant across the Caribbean later during this time interval. Outside the Dominican Republic, this species occurs in the following strata: (1) the lower Miocene Nariva Formation of Trinidad; (2) the middle Miocene Tamana Formation of Trinidad; and (3) the upper Pliocene La Cruz Formation of Cuba.

Montastraea trinitatis

(Vaughan *in* Vaughan and Hoffmeister, 1926)

Plate 18, figure 8; Plate 20, figure 3;
Plate 22, figures 1–4, 6; Plate 23, figures 1–6;
Plate 24, figures 1–3, 5, 6;
Text-figures 3, 4, 5, 10, 11, 14, 17

not *Madrepora annularis* Ellis and Solander, 1786, p. 169, pl. 53, figs. 1, 2.
not *Phyllocoenia limbata* Duncan, 1863, p. 433.
?*Heliastraea altissima* Duncan, 1868, p. 12–13, pl. 2, fig. 3 (not seen).
?*Orbicella cumutensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926, pp. 121–122, pl. 3, figs. 3, 3a.
Orbicella trinitatis Vaughan *in* Vaughan and Hoffmeister, 1926, pp. 122–123, pl. 4, figs. 1, 1a.
?*Orbicella annularis* (Ellis and Solander). Coryell and Ohlsen, 1929, pp. 194–195, pl. 28, fig. 2.
?*Orbicella limbata* (Duncan). Coryell and Ohlsen, 1929, p. 197, pl. 29, fig. 3.

Description.—Colony ranging from small (diameter, 3 cm) knobs to large (maximum diameter, 20 cm) hemispherical mounds. Colony surface smooth, well-rounded. Growth bands highly regular and well-developed at 4–6 mm intervals. Epitheca reduced to absent.

Calices highly variable in size, shape, and orientation. Generally elliptical to circular, small to intermediate in size (2.6–4.0 mm), deep (1–3 mm depth), and closely-spaced (nearest neighbor distance, 3–5 mm). Corallite wall relatively thick (0.3–1.3 mm), projecting slightly (0.3–0.6 mm) above the colony surfacee.

Costae equal to subequal, moderately thick (0.3–0.47 mm), short (less than 1 mm), and discontinuous with strongly beaded margins. Septa in three to four cycles, ranging from 24 to 48 in number, with the first and second cycles extending to the columella. First cycle strong (0.08–0.20 mm thick) and slightly thicker than the second. Tertiary septa free, generally three-fourths as long as the first two cycles; fourth cycle free, short. Columella trabecular, weak (0.89–1.52 mm thick), formed by the inner margins of the primary and secondary septa.

Endothecal dissepiments well-developed (0.05–0.08 mm), at 0.8 mm intervals. Exothecal dissepiments thin (0.12 mm), at 0.8 mm intervals. Exothecal voids roughly equidimensional (0.8 mm).

Holotype.—USNM 353657 (refigured here: Pl. 22, fig. 3; Pl. 23, fig. 1).

Measurements of the holotype.—Means of six calices: **CD**, 4.02; **NS**, 27.3; **NND**, 1.48; **CLW**, 1.57; **TT**, 0.32; **SLT**, 0.50; **STP**, 0.17; **STS**, 0.12; **CST**, 0.28; colony length, 50; colony width, 25; colony height, 18.

Type locality.—Locality USGS 8299, Cumuto Road, Manzanilla Formation, Trinidad, upper Miocene.

Material.—Thirty-nine colonies from 10 localities. Twelve specimens sectioned and measured.

Remarks.—Occasional Dominican Republic specimens of *M. trinitatis* have strongly developed paliform lobes that closely resemble Recent Indo-Pacific *Plesiastrea* (Pl. 24, figs. 1, 2). Only three specimens have been assigned to *M. altissima* in the literature: (1) Duncan's (1868) holotype lost prior to Vaughan's (1919) monograph; and (2) two specimens mentioned in Vaughan *in* Vaughan and Hoffmeister (1926), one of which is refigured in Plate 23, figure 6. Canonical discriminant analysis shows that the latter two specimens lie close to the *M. trinitatis* cluster. Therefore, *M. altissima* is questionably synonymized with *M. trinitatis*. As found also by Gregory (1895) and Vaughan (1919), *M. altissima* differs from *M. annularis* by having larger calices and four septal cycles.

Hoffmeister (*in* Vaughan and Hoffmeister, 1926) distinguished *Orbicella cumutensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926 (USNM 353678, refigured herein on Pl. 18, fig. 8 and Pl. 20, fig. 3) on the basis of its fewer septa (two full cycles with a third incomplete) and the equal thickness of the first and second cycles. This morphology more closely resembles that of *M. trinitatis* than that of *M. limbata*.

Coryell and Ohlsen's (1929) specimens of "*O. annularis* (Ellis and Solander)" (AMNH 23064) and "*O. limbata* (Duncan)" (AMNH 23069) are strongly recrystallized and therefore difficult to identify using the criteria described herein; however, their relatively numerous septa, elliptical corallite shape, and well-developed paliform lobes more strongly resemble *M. trinitatis*.

Variability.—Variability in *Montastraea trinitatis* is high in corallite size and theca and septum thickness. Trends across colonies are enormously variable. From colony top to bottom, corallites are more widely spaced, smaller, and more irregularly shaped, and costae are more prominent.

Comparison.—Study of Mahalanobis' distances between species shows that *M. trinitatis* is closest morphologically to *M. brevis*. As stated previously, it is distinguished by its larger, more regular, mound-shaped colonies and its smaller, more closely spaced, elliptical calices. The septa are more numerous, the primary and secondary septa are roughly equal in thickness, and the paliform lobes notably well-developed. This species is distinguished from the common Recent species *M. annularis* by the greater variability in size and shape of its calices, its elliptical calice shape, and its strong paliform lobes.

Occurrence.—Río Cana: Mao Formation (loc. NMB 16884). Río Yaque del Norte: Baitoa Formation (locs. NMB 16943, 16944, 16945, 17273, 17276, 17277, 17282, 17283, 17284; loc. USGS 8668). Río Gurabo: Gurabo Formation (loc. TU 1208).

Distribution.—*M. trinitatis* ranges in age from early Miocene to early Pliocene. Outside the Dominican Republic, it occurs in: (1) the lower Miocene Larés Formation of Puerto Rico; (2) the middle Miocene La Boca Formation of Panama, Anguilla Formation of Anguilla, and Tamana Formation of Trinidad; and (3) the upper Miocene Manzanilla Formation of Trinidad.

Genus **SOLENASTREA**
Milne Edwards and Haime, 1848

Palaeoplesiastraea Chevalier, 1961, p. 264.

Type species.—*Astrea turonensis* Michelin, 1847, p. 312, pl. 75, figs. 1, 2.

Diagnosis.—Colonies massive, encrusting, plocoid. Costae weakly developed. Coenosteum trabecular. Wall structure septothecate with regularly dentate septal margins. Trabecular columella with paliform lobes opposite the first two septal cycles.

Remarks.—*Solenastrea* occurs today only in the Caribbean and western Atlantic regions, extending from North Carolina to Venezuela. It consists of two species that tend to occur sporadically in shallow nearshore areas and in turbid, deeper, offshore areas at 15 to 45 m depth, except in Curaçao, where *S. bournoni* Milne Edwards and Haime, 1849 is common at depths greater than 5 m.

Solenastrea arose in the Oligocene in the Mediterranean (Vaughan and Wells, 1943) and, during the early Miocene, its distribution ranged from the Mediterranean across to the Caribbean. Diversity in the Mediterranean during the early to middle Miocene was high; however, the genus became extinct in the Mediterranean at the end of the Miocene during the so-called Mediterranean salinity crisis. In the Caribbean region, the genus consisted of only three species [*S. hyades* (Dana, 1846), *S. bournoni*, and *S. fairbanksi* (Vaughan, 1900)], two of which have extended from

Miocene to Recent time. Altogether eight valid Neogene species of *Solenastrea* and three varieties have been described (Table 3).

Solenastrea bournoni
Milne Edwards and Haime, 1849

Plate 25, figures 1–8; Plate 26, figures 1–6;
Plate 27, figures 1–6;
Text-figures 3, 4, 6, 7, 12, 13, 15, 18

Solenastrea bournoni Milne Edwards and Haime, 1849, p. 121.
Plesiastraea distans Duncan, 1864, p. 37, pl. 4, figs. 4a, b.
Plesiastraea globosa Duncan, 1864, p. 38, pl. 4, fig. 5.
Solenastraea verhelsti Milne Edwards and Haime. Duncan, 1864, p. 40.
?*Stephanocoenia fairbanksi* Vaughan, 1900, p. 151, pl. 17, figs. 11, 11a.
?*Stephanocoenia fairbanksi* var. *columnaris* Vaughan, 1900, p. 151, pl. 17, figs. 10, 10a.
?*Solenastrea fairbanksi* var. *normalis* Vaughan, 1917, p. 373, pl. 96, figs. 2, 2a, 2b, 2c; pl. 97, figs. 1, 1a.
?*Solenastrea fairbanksi* var. *minor* Vaughan, 1917, p. 373, pl. 97, figs. 2, 2a, 2b, 2c.
Cyphastrea tampae Weisbord, 1973, pp. 54–55, pl. 25, figs. 1–3.
Solenastrea bournoni Edwards and Haime. Weisbord, 1974, pp. 387–391, pl. 42, figs. 2–5, fig. 1 (not seen); not pl. 44, figs. 4, 5.

Description.—Colony small, irregular knobs and spheres (colony diameter 2.1 cm) to larger hemispherical mounds (colony diameter, 12.0 cm; height, 10.5 cm) and columns (colony diameter, 9.0 cm; height, 17 cm). Colony surface generally smooth and well-rounded, with occasional lumps or protuberances. Some colonies showing repeated episodes of partial mortality and subsequent overgrowth. Growth bands highly regular and well-developed, at 4–6 mm intervals. Epitheca absent to weak. Elongate costae extend to the colony edge.

Calices circular, small to intermediate in size (**CD**, 2.8– 6.0 mm), moderate in depth (0.5–1.0 mm), and moderate to widely spaced (2.0–5.0 mm). Size and spacing of corallites vary widely among colonies, even from the same locality. Corallite wall relatively thin (**TT**, 0.2–0.8 mm), projecting slightly above the colony surface.

Costae thin, equal, and discontinuous, with a granulated surface. They sometimes extend to those of adjacent calices. Septal teeth strong. Septa in three cycles, 24 in number, with the first and the second cycles extending to the columella. First and second cycles relatively thick and greater than the third cycle. Third cycle one-fourth to one-half the length of the second cycle and generally free. Columella trabecular, relatively thick (**CLW**, 0.45–1.8 mm), formed by the inner margins of the primary and secondary septa. Paliform lobes usually well-developed before the primary and secondary septa.

Endothecal dissepiments thin (0.02–0.04 mm), at 0.5 mm intervals. Exothecal voids wide (0.5–0.9 mm) and thin-walled (0.05 mm).

Holotype.—MNHNP 794 (refigured here: Pl. 26, fig. 1).

Measurements of the holotype.—Means of seven calices: **CD**, 2.47; **NND**, 0.73; **NS**, 24.0; **CLW**, 0.84; **TT**, 0.21; **CST**, 0.32; **ST**, 0.08; **SLT**, 0.30; **CA**, 0.90.

Type locality.—Recent. Locality unknown.

Material.—Fifty-eight colonies from 35 localities. Twelve colonies measured.

Remarks.—Calice size and spacing are enormously variable in this species which, as found by Vaughan (1919), encompasses Duncan's two species *Plesiastraea distans* Duncan, 1864 and *Plesiastraea globosa* Duncan, 1864 from the "silt of the sandstone plain" of Heneken (1853) in the Dominican Republic. Duncan's (1864) specimen of "*Solenastraea verhelsti* Milne Edwards and Haime" [BM(NH) 28809 = USNM 155271] also clearly lies within the range of variation.

The range of variation is so extensive in this species that, at first, this group was separated into two subgroups. However, although the two forms were statistically significantly different, corallites similar to the small corallite form were sometimes found on the upper surface and center of larger colonies of the large corallite form. Therefore, without more characters and a larger sample size, the two groups were not separated. The single specimen (the holotype: USNM 68284) of *Solenastrea fairbanksi minor* Vaughan, 1917 strongly resembles the small corallite form and is questionably synonymized. Topotypes of other subspecies of *S. fairbanksi* statistically lie within the *S. bournoni* cluster (Text-fig. 18), although preliminary study of the primary types suggests they are closer to *S. hyades* (Table 10). These species are therefore also only questionably synonymized with *S. bournoni*. The holotype of *Cyphastrea tampae* Weisbord, 1973 (USNM 66161) clearly lies within the range of variation of *S. bournoni*.

Variability.—Trends across colonies are not pronounced. From colony top to bottom, corallites increase in size and spacing, and costae become more prominent.

Comparison.—*S. bournoni* is distinguished from *S. hyades* primarily by its larger, more regular, and well-rounded colonies; its smaller calices; and its free third septal cycle. It also has better-developed paliform lobes and a stronger columella. Its colony form is in many ways similar to *S. fairbanksi* (Vaughan, 1900), whose corallite size is intermediate between *S. bournoni* and *S. hyades*, and whose third septal cycle is either fused or free.

Occurrence.—Río Cana: Cercado Formation (locs. NMB 16855, 16856), Gurabo Formation (loc. NMB 16814), and Mao Formation (locs. NMB 16875, 16876, 16884). Río Gurabo: Gurabo Formation (locs. NMB 15837, 15844, 15845, 15846, 15850, 15851, 15853, 15855, 15857, 15858, 15885, 15887, 16811, 16883, 16934) and Mao Formation (locs. NMB 15822, 15830; loc. TU 1344). Río Mao: ?Gurabo Formation (loc. NMB 16911; loc. USGS 8734). Río Yaque del Norte: Tabera Group (loc. NMB 17279) and Baitoa Formation (locs. NMB 16935, 16937, 16943, 16944, 17280, 17282, 17283, 17284, 17289; loc. TU 1442).

Distribution.—*S. bournoni* ranges in age from late Oligocene to Recent. In addition to the Dominican Republic, it occurs in the lower Miocene Tampa Formation of Florida, and the Pliocene Imperial Formation of south-central California; the upper Pliocene La Cruz Formation of Cuba, Moín Formation of Costa Rica, and Tamiami Formation of Florida; and the Pleistocene Caloosahatchee Formation of Florida. Today its distribution extends from Florida across the Caribbean to Venezuela. It is especially abundant on reefs near Curaçao at depths greater than 15 m (Roos, 1971).

Solenastrea hyades (Dana, 1846)

Plate 28, figures 1–6; Plate 29, figures 1–6;
Text-figures 3, 4, 6, 7, 12, 13, 15, 18

Astraea hyades Dana, 1846, p. 212, pl. 10, fig. 15 (not seen).
Astraea excelsa Dana, 1846, p. 212, pl. 10, fig. 16.
Montastrea davisina Weisbord, 1973, pp. 46–47, pl. 20, figs. 1–3.
Montastrea peninsularis Weisbord, 1973, pp. 47–48, pl. 20, figs. 4, 5.
Solenastrea hyades (Dana). Weisbord, 1974, pp. 391–395, pl. 43, figs. 3–6; pl. 43, figs. 1, 2 (not seen); pl. 44, figs. 1–3.
Solenastrea cf. *S. bournoni* Edwards and Haime. Weisbord, 1974, pp. 387–391, pl. 44, figs. 4, 5.

Description.—Colony encrusting, small knobs (colony diameter, 3.0 cm; height, 2.0 cm) to moderate-sized (colony diameter, roughly 9 cm) spherical mounds. Colony surface irregular to smooth, well-rounded. Often heavily bored by bivalves. Growth bands highly irregular at 2–4 mm intervals. Epitheca absent to weak. Elongate costae extend to the colony edge.

Calices generally circular, sometimes distorted, intermediate to large in size (**CD**, 4.4–7.3 mm), variable in depth (0.5–1.5 mm), and narrow to moderately spaced (2.5–5.5 mm). Corallite wall thick (**TT**, 0.3–0.6 mm), projecting slightly above the colony surface.

Costae equal, short, granulated. Septal teeth strong. Septa in three cycles, 24 in number with the first and second cycles extending to the columella. First cycle thin, equal in thickness to the second and third cycles. Third cycle fuses with the second cycle and is about three-fourths its length. Columella trabecular, thin (**CLW**, 0.95–2.05 mm), weak; formed by the inner margins of the primary and secondary septa.

Endothecal dissepiments thin (0.02–0.04 mm), at 0.4 mm intervals. Exothecal voids narrow (0.3–0.6 mm) and thick-walled (0.8 mm).

Holotype.—The holotype cannot be found at the USNM, MCZ, or YPM. A specimen (YPM 1586) of Verrill (1901) was therefore studied and is refigured here on Plate 28, figures 1 and 5. The holotype of *Astraea excelsa* Dana, 1846 (YPM 1727, refigured here on Pl. 28, fig. 3) was also studied.

Measurements of the holotype of A. excelsa *Dana.*—Means of ten calices: **CD**, 5.63; **NND**, 1.97; **NS**, 24.2; **CLW**, 1.18; **TT**, 0.72; **CST**, 0.53; **ST**, 0.12; **SLT**, 1.34; **CA**, 0.40; colony length, 52; colony width, 47; colony height, 122.

Type locality.—Recent. West Indies.

Material.—Eight colonies from four localities. Three colonies measured.

Remarks.—As stated by Vaughan (1919), *S. hyades* and *S. excelsa* differ only in the density of the exotheca and development of the costae, two characters found to be highly plastic in suites of Recent specimens from Florida. The two named species are therefore synonymized. In extreme cases, *S. hyades* may intergrade morphologically with *S. bournoni*, and the two species are sometimes difficult to distinguish.

Cursory examination of the coenosteum and septal arrangement in type specimens of *Montastrea davisina* Weisbord, 1973 (UF 8280) and *Montastrea peninsularis* Weisbord, 1973 (UF 8281) from the Tampa Formation of south Florida suggest that they clearly belong to *S. hyades* as described herein. Weisbord's (1974) specimen of "*Solenastrea* cf. *S. bournoni* Edwards and Haime" from the Caloosahatchee Formation of south Florida also appears to belong to *S. hyades*.

Variability.—Trends across colonies are not pronounced. From colony top to bottom, corallites increase only slightly in size and spacing.

Comparison.—As explained previously, *S. hyades* is distinguished from *S. bournoni* by its encrusting, irregular colony shape, its larger calices, its fused third septal cycle, its relatively thick corallite wall, its more extensive coenosteum, its thin columella, and its lack of paliform lobes.

Occurrence.—Río Cana: Cercado Formation (loc. NMB 16853). Río Gurabo: Gurabo Formation (loc. NMB 15891). Río Yaque del Norte: Baitoa Formation (locs. NMB 16939, 17284).

Distribution.—*S. hyades* ranges in age from early Miocene to Recent. In addition to the Dominican Republic, it occurs in the lower Miocene Tampa Formation of Florida; the upper Pliocene Tamiami Formation of Florida and La Cruz Formation of Cuba; and the Pleistocene Caloosahatchee Formation of Florida. Today its distribution extends from North Carolina to Venezuela.

Appendix Ia.—Means (±1 standard deviation) of all corallite characters in the seven species of *Montastraea* herein described. Abbreviations for characters are explained in Table 5. "n" = number of colonies measured. Eight to 10 corallites were measured in each colony.

	M. limbata (*n = 31*)	*M. trinitatis* (*n = 13*)	*M. brevis* (*n = 7*)	*M. canalis* (*n = 11*)	*M. cylindrica* (*n = 8*)	*M. cavernosa* (*n = 8*)	*M. endothecata* (*n = 7*)
*CD	2.42 (±0.24)	3.04 (±0.42)	3.63 (±0.26)	5.02 (±0.72)	4.53 (±0.51)	6.70 (±0.44)	7.98 (±0.80)
*NS	24.0 (±0.9)	30.6 (±3.7)	28.1 (±3.1)	39.1 (±3.6)	30.8 (±7.6)	42.4 (±4.3)	42.8 (±7.2)
*NND	1.56 (±0.50)	1.42 (±0.34)	2.73 (±0.49)	2.44 (±0.80)	4.29 (±1.24)	3.91 (±1.41)	4.30 (±1.28)
CND	0.89 (±0.39)	0.54 (±0.32)	1.74 (±0.43)	0.97 (±0.39)	3.16 (±1.10)	2.76 (±1.36)	2.36 (±1.55)
CNNV	0.19 (±0.13)	0.08 (±0.04)	0.46 (±0.17)	0.21 (±0.18)	0.72 (±0.49)	0.56 (±0.39)	0.45 (±0.20)
CNP	3.56 (±1.29)	4.40 (±2.13)	3.69 (±0.93)	4.31 (±2.21)	2.16 (±0.95)	2.60 (±1.06)	4.04 (±1.47)
*CLW	0.95 (±0.10)	1.15 (±0.20)	1.29 (±0.14)	2.02 (±0.28)	1.90 (±0.27)	2.57 (±0.25)	3.22 (±0.30)
CLNV	0.29 (±0.07)	0.43 (±0.07)	0.56 (±0.16)	0.85 (±0.26)	0.73 (±0.28)	0.95 (±0.22)	1.56 (±0.42)
*TT	0.34 (±0.14)	0.59 (±0.28)	0.46 (±0.11)	0.84 (±0.39)	0.50 (±0.16)	0.60 (±0.24)	1.01 (±0.27)
SLP	0.73 (±0.08)	0.93 (±0.12)	1.12 (±0.10)	1.38 (±0.16)	1.29 (±0.17)	1.92 (±0.14)	2.22 (±0.25)
SLS	0.62 (±0.09)	0.78 (±0.15)	1.06 (±0.13)	1.26 (±0.17)	1.04 (±0.13)	1.76 (±0.16)	2.13 (±0.20)
*SLT	0.186 (±0.050)	0.234 (±0.087)	0.477 (±0.056)	0.408 (±0.102)	0.246 (±0.150)	0.545 (±0.098)	0.764 (±0.165)
*STP	0.101 (±0.029)	0.136 (±0.033)	0.171 (±0.028)	0.146 (±0.041)	0.157 (±0.038)	0.194 (±0.032)	0.262 (±0.061)
*STS	0.058 (±0.012)	0.093 (±0.024)	0.082 (±0.009)	0.079 (±0.028)	0.083 (±0.020)	0.095 (±0.016)	0.127 (±0.025)
STT	0.042 (±0.011)	0.053 (±0.010)	0.064 (±0.012)	0.062 (±0.014)	0.047 (±0.018)	0.066 (±0.017)	0.092 (±0.020)
CST	0.326 (±0.069)	0.390 (±0.049)	0.412 (±0.048)	0.473 (±0.063)	0.483 (±0.130)	0.570 (±0.065)	0.646 (±0.081)

* Characters whose means and standard deviations are diagrammed in Text-figure 14.

Appendix Ib.—Means (±1 standard deviation) of all calical characters in the two species of *Solenastrea* herein described. Abbreviations for characters are explained in Table 6. "n" = number of colonies measured. Eight to 10 corallites were measured in each colony.

	S. bournoni (*n = 12*)	*S. hyades* (*n = 3*)
*CD	2.28 (±0.36)	2.82 (±0.47)
*NND	0.94 (±0.36)	0.80 (±0.19)
NS	24.0 (±0.3)	23.6 (±0.9)
*PA	0.86 (±0.16)	1.03 (±0.15)
CLW	0.52 (±0.15)	0.72 (±0.18)
*TT	0.139 (±0.037)	0.140 (±0.033)
CST	0.343 (±0.039)	0.371 (±0.060)
ST	0.051 (±0.006)	0.050 (±0.008)
*SLT	0.62 (±0.12)	0.81 (±0.11)
CA	0.38 (±0.35)	0.46 (±0.27)

* Characters whose means and standard deviations are diagrammed in Text-figure 15.

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PLATES

EXPLANATION OF PLATE 1

AGATHIPHYLLIA

Whole colonies and transverse and longitudinal thin-sections. Oligocene and Miocene specimens of Caribbean *Agathiphyllia* are frequently confused with *Montastraea*. *Agathiphyllia* is distinguished by the presence of synapticulae (best revealed in thin-section), a well-developed palar crown, and generally large calices.

Figure Page

1, 6. ***Agathiphyllia tenuis*** (Duncan, 1863) 35

1. Holotype. BM(NH) R28627. Oligocene, "Marl Formation", Antigua. Polished surface showing synapticular wall structure, ×10.

6. Figured specimen. USNM 63495 (NF363D). Oligocene, locality USGS 6881, Antigua Formation, Antigua. Longitudinal thin-section showing synapticular wall structure, ×10.

2, 3. ***Agathiphyllia antiguensis*** (Duncan, 1863) 35

2. Figured specimen. BM(NH) R365 (original specimen of *Astraea costata* Duncan, 1863). Oligocene, Antigua. Polished surface showing synapticulae within a corallite, ×10.

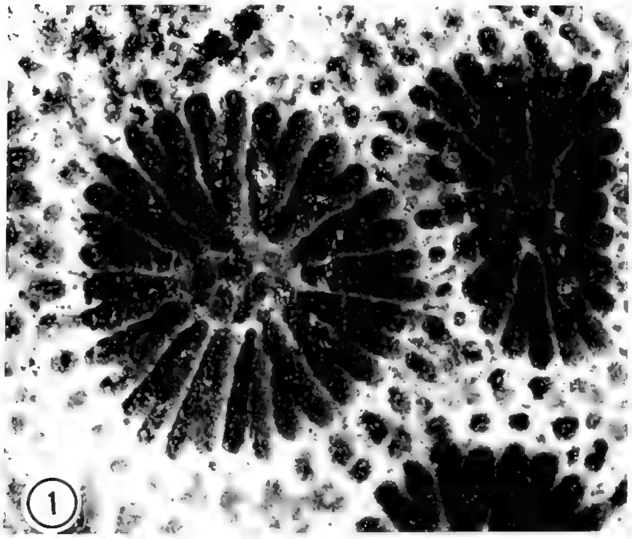
3. Figured specimen. USNM 63496 (NF373B). Oligocene, locality USGS 6854, Antigua Formation, Antigua. Transverse thin-section showing synapticulae, ×10.

