Journal of Paleontology, 93(1), 2019, p. 1–24

0022-3360/15/0088-0906
doi: 10.1017/jpa.2018.45

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Early Miocene shallow-water corals from La Guajira, Colombia: part I, Acroporidae–Montastraeidae

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Abstract.—We document for the first time Miocene corals from the Siamaná and Jimol formations of the Cocinetas Basin in La Guajira Peninsula, northern Colombia. This is the first of two contributions dedicated to the description and detailed illustration of morphospecies collected during two scientific expeditions (2011, 2014) to the remote region. Here we report coral morphospecies attributed to the families Acroporidae, Agathiphylliidae, Astrocoeniidae, Caryophylliidae, Diploastraeidae, Merulinidae, and Montastraeidae. Eighteen species belonging to these seven families, included in nine genera, are described. Fifteen species are assigned to established taxa, while three remain in open nomenclature. Of the species identified, only *Montastraea cavernosa* (Linnaeus, 1767) exists today. The coral taxa described are typical of the Oligocene–Miocene transition and were important components of shallow-water reefs in the Caribbean and Gulf of Mexico region during this period. The occurrence of *Agathiphyllia* spp., *Antiguastrea*, and *Diploastrea* spp. confirms the presence of these genera in the Miocene of the Southern Caribbean. Coral assemblages suggest that the La Guajira coral community thrived in calm and shallow waters.

Introduction

Shallow-water reef corals play a fundamental ecological and structural role in tropical marine ecosystems. For this reason, their distribution across time and space is of great interest to paleontologists, biologists, and environmental managers (Greenstein, 2007; Pandolfi and Jackson, 2007; Bennington and Aronson, 2012). An understanding of coral biodiversity and the processes that have influenced taxonomic composition of reef corals over geological timescales is useful in understanding how reef ecosystems will respond to present-day environmental stressors (Pandolfi, 2011; van Woesik et al., 2012; López-Pérez, 2017).

Paleontological studies of zooxanthellate corals in Caribbean shallow waters date back to the start of the twentieth century (e.g., Vaughan, 1900, 1901, 1919). Since then, numerous studies and taxonomical descriptions based on the morphology of the skeleton have been carried out (e.g., Vaughan, 1919; Wells, 1936, 1956; Vaughan and Wells, 1943; Weisbord, 1971, 1973; Frost and Langenheim, 1974). Subsequently, more detailed descriptions of the families Astrocoeniidae and Faviidae were provided by Foster (1987), Budd (1991), Budd et al. (1992, 1994), and Budd and Johnson (1999). Since publication of these works, there have been important advances in the taxonomy and phylogeny of cnidarians, particularly of the order Scleractinia (Fukami et al., 2004; Budd and Stolarski, 2009, 2011; Budd et al., 2010, 2012), clarifying, in part, their phylogenetic relationships, as well as the key macrostructural, micromorphological, and microstructural key characters for the classification of fossils and recent samples. As such, it is a fitting time to reestablish the morphologic basis for identification of Cenozoic coral species. Furthermore, phenotypic description of taxa from diverse localities provides a critical source of information in establishing regional variability and assessing evolutionary processes in time and space (Jablonski and Shubin, 2015).

In addition to significant advances in coral systematics, a number of recent works have contributed updated paleoecological information on coral communities of the Caribbean and western Atlantic region (e.g., Geister, 1975, 1983, 1992; Budd et al., 1995, 1996, 2011; Budd, 2000; Johnson, 2001, 2007; Klaus and Budd, 2003; Stemann, 2003; Johnson et al., 2008, 2009; Klaus et al., 2012). Three important events of coral faunal turnover and speciation have been recognized within the region: the Eocene-Oligocene (ca. 34 Ma), the Oligocene-Miocene (ca. 23 Ma), and the Pliocene-Pleistocene (ca. 2.6 Ma) (Budd et al., 1994, 2011; Budd, 2000). According to these studies, at the Oligocene–Miocene transition, reef-building capacity was greatly reduced due to the loss of an estimated 50% of zooxanthellate corals (Edinger and Risk, 1994, 1995; Budd, 2000; Johnson et al., 2008, 2009).

Although these studies have provided insights into the coral diversity during important periods of speciation and extinction, few have addressed the Oligocene to Miocene transition in the southern Caribbean–northern South America region (Johnson et al., 2009), and no significant study has been performed on the continental fossil reefs of Colombia. The current study is based on new coral collections from early Miocene reefs of the Cocinetas Basin in La Guajira Peninsula, northern Colombia. The purpose of this work is to provide a taxonomical account of this collection that will serve for future work on the Cenozoic corals of the southern Caribbean. We describe the morphospecies included in seven of the 12 families found, along with their occurrences in other regions and paleoenvironmental significance.

Geologic setting

The coral specimens of the present study were collected from the Siamaná and Jimol formations in the Cocinetas Basin, in the La Guajira Peninsula, northeast Colombia (Fig. 1). The Siamaná Formation ranges from the late Oligocene to the early Miocene (Fig. 2) (Teatin, 1991; Silva-Tamayo et al., 2017). The formation is exposed in the remote northeastern foothills of the Serranía de Cocinas, south of Serranía de Jarara and west of Serranía de Macuira (Fig. 1.2). The lower Miocene deposits are characterized by shallow reefal limestones onlapping basement paleohighs (Renz, 1960; Lockwood, 1965; Rollins, 1965; Macellari, 1995). The thickness of the Siamaná Formation is highly variable, ranging from a few meters south of Serranía de la Macuira (Zapata, 2010) to over 240 m near Uitpa (Rollins, 1965) and over 450 m south of Serranía de Jarara (Lockwood, 1965).

The Siamaná Formation is conformably overlain by the early Miocene Uitpa Formation, which in turn is overlain by the latest early Miocene Jimol Formation (Fig. 2) (Moreno et al., 2015). The Uitpa Formation is composed of deepwater silts and shales, with abundant macrofauna (Carrillo-Briceño et al., 2016). Fine-grained, calcareous sandstone interbeds are common in the lower and upper parts of this formation (Thomas, 1972). Conformably overlying the Uitpa Formation is the Jimol Formation, which is mainly composed of lithic sandstones and mudstones with high fossil content (Hendy et al., 2015; Moreno et al., 2015). According to Moreno et al. (2015), the formation comprises shallow marine deposits with hermatypic zooxanthellate corals and was deposited in an inner shelf at less than 50 m depth.