4. ***Montastraea endothecata*** (Duncan, 1863) 40

Figured specimen. USNM 324844 (NF119A) [one of Vaughan's (1919) specimens of *Orbicella costata* (Duncan)]. Middle Miocene, locality USGS 6894, Anguilla Formation, Anguilla. Transverse thin-section showing no synapticulae and a strongly whorled columella, ×10.

5. ?***Agathiphyllia hilli*** (Vaughan, 1919) 35

Figured specimen. USNM 325214 [one of Vaughan's (1919) specimens of *Cyathomorpha anguillensis* Vaughan]. Middle Miocene, Anguilla Formation, Anguilla. Upper colony surface showing large calices and a well-developed palar crown, ×1.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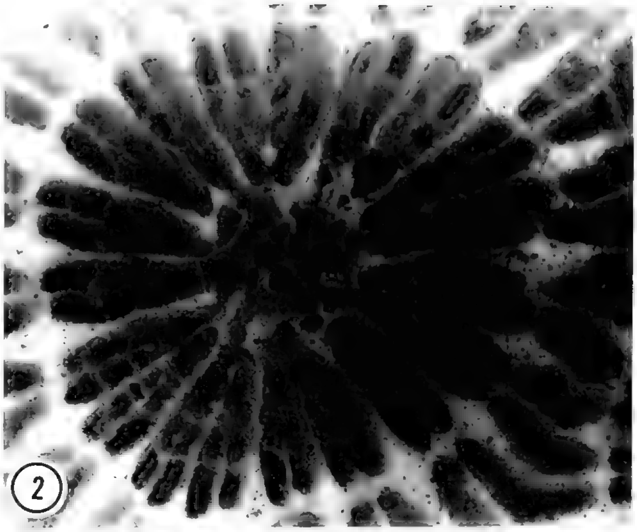
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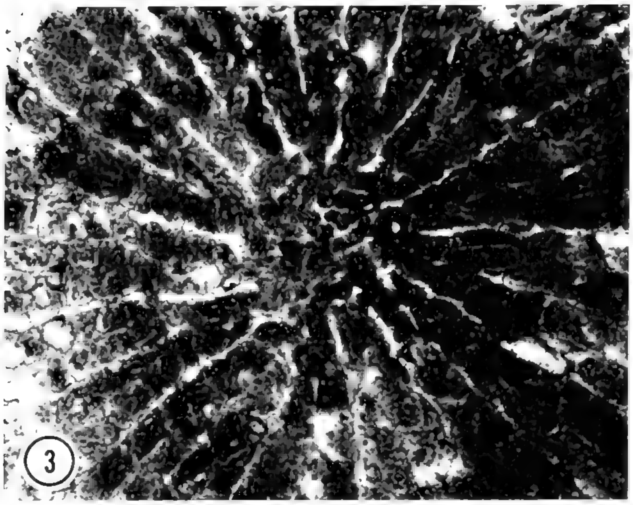
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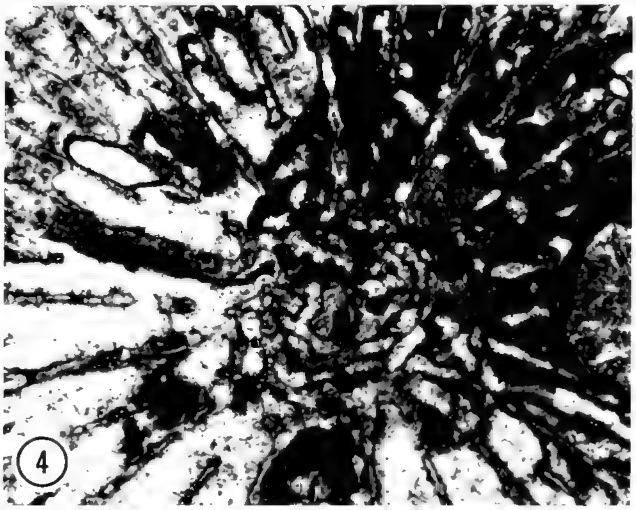
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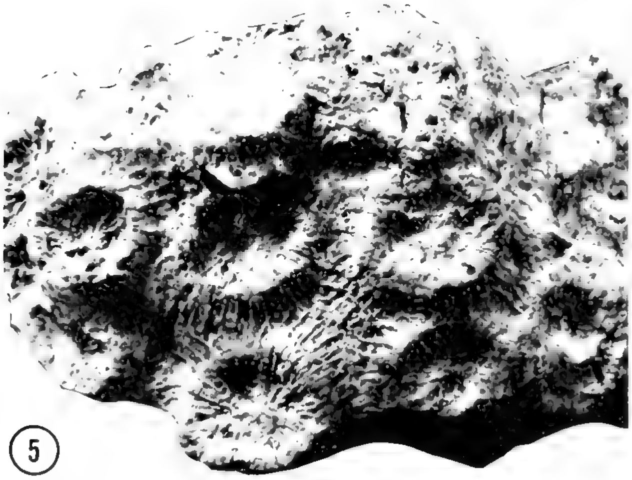
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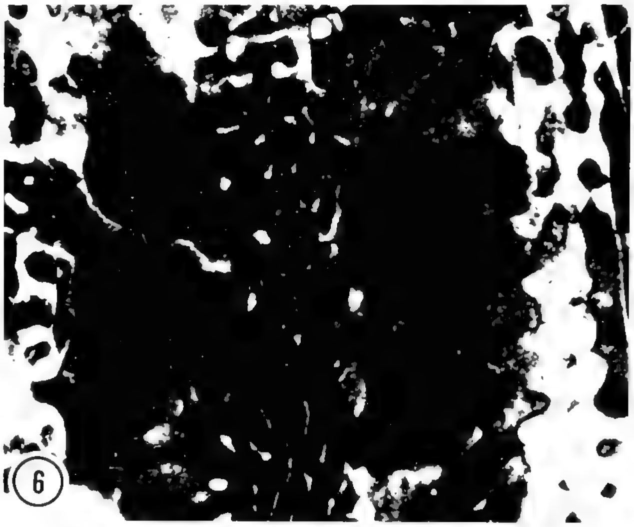
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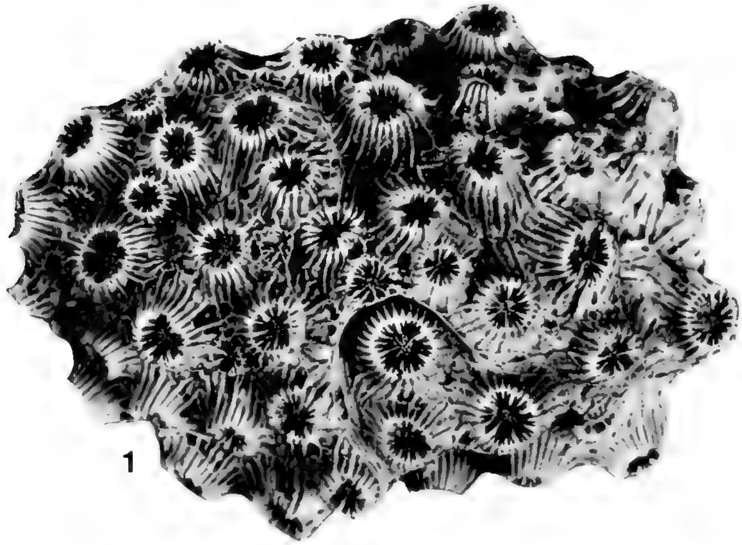

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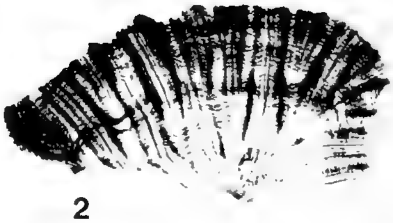

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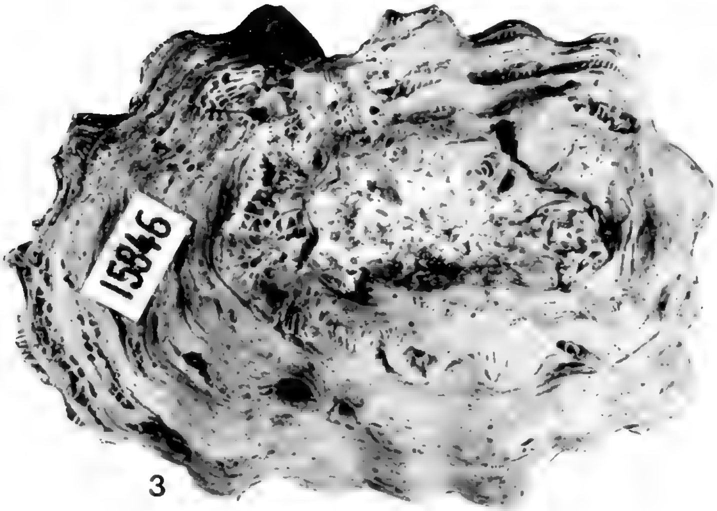

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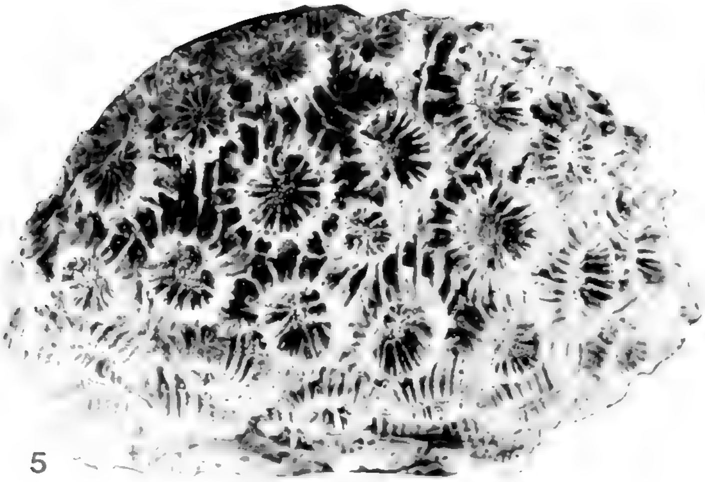

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EXPLANATION OF PLATE 2

Montastraea brevis (Duncan) .... page 35

Whole colonies and x-radiograph of a colony. Colonies form small discoidal to ellipsoidal masses. Corallites are intermediate in size, and are moderately to widely spaced. The epitheca is well-developed on the colony undersurface.

Figure

1. Figured Specimen. NMB D5575. Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of an ellipsoidal colony, ×2.
2. Figured Specimen. NMB D5726. Upper Miocene, locality NMB 16934, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph of a typical colony, ×1.
3. Figured Specimen. NMB D5575. Same specimen as figure 1. Colony undersurface showing the epitheca, ×2.
4. Figured specimen. NMB D5595. Upper Miocene, locality NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of an ellipsoidal colony, ×2.
5. Holotype. BM(NH) R28767. Neogene, "Nivajé Shale", Dominican Republic. Upper colony surface, ×2.
6. Figured Specimen. NMB D5582. Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of discoidal colony, ×2.

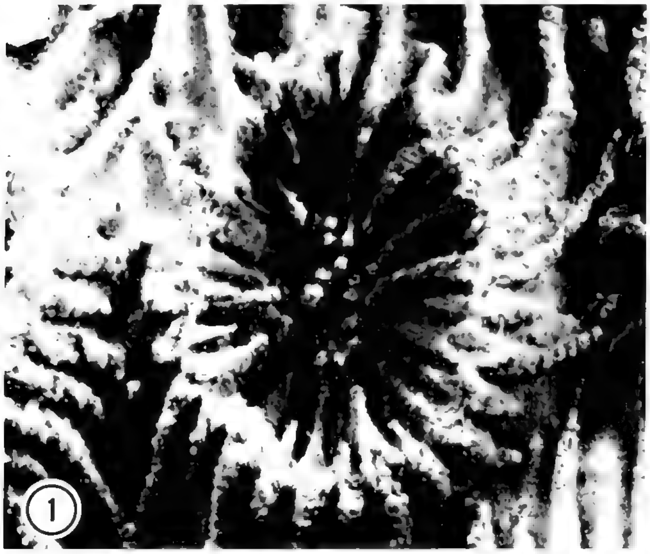
EXPLANATION OF PLATE 3

Montastraea brevis (Duncan) .... page 35

Close-ups of calical surfaces and transverse thin-sections. The septa are arranged in three to four cycles from which extend prominent costae. The wall is relatively thin and elevated moderately above the colony surface.

Figure

1. Holotype. BM(NH) R28767. Same specimen as Plate 2, figure 5. Calical surface, ×10.
2. Figured specimen. USNM 66830 (NF493). Neogene, locality USGS 7780, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
3. Figured specimen. NMB D5583. Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
4. Figured specimen. NMB D5586. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
5. Figured specimen. USNM 86904. Upper Miocene, locality TU 1215, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
6. Figured specimen. NMB D5726. Same specimen as Plate 2, figure 2. Transverse thin-section, ×10.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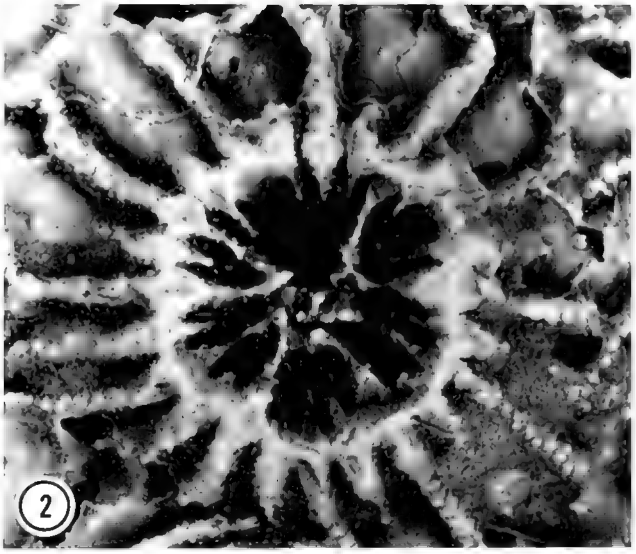
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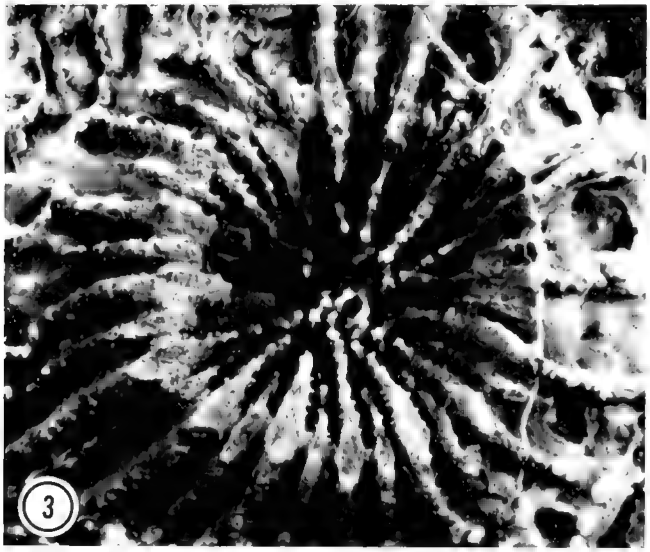
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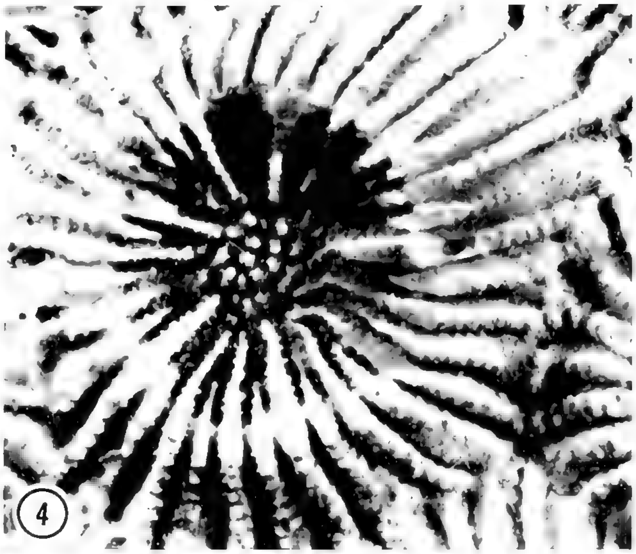
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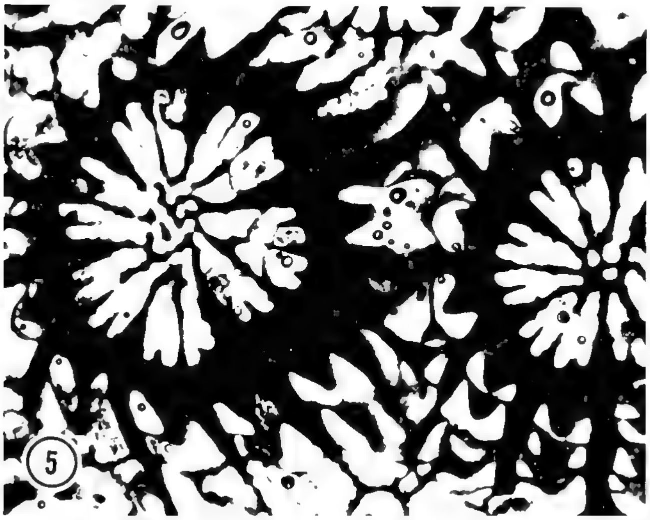
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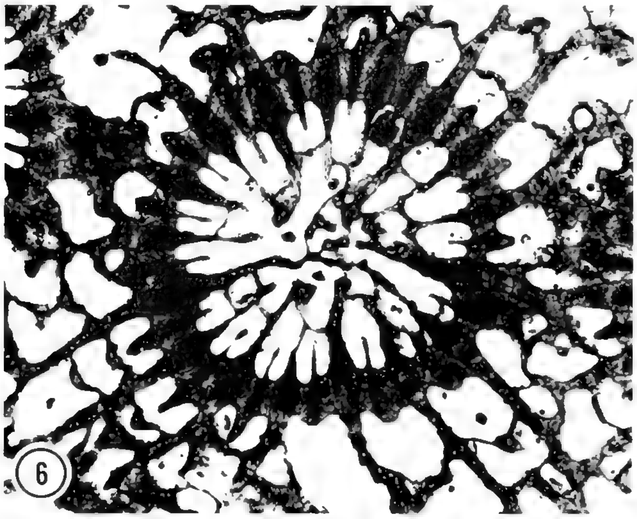
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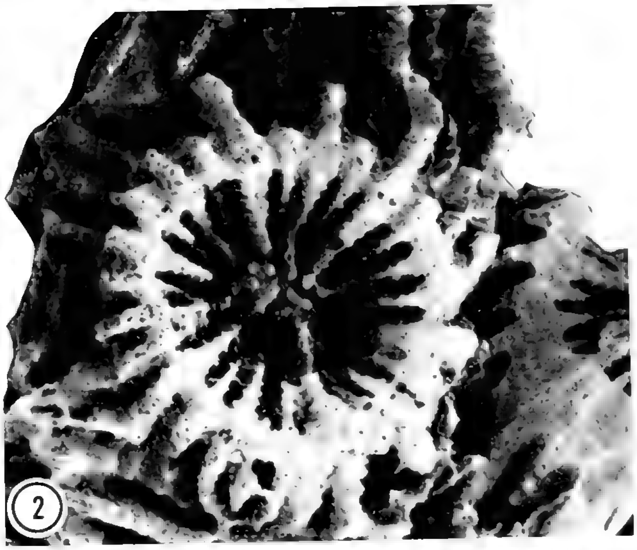
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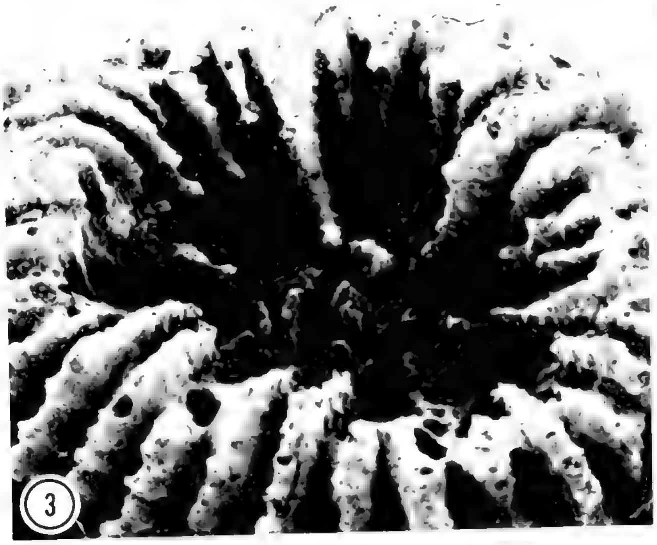
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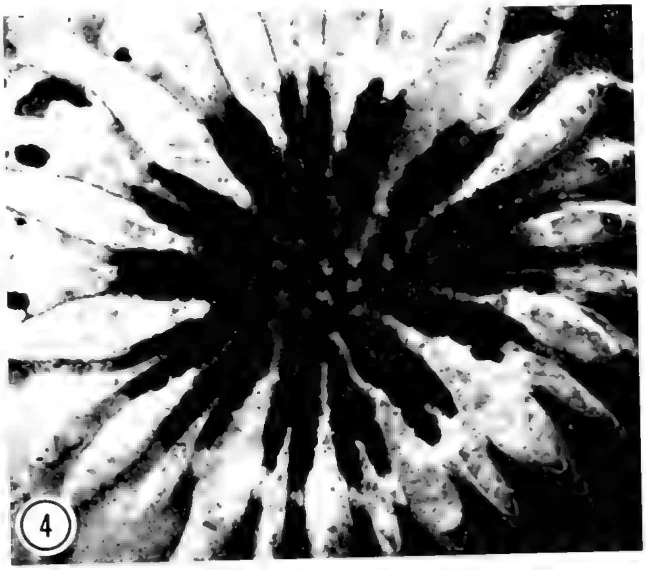
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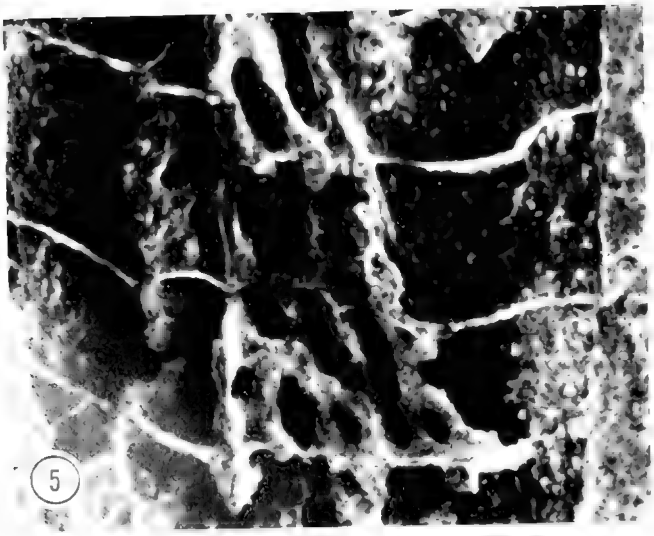
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EXPLANATION OF PLATE 4

Montastraea brevis (Duncan) .... page 35

SEM photographs and longitudinal thin-section. The columella is small and has a strongly whorled, papillate appearance formed by the inner margins of the primary and secondary septa. Endo- and exothecal dissepiments are moderately well-developed.

Figure

1. Figured specimen. NMB D5726. Same specimen as Plate 2, figure 2. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5585. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. SEM photograph of calical surface, ×10.
3. Figured specimen. NMB D5585. Same specimen as Plate 4, figure 2. SEM photograph of calical surface, ×15.
4. Figured specimen. NMB D5726. Same specimen as Plate 4, figure 1. SEM photograph of calical surface, ×15.
5. Figured specimen. NMB D5585. Same specimen as Plate 4, figure 2. SEM photograph of longitudinal break, ×20.
6. Figured specimen. NMB D5726. Same specimen as Plate 4, figure 1. Longitudinal thin-section, ×10.

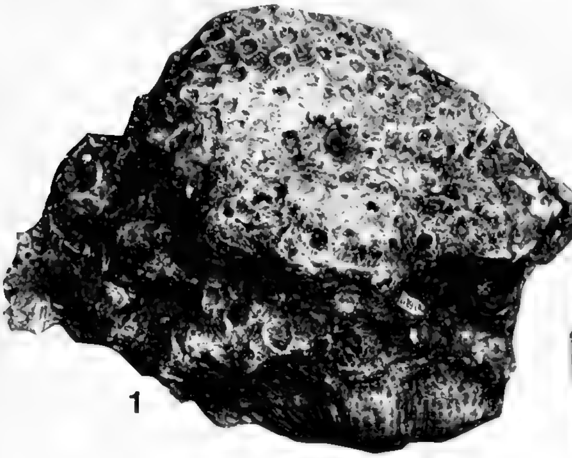
EXPLANATION OF PLATE 5

Montastraea canalis (Vaughan) .... page 36

Whole colonies and x-radiograph of a colony. Colonies form intermediate-sized hemispherical to domal mounds. Corallites are intermediate in size and relatively closely spaced.

Figure

1. Figured specimen. NMB D5615. Lower Pliocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. Side of a larger hemispherical colony, × ½.
2. Holotype. USNM 324862. Middle Miocene, locality USGS 6016, La Boca Formation, Panama. Surface of a small spherical colony, × 1.
3. Figured specimen. NMB D5610. Lower Pliocene, locality NMB 16815, Río Cana, Gurabo Formation, Dominican Republic. Surface of a plate-shaped colony fragment, × 1.
4. Figured specimen. NMB D5639. Lower Pliocene, locality NMB 16881, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, × 1.
5. Figured specimen. NMB D5552. Middle Pliocene, locality NMB 15830, Río Gurabo, Mao Formation, Dominican Republic. Surface of a colony fragment, × 1.
6. Figured specimen. NMB D5619. Lower Pliocene, locality NMB 16817, Río Cana, Gurabo Formation, Dominican Republic. X-radiograph, × 1.
7. Synonym of *M. endothecata* (Duncan). USNM 324861 [original paratype of *Orbicella canalis* Vaughan]. Middle Miocene, locality USGS 6444, La Boca Formation, Panama. Colony surface, × 1.
8. Figured specimen. NMB D5613. Lower Pliocene, locality NMB 16815, Río Cana, Gurabo Formation, Dominican Republic. Colony surface, × 1.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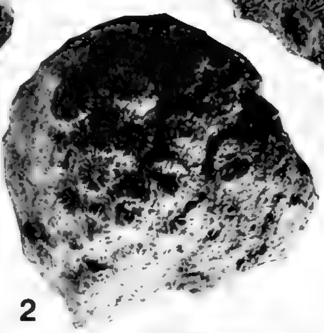
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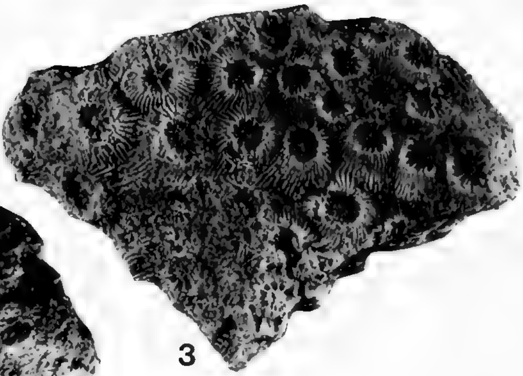
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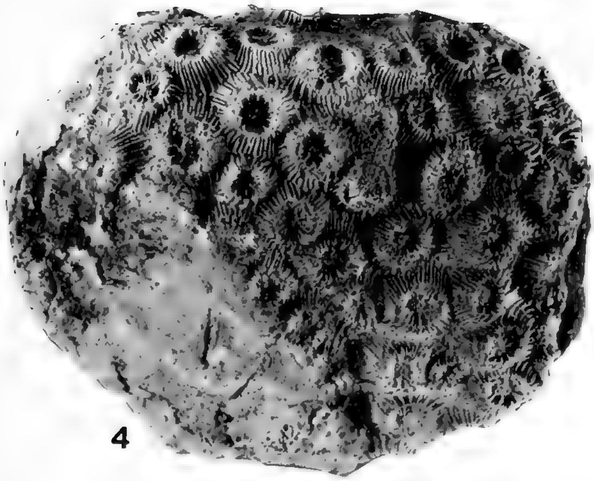
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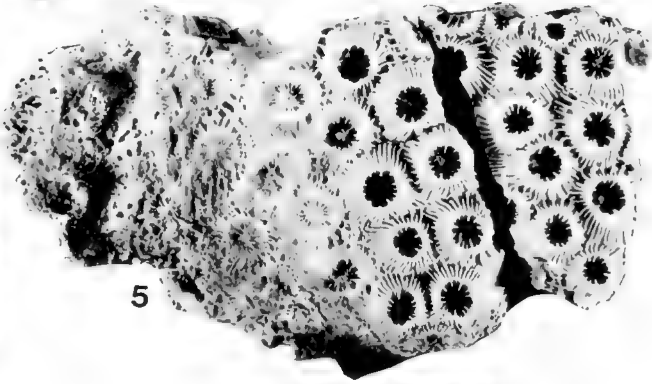
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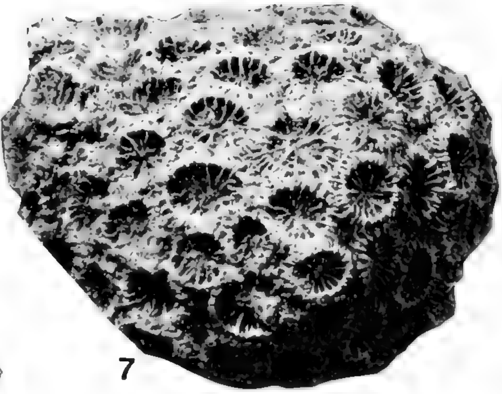
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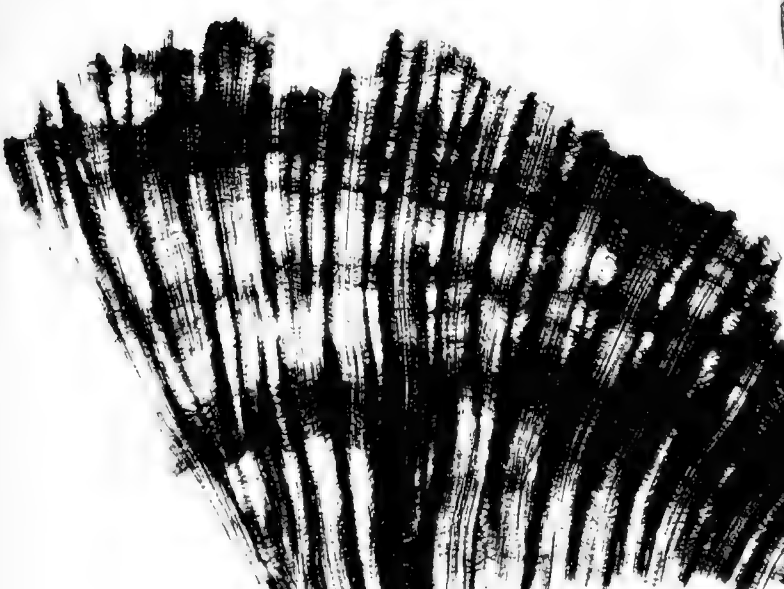
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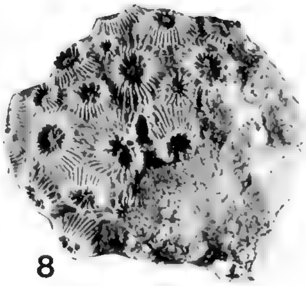
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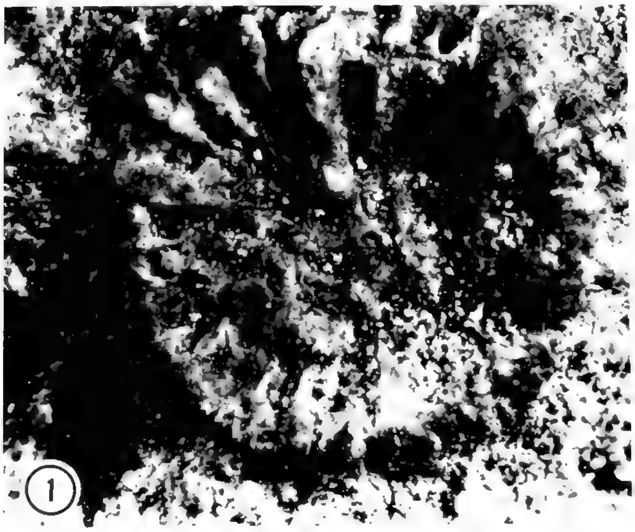
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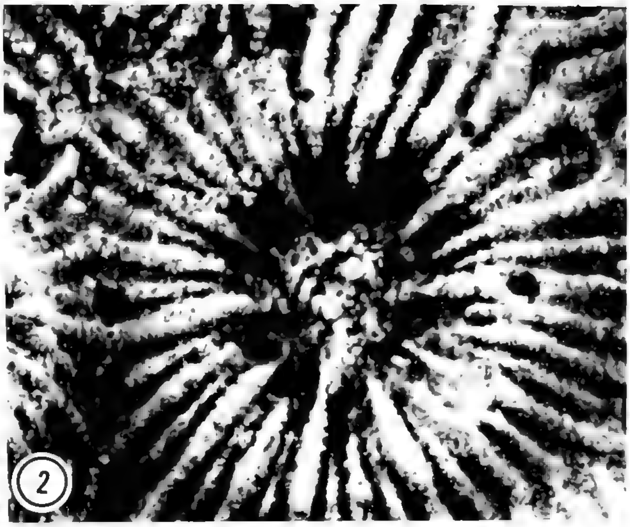
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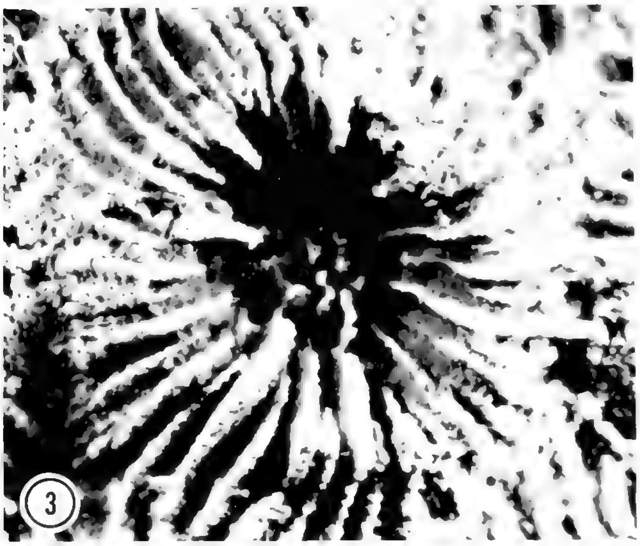
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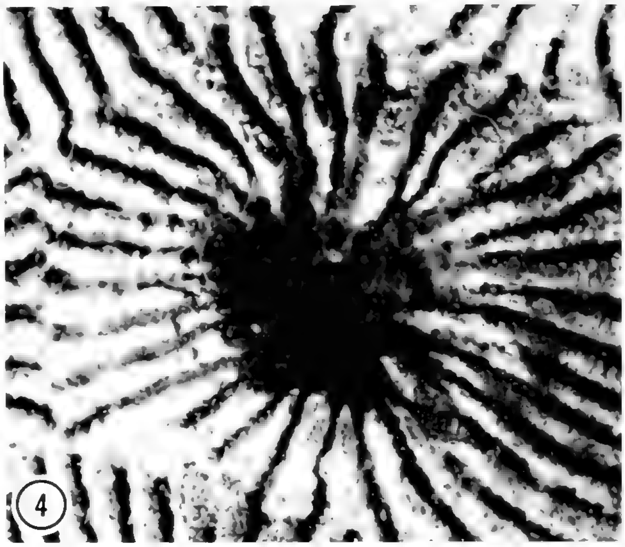
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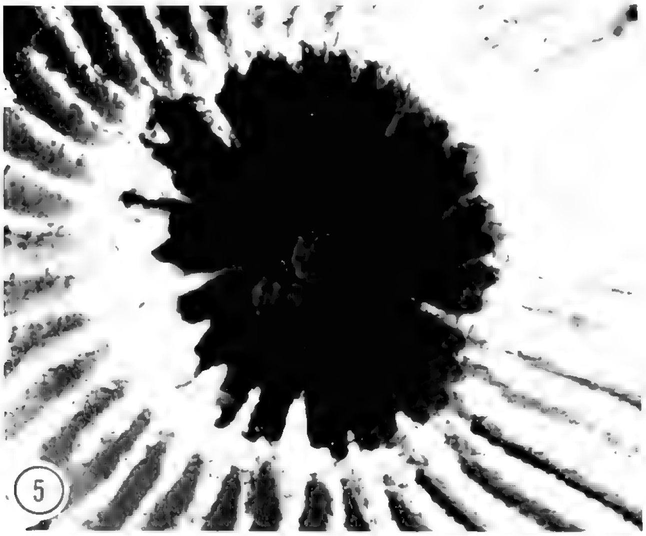
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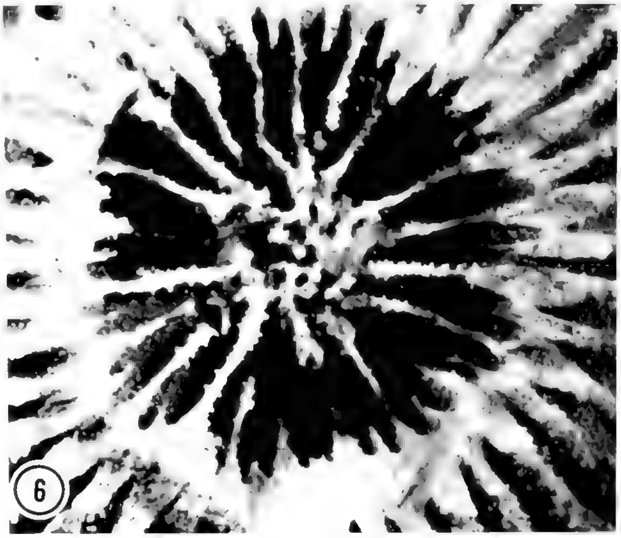
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EXPLANATION OF PLATE 6

Montastraea canalis (Vaughan) . . . . page 36

Close-ups of calical surfaces. The septa are arranged in three to four cycles from which extend prominent costae, usually equal in size. The wall is thick, and it projects distinctively above the colony surface.

Figure

1. Holotype. USNM 324862. Same specimen as Plate 5, figure 2. Calical surface, ×10.
2. Figured specimen. NMB D5613. Same specimen as Plate 5, figure 8. Calical surface, ×10.
3. Figured specimen. NMB D5611. Lower Pliocene, locality NMB 16815, Río Cana, Gurabo Formation, Dominican Republic. Calical surface, ×10.
4. Figured specimen. NMB D5614. Lower Pliocene, locality NMB 16815, Río Cana, Gurabo Formation, Dominican Republic. Calical surface, ×10.
5. Figured specimen. NMB D5552. Lower Pliocene, locality NMB 16815, Río Cana, Gurabo Formation, Dominican Republic. Calical surface, ×10.
6. Figured specimen. NMB D5731. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Calical surface, ×10.

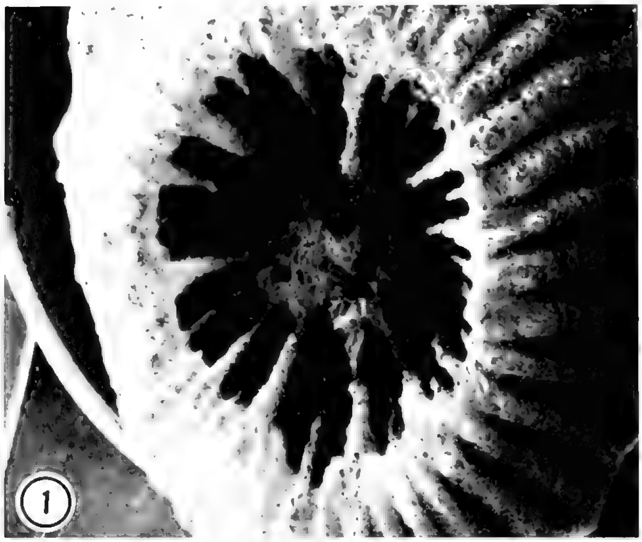
EXPLANATION OF PLATE 7

Montastraea canalis (Vaughan) .... page 36

SEM photographs and thin-sections. The columella is strong, and is intermediate in size. The primary septa are slightly thicker than the other septal cycles. Endothecal dissepiments are weakly developed, whereas exothecal dissepiments are well-developed.

Figure

1. Figured specimen. NMB D5552. Same specimen as Plate 6, figure 5. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5615. Same specimen as Plate 5, figure 1. SEM photograph of calical surface, ×10.
3. Figured specimen. NMB D5739. Lower Miocene, locality NMB 16944, Río Yaque del Norte, Baitoa Formation, Dominican Republic. SEM photograph of calical surface, ×10.
4. Figured specimen. NMB D5636. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Transverse thin-section, ×10.
5. Figured specimen. NMB D5739. Same specimen as Plate 7, figure 3. SEM photograph of longitudinal break, ×10.
6. Figured specimen. NMB D5738. Lower Miocene, locality NMB 16944, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Longitudinal thin-section, ×10.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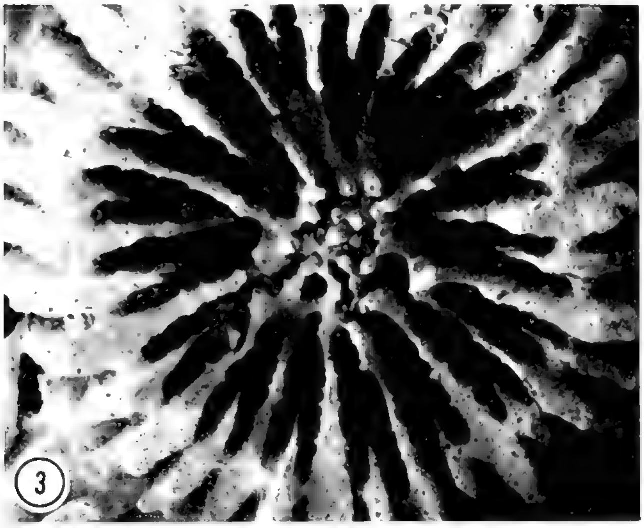
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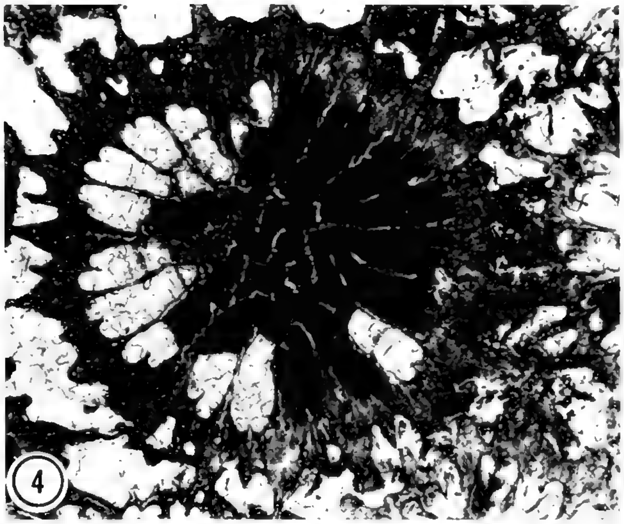
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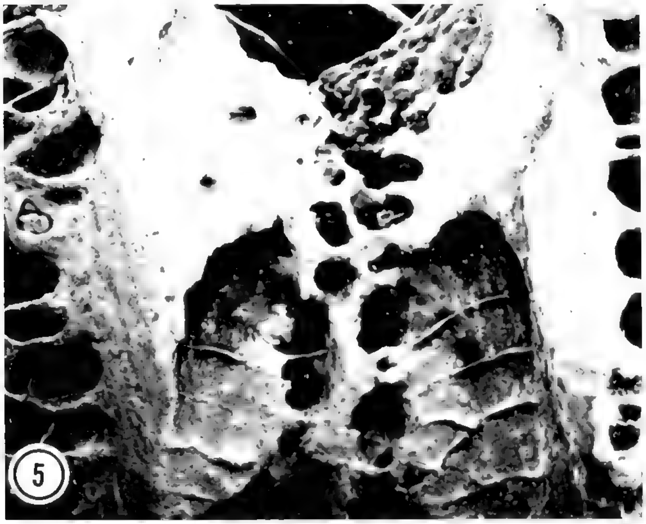
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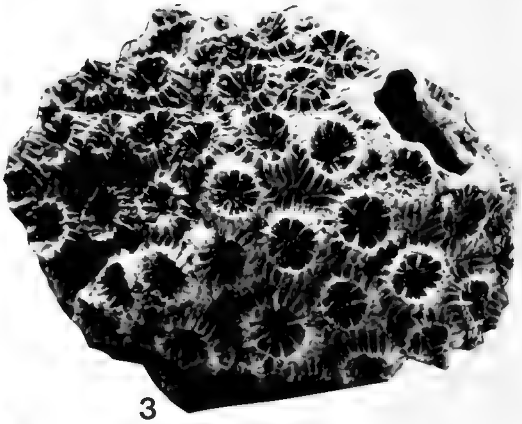

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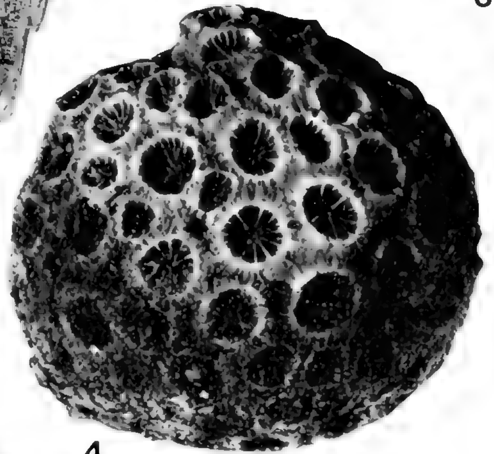

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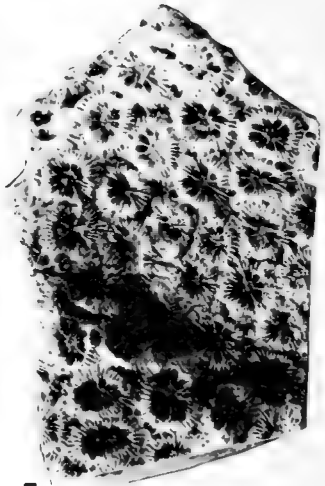

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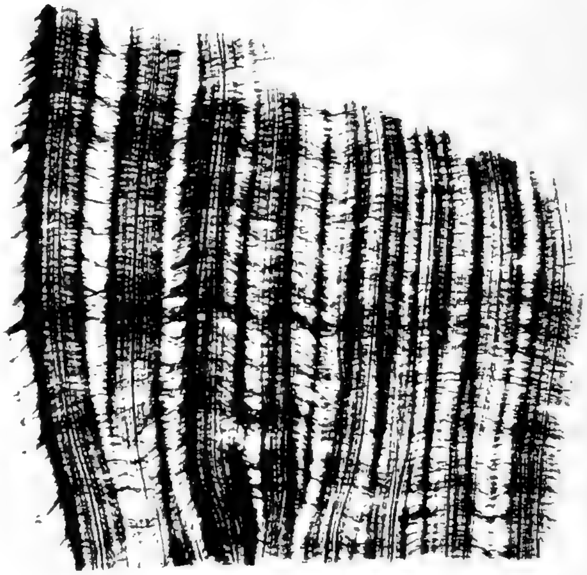

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Explanation of Plate 8

Montastraea cavernosa (Linnaeus) and two early Miocene species that are often confused with ***M. cavernosa***

Whole colonies and x-radiograph of a colony. Colony morphology ranges from small to large hemispherical mounds. The corallites are intermediate to large in size and moderately spaced.

Figure Page

1, 4, 6, 7. ***Montastraea cavernosa*** (Linnaeus) 37

- 1, 7. Figured specimen. NMB D5579. Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. 1, longitudinal break through colony, ×½; 7, X-radiograph, ×1.
- 4. Figured specimen. NMB D5750. Lower Miocene, locality NMB 17279, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Colony surface, ×1.
- 6. Figured specimen. NMS catalogue number unknown [presumably Esper's (1795) specimen of *M. cavernosa*]. Recent, unknown locality. Colony side, ×½.

2, 3. ***Orbicella tampaensis*** Vaughan 36

- 2. Holotype. USNM 324900. Lower Miocene, locality USGS 2115, Tampa Formation, Florida. Colony surface, ×1.
- 3. Paratype [synonym of *M. canalis* (Vaughan)]. USNM 324901. Lower Miocene, locality USGS 2115, Tampa Formation, Florida. Colony surface, ×1.

5. ***Orbicella bainbridgensis*** Vaughan 40

Holotype [synonym of *M. endothecata* (Duncan)]. USNM 324881. Lower Miocene, locality USGS 3383, Chattahoochee Formation, Georgia. Upper colony surface, ×1.

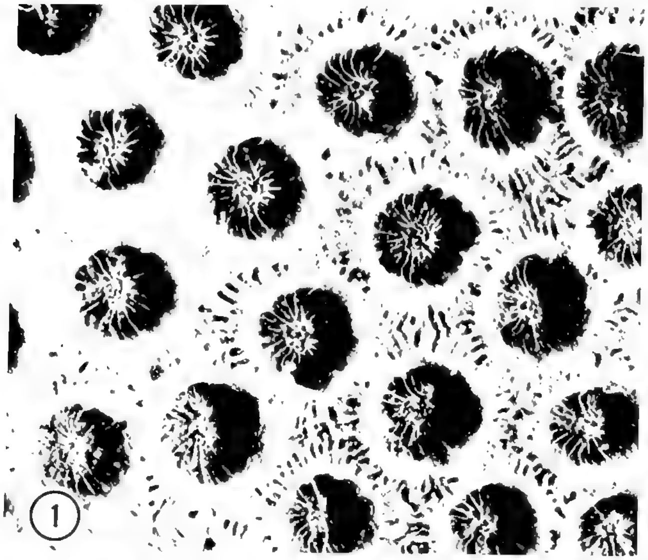
EXPLANATION OF PLATE 9

Montastraea cavernosa (Linnaeus) . . . . page 37

Close-ups of calical surfaces. The septa are arranged in four to five septal cycles from which extend costae, subequal in size. The wall is relatively thin, and it projects moderately above the colony surface.