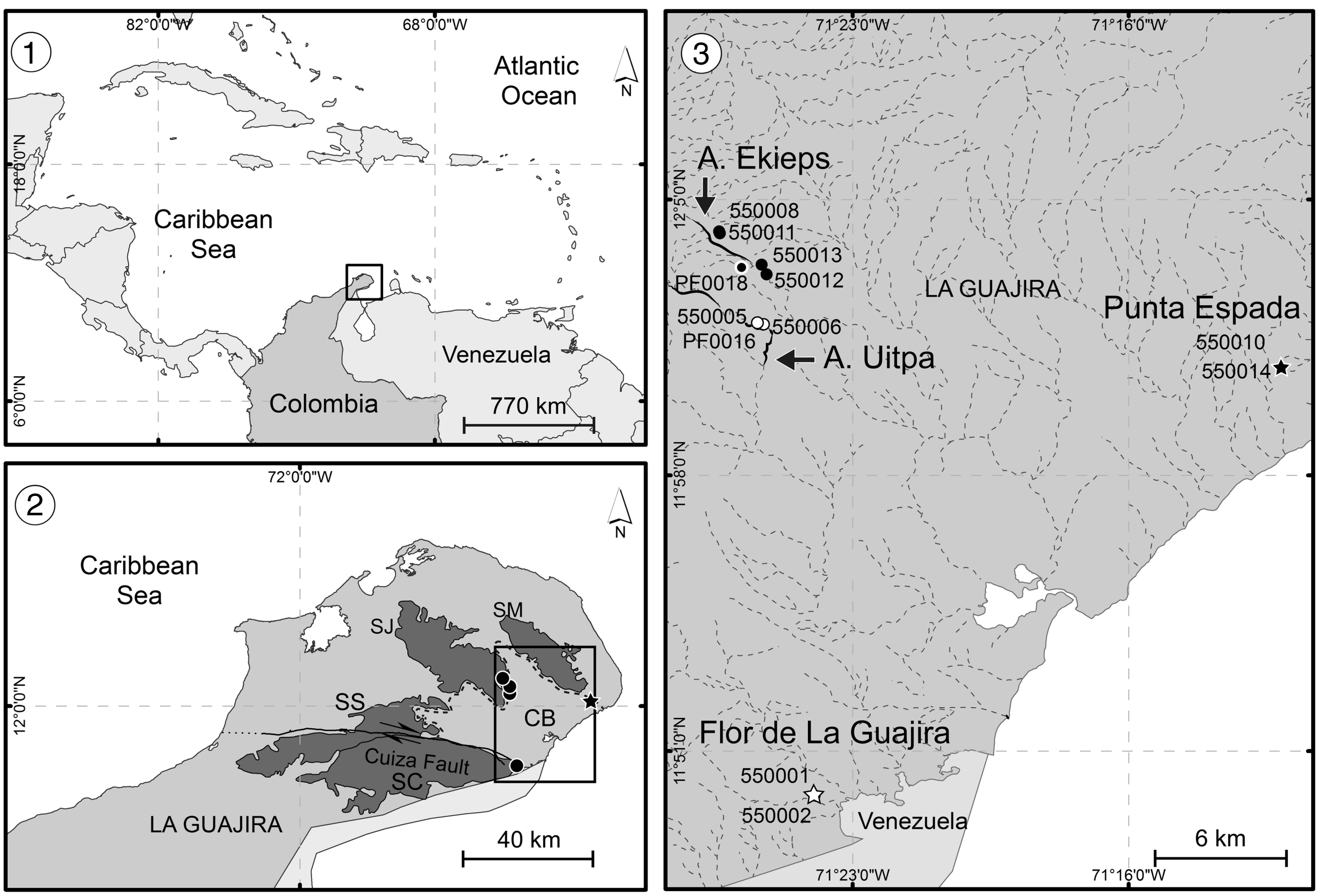

Figure 1. (**1**) General location of the La Guajira Peninsula along the southern margin of the Caribbean Sea. (**2**) Location of Cocinetas Basin (CB), flanked by the Serranía de la Macuira (SM), Serranía de Jarara (SJ), Serranía de Simarua (SS), Serranía de Cocinas (SC), and Cuiza fault; the black circles indicate stations from the Siamaná Formation (early Miocene) and the black star indicates station from the Jimol Formation (late early Miocene). (**3**) Localities and stations: Arroyo Ekieps indicated by black circles; Arroyo Uitpa indicated by white circles with a black border; PF0018 station, corresponding to the SW Ekieps locality, indicated by the black circle with a white border; Flor de La Guajira indicated by the white star with a black border; and Punta Espada indicated by a black star.

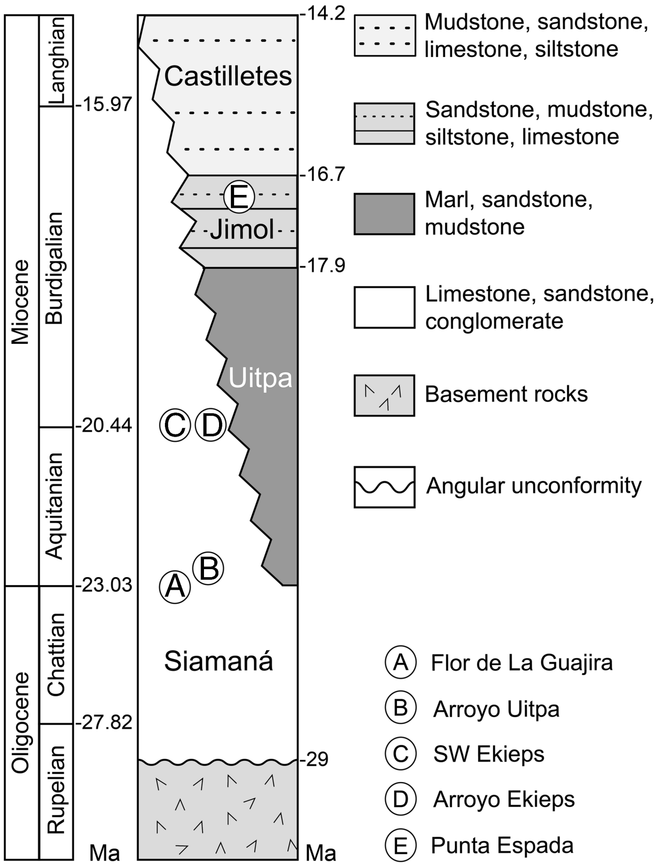

Figure 2. The Cocinetas Basin general stratigraphy showing the positions of the localities studied (A–E). Ages and lithological characteristics of the Siamaná, Uitpa, Jimol, and Castilletes formations following Moreno et al. (2015) and Silva-Tamayo et al. (2017).

Materials and methods

Fossil coral samples were collected in two expeditions carried out in 2011 and 2014, at five localities in the Cocinetas Basin: Arroyo Uitpa, Arroyo Ekieps, SW Ekieps, Flor de La Guajira, and Punta Espada (Fig. 1; Table 1). Samples were collected along 10 m horizontal transects. To increase sampling of taxa, some additional specimens were obtained outside of linear transects. The ages of the units studied in the Siamaná Formation were estimated by Silva-Tamayo et al. (2017) through $^{87}Sr/^{86}Sr$ values in fossil coralline algae. The numerical dating was confirmed by biostratigraphic data based on larger benthic foraminifera (*Myogypsina*, *Amphistegina*, operculinoids, and archaiasinids) determined by Dr. W. Renema in thin sections from the outcrops. The dating of the Jimol Formation was performed by Moreno et al. (2015) and Hendy et al. (2015) through $^{87}Sr/^{86}Sr$ and biostratigraphy based on mollusk shells.

All coral samples were cleaned and brushed with water to remove the sediment. Taxonomic identification was guided by the works of Vaughan (1919), Coryell and Ohlsen (1929), Wells (1956), Frost and Langenheim (1974), Budd (1991), Budd et al. (1992, 1994, 2010), Johnson (2001, 2007), Johnson et al. (2009), Wallace (2012), and Huang et al. (2014). The taxonomic assignment was based on macrostructural features, such as colony shape, septum development, calice size and shape, calicular wall, morphology of the columella, presence/absence of pali and coenosteum characteristics (Budd and Stolarski, 2011), and microstructural characters related to septal face granulation (Budd et al., 2012). Morphologic investigations were performed with a stereomicroscope under 2x and 4x magnification. Basic morphometric data (Table 2) were measured with a digital caliper. Pictures of colonies were taken with a Canon EOS D60 digital camera. Micromorphological images of some specimens were obtained with a Quanta 400 FEI scanning electron microscope (SEM) after mounting specimens on stubs with double-sided tape or CCC carbon adhesive and sputter-coating with conductive carbon and gold. Thin sections were used to examine corallites in samples with poor preservation of the calicular surface.