Figure

1. Figured specimen. NMS catalogue number unknown. Same specimen as Plate 8, figure 6. Calical surface, ×2.
2. Synonym of *M. canalis* (Vaughan), which closely resembles *M. cavernosa*, paratype of *Orbicella tampaensis* var. *silecensis* Vaughan. USNM 324896. Lower Miocene, locality USGS 7754, Tampa Formation, Florida. Calical surface, ×1.
3. Figured specimen. NMB D5596. Upper Miocene, locality NMB 15858, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
4. Figured specimen. SUI 48763. Recent, Discovery Bay, Jamaica, lagoon locality of Foster (1980), depth = 16 m. SEM photograph of calical surface, ×10.
5. Figured specimen. NMB D5750. Same specimen as Plate 8, figure 4. Calical surface, ×10.
6. Figured specimen. NMB D5931. Upper Miocene, locality NMB 15836, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.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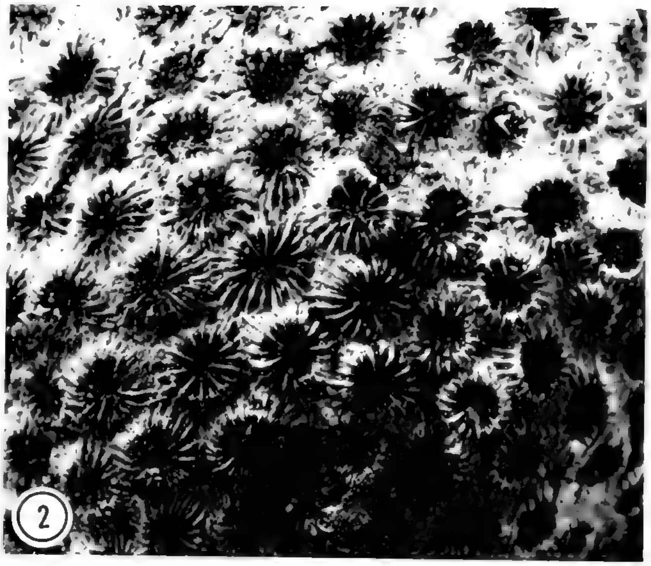
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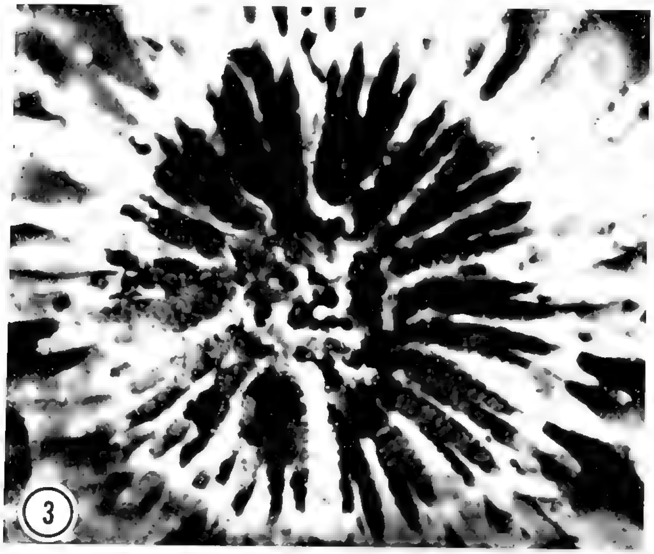
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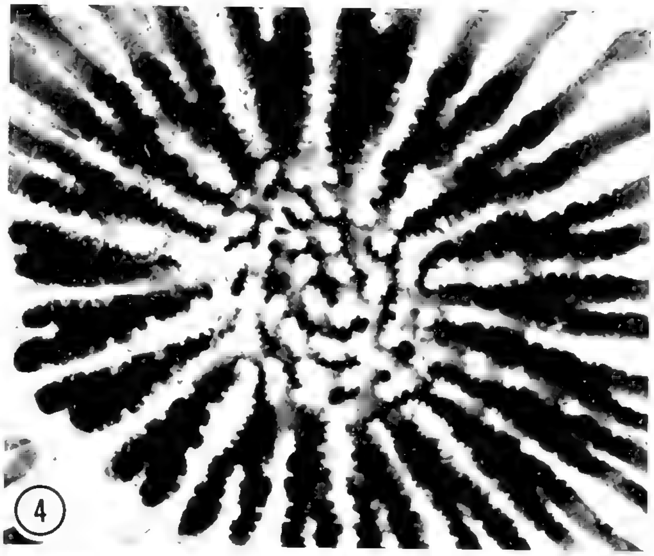
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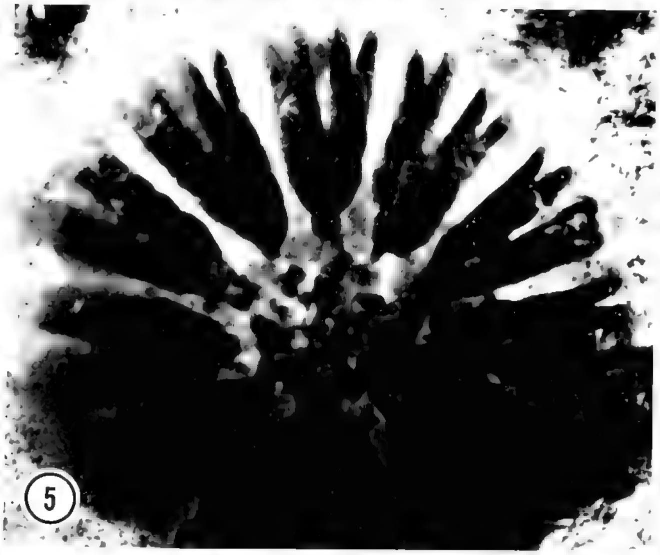
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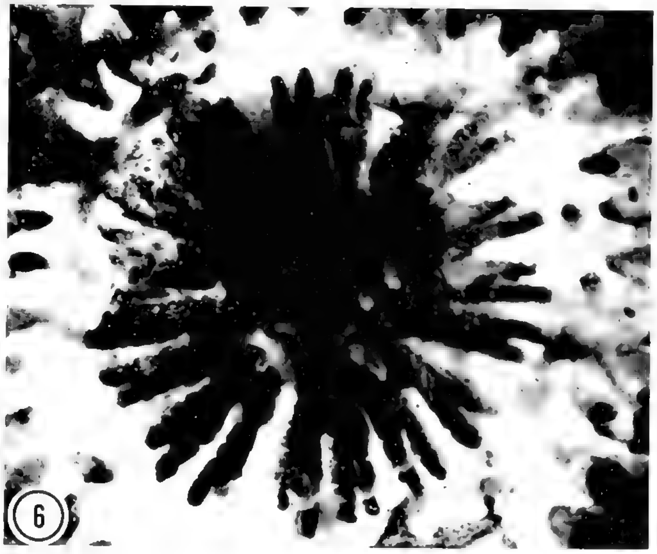
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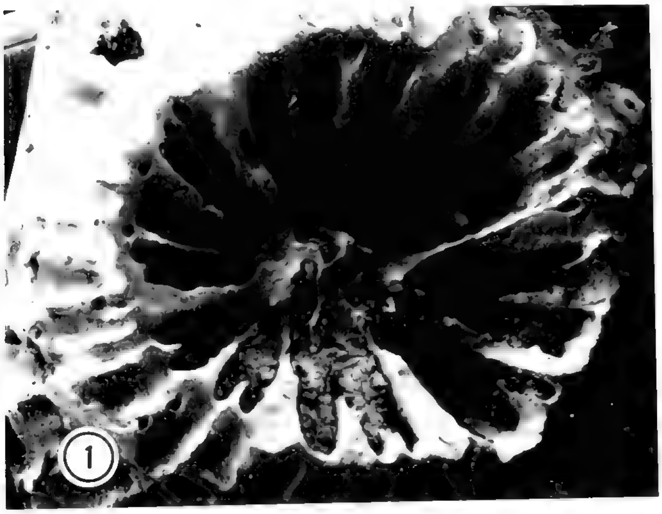
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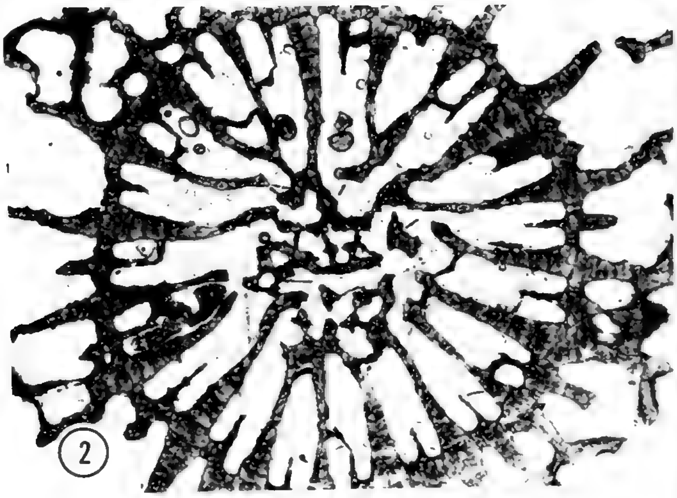
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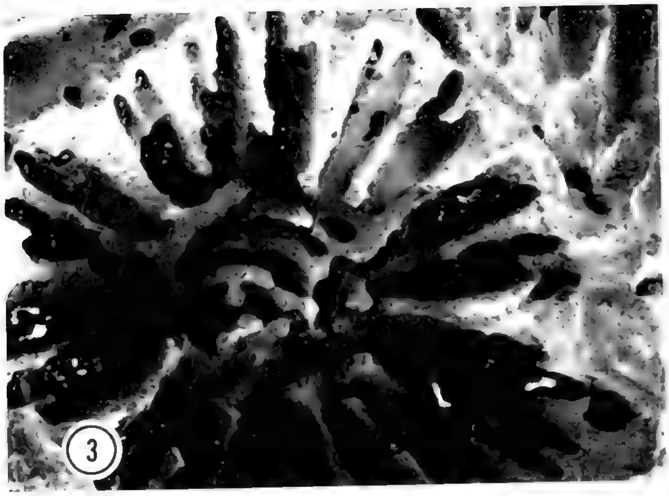
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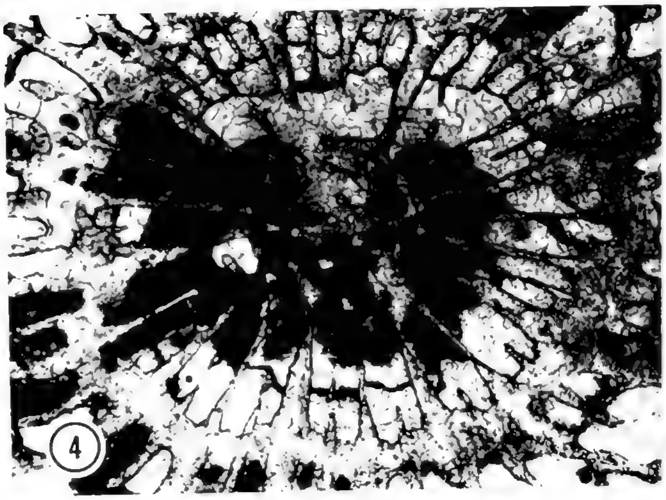
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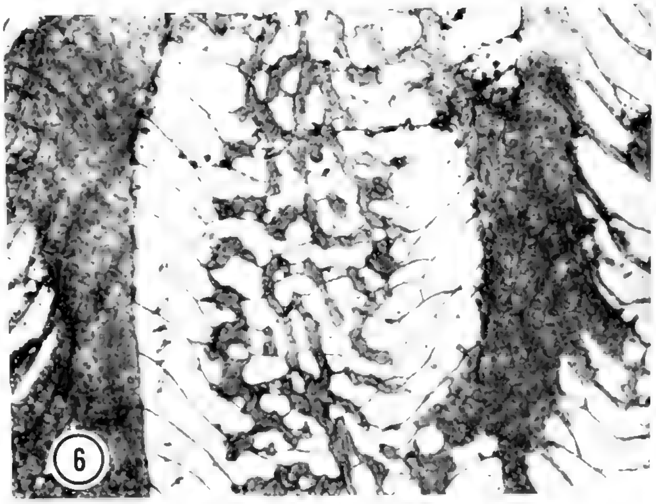
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EXPLANATION OF PLATE 10

Montastraea cavernosa (Linnaeus) . . . . page 37

SEM photographs and thin-sections. The columella is intermediate in size and in depth, papillate, and whorled. The first and second septal cycles are generally equal and the third often extends completely to the columella. Endo- and exothecal dissepiments are thin, and are closely spaced.

Figure

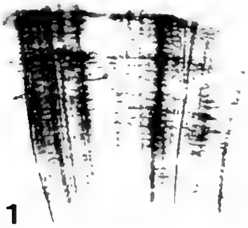
1. Figured specimen. NMB D5596. Same specimen as Plate 9, figure 3. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5579. Same specimen as Plate 8, figure 1. Transverse thin-section, ×10.
3. Figured specimen. NMB D5931. Same specimen as Plate 9, figure 6. SEM photograph of calical surface, ×10.
4. Figured specimen. NMB D5709. Upper Miocene, locality NMB 16921, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
5. Figured specimen. NMB D5596. Same specimen as Plate 10, figure 1. SEM photograph of longitudinal break, ×10.
6. Figured specimen. NMB D5701. Upper Miocene, locality NMB 16911, Río Mao, ?Gurabo Formation, Dominican Republic. Longitudinal thin-section, ×10.

EXPLANATION OF PLATE 11

Montastraea cylindrica (Duncan) . . . . page 39

Whole colonies, colony fragments, and x-radiograph of a colony. Colony morphology consists of intermediate-sized to large, flattened mounds. The corallites are intermediate in size, strongly exsert, and widely spaced.

Figure
1. Figured specimen. NMB D5578. Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, × 1.
2. Figured specimen. NMB D5577. Upper Miocene, locality NMB 15846, Río Gurabo, Gurabo Formation, Dominican Republic. Upper colony surface, × 1.
3. Figured specimen. USNM 155277 [one of Duncan's (1863) original specimens]. Neogene, "Nivajé Shale", Dominican Republic. Upper colony surface, × 1.
4. Figured specimen. NMB D5578. Same specimen as Plate 11, figure 1. X-radiograph, × 1.
5. Figured specimen. NMB D5561. Upper Miocene, locality NMB 15838, Río Gurabo, Gurabo Formation, Dominican Republic. Upper colony surface, × 1.
6. Figured specimen. NMB D5557. Upper Miocene, locality NMB 15838, Río Gurabo, Gurabo Formation, Dominican Republic. Colony side, × ½.
7. Figured specimen. NMB D5646. Lower Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Surface of a plate-shaped colony, × ½.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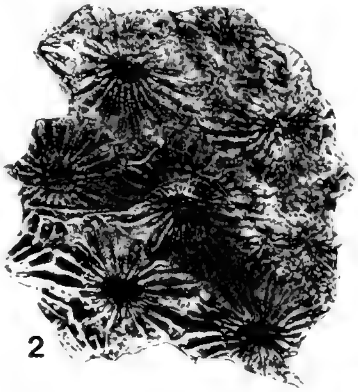
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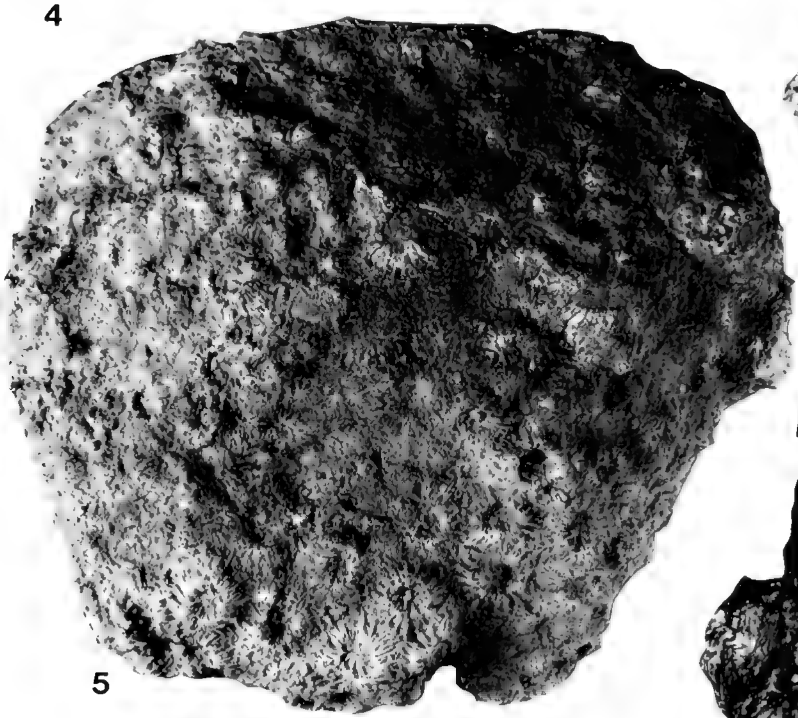
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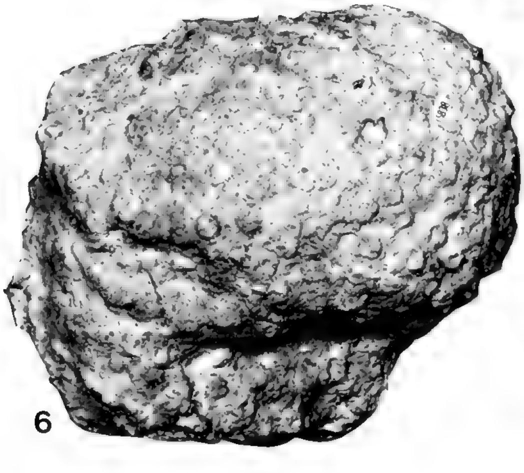
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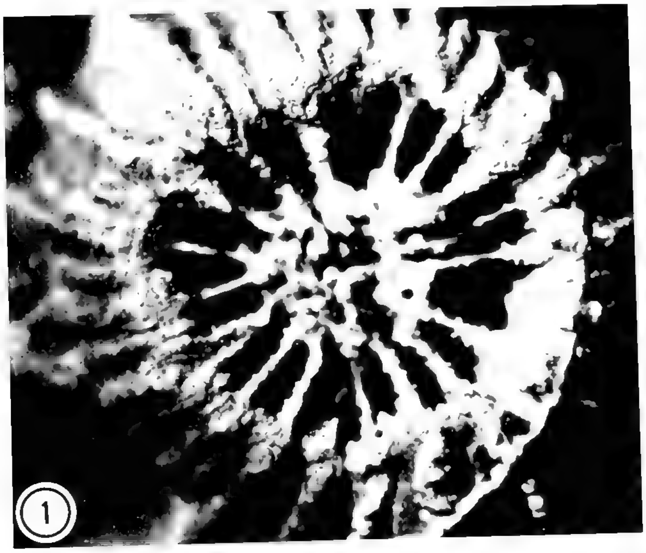
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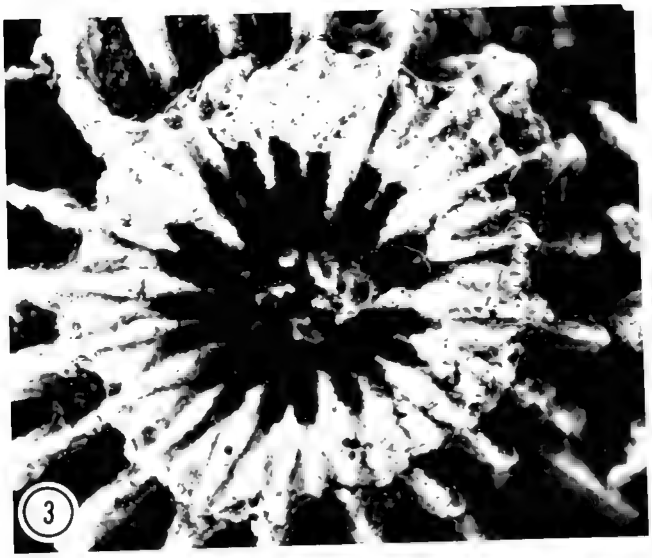
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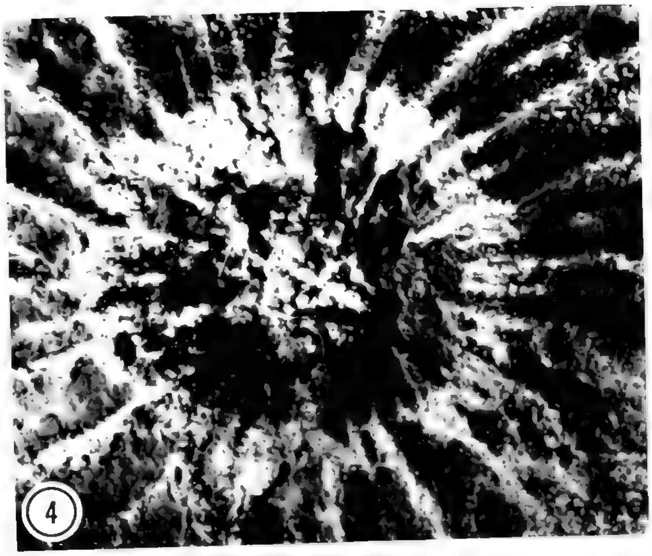
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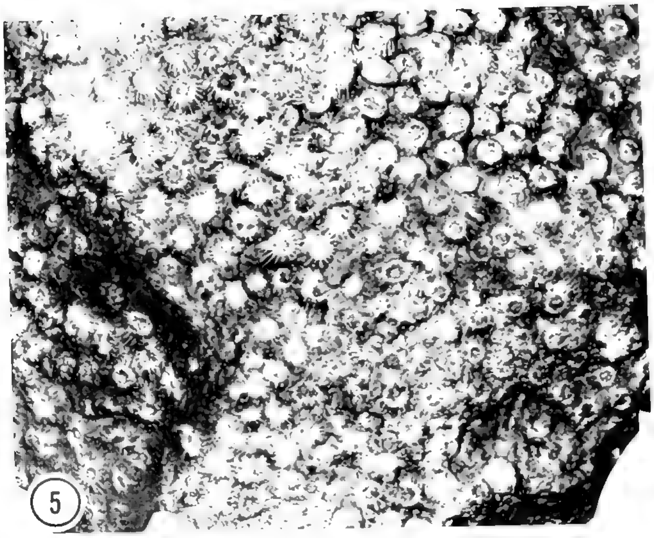
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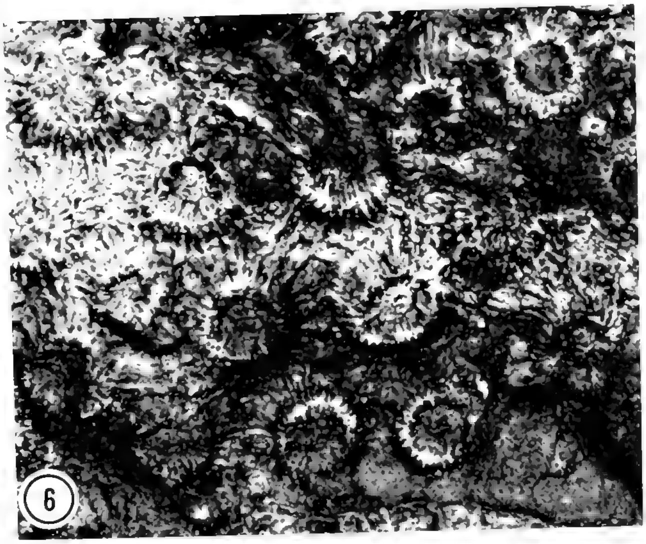
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EXPLANATION OF PLATE 12

Montastraea cylindrica (Duncan) .... page 39

Whole colony and close-ups of calical surfaces. The septa are relatively few in number, and are arranged in three cycles, with a weak fourth cycle sometimes developed. The costae are thin, exsert, and subequal. The corallite wall is thin to intermediate in thickness.

Figure

1, 2. Holotype. BM(NH) R28790. Neogene, "Tuffaceous Limestone", Dominican Republic. 1, calical surface, ×10; 2, calical surface, ×10.

3. Figured specimen. USNM 155277. Same specimen as Plate 11, figure 3. Calical surface, ×10.

4. Figured specimen. NMB D5559. Upper Miocene, locality NMB 15838, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.

5. Figured specimen. NMB D5649. Lower Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. Colony surface, ×½.

6. Figured specimen. NMB D5566. Upper Miocene, locality NMB 15841, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×2.

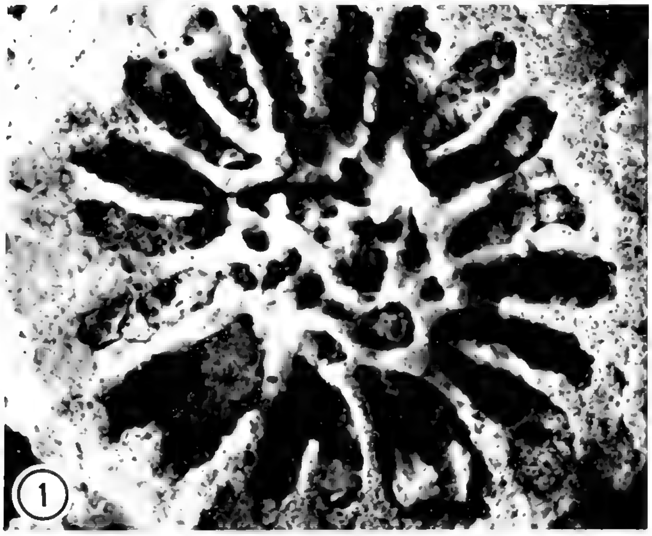
EXPLANATION OF PLATE 13

Montastraea cylindrica (Duncan) .... page 39

SEM photographs and thin-sections. The columella is thick and prominent, and is formed by the inner margins of the first three septal cycles. Endo- and exothecal dissepiments are thin and closely spaced.

Figure

1. Figured specimen. NMB D5657. Lower Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5566. Same specimen as Plate 12, figure 6. Transverse thin-section, ×10.
3. Figured specimen. NMB D5649. Same specimen as Plate 12, figure 5. SEM photograph of calical surface, ×10.
4. Figured specimen. NMB D5646. Same specimen as Plate 11, figure 7. Transverse thin-section, ×10.
5. Figured specimen. BM(NH) R28856 [one of Duncan's (1863) original specimens]. Neogene, "Nivajé Shale", Dominican Republic. Longitudinal break, ×10.
6. Figured specimen. NMB D5566. Same specimen as Plate 13, figure 2. Longitudinal thin-section, ×10.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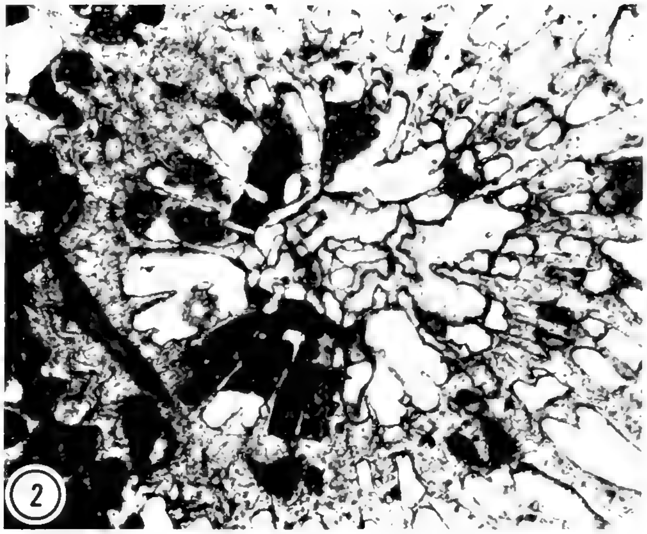
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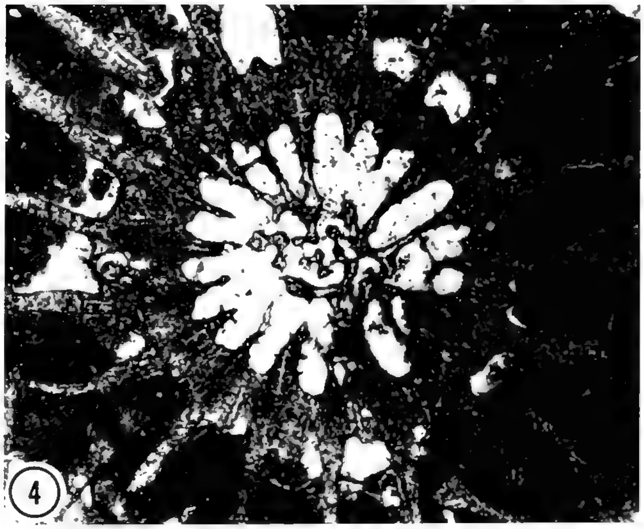
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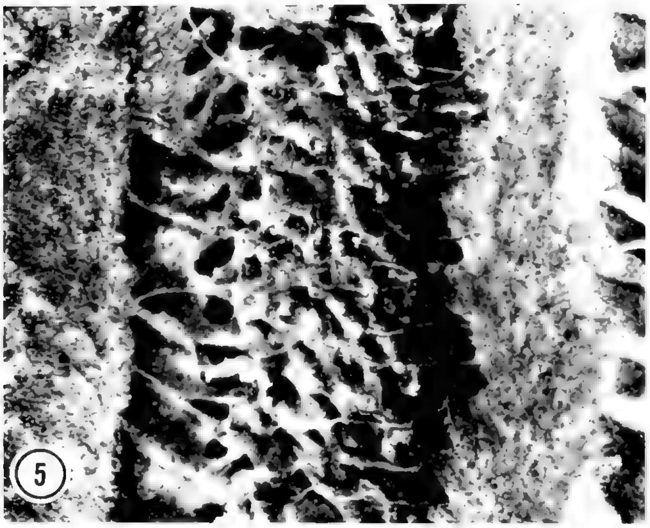
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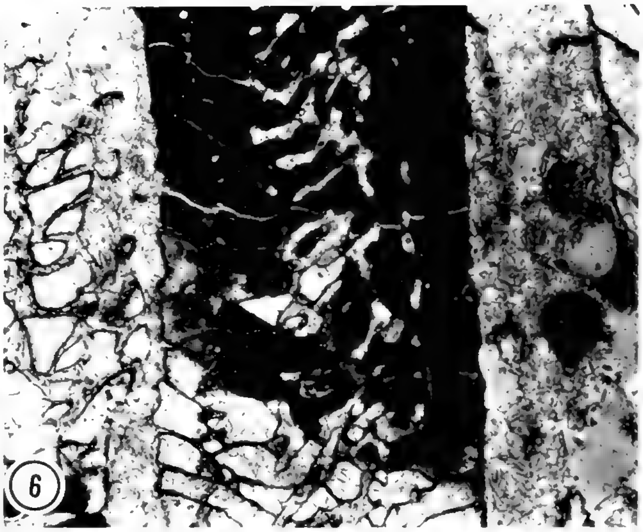
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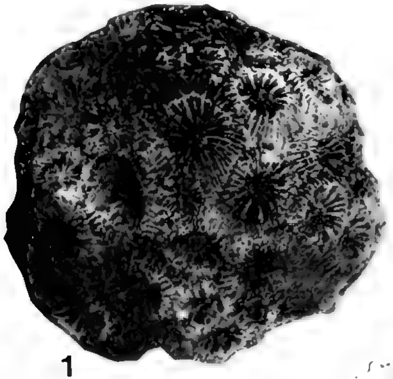

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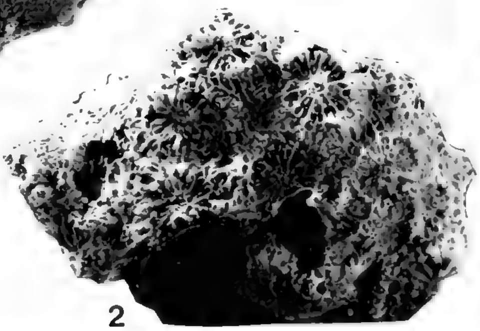

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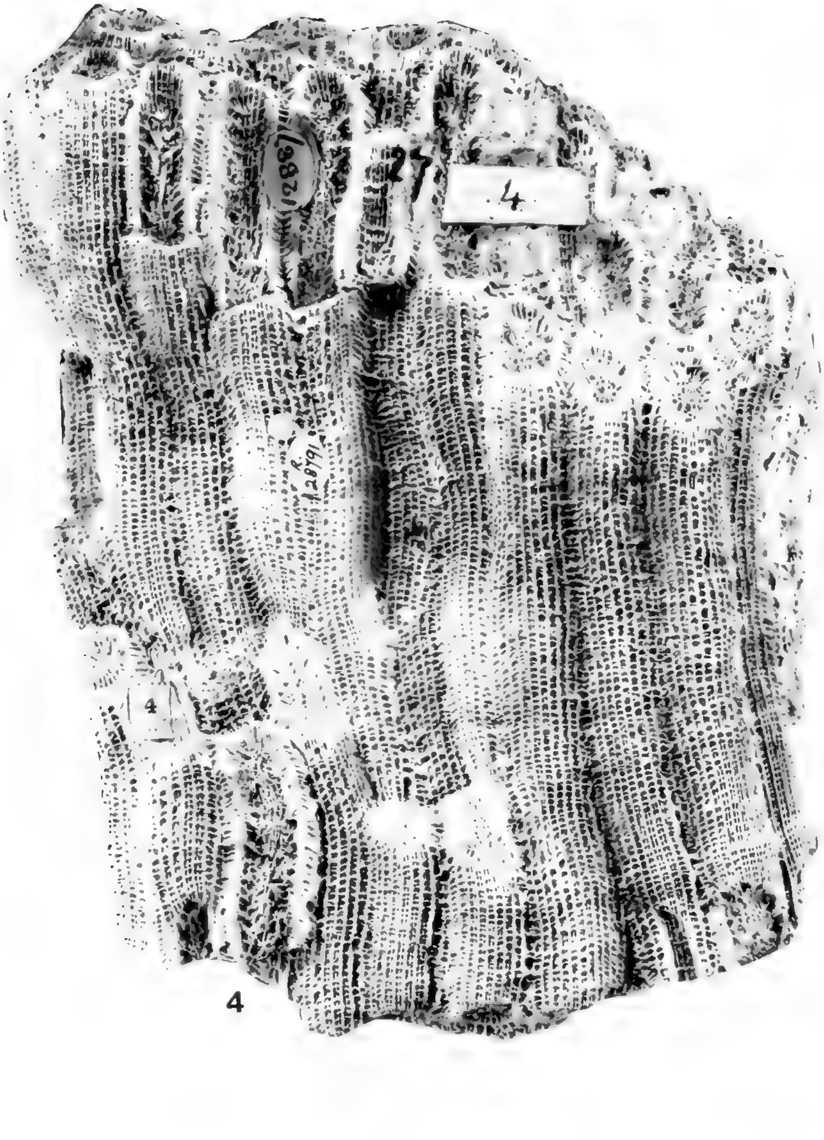

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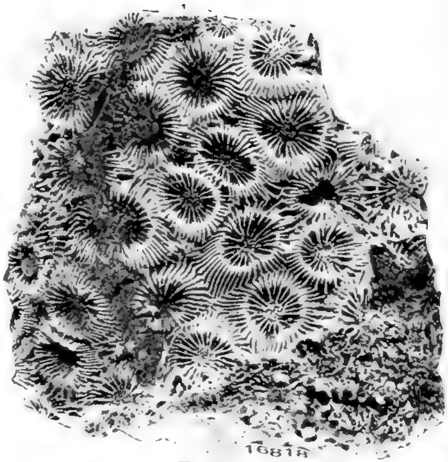

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EXPLANATION OF PLATE 14

Montastraea endothecata (Duncan) . . . . page 40

Whole colonies and colony fragments. Colonies generally form large hemispherical mounds. Corallites are large in size, with variable, intermediate spacing.

Figure

1. Figured specimen. USNM 66867 (NF425). Upper Miocene, locality USGS 8539, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.
2. Possible synonym of *Montastraea canalis* (Vaughan), which resembles *M. endothecata*. USNM 324883 [Vaughan's (1919) hypotype of *Heliastraea insignis* Duncan]. Neogene, Aruba. Upper colony surface, ×1.
3. Figured specimen. BM(NH) R28874 = USNM 155276 [one of Duncan's (1863) original specimens]. Neogene, "Nivajé Shale", Dominican Republic. Colony side, ×1
4. Holotype. BM(NH) R28791. Neogene, "Nivajé Shale", Dominican Republic. Longitudinal break, ×1.
5. Figured specimen. NMB D5623. Lower Pliocene, locality NMB 16818, Río Cana, Gurabo Formation, Dominican Republic. Surface of a colony fragment, ×1.

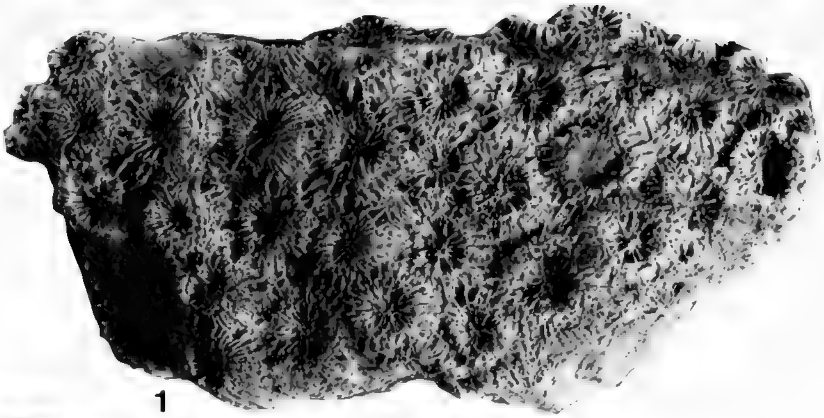
EXPLANATION OF PLATE 15

Montastraea endothecata (Duncan) .... page 40

Whole colonies and colony fragments. Colonies generally form large hemispherical mounds. Corallites are large in size with variable intermediate spacing.

Figure

1. Figured specimen. NMB D5723. Upper Miocene, locality NMB 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Upper colony surface, ×1.
2. Figured specimen. NMB D5618. Lower Pliocene, locality NMB 16818, Río Cana, Gurabo Formation, Dominican Republic. Longitudinal break, ×¾.
3. Figured specimen. NMB D5718. Upper Miocene, locality NMB 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×¾.
4. Figured specimen. USNM 66867 (NF424). Upper Miocene, locality USGS 8538, Río Gurabo, Gurabo Formation, Dominican Republic. Colony surface, ×1.



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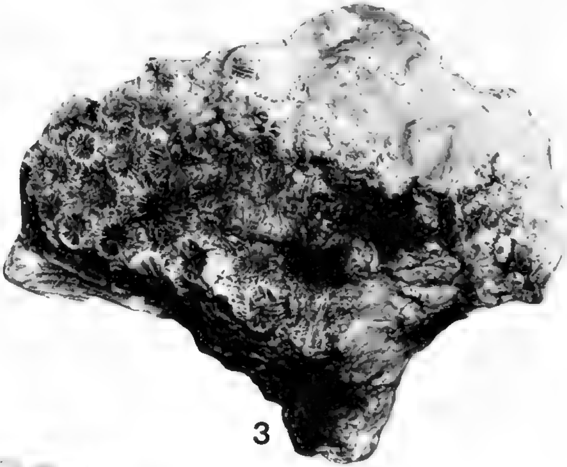

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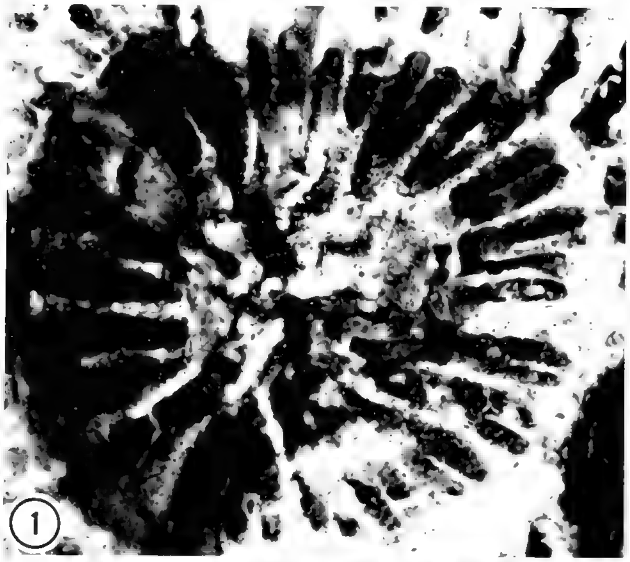
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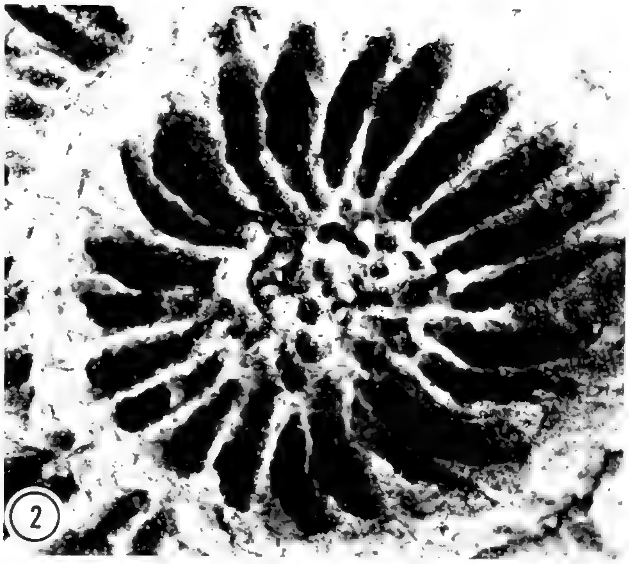
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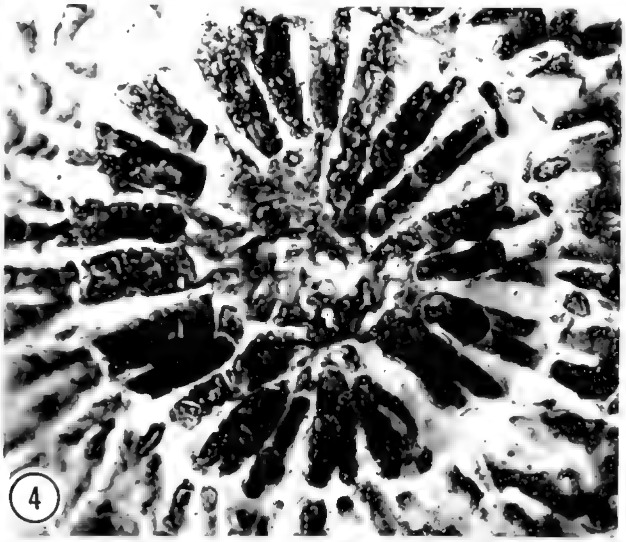
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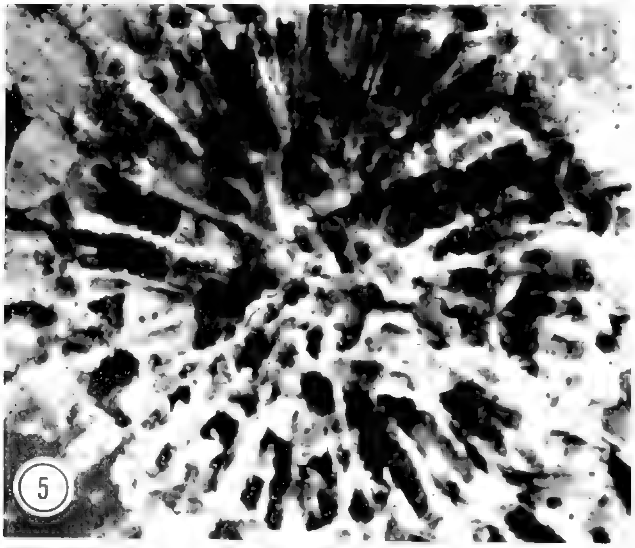
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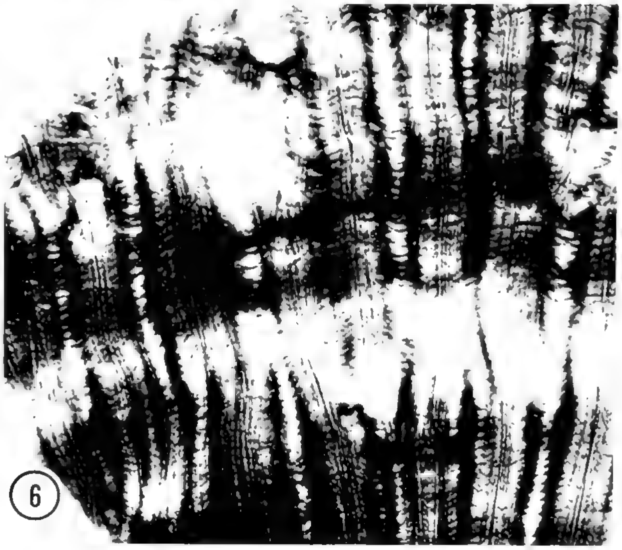
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EXPLANATION OF PLATE 16

Montastraea endothecata (Duncan) . . . . page 40

X-radiograph of a colony and close-ups of calical surfaces. The septa are arranged in four to five cycles, and the costae alternate in thickness. The corallite wall is relatively thick, and it projects slightly above the colony surface.

Figure

1. Holotype. BM(NH) R28791. Same specimen as Plate 14, figure 4. Calical surface, ×10.
2. Figured specimen. BM(NH) R28874 = USNM 155276. Same colony as Plate 14, figure 3. Calical surface, ×10.
3. Figured specimen. USNM 66867 (NF424). Same specimen as Plate 15, figure 4. Calical surface, ×10.
4. Figured specimen. USNM 66867 (NF425). Same specimen as Plate 14, figure 1. Calical surface, ×10
5. Figured specimen. NMB D5723. Same specimen as Plate 15, figure 1. Calical surface, ×10.
6. Figured specimen. NMB D5618. Same specimen as Plate 15, figure 2. X-radiograph, ×1.

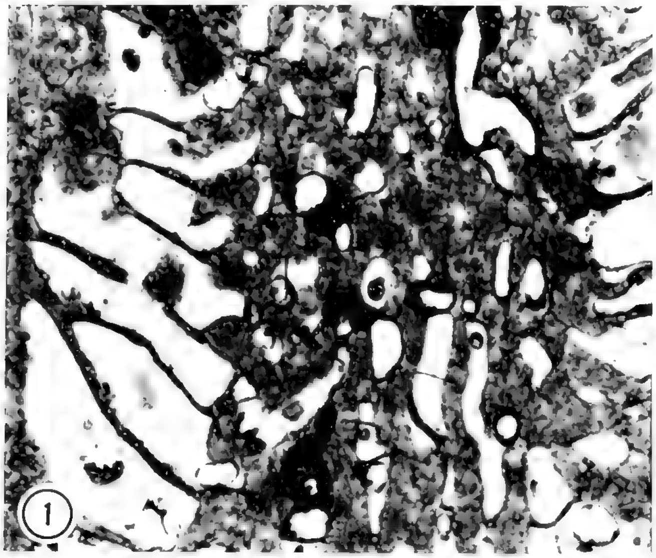
EXPLANATION OF PLATE 17

Montastraea endothecata (Duncan) . . . . page 40

SEM photographs and thin-sections. The columella is papillate, wide, complex, and strongly whorled. The first and second septal cycles are equal and the fourth and fifth are short, thin and free. Endo- and exothecal dissepiments are well-developed and widely spaced.

Figure

1. Figured specimen. NMB D5621. Lower Pliocene, locality NMB 16818, Río Cana, Gurabo Formation, Dominican Republic. Longitudinal thin-section, × 10.
2. Figured specimen. NMB D5621. Same specimen as Plate 17, figure 1. Transverse thin-section, × 10.
3. Figured specimen. USNM 86902. ?Lower Pliocene, locality TU 1405, Rio Yaque del Norte, Arroyo Babosico. Dominican Republic. SEM photograph of a longitudinal break, × 15.
4. Figured specimen. USNM 86902. Same specimen as Plate 17, figure 3. SEM photograph of calical surface, × 10.
5. Holotype. BM(NH) R28791. Same specimen as Plate 14, figure 4. Longitudinal break, × 10.
6. Figured specimen. USNM 86902. Same specimen as Plate 17, figure 3. SEM photograph of calical surface, × 10.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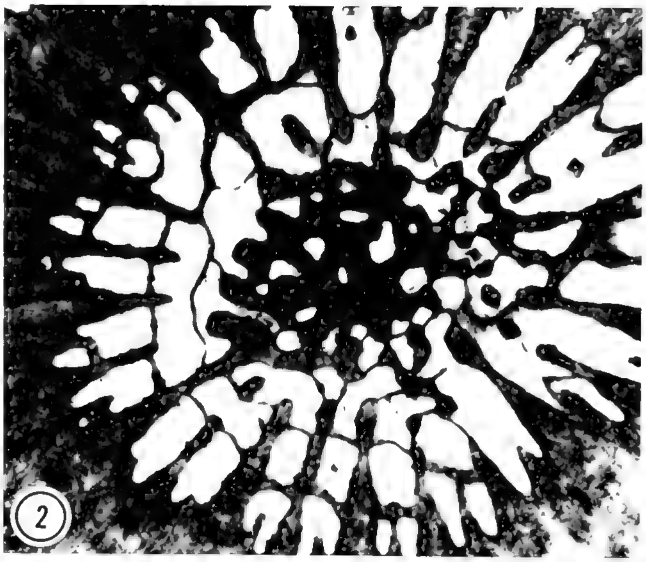
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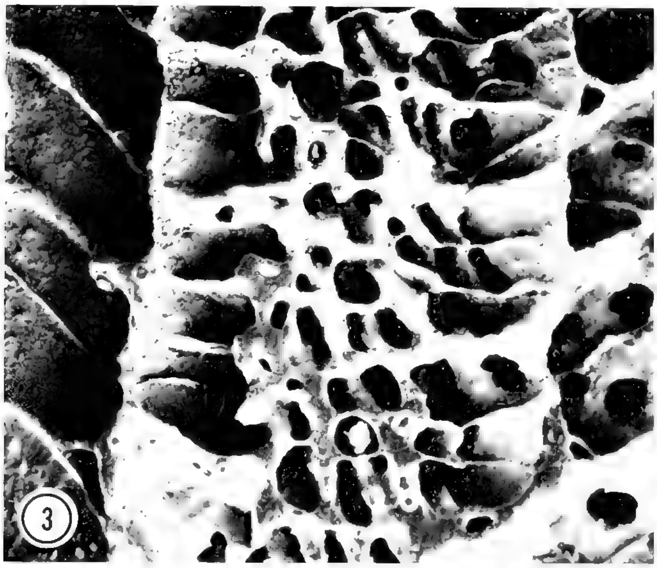
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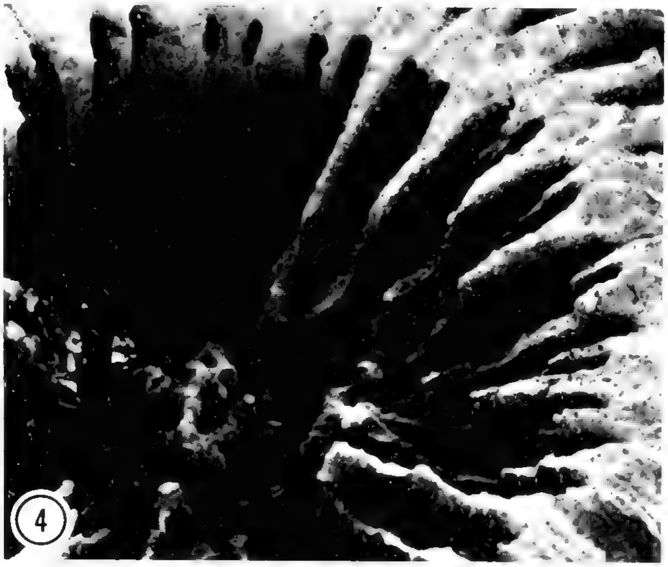
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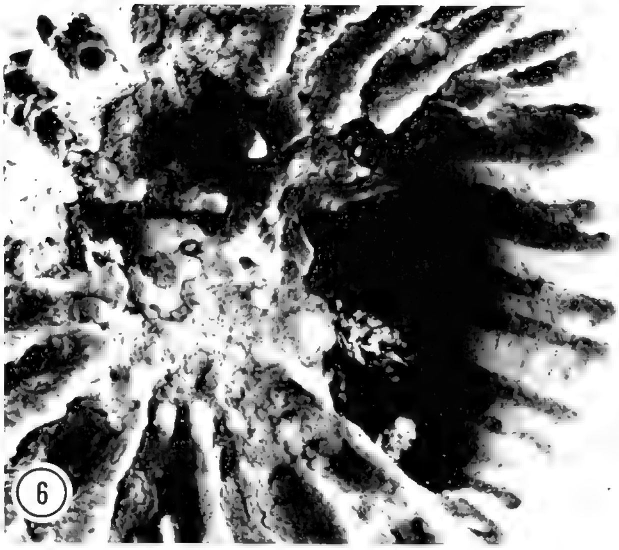
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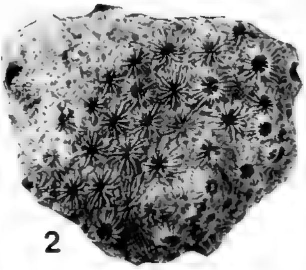

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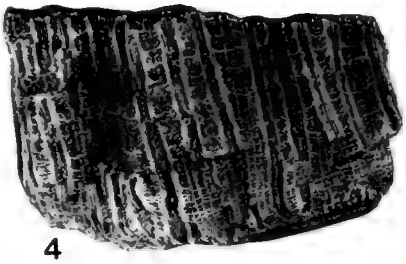

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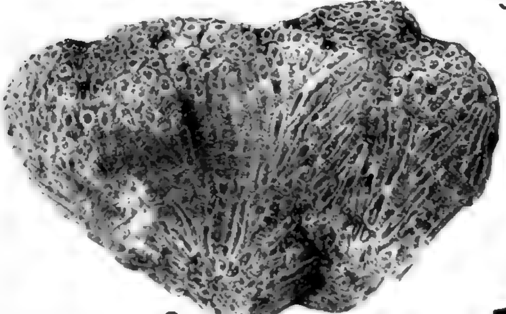

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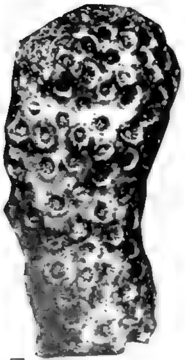

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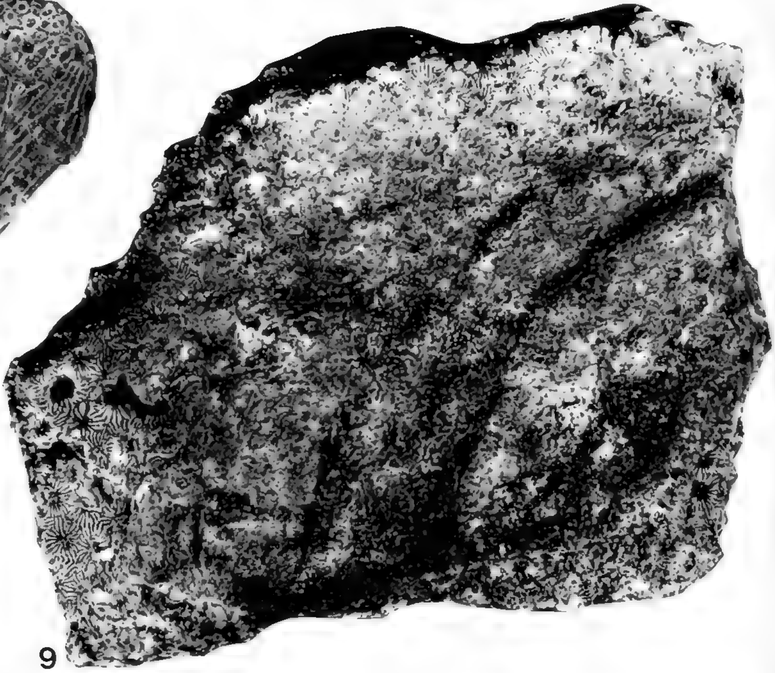

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EXPLANATION OF PLATE 18

Montastraea limbata (Duncan) . . . . page 41

Whole colonies and colony fragments. Colony morphology is highly variable, ranging from columns to irregular mounds to plates. Corallites are small and are widely spaced.