The systematic paleontology is presented in alphabetical order, at both family and genus levels. References for the occurrence information provided on each species for the Caribbean region, such as formation, depositional age, and country, are compiled in Table 3. A total of 273 lots were collected from the Siamaná (240 lots) and Jimol (33 lots) formations. The specimens were classified into two orders (Scleractinia and Anthoathecata: Milleporidae), 12 families, 15 genera, and 26 species. The present work includes seven families (Table 2), and the second part includes the families Mussidae, Pocilloporidae, Poritidae, Siderastreidae, and Milleporidae.

Repositories and institutional abbreviations.—The reference collection has been deposited at the Mapuka Museum of the Universidad del Norte, Barranquilla-Colombia, with the repository acronym MUN-STRI followed by the catalog number, which appears in the section of material for each species. The type samples are deposited in the following institutions: The Natural History Museum, London, United Kingdom (NHMUK); U.S. National Museum of Natural History, Washington, USA (USNM); numbers preceded by 'M' are from mollusk series.

Systematic paleontology

Class Anthozoa Ehrenberg, 1834
Subclass Hexacorallia Haeckel, 1896
Order Scleractinia Bourne, 1900
Family Acroporidae Verrill, 1902
Genus *Acropora* Oken, 1815

Type species.—*Millepora muricata* Linneaus, 1758; by original designation.

Acropora panamensis Vaughan, 1919
Figure 3.1, 3.2

1919 *Acropora panamensis* Vaughan, p. 480, pl. 141, figs. 1, 1a, b, 2.
1974 in part *Acropora panamensis*; Frost and Langenheim, p. 188, pl. 56, figs. 4–7, pl. 57, figs. 1–5.

Holotype.—USNM M325042, from La Boca Formation, Panama. Middle Miocene.

Table 1. Coordinates of the stations and locations studied. Station nomenclature follows the STRI procedure: the first two characters correspond to collector and the rest to station code. The ages of the Siamaná Formation were estimated by Silva-Tamayo et al. (2017) through strontium isotopes; the uncertainty at Flor de La Guajira because to part of the material is reworked. Age of the Jimol Formation was estimated by Hendy et al. (2015) and Moreno et al. (2015) by means of biostratigraphic analyses.

Formation	Locality	Station code	Latitude N	Longitude W	Age
Jimol	Punta Espada	550010	12°00'46.0"	71°12'07.2"	Burdigalian
Jimol	Punta Espada	550014	12°00'46.0"	71°12'07.2"	Burdigalian
Siamaná	Arroyo Ekieps	550008	12°04'11.02"	71°26'23.09"	Aquitanian–Burdigalian
Siamaná	Arroyo Ekieps	550011	12°04'08.06"	71°26'22.2"	Aquitanian–Burdigalian
Siamaná	Arroyo Ekieps	550012	12°03'5.70"	71°25'10.80"	Aquitanian–Burdigalian
Siamaná	Arroyo Ekieps	550013	12°03'20.5"	71°25'18.4"	Aquitanian–Burdigalian
Siamaná	SW Ekieps	PF0018	12°03'17.60"	71°25'49.00"	Aquitanian–Burdigalian
Siamaná	Arroyo Uitpa	PF0016	12°01'50.5"	71°25'21.8"	Aquitanian
Siamaná	Arroyo Uitpa	550005	12°01'50.04"	71°25'24.04"	Aquitanian
Siamaná	Arroyo Uitpa	550006	12°01'49.0"	71°25'16.07"	Aquitanian
Siamaná	Flor de La Guajira	550001	11°49'52.08"	71°23'58.07"	Aquitanian?
Siamaná	Flor de La Guajira	550002	11°49'52.08"	71°23'58.07"	Aquitanian?

Occurrence.—Late Oligocene to Pleistocene. First occurrences from the late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003). Early Miocene in Culebra Formation, Panama (Johnson and Kirby, 2006); Siamaná Formation, Colombia. Middle Miocene in Valiente Formation, Panama (Klaus et al., 2012). Middle Miocene–late Pliocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Latest occurrences from the Pleistocene in drilling cores from the Bahamas (Budd and Manfrino, 2001).

Description.—Corallum cuneiform to ?caespitose in shape. Thick branches of blunt to acuminate tips, 1.0–2.5 cm in mid-branch diameter. Multiple axial corallites per branch, hardly distinguishable from radial corallites, 3 mm in outer diameter. Radial corallites nariform, appressed tubular to immersed in shape, calices rounded to slightly oval, 1.0–1.4 mm in diameter, radial spacing of 3.5–3.7 mm, and wall thickness of 1 mm. Both kinds of corallites with three synapticular rings; and septa hexamerally arranged in two cycles, S1 reach the center of the corallite, S2 rudimentary. Columella absent. Corallite wall and coenosteum reticulo-costate sometimes constituted by simple pointed spinules.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550013: MUN-STRI-17331, MUN-STRI-17325, MUN-STRI-17327. SW Ekieps, station PF0018: MUN-STRI-37928.

Remarks.—*Acropora panamensis* could be easily confused with *A. saludensis* Vaughan, 1919, a species commonly present in the same stratigraphic units (Vaughan, 1919; Budd et al., 1994). They differ from each other by corallite diameter, smaller in *A. panamensis* (1.2–1.5 mm) than in *A. saludensis* (1.8–2.2 mm). In addition, the coenosteum is costulate in *A. panamensis* and porous in *A. saludensis* (Budd et al., 1994). The Siamaná samples also share some morphologic characteristics with the genus *Isopora*; for example, they have two or more axial corallites per branch and cuneiform colonies as reported by Wallace (1999) and Wallace et al. (2007). These characteristics have been also observed in other Caribbean localities (Budd and Wallace, 2008); however, the coenosteum characteristics define them as *Acropora*. On the other hand, the Siamaná specimens differ, in part, from the description given by Frost and Langenheim (1974) in the size and number of septal cycles of the leading corallites. In the Siamaná Formation, *A. panamensis* occurs with *Porites baracoaensis* Vaughan, 1919, *Montastraea canalis* (Vaughan, 1919), *Montastraea cavernosa* (Linnaeus, 1767), and *Colpophyllia willoughbiensis* (Vaughan, 1919), among others.

Acropora sp. indet.
Figure 3.3

Occurrence.—Early Miocene from Siamaná Formation, Colombia.

Description.—Corallum plocoid, probably arborescent or corymbose-caespitose. Cylindrical to slightly flattened branches, 6.6–13.0 mm in diameter. One axial corallite per branch, 1.3–1.5 mm in inner diameter, and wall thickness around 1 mm. In some places the corallites are vertically aligned, but this pattern changes to intercalate laterally. Radial corallites spaced 2.4–4.2 mm apart, calices rounded, 0.9–1.0 mm in inner diameter, and wall thickness of 0.7–0.8 mm. Axial and radial corallites surrounded by two synapticular rings; septa hexamerally arranged in two complete cycles; S1 reach the center of corallites, and S2 often half width of S1. Columella absent. Corallite wall and coenosteum reticulo-costate with simple spinules.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-43531, MUN-STRI-43532; station 5500013: MUN-STRI-43533.

Remarks.—The samples are broken fragments, most of them without tips, and with poor preservation, limiting the identification to the genus level. Specimens are assigned to *Acropora* based on the protuberant morphology of corallites, the absence of columella, and the spinose and costate pattern of the coenosteum. Samples of *Acropora* sp. indet. closely resemble *Acropora saludensis*; however, the Siamaná specimens do not have the dense and elaborate coenosteum characteristic of this species (Budd and Wallace, 2008). Specimens were found associated with *Porites* spp., *Montastraea* spp., and *Siderastrea* spp.

Table 2. Species list and summary of the main characters used to identify taxa from the Siamaná and Jimol formations. Colony: B = branching; M = massive; D = dendroid. CD = calicular diameter. ICD = intercalicular distance. Coenosteum: Cos = costae present; Sp = spinose. No. cycles: inc. = incomplete. Columella: St = styliform; L = lamellar; T = trabecular; A = absent. In all characters (—) means not determined. Siamaná EM (early Miocene) localities: AE = Arroyo Ekieps; SWE = SW Ekieps; AU = Arroyo Uitpa; FG = Flor de La Guajira. Jimol LEM (late early Miocene) localities: PE = Punta Espada.

		Morphologic characters							Formations	
Family	Species	Colony	CD (mm)	ICD (mm)	Coenosteum	No. septa	No. cycles	Columella	Siamaná EM	Jimol LEM
Acroporidae	*Acropora panamensis*	B	—	—	Cos, Sp	12	2	A	AE, SWE	
	Acropora sp. indet.	B	—	—	Cos	12	2	A	AE	
	Alveopora tampae	B	1.9–2.9	—	—	—	—	—	AE	
Agathiphylliidae	*Agathiphyllia antiguensis*	M	7.0–10.0	0.0–3.0	Cos	38–40	4	T	AE	
	Agathiphyllia tenuis	M	3.0–5.0	0.0–2.0	Cos	20–31	3	T	AE, SWE, AU	
Astrocoeniidae	*Astrocoenia decaturensis*	M	1.5–1.9	0.30	—	16	2	St	AE, SWE, AU	
	Astrocoenia portoricensis	B	1.5–2.0	0.2–0.6	—	16	2	St	AE, AU	
	Astrocoenia sp. indet.	M	2.0–3.0	1.0–2.0	Sp	20	2	St	AU	
Caryophylliidae	sp. indet.	D	4.0–8.0	—	—	48	4	A	AE	
Diploastraeidae	*Diploastrea crassolamellata*	M	5.0–7.0	1.0–2.0	Cos	18–21	3	T	AU, FG	
	Diploastrea magnifica	M	5.0–10.0	3.0–6.0	Cos	42–48	4 inc.	T	AE, AU, FG	
Merulinidae	*Antiguastrea cellulosa*	M	3.0–4.0	0.5–1.0	—	48	4	L	AE, SWE, AU	
	Goniastrea canalis	M	2.5–5.0	0.8–1.5	—	28–33	3	T	AE	
	Orbicella imperatoris	M	3.2–4.0	1.7–4.2	Cos	24	3	?T	FG	PE
	Orbicella limbata	M	3.5–4.2	0.4–1.3	Cos	24	3	T	FG	
Montastraeidae	*Montastraea canalis*	M	4.0–8.0	3.0–6.0	Cos	42–49	4	T	AE, SWE, AU	
	Montastraea cavernosa	M	5.0–7.0	1.5–4.5	Cos	48	4	T	AE, SWE, AU, FG	
	Montastraea endothecata	M	4.5–10	1.0–12.0	Cos	37–40	4 inc.	T	AE, SWE	

Genus *Alveopora* Blainville, 1830

Type species.—*Madrepora daedalea* Forsskål, 1775; by subsequent designation (Wells, 1936).

Alveopora tampae Weisbord, 1973
Figure 3.4–3.6

1973 *Alveopora tampae* Weisbord, p. 37, pl. 6, figs. 4–6, pl. 7, figs. 4, 5.

Holotype.—USNM 66160, from Arcadia Formation (Tampa Member), Florida, USA. Late Miocene.

Occurrence.—Late Oligocene to Miocene. First occurrences in Antigua Formation, Antigua and Barbuda (Johnson, 2007). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003); Arcadia Formation (Tampa Member), Florida, USA (Weisbord, 1973). Early Miocene in Castillo and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation in Colombia. Middle Miocene in Baitoa Formation, Dominican Republic (Budd et al., 1994).

Description.—Corallum plocoid and columniform. Columns thick of blunt tips, slightly compressed transversely, 2.5–3.5 cm in diameter. Corallites circular to polygonal, 1.9–2.9 mm in diameter, separated by a calicular wall formed of 11–12 rods of 0.3–0.5 mm thickness. Synapticulae linked the rods of the wall. Septal spines thin, irregularly arranged in different levels, sometimes fused in the axis of the corallite.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-43504; station 550011 MUN-STRI-17268, MUN-STRI-43508, MUN-STRI-17274; station 550012: MUN-STRI-43517; station 550013: MUN-STRI-43524, MUN-STRI-17323. SW Ekieps, station PF0018: MUN-STRI-37892.

Remarks.—The samples are recrystallized and poorly preserved. However, they are easily distinguishable due to large column thickness and the typical spiny septa and absence of a columella. The genus *Alveopora* was included in the family Poritidae but later transferred to the family Acroporidae based on molecular analysis and morphological features (Kitano et al., 2014). In the Siamaná Formation, *Alveopora* inhabited patch and fringing reefs in association with *Agathiphyllia tenuis* (Duncan, 1863), *Millepora alcicornis* Linnaeus, 1758, *Porites anguillensis* Vaughan, 1919, *P. portoricensis* Vaughan, 1919, *Siderastrea siderea* (Ellis and Solander, 1786), and *Goniastrea canalis* Vaughan, 1919.

Family Agathiphylliidae Vaughan and Wells, 1943
Genus *Agathiphyllia* Reuss, 1864

Type species.—*Agathiphyllia explanata* Reuss, 1864; by subsequent designation (Vaughan, 1919).

Remarks.—*Agathiphyllia*, *Montastraea*, and *Antiguastrea* show several similar external morphological characters, for which

 https://doi.org/10.1017/jpa.2018.45

Table 3. Summary of the ages and locations of the Caribbean region stratigraphic units and references used to create the range chart (Fig. 6) and species occurrences (Table 4). Sources with (*) are stratigraphic works without coral records. E = early; M = middle; L = late.