Figure

1. Holotype. BM(NH) R28780. Neogene, "Yellow Shale", Dominican Republic. Colony side, ×1.7.
2. Figured specimen. NMB D5590. Upper Miocene, locality NMB 15853, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of a colony fragment, ×1.
3. Figured specimen. NMB D5569. Upper Miocene, locality NMB 15841, Río Gurabo, Gurabo Formation, Dominican Republic. Upper surface of a colony fragment, ×1.
4. Figured specimen. NMB D5706. Upper Miocene, locality NMB 16911, Río Mao, ?Gurabo Formation, Dominican Republic. Longitudinal break through a colony fragment, ×1.
5. Possible synonym. USNM 353654 [holotype of *Orbicella limbata* var. *pennyi* Vaughan *in* Vaughan and Hoffmeister, 1926]. Lower Miocene, locality USGS 8298, Nariva Formation, Trinidad. Upper colony surface, ×1.
6. Figured specimen. USNM 66854 (NF434). Upper Miocene, locality USGS 8540, Río Gurabo, Gurabo Formation, Dominican Republic. Colony side, ×½.
7. Figured specimen. BM(NH) R28830. Neogene, "Silt of the Sandstone Plain", Dominican Republic. Side of a columnar-shaped colony, ×1.
8. Possible synonym of *Montastraea trinitatis* (Vaughan), which resembles *M. limbata*. USNM 353678 [holotype of *Orbicella cumutensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926]. Middle Miocene, locality USGS 9217, Brasso Formation, Trinidad. Surface of colony fragment, ×1.
9. Synonym. BM(NH) R28781. Holotype of *Phyllocoenia sculpta* var. *tegula* Duncan. Neogene, "Nivajé Shale", Dominican Republic. Surface of a plate-shaped colony, ×1.

EXPLANATION OF PLATE 19

Montastraea limbata (Duncan) .... page 41

Whole colonies, colony fragments, and x-radiograph of a colony. In columnar forms, columns grow upward at a rapid rate from an irregular, encrusting base. They sometimes are tall, and they may anastomose to form thickets. Corallite size and spacing vary widely among colonies.

Figure

1. Figured specimen. NMB D5654. Lower Pliocene, locality NMB 16884, Río Cana, Mao Formation, Dominican Republic. X-radiograph, × 1.
2. Figured specimen. USNM 66827 (NF439). Neogene, loc. USGS 7775, Río Gurabo, Gurabo Formation, Dominican Republic. Colony side, × 1.
3. Figured specimen. NMB D5608. Lower Pliocene, locality NMB 16814, Río Cana, Gurabo Formation, Dominican Republic. Upper surface of a plate-shaped colony, × ½.
4. Figured specimen. NMB D5725. Upper Miocene, locality NMB 16934, Río Gurabo, Gurabo Formation, Dominican Republic. Side of a columnar-shaped colony, × 1.
5. Figured specimen. NMB D5746. Lower Miocene, locality NMB 17277, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Side of a columnar thicket, × ½.
6. Figured specimen. NMB D5549. Lower Pliocene, locality NMB 15822, Río Gurabo, Mao Formation, Dominican Republic. Side of a columnar-shaped colony, × 1.


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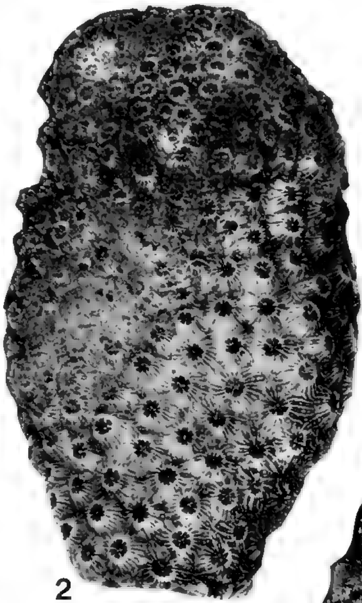
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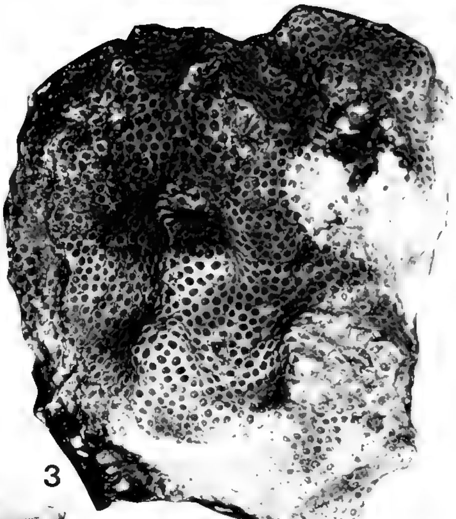
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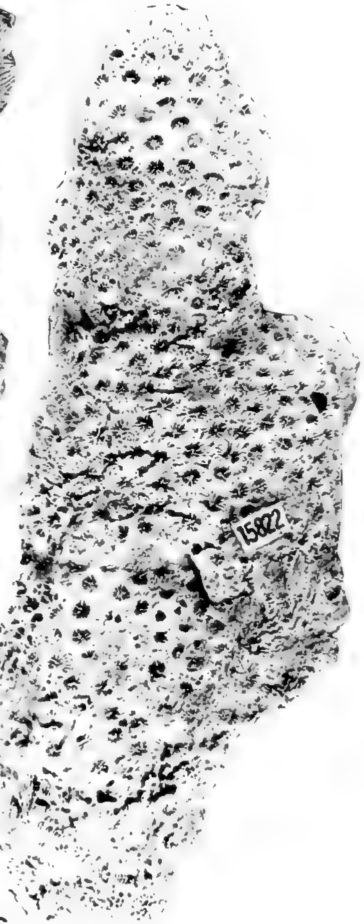

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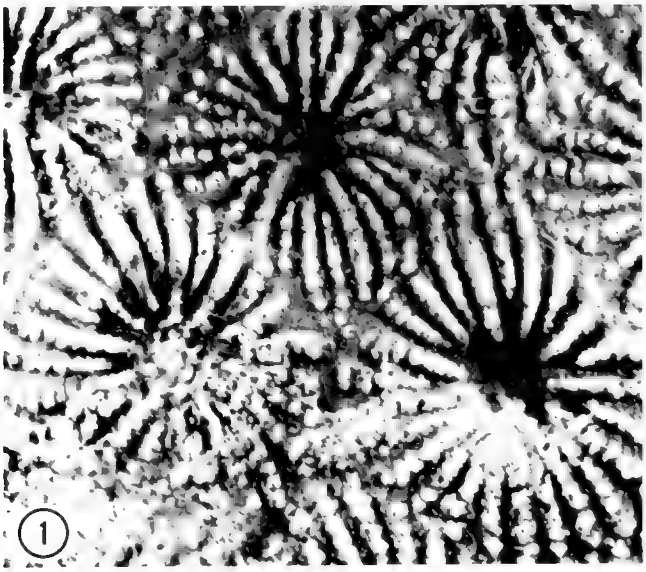
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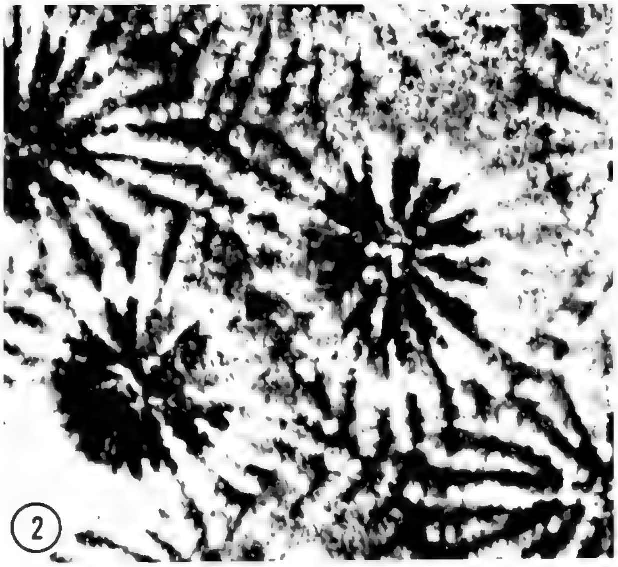
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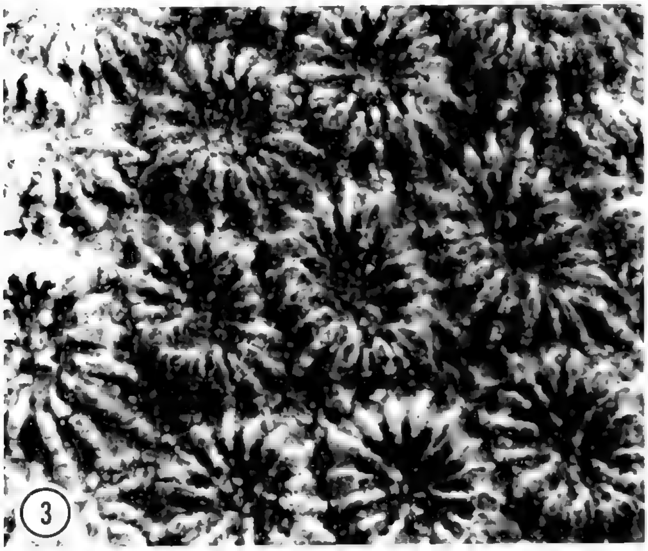
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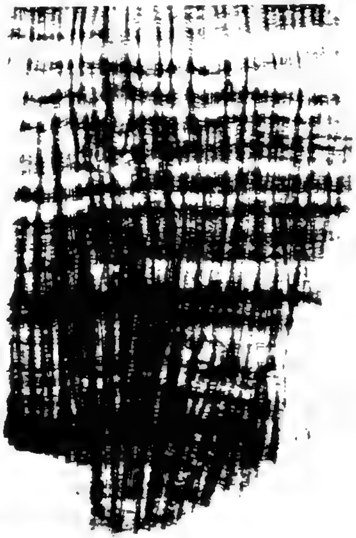
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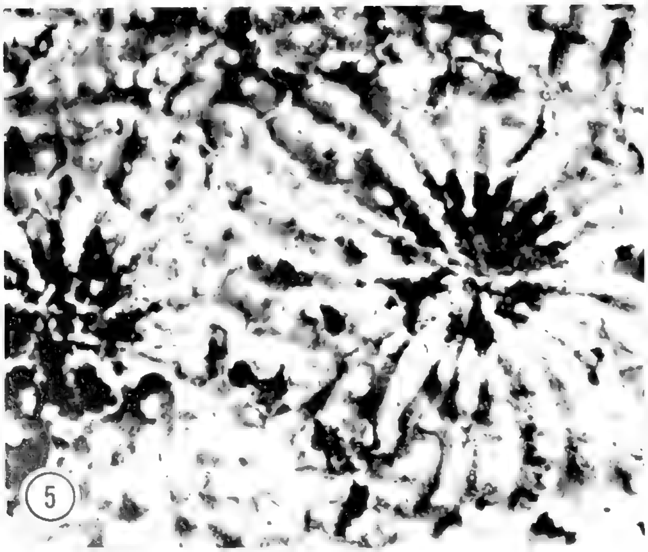
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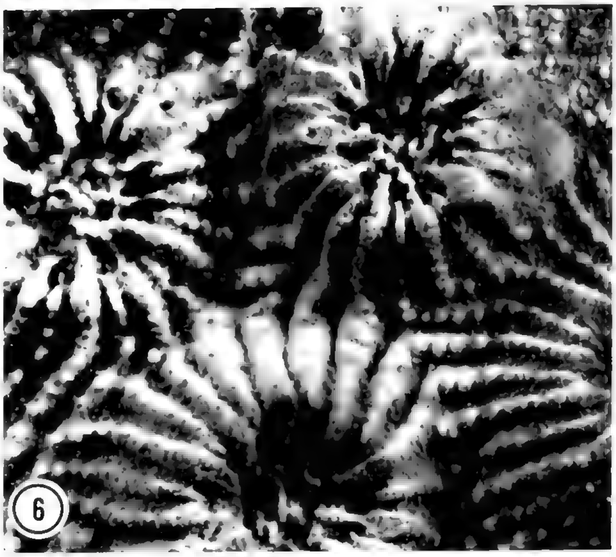
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EXPLANATION OF PLATE 20

Montastraea limbata (Duncan) . . . . page 41

Close-ups of calical surfaces and transverse thin-sections, and x-radiograph. The septa are arranged in three complete cycles from which extend elongate, equal-sized costae with finely dentate to beaded margins.

Figure

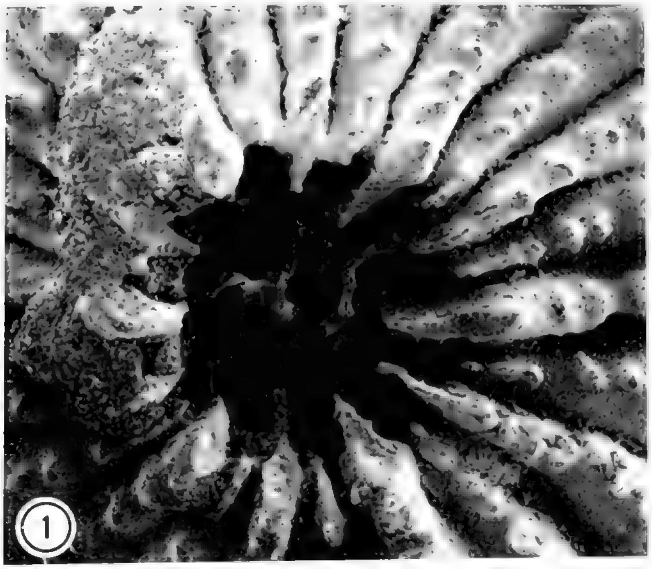
1. Holotype. BM(NH) R28780. Same specimen as Plate 18, figure 1. Calical surface, ×10.
2. Synonym. BM(NH) R28755, holotype of *Plesiastraea ramea* Duncan. Neogene, "Silt of the Sandstone Plain", Dominican Republic. Calical surface, ×10.
3. Possible synonym of *Montastraea trinitatis* (Vaughan), which resembles *M. limbata*. USNM 353678, holotype of *Orbicella cumutensis* Hoffmeister *in* Vaughan and Hoffmeister, 1926. Same specimen as Plate 18, figure 8. Calical surface, ×10.
4. Figured specimen. NMB D5593. Upper Miocene, locality NMB 15855, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, ×1.
5. Figured specimen. NMB D5580. Upper Miocene, locality NMB 15847, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
6. Figured specimen. NMB D5720. Upper Miocene, locality NMB 16933, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.

EXPLANATION OF PLATE 21

Montastraea limbata (Duncan) .... page 41

SEM photographs and thin-sections. The columella is wide and porous and formed by the inner ends of the first and second septal cycles. The first septal cycle is thicker than the second, and the third cycle is thin, short, and free. Endo- and exothecal dissepiments are well-developed.

Figure
1. Figured specimen. NMB D5725. Same specimen as Plate 19, figure 4. SEM photograph of calical surface, ×20.
2. Figured specimen. NMB D5546. Upper Miocene, locality NMB 15808, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×20.
3. Figured specimen. NMB D5608. Same specimen as Plate 19, figure 3. SEM photograph of calical surface, ×20.
4. Figured specimen. NMB D5628. Upper Miocene, locality NMB 16853, Río Cana, Cercado Formation, Dominican Republic. Transverse thin-section, ×10.
5. Figured specimen. USNM 86903. Upper Miocene, locality TU 1215, Río Gurabo, Gurabo Formation, Dominican Republic. SEM photograph of longitudinal break, ×25.
6. Figured specimen. NMB D5608. Same specimen as Plate 21, figure 3. Longitudinal thin-section, ×10.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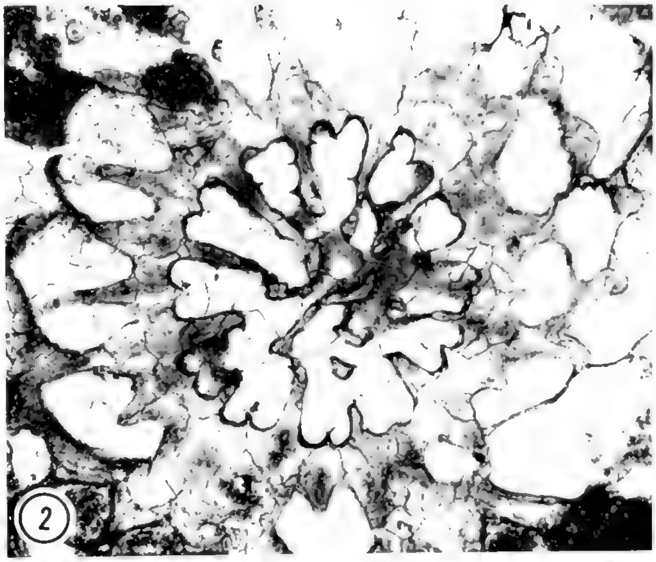
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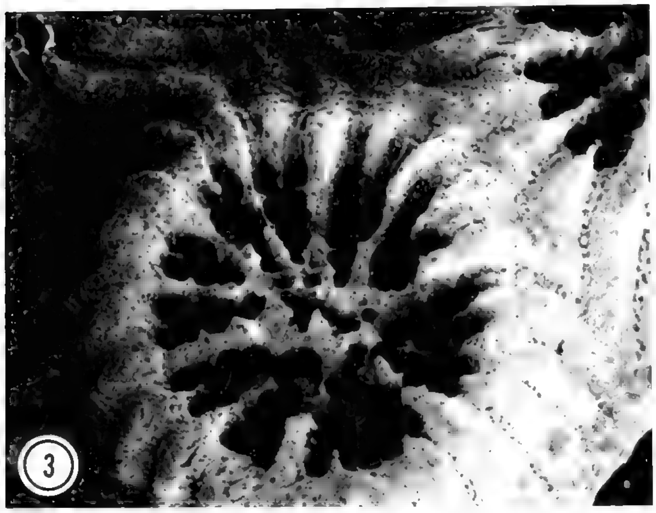
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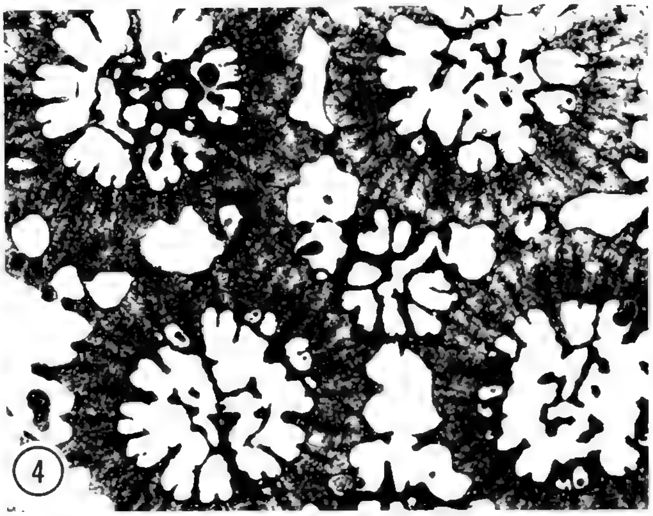
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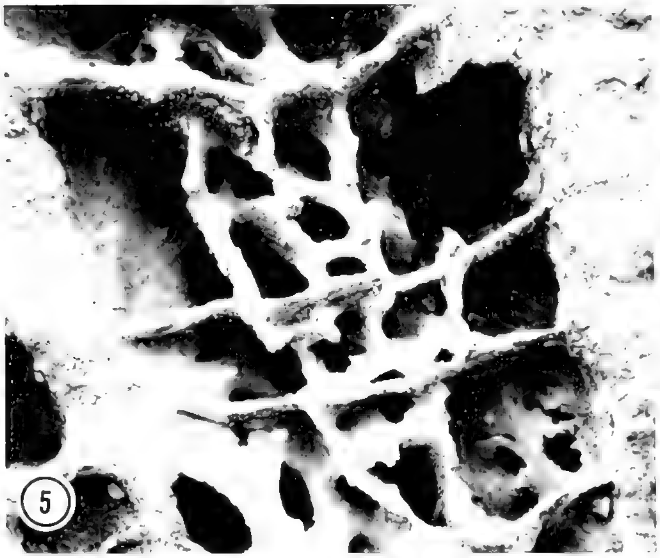
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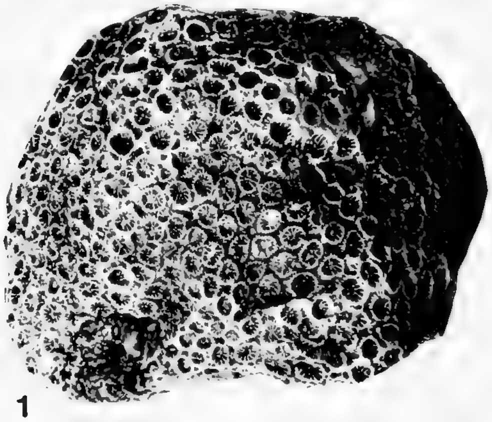
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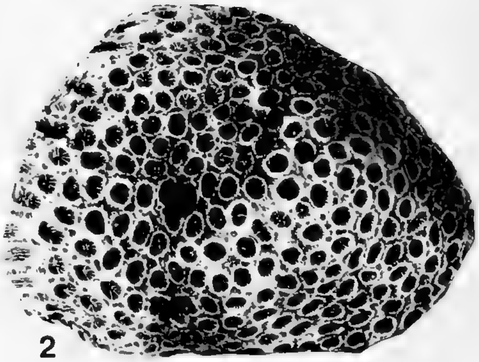
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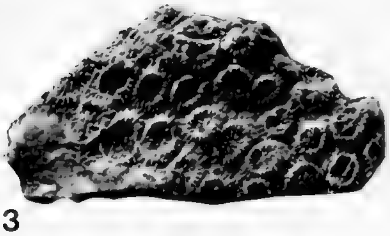
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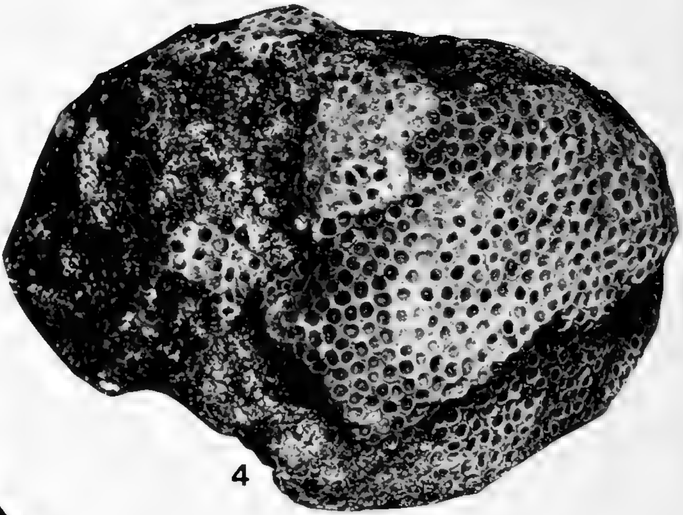
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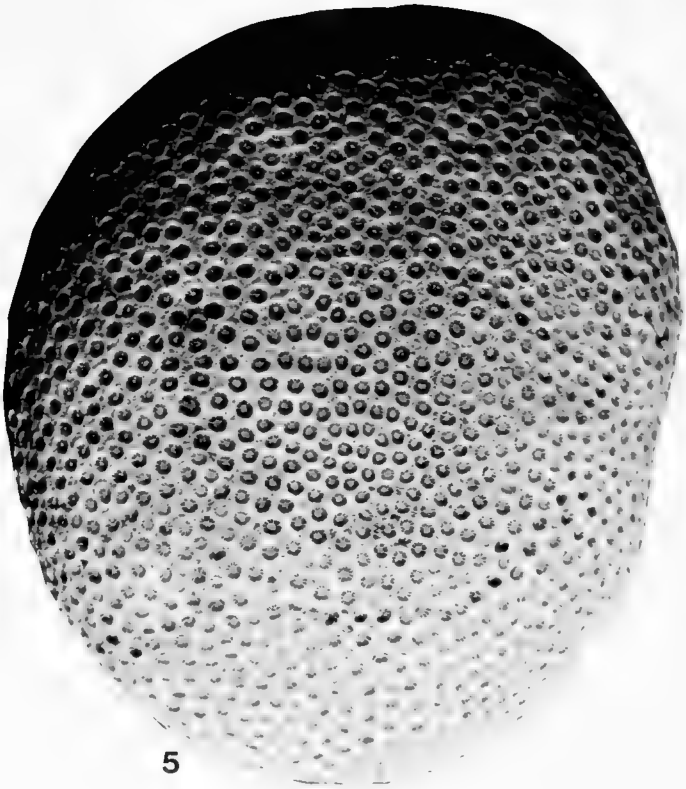
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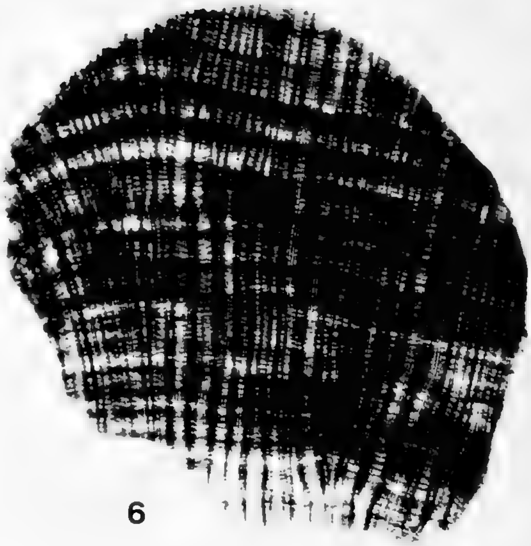
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EXPLANATION OF PLATE 22

Montastraea trinitatis (Vaughan) .... page 42

Whole colonies, colony fragments, and x-radiograph of a colony. Colony morphology ranges from relatively small knobs to large hemispherical mounds. Corallites are closely spaced, and are variably small to intermediate in size, sometimes elliptical in shape.