Geologic age	Absolute age (Ma)		Formation	Country	Source
L. Pleistocene	0.2	0.1	Falmouth	Jamaica	Budd and McNeill, 1998; James-Williamson and Mitchell, 2012*; James-Williamson et al., 2014*.
M–L. Pleistocene	0.5	0.1	Santo Domingo Terraces	Dominican Republic	Budd et al., 1994, 1996.
M–L. Pleistocene	0.5	0.1	Key Largo	USA, Florida	Weisbord, 1974; Budd et al., 1994, 1996.
M–L. Pleistocene	0.8	0.1	San Luis (San Andrés Terraces)	Colombia	Budd et al., 1994, 1996; Vargas, 2004*; Díaz and García-Llano, 2010*.
E. Pleistocene	1.2	0.8	Urracá	Panama	Klaus et al., 2012.
E. Pleistocene	2.2	1.4	Isla Colón	Panama	Klaus et al., 2012.
E. Pleistocene	1.6	1.1	Manchioneal	Jamaica	Budd and McNeill, 1998; James-Williamson and Mitchell, 2012*; James-Williamson et al., 2014*.
E. Pleistocene	1.8	0.1	Caloosahatchee and Glades	USA, Florida	Budd et al., 1994, 1996.
E. Pleistocene	2.2	1.8	Hope Gate	Jamaica	Budd and McNeill, 1998; James-Williamson et al., 2014*.
E. Pleistocene	2.5	1.8	Highest Terrace	Curaçao	Budd et al., 1998.
E. Pleistocene	2.5	1.8	Old Pera	Jamaica	Budd and McNeill, 1998; James-Williamson and Mitchell, 2012*; James-Williamson et al., 2014*.
L. Pliocene–E. Pleistocene	2.9	1.5	Moin	Costa Rica	Budd et al., 1999.
L. Pliocene	3.8	2.5	Layton (Bowden Member)	Jamaica	Budd and McNeill, 1998; Budd et al., 1996; James-Williamson et al., 2014*.
L. Pliocene–E. Pleistocene	3.5	1.6	La Cruz	Cuba	Budd et al., 1998, 1999.
L. Pliocene–E. Pleistocene	3.5	1.0	Matanzas	Cuba	Budd et al., 1999.
L. Pliocene	3.5	2.9	Quebrada Cholcolate	Costa Rica	Budd et al., 1999.
E. Pliocene	4.2	3.3	Mao	Dominican Republic	Budd et al., 1994, 1996; Budd and Klaus, 2001; Klaus et al., 2008.
Pliocene–E. Pleistocene	4.9	1.9	Tamiami	USA, Florida	Klaus et al., 2017.
E. Pliocene	5.2	4.3	Río Banano (Brazo Seco)	Costa Rica	Budd et al., 1999.
L. Miocene–E. Pliocene	5.5	4.8	Gurabo	Dominican Republic	Budd et al., 1994, 1996; Klaus et al., 2008.
L. Miocene	5.8	5.6	Old Bank	Panama	Klaus et al., 2012.
L. Miocene	6.2	5.8	Cercado	Dominican Republic	Budd et al., 1994, 1996; Budd and Klaus, 2001; Klaus et al., 2008.
M. Miocene	12.0	11.0	Valiente	Panama	Coates et al., 2003*; Klaus et al., 2012.
M. Miocene–E. Pleistocene	14.1	1.8	Seroe Domi	Curaçao	Budd et al., 1998.
M–L. Miocene	15.9	5.3	San Andrés	Colombia	Geister, 1975; Vargas, 2004*; Díaz and García-Llano, 2010*.
E–M. Miocene	16.0	11.6	Tamana	Trinidad and Tobago	Johnson, 2001; Wilson et al., 2011*.
E–M. Miocene	17.3	13.1	Baitoa	Dominican Republic	Foster, 1986; Saunders et al., 1986*; Budd et al., 1994.
Latest E. Miocene	17.9	16.7	Jimol	Colombia	Hendy et al., 2015*; Moreno et al. 2015*; this work.
E–M. Miocene	18.0	15.0	Chipola	USA, Florida	Budd et al., 1996.
E–M. Miocene	22.0	15.0	Providencia Island	Colombia	Geister, 1992.
E–M. Miocene	22.0	15.0	Santa Ana	Mexico	Frost and Langenheim, 1974.
E. Miocene	19.3	17.2	Castillo	Venezuela	Johnson et al., 2009; Rincon et al., 2014*.
E. Miocene	22.0	16.2	Anguilla	Anguilla	Budd et al., 1995.
E. Miocene	22.0	17.6	Culebra	Panama	Kirby et al., 2008*; Johnson and Kirby, 2006.
E. Miocene	23.0	20.4	San Luis	Venezuela	Johnson et al., 2009; Albert-Villanueva et al., 2017*.
E. Miocene	23.0	20.4	Agua Clara (Caurderalito Member)	Venezuela	Johnson et al., 2009; Quiroz and Jaramillo, 2010*.
E. Miocene	23.7	23.0	Pedregoso	Venezuela	Johnson et al., 2009; Montero-Serrano et al., 2010*.
L. Oligocene–E. Miocene	26.0	22.3	Arcadia (Tampa Member)	USA, Florida	Weisbord, 1973; Budd et al., 1994; Brewster-Wingard et al., 1997*.
L. Oligocene–E. Miocene	27.8	20.4	Browns Town	Jamaica	Stemann, 2003; Mitchell, 2004*, 2013*.
L. Oligocene–E. Miocene	27.8	20.4	Newport	Jamaica	Stemann, 2003; Mitchell, 2004*, 2013*.
L. Oligocene–M. Miocene	29.0	14.2	Siamaná	Colombia	Silva-Tamayo et al., 2017*; this work.
L. Oligocene	26.5	24.7	Lares	Puerto Rico	Frost et al., 1983; Ortega-Ariza et al., 2015*.
L. Oligocene	27.8	26.3	Antigua	Antigua and Barbuda	Frost and Weiss, 1979; Weiss, 1994; Johnson, 2007; Robinson et al., 2017*.
L. Oligocene	28.0	24.0	La Quinta	Mexico	Frost and Langenheim, 1974.
L. Oligocene	28.0	24.0	Anahuac	USA, Texas	Frost and Schafersman, 1978; Swanson et al., 2013*.
L. Oligocene	28.1	23.7	Tabera	Dominican Republic	Budd et al. 1994, 1996.
E. Oligocene	32.0	28.0	Rancho Berlín	Mexico	Frost and Langenheim, 1974.
L. Eocene	40.0	36.0	Gatuncillo	Panama	Woodring, 1957; Budd et al., 1992.
M. Eocene	46.0	40.0	St. Bartholomew	St. Bartholomew	Vaughan, 1919.
Maastrichtian	72.1	66.0	Cardenas	Mexico	Baron-Szabo et al., 2006.

they are often confused, in particular when samples are poorly preserved by effects of diagenetic processes (Neil-Champagne, 2010). The Agathiphylliids are characterized by rounded corallites, synapticulothecal wall, trabecular columella, and paliform lobes. By contrast, *Antiguastrea* has circular to polygonal corallites, parathecal wall, and lamellar columella, with no paliform lobes. On the other hand, *Montastraea* has a septothecal wall, the circular corallites are larger and more exsert