Figure

1. Figured specimen. NMB D5754. Lower Miocene, locality NMB 17283, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Upper colony surface, ×1.
2. Figured specimen. NMB D5737. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Upper colony surface, ×1.
3. Holotype, USNM 353657. Middle Miocene, locality USGS 8299, Manzanilla Formation, Trinidad. Surface of colony fragment, ×1.
4. Figured specimen. NMB D5741. Lower Miocene, locality NMB 16945, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Upper colony surface, ×½.
5. Holotype of *Madrepora annularis* Ellis and Solander, a species closely related to *M. trinitatis*. Hunterian Museum, Glasgow. Recent, locality unknown. Upper colony surface, ×1 (photo by Trevor Graham of the Hunterian Museum).
6. Figured specimen. NMB D5732. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. X-radiograph, ×1.

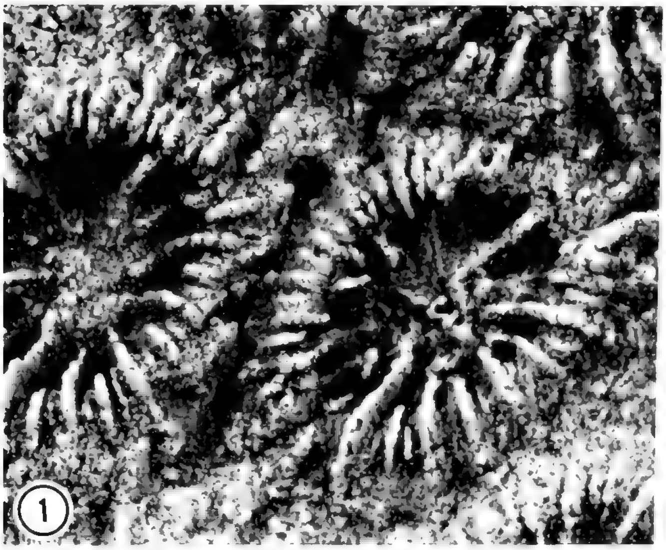
EXPLANATION OF PLATE 23

Montastraea trinitatis (Vaughan) . . . . page 42

Close-ups of calical surfaces and transverse thin-sections. The septa are arranged in three to four septal cycles with the fourth cycle ranging from absent to completely developed. The costae are weakly developed, and are roughly equal in thickness.

Figure

1. Holotype. USNM 353657. Same specimen as Plate 22, figure 3. Calical surface, ×10.
2. Figured specimen. USNM 66852 (NF492). Miocene, locality USGS 8668, Baitoa, Dominican Republic. Calical surface, ×10.
3. Figured specimen. NMB D5741. Same specimen as Plate 22, figure 4. Calical surface, ×10.
4. Figured specimen. NMB D5732. Same specimen as Plate 22, figure 6. Calical surface, ×10.
5. Figured specimen. NMB D5741. Same specimen as Plate 23, figure 3. Transverse thin-section, ×10.
6. Possible synonym. USNM 353656 [hypotype of *Heliastraea altissima* Duncan of Vaughan *in* Vaughan and Hoffmeister, 1926]. Middle Miocene, locality USGS 8297, Tamana Formation, Trinidad. Transverse thin-section, ×10.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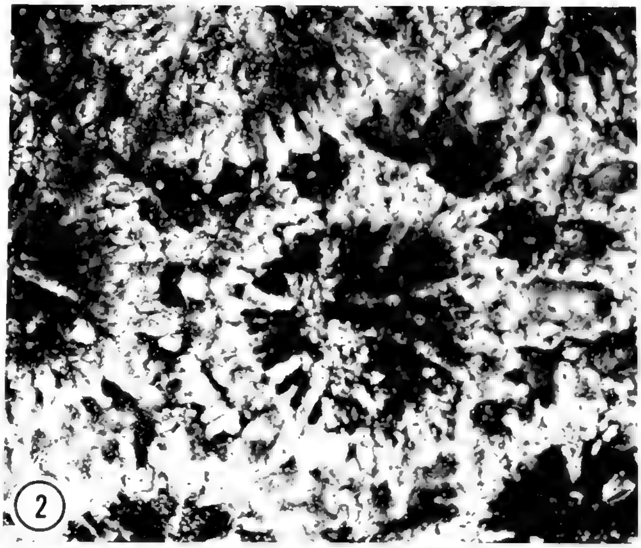
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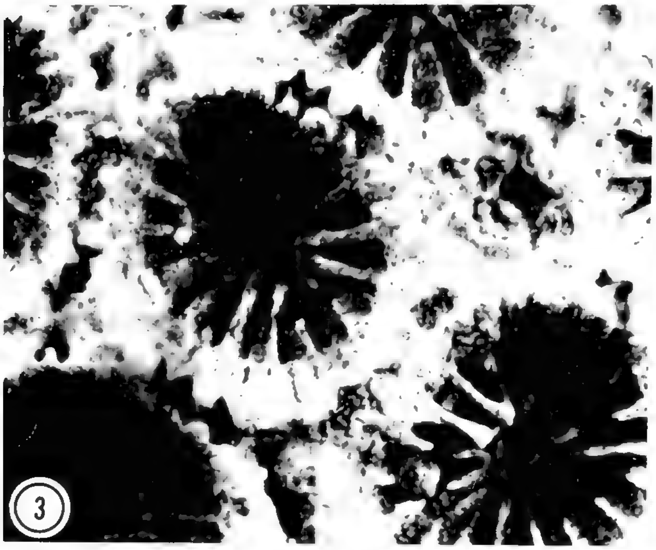
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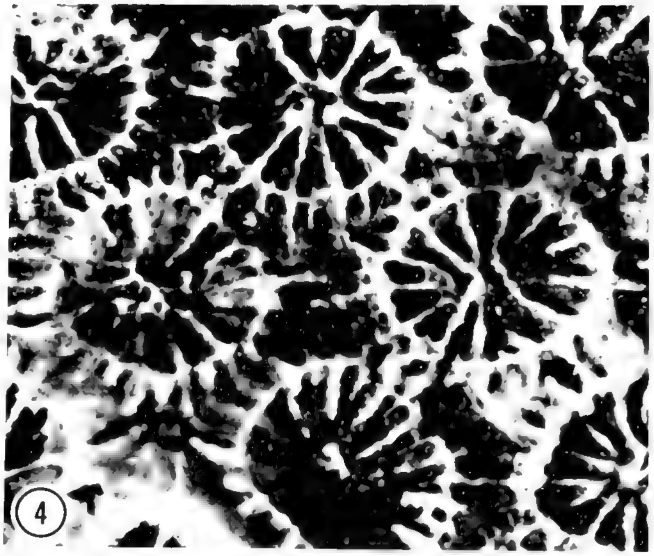
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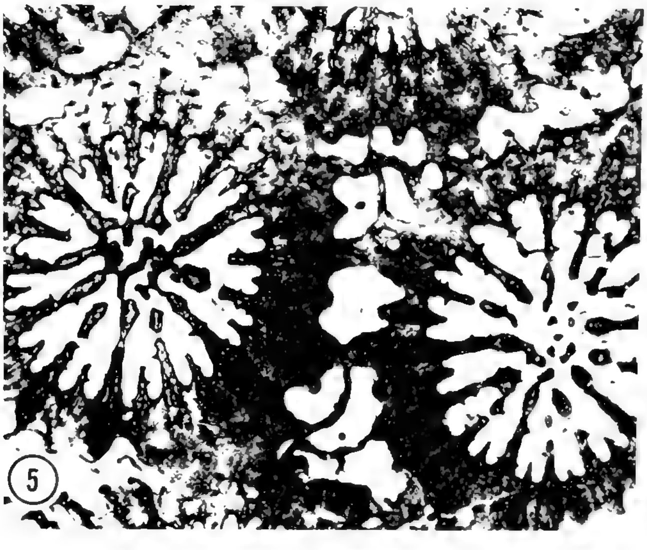
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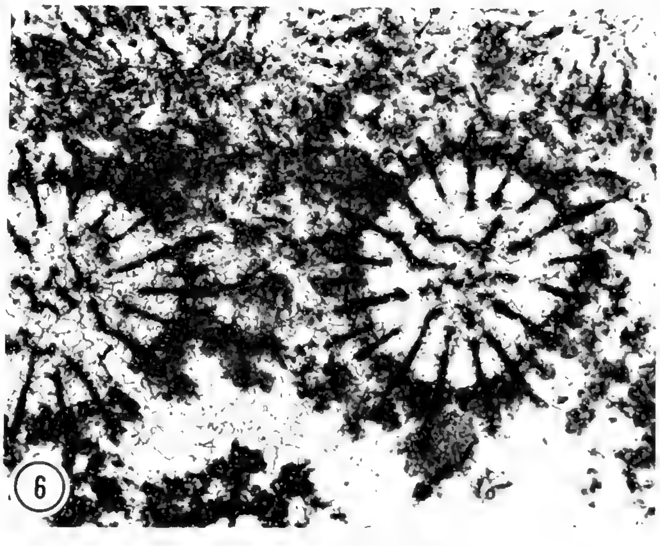
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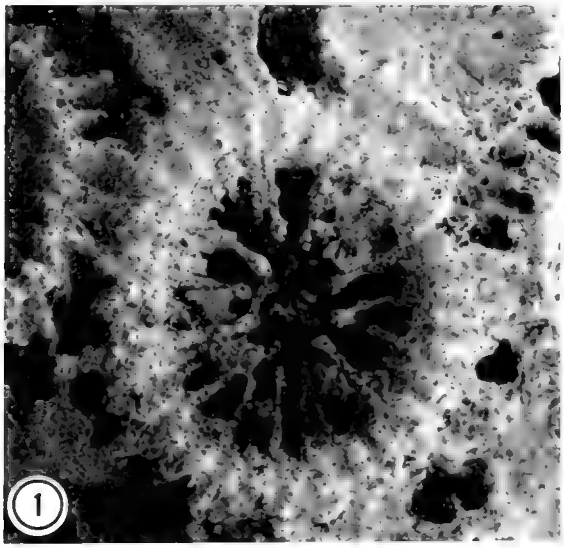
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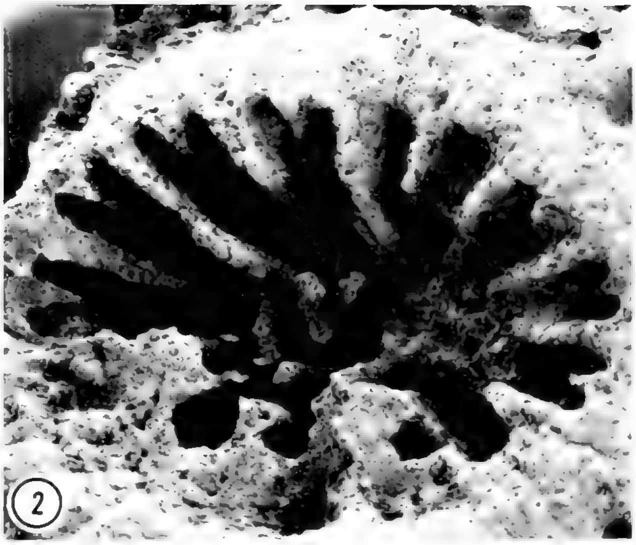
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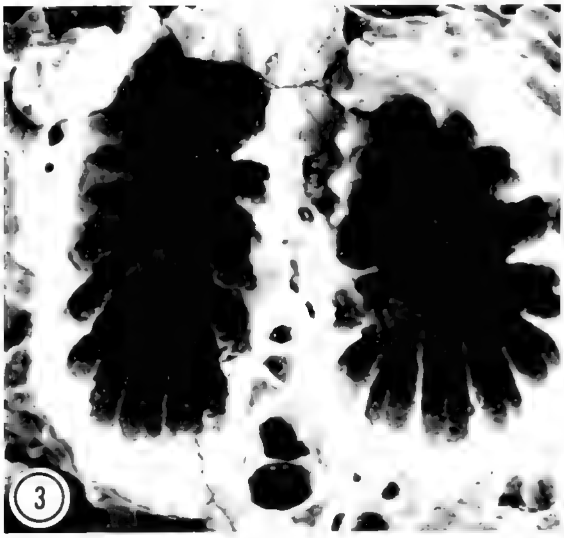
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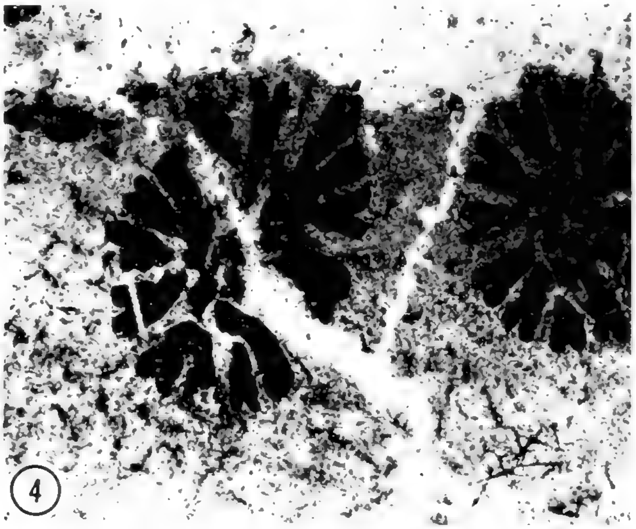
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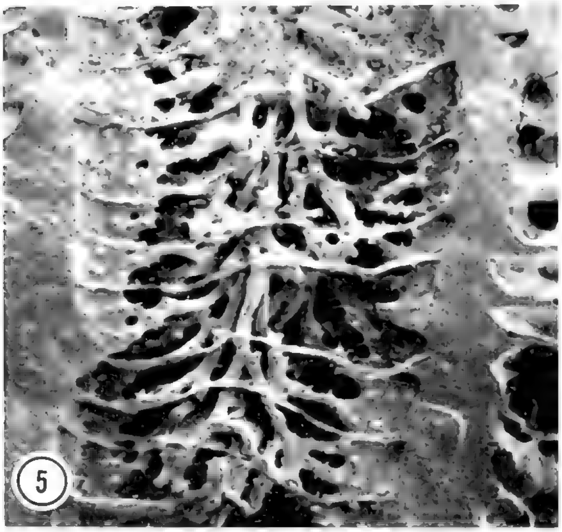
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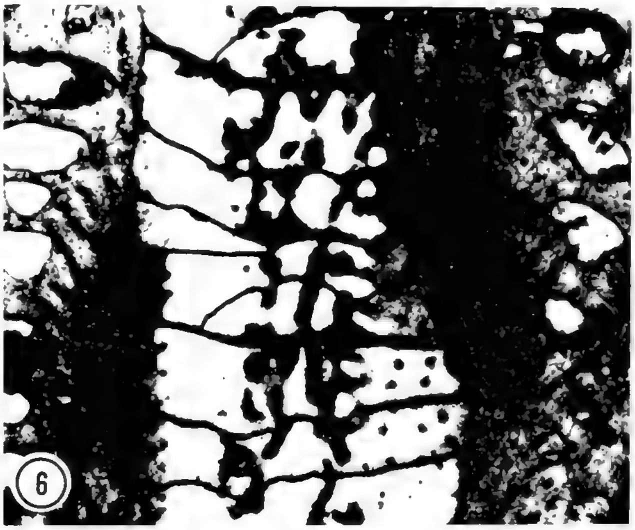
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EXPLANATION OF PLATE 24

Montastraea trinitatis (Vaughan) .... page 42

SEM photographs and transverse and longitudinal thin-sections. The columella generally is weak; however, strong, erect paliform teeth are developed in front of the first and second septal cycles. The endothecal and exothecal dissepiments and corallite wall are thick and well-developed.

Figure

1. Figured specimen. NMB D5735. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5735. Same specimen as Plate 24, figure 1. SEM photograph of calical surface, ×20.
3. Figured specimen. NMB D5730. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. SEM photograph of calical surface, ×10.
4. Possible synonym of *Montastraea limbata* (Duncan), which resembles *M. trinitatis*. USNM 353654 [holotype of *Orbicella limbata* var. *pennyi* Vaughan *in* Vaughan and Hoffmeister, 1926]. Lower Miocene, locality USGS 8298, Nariva Formation, Trinidad. Transverse thin-section, ×10.
5. Figured specimen. NMB D5730. Same specimen as Plate 24, figure 3. SEM photograph of longitudinal break, ×20.
6. Figured specimen. NMB D5729. Lower Miocene, locality NMB 16943, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Longitudinal thin-section, ×15.

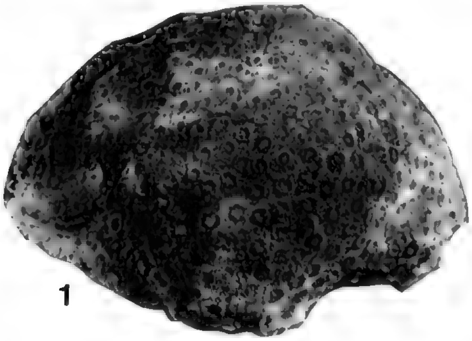
EXPLANATION OF PLATE 25

Solenastrea bournoni Milne Edwards and Haime . . . . page 44

Whole colonies and x-radiograph of a colony. Colony morphology is extremely variable, ranging from small, irregular knobs and spheres to larger, massive, hemispherical, and columnar mounds. Upward colony growth is highly regular. Corallites are relatively small and widely spaced.

Figure

1. Figured specimen. NMB D5589. Upper Miocene, locality NMB 15851, Río Gurabo, Gurabo Formation, Dominican Republic. Colony side, × 1.
2. Figured specimen. NMB D5753. Lower Miocene, locality NMB 17283, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Side of a small irregular knob-shaped colony, × 1.
3. Synonym. BM(NH) R28871 [holotype of *Plesiastraea globosa* Duncan]. Neogene, "Silt of the Sandstone Plain", Dominican Republic. Longitudinal cut through the growth axis of a colony, × 1.
4. Figured specimen. NMB D5603. Lower Pliocene, locality NMB 16811, Río Gurabo, Gurabo Formation, Dominican Republic. X-radiograph, × 1.
5. Figured specimen. NMB D5641. Upper Miocene, locality NMB 16883, Río Cana, Gurabo Formation, Dominican Republic. Upper colony surface, × 1.
6. Figured specimen. USNM 66843 (NF488). ?Lower Pliocene, locality USGS 8734, Río Mao, Gurabo Formation, Dominican Republic. Upper colony surface, × 1.
7. Synonym. BM(NH) R28758 [holotype of *Plesiastraea distans* Duncan]. Neogene, "Nivajé Shale", Dominican Republic. Upper colony surface, × 1.
8. Figured specimen. NMB D5587. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Upper colony surface, × 1.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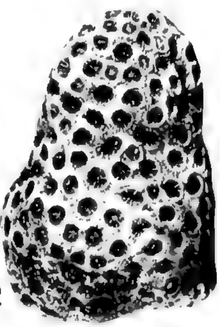
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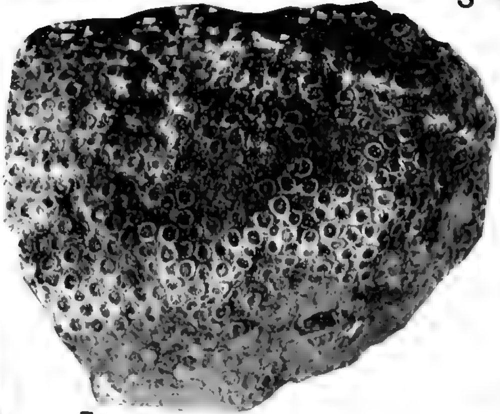
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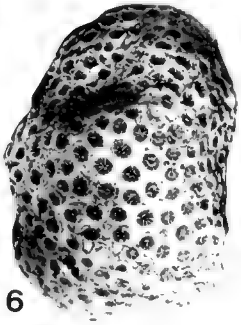
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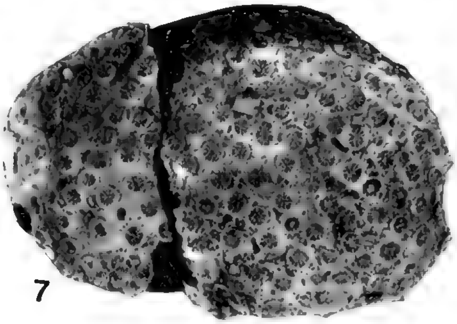
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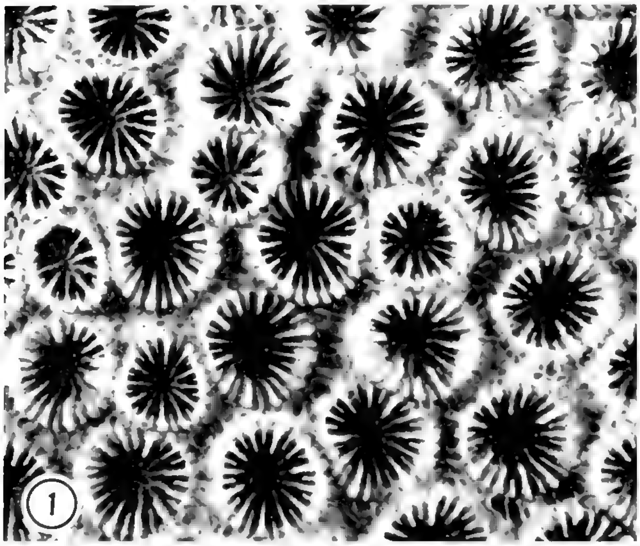
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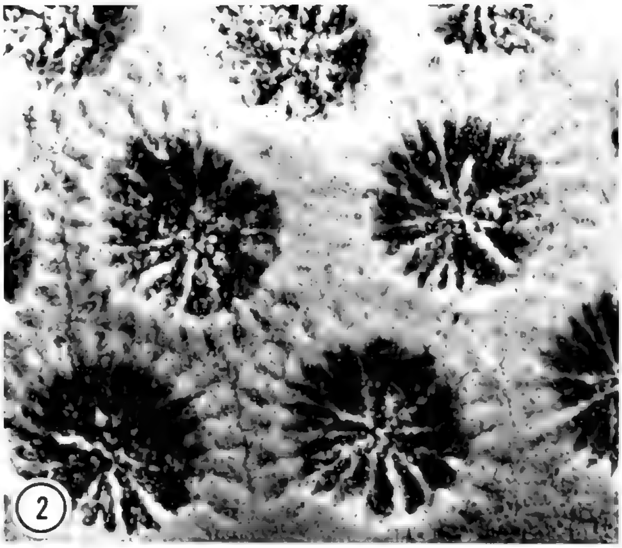
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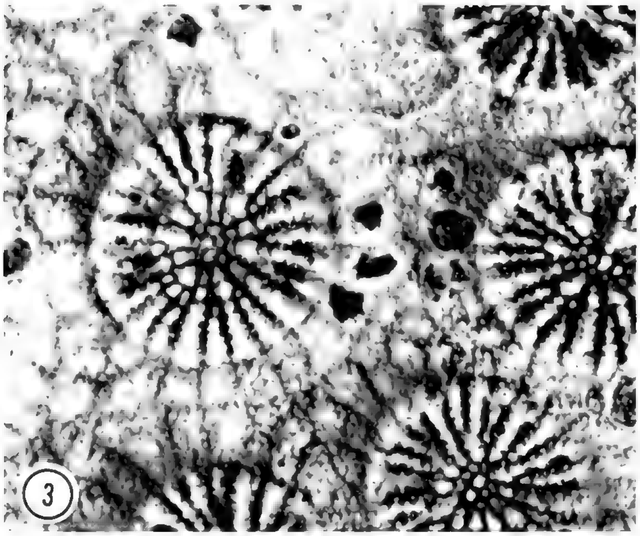
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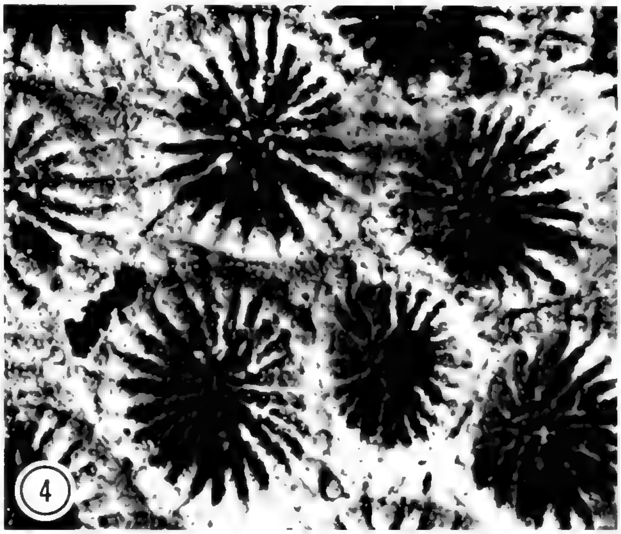
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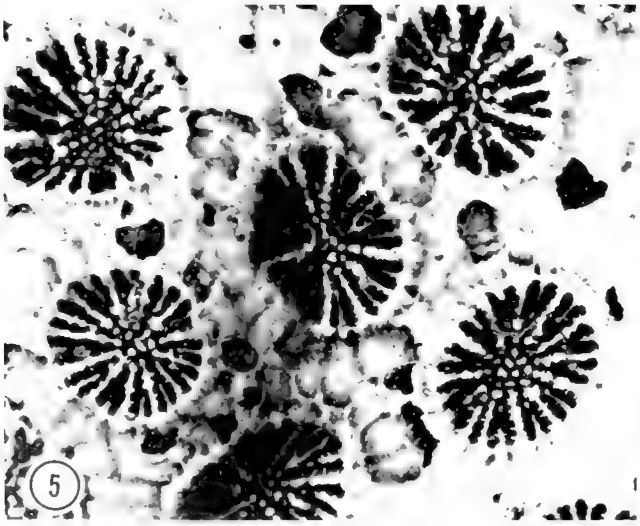
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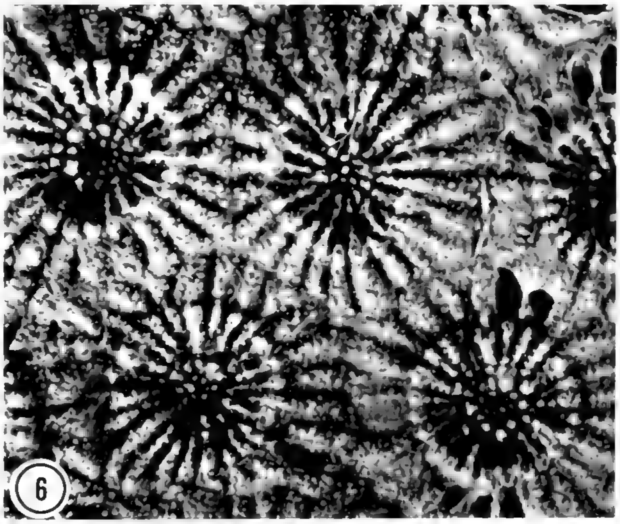
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EXPLANATION OF PLATE 26

Solenastrea bournoni Milne Edwards and Haime .... page 44

Close-ups of calical surfaces. The septa are arranged in three complete cycles with the first and second cycles extending to the columella. The third cycle is short, and usually is free, and the corallite wall is elevated.