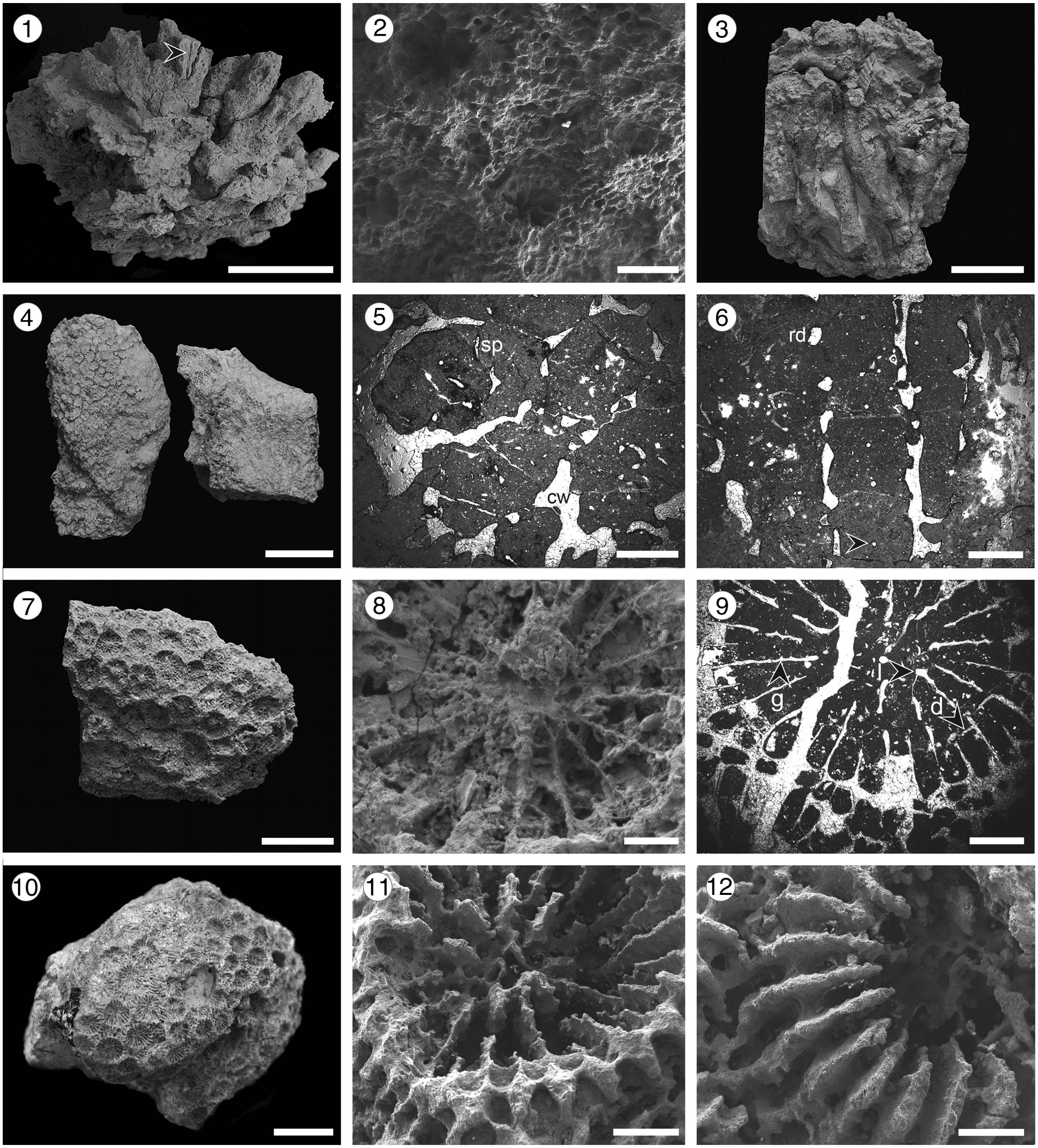

Figure 3. (**1, 2**) *Acropora panamensis* Vaughan, 1919: (**1**) morphology of the colony (MUN-STRI-17331), showing an axial corallite 1.4 cm in length (black arrow) cut laterally; (**2**) detail of the corallites, showing the septal arrangement and coenosteum reticulo-costate (MUN-STRI-17327). (**3**) Colony of *Acropora* sp. indet. (MUN-STRI-43531). (**4–6**) *Alveopora tampae* Weisbord, 1973 (MUN-STRI-43508): (**4**) morphology of the colony; (**5**) transverse thin section showing the calicular wall (cw) and fragments of the septal spines (sp); (**6**) longitudinal thin section showing the rods of the wall (rd) and insertion of the spines (black arrow). (**7–9**) *Agathiphyllia antiguensis* (Duncan, 1863) (MUN-STRI-17309): (**7**) morphology of the colony; (**8**) detail of the corallites; (**9**) transverse thin section showing the (d) endothecal dissepiments, (g) septal granules, and (l) paliform lobes. (**10–12**) *Agathiphyllia tenuis* (Duncan, 1863) (MUN-STRI-17275): (**10**) general view of the colony; (**11**) detail of the palar crown and granules of the pali and septa; (**12**) detail of the septa and costae. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. (**1, 7**) Scale bars = 3 cm; (**2, 8, 11, 12**) scale bars = 1 mm; (**3**) scale bar = 4 cm; (**4**) scale bar = 2 cm; (**5**) scale bar = 800 μ; (**6, 9**) scale bars = 600 μ; (**10**) scale bar = 1 cm.

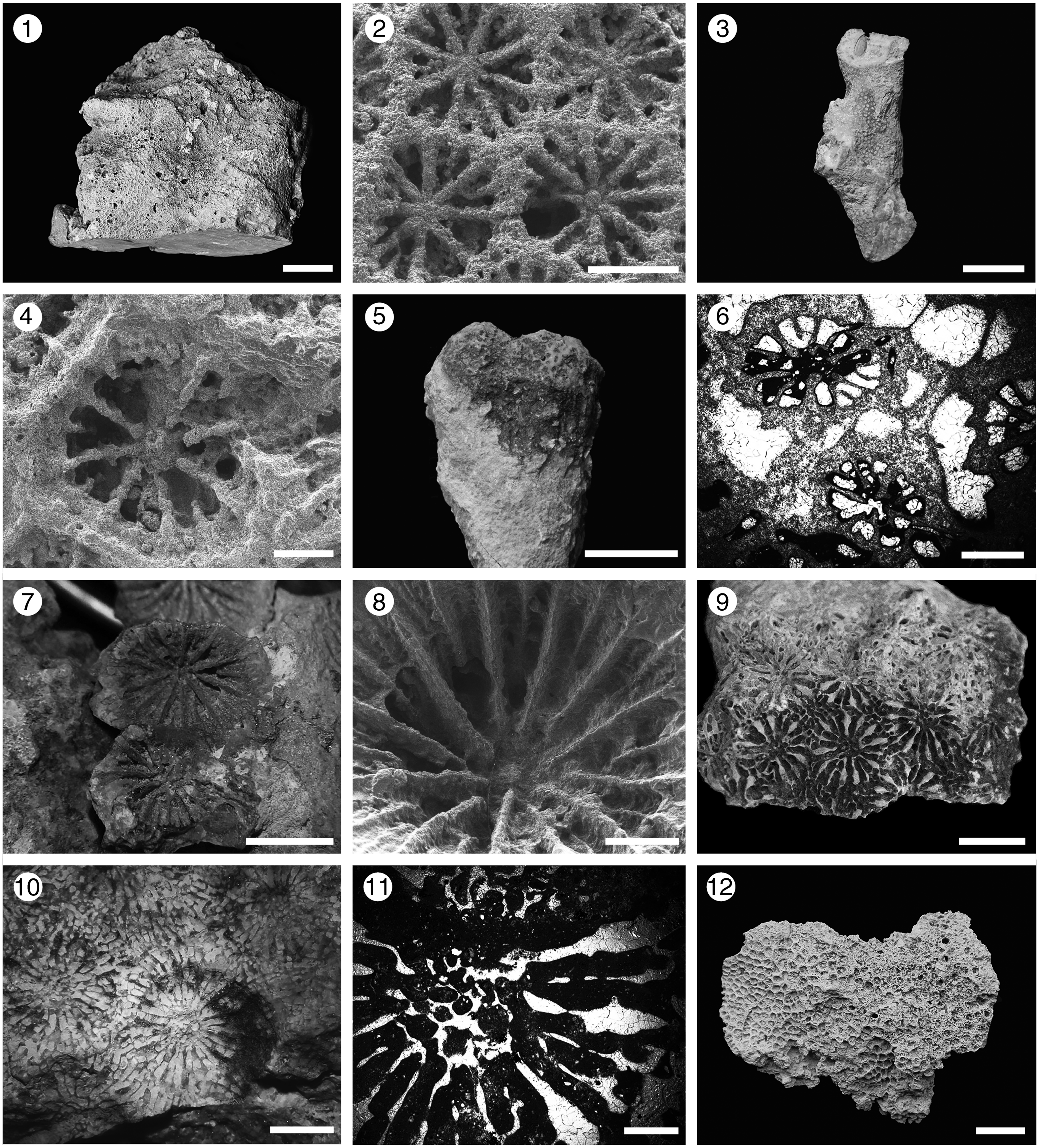

Figure 4. (**1, 2**) *Astrocoenia decaturensis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17294): (**1**) general view of the colony; (**2**) detail of the corallites. (**3, 4**) *Astrocoenia portoricensis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17311): (**3**) morphology of the colony; (**4**) detail of the corallites, septa, and granules. (**5, 6**) *Astrocoenia* sp. indet. from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-43497): (**5**) morphology of the colony; (**6**) transverse thin section. (**7, 8**) Caryophylliidae gen. indet. sp. indet. from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-43528): (**7**) phaceloid corallites; (**8**) detail of the rudimentary columella and septal granules. (**9**) *Diploastrea crassolamellata* (Duncan, 1863) from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-17635), detail of corallites. (**10, 11**) *Diploastrea magnifica* (Duncan, 1863) from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-43496): (**10**) surface of the corallites; (**11**) transverse thin section showing the columella and thick septal edges. (**12**) *Antiguastrea cellulosa* (Duncan, 1863) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17224), colony morphology. (**1, 12**) Scale bars = 2 cm; (**2, 8**) scale bars = 1 mm; (**3**) scale bar = 2.5 cm; (**4**) scale bar = 0.5 mm; (**5**) scale bar = 3.5 cm; (**6, 11**) scale bars = 600 μ; (**7**) scale bar = 4 mm; (**9**) scale bar = 7 mm; (**10**) scale bar = 5 mm.

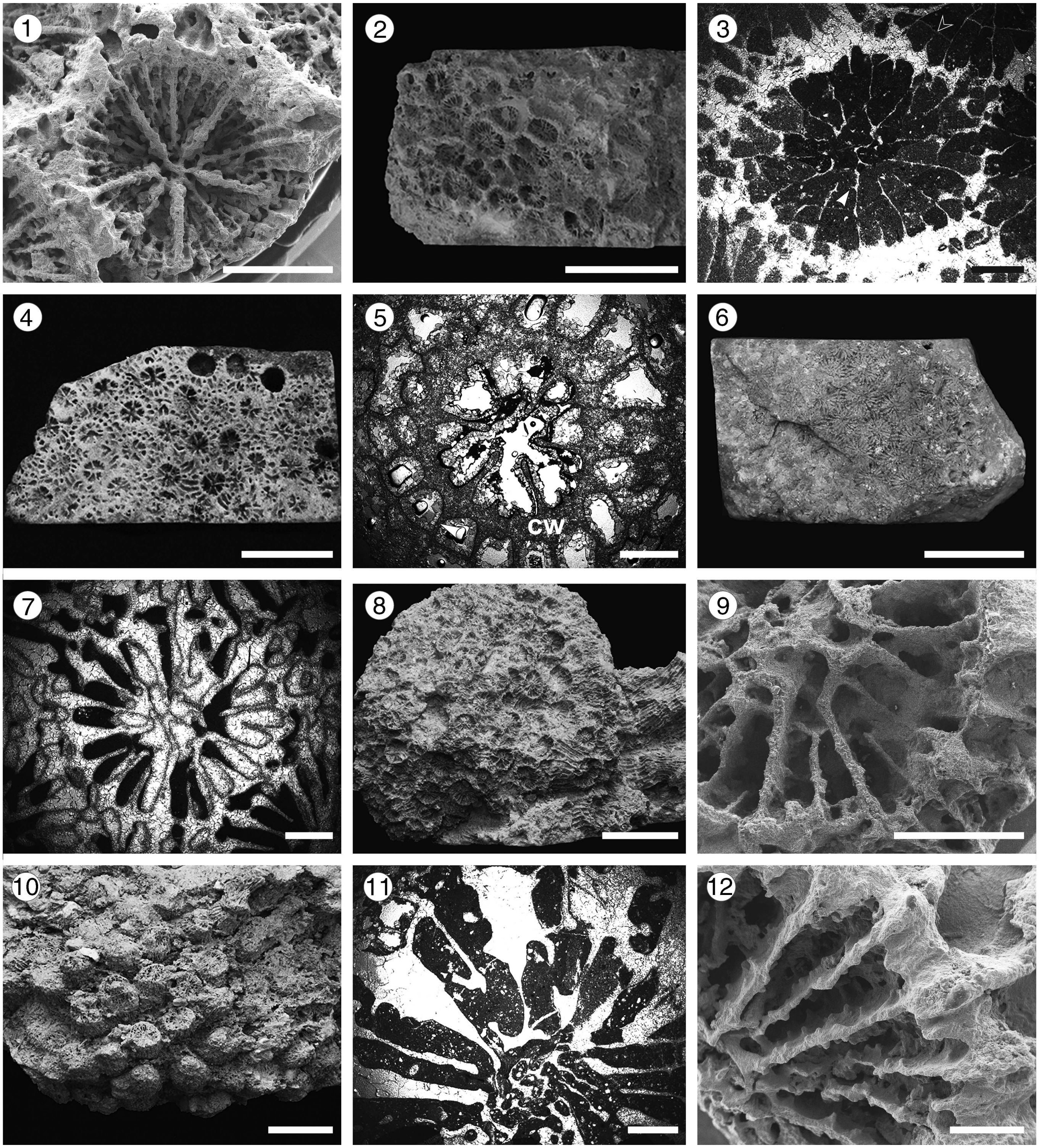

Figure 5. (**1**) *Antiguastrea cellulosa* (Duncan, 1863) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17224), detail of corallite. (**2, 3**) *Goniastrea canalis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17332): (**2**) fragment of the colony; (**3**) transverse thin section, showing the septal arrangement, dissepiments (black arrow), and septal granules (white arrow). (**4, 5**) *Orbicella imperatoris* Vaughan, 1919 from the Jimol Formation, Punta Espada: (**4**) fragment of the colony (MUN-STRI-17344); (**5**) transverse thin section showing the calicular wall (cw), septal arrangement, and costae (white arrow) (MUN-STRI-43539). (**6, 7**) *Orbicella limbata* (Duncan, 1863) from Siamaná Formation, Flor de La Guajria (MUN-STRI-17185): (**6**) colony; (**7**) transverse thin section showing the septal arrangement. (**8, 9**) *Montastraea canalis* (Vaughan, 1919) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17283): (**8**) fragment of the colony; (**9**) detail of the columella, septocostae, and septal arrangement. (**10, 11**) *Montastraea cavernosa* (Linnaeus, 1767) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17306): (**10**) morphology of the colony; (**11**) transverse thin section. (**12**) *Montastraea endothecata* Duncan, 1863 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17225), detail of the columella and septal granules. (**1, 9**) Scale bars = 2 mm; (**3, 7, 11**) scale bars = 500 μ; (**2, 4, 6**) scale bars = 1.5 cm; (**5**) scale bar = 600 μ; (**8, 10**) scale bars = 2 cm; (**12**) scale bar = 1 mm.