Figure

1. Holotype. MNHNP 794. Recent, locality unknown. Calical surface, ×5.
2. Figured specimen. BM(NH) R28871. Same specimen as Plate 25, figure 3. Calical surface, ×10.
3. Figured specimen. BM(NH) R28758. Same specimen as Plate 25, figure 7. Calical surface, ×10.
4. Figured specimen. NMB D5572. Upper Miocene, locality NMB 15845, Río Gurabo, Gurabo Formation, Dominican Republic. Calical surface, ×10.
5. Figured specimen. USNM 66843 (NF488). Same specimen as Plate 25, figure 6. Calical surface, ×10.
6. Figured specimen. NMB D5589. Same specimen as Plate 25, figure 1. Calical surface, ×10.

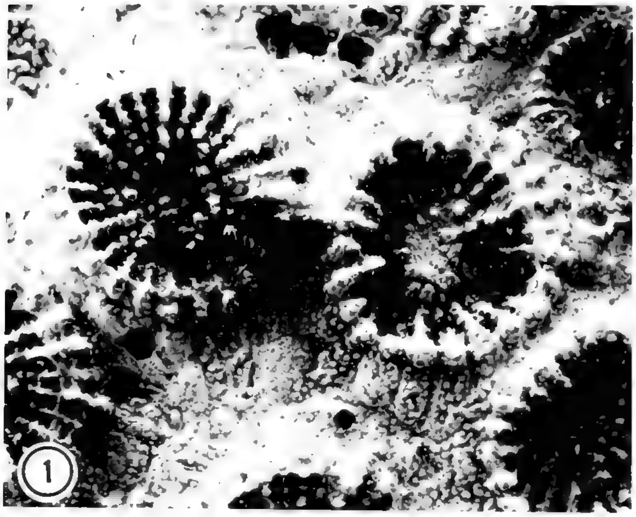
EXPLANATION OF PLATE 27

Solenastrea bournoni Milne Edwards and Haime .... page 44

SEM photographs and thin-sections. The columella is porous and wide with often well-developed paliform lobes in front of the first and second cycles. The corallite wall and exothecal dissepiments are thin.

Figure

1. Figured specimen. USNM 86910. Miocene, locality TU 1442, Río Yaque del Norte, Dominican Republic. SEM photograph of calical surface, ×10.
2. Figured specimen. NMB D5584. Upper Miocene, locality NMB 15850, Río Gurabo, Gurabo Formation, Dominican Republic. Transverse thin-section, ×10.
3. Figured specimen. NMB D5641. Same specimen as Plate 25, figure 5. SEM photograph of calical surface, ×15.
4. Figured specimen. NMB D5794. Lower Pliocene, locality NMB 15822, Río Gurabo, Mao Formation, Dominican Republic. Transverse thin-section, ×10.
5. Figured specimen. USNM 86911. Lower Pliocene, locality TU 1344, Río Gurabo, Mao Formation, Dominican Republic. SEM photograph of a longitudinal break, ×25.
6. Figured specimen. NMB D5584. Same specimen as Plate 27, figure 2. Longitudinal thin-section, ×10.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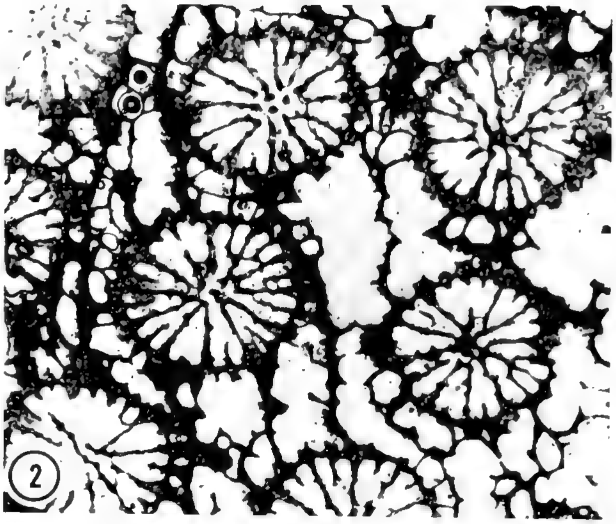
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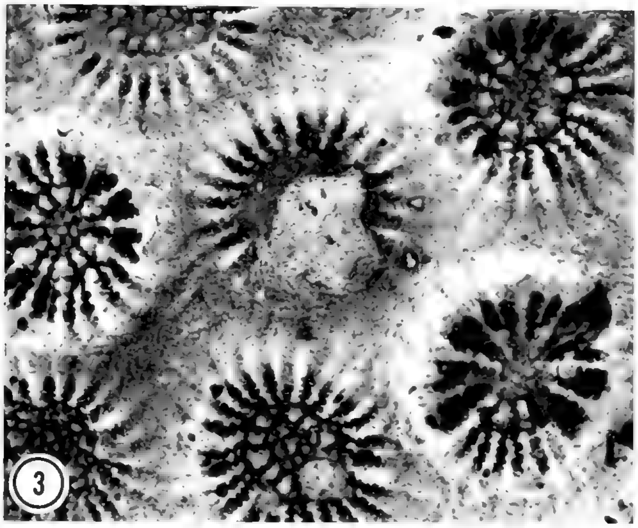
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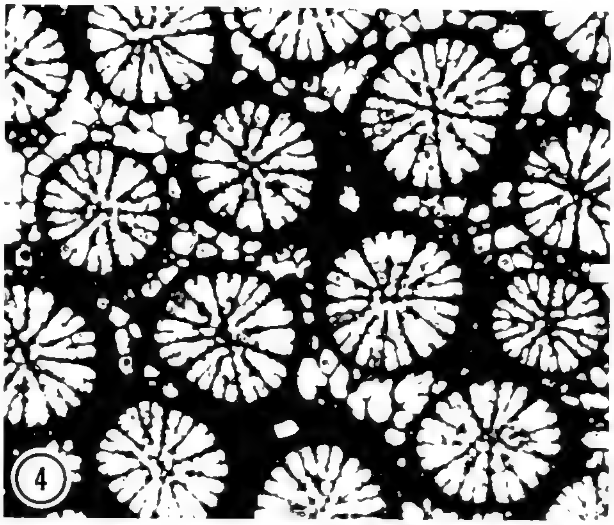
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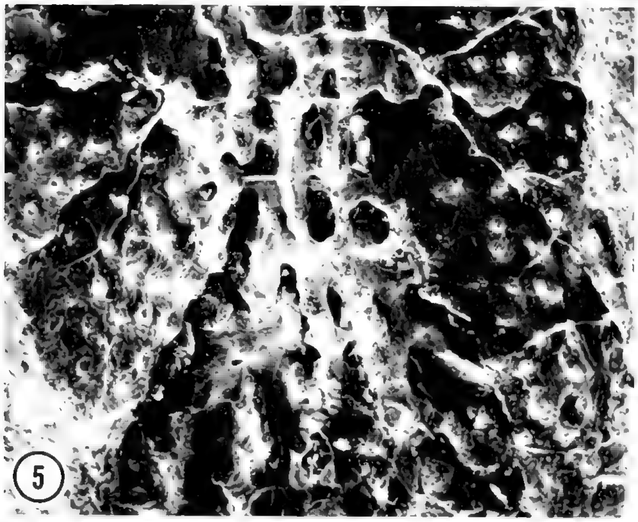
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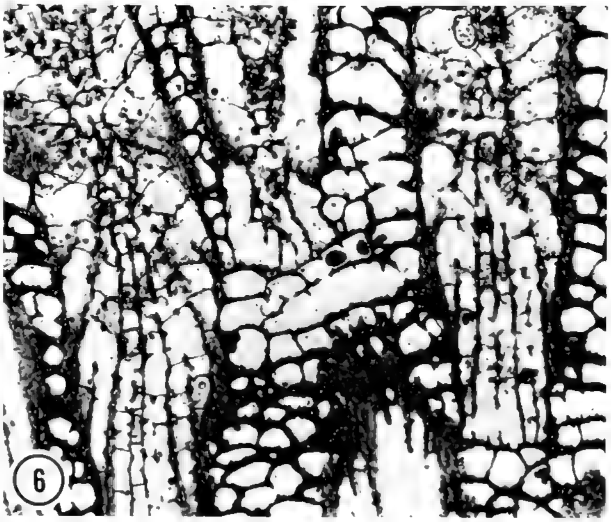
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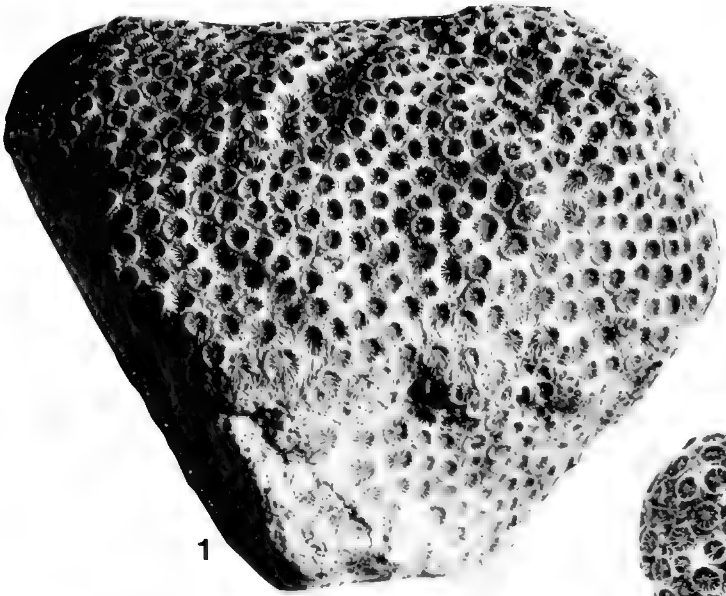
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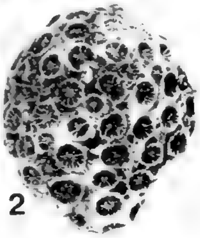
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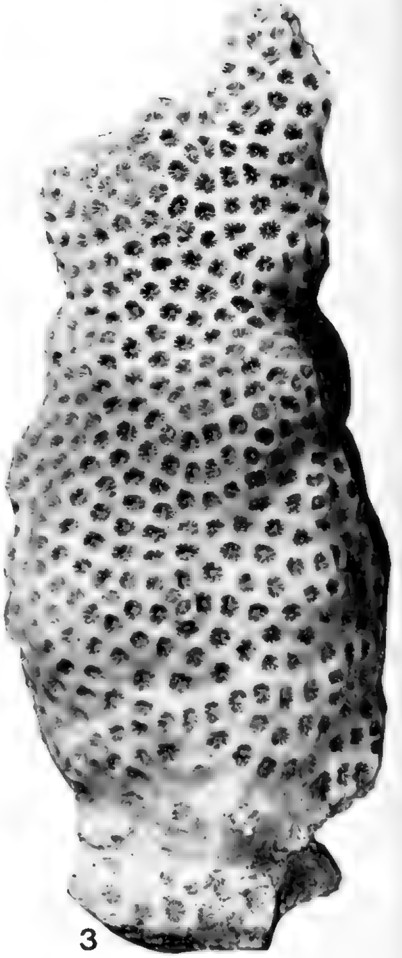
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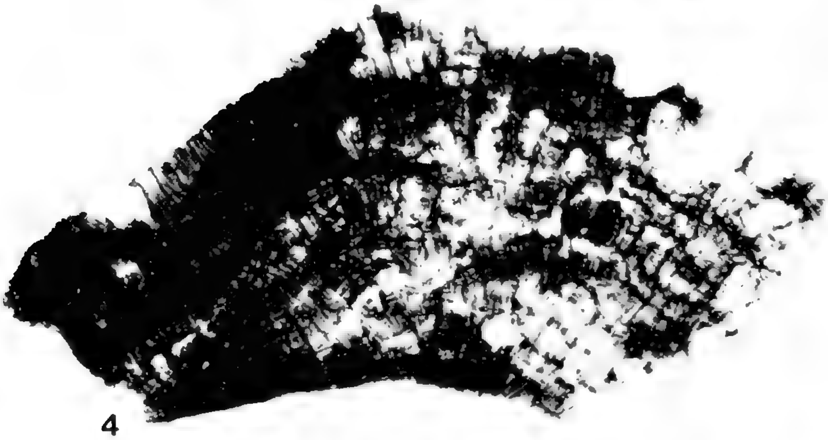
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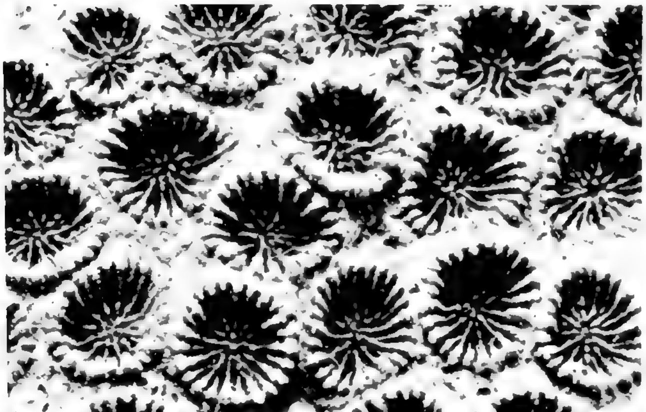
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EXPLANATION OF PLATE 28

Solenastrea hyades (Dana) .... page 45

Whole colonies, x-radiograph, and close-ups of calical surfaces. Colonies generally are encrusting knobs or moderate-sized hemispherical mounds. Upward colony growth is highly irregular. Corallites are relatively large, and are variably spaced.

Figure

1. Figured specimen. YPM 1586 [Verrill's (1901) specimen of *S. hyades* (Dana)]. Recent, St. Thomas. Colony side, ×½.
2. Figured specimen. NMB D5727. Upper Miocene, locality NMB 16939, Río Yaque del Norte, Baitoa Formation, Dominican Republic. Upper surface of a knob-shaped colony, ×1.
3. Synonym. YPM 1727 [holotype of *Astraea excelsa* Dana]. Recent, West Indies. Side of a columnar-shaped colony, ×1
4. Figured specimen. NMB D5627. Upper Miocene, locality NMB 16853, Río Cana, Cercado Formation, Dominican Republic. X-radiograph, ×1.
5. Figured specimen. YPM 1586. Same specimen as Plate 28, figure 1. Calical surface, ×5.
6. Synonym. UF 8291 [holotype of *Montastrea peninsularis* Weisbord]. Lower Miocene, Tampa Formation, Ballast Point, Florida. Calical surface, ×10.

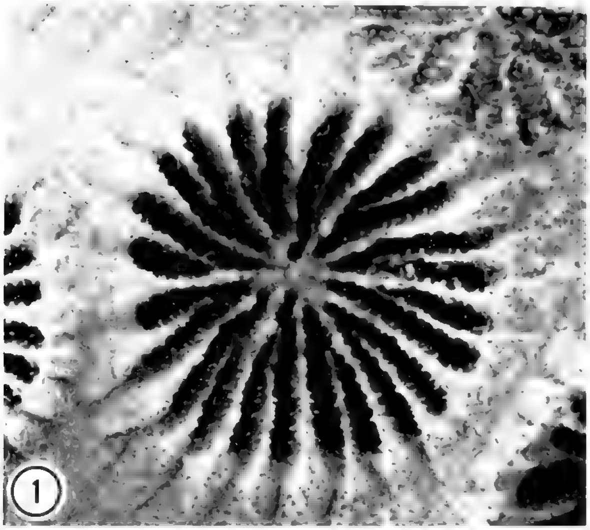
EXPLANATION OF PLATE 29

Solenastrea hyades (Dana) .... page 45

SEM photographs and thin-sections. The columella is thin and less porous, with few or no paliform lobes. The third septal cycle is relatively long, and it fuses with the second septal cycle. The corallite wall and exothecal dissepiments are relatively thick.

Figure

1. Figured specimen. USNM 36662 (NF499). Recent, 3–7 m depth, Cedar Key, Florida. SEM photograph of a calice, ×20.
2. Figured specimen. USNM 36662 (NF499). Same specimen as Plate 29, figure 1. Transverse thin-section, ×10.
3. Figured specimen. NMB D5627. Same specimen as Plate 28, figure 4. SEM photograph of a calice, ×20.
4. Figured specimen. NMB D5627. Same specimen as Plate 29, figure 3. Transverse thin-section, ×10.
5. Figured specimen. NMB D5627. Same specimen as Plate 29, figure 3. SEM photograph of a longitudinal break, ×20.
6. Figured specimen. USNM 36662 (NF499). Same specimen as Plate 29, figure 1. Longitudinal thin-section, ×10.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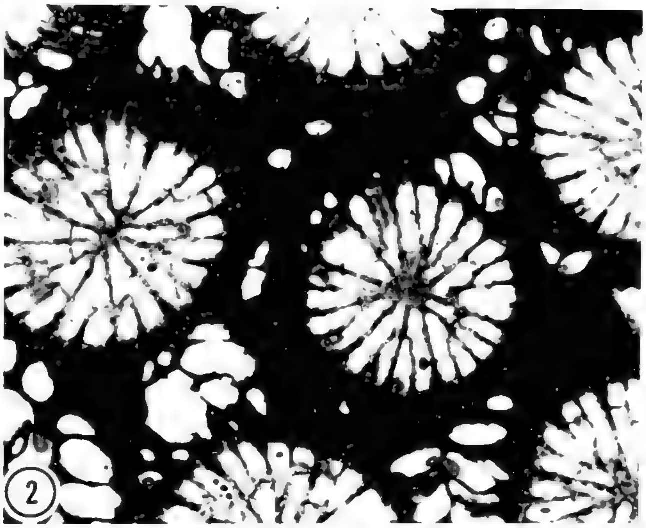
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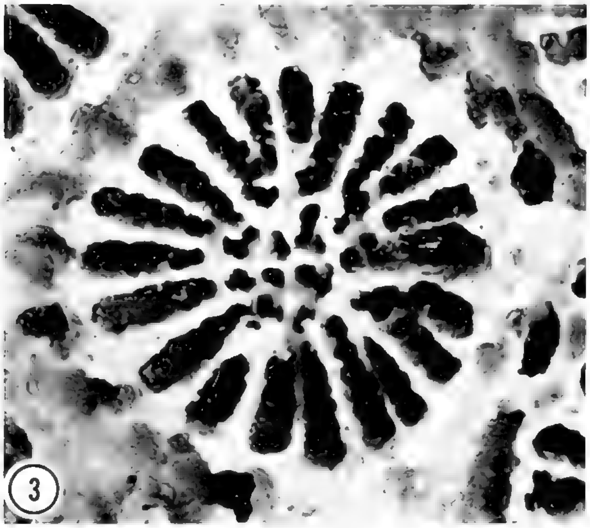
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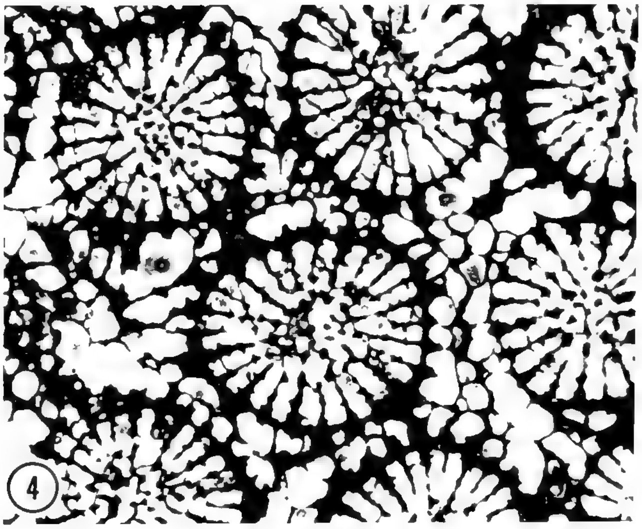
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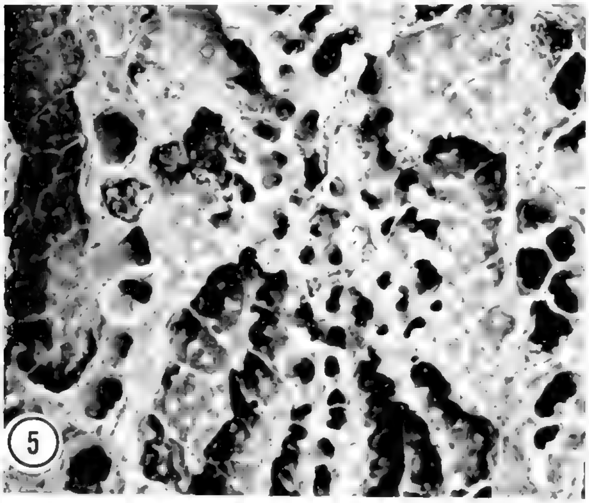
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Note: Page numbers are in light face; plate numbers are in **bold face** type; the page numbers on which principal discussions occur are in *italics*.

PREPARATION OF MANUSCRIPTS

Bulletins of American Paleontology usually comprises two or more separate monographs in two volumes each year. This series is a publication outlet for significant longer paleontological monographs for which high quality photographic illustrations and the large quarto format are a requisite.

Manuscripts submitted for publication in this monograph series must be typewritten, and double-spaced *throughout* (including direct quotations and references). All manuscripts should contain a table of contents, lists of text-figures and (or) tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be stated in the metric system, alone or in addition to the English system equivalent. The maximum dimensions for photographic plates are 178 mm × 229 mm (7″ × 9″; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼″) or full page (178 mm; 7″) width, but arrangements can be made to publish text-figures that must be larger. Any lettering in illustrations should follow the recommendations of Collinson (1962).

Authors must provide three (3) copies of the text and accompanying illustrative material. The text and line-drawings may be reproduced xerographically, but glossy prints at publication scale must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

All dated text-citations must be referenced. Additional references may be listed separately if their importance can be demonstrated by a short general comment, or individual annotations. Referenced publication titles must be spelled out in their entirety. Citations of illustrations within the monograph bear initial capitals (*e.g.*, Plate, Text-figure), but citations of illustrations in other articles appear in lower-case letters (*e.g.*, plate, text-figure).

Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays. These photomounts should be retained by the author until the manuscript has been formally accepted for publication. Explanations of text-figures should be interleaved on separate numbered pages within the text, and the approximate position of the text-figure in the text should be indicated. Explanations of plates follow the Bibliography.

Authors are requested to enclose $10 with each manuscript submitted, to cover costs of postage during the review process.

Collinson, J.
1962. *Size of lettering for text-figures.* Journal of Paleontology, vol. 36, p. 1402.