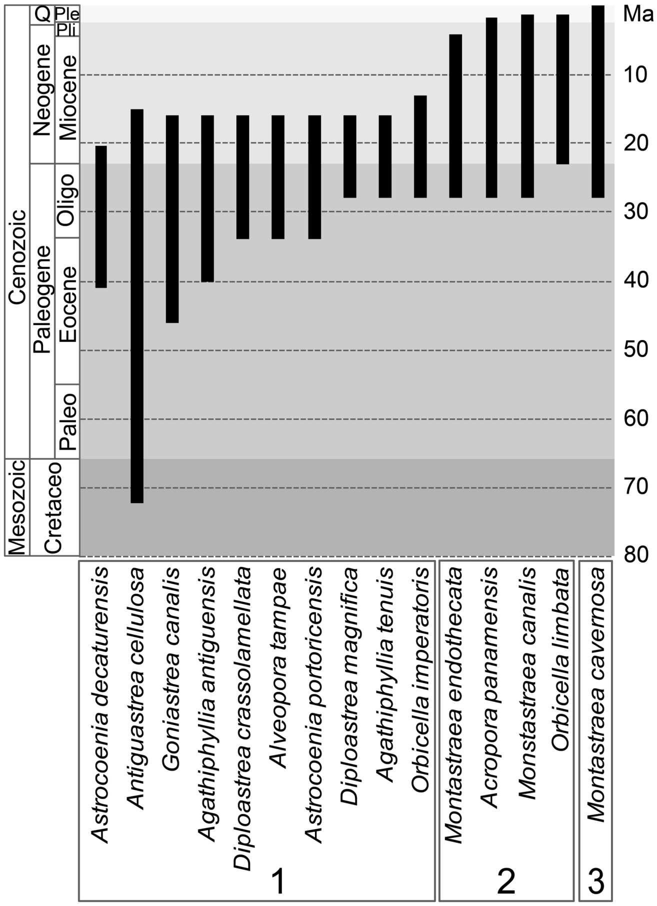

Figure 6. Range chart of first and last occurrences of species recorded in this study in the Greater Caribbean. Box 1: extinct species at the end of the early Miocene and middle Miocene; box 2: extinct species in the late Pliocene and Pleistocene; box 3: extant species. Reference sources of stratigraphic units, ages, and countries are provided in Table 3.

than in *Agathiphyllia*, and the columella is larger and usually trabecular to spongy (Frost and Langenheim, 1974; Neil-Champagne, 2010). The genus *Agathiphyllia* is globally extinct (Budd, 2000).

Agathiphyllia antiguensis (Duncan, 1863)
Figure 3.7–3.9

1863 *Astraea antiguensis* Duncan, p. 419, pl. 13, fig. 8.
1919 *Cyathomorpha antiguensis*; Vaughan, p. 463, pl. 129, fig. 2, pl. 130, figs. 1, 1a, 2, 2a, 3, pl. 131, figs. 1, 1a, b, 2–4, pl. 132, figs. 1, 2, 2a, b, pl. 133, fig. 1.

Holotype.—NHMUK R28629, from Antigua Formation, Antigua. Late Oligocene.

Occurrence.—Late Eocene to early Miocene. First occurrences in Gatuncillo Formation, Panama (Budd et al., 1992). Early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Early Miocene in Castillo and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation in Colombia.

Description.—Corallum massive and plocoid, with extratentacular budding. Corallites rounded to oval in shape, 7–10 mm in diameter. They bear 38–40 septa, hexamerally arranged in four cycles with the fourth one rarely complete. S1 and S2 reach the columella, S3 not always, while S4 has one-fourth the width of S1–2. Septal faces bear pointed granules. Primary and secondary septa bear paliform lobes only observed in transverse section. Trabecular columella, 1.3–3.2 mm in diameter, usually occupying one-third of corallite diameter into a shallow fossa. Synapticulothecal wall and costate coenosteum.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550012: MUN-STRI-17304, MUN-STRI-17309; station 550013: MUN-STRI-17328.

Remarks.—The samples of *Agathiphyllia antiguensis* from the Siamaná Formation are poorly preserved and do not conserve either the paliform crown or complete septa. Nevertheless, the synapticulothecal wall is typical of the species. *Agathiphyllia antiguensis* was a framework component of fringing reefs in the Siamaná Formation, associated with *Porites* spp., *Montastraea* spp., and *Siderastrea* spp., among others.

Agathiphyllia tenuis (Duncan, 1863)
Figure 3.10–3.12

1863 *Astraea tenuis* Duncan, p. 421, pl. 13, fig. 11.
1919 *Cyathomorpha tenuis*; Vaughan, p. 467, pl. 132, fig. 3, 3a, pl. 133, figs. 2, 3, 3a, b.

Holotype.—NHMUK R28627, from Marl Formation, Antigua. Miocene.

Occurrence.—Late Oligocene to middle Miocene. Oldest occurrences in Lares Formation, Puerto Rico (Frost et al., 1983) and Antigua Formation, Antigua and Barbuda (Johnson, 2007). Late Oligocene–early Miocene in Browns Town Formation, Jamaica (Stemann, 2003). Early Miocene in the southern Caribbean in Castillo and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia. Latest occurrences from middle Miocene in Baitoa Formation, Dominican Republic (Budd et al., 1994).

Description.—Corallum massive and plocoid, with extratentacular budding. Corallites rounded to slightly compressed in shape, 3–5 mm in diameter. They bear 20–31 septa, hexamerally arranged in three cycles. S1 and S2 reach the columella, while S3 is one-third the width of S1–2. Pali present before S1 and S2, forming two circular crowns encircling a trabecular columella. Faces of septa, costae, and pali finely spinose. Fossa shallow to moderately deep. Synapticulothecal wall. Costae are thick and converge with the adjacent calices.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-17275, MUN-STRI-43509, MUN-STRI-43513; station 550012: MUN-STRI-43518. Arroyo Uitpa, station 550006: MUN-

STRI-37877. SW Ekieps, station PF0018: MUN-STRI-37890, MUN-STRI-37893, MUN-STRI-37894, MUN-STRI-37900, MUN-STRI-37901, MUN-STRI-37903.

Remarks.—*Agathiphyllia tenuis* differs from *A. antiguensis* by the number of cycles and size of the corallites. In the Siamaná Formation, *A. tenuis* occurs with *Porites* spp., *Montastraea* spp., *Siderastrea* spp., and *Colpophyllia* as a builder of patch and fringing reefs.

Family Astrocoeniidae Koby, 1890
Genus *Astrocoenia* Milne-Edwards and Haime, 1848

Type species.—*Astrea numisma* Defrance, 1826; by original designation.

Remarks.—Within the family Astrocoenidae, the specimens of *Astrocoenia* resemble species of *Madracis* recorded from the Caribbean Oligocene–Miocene (Table 4) in their corallum shape and characteristic styliform columella. However, *Madracis* specimens may be distinguished from *Astrocoenia* by their septal arrangement in groups of six, eight, or 10, a diagnostic characteristic in *Madracis* spp. (Cairns, 2000).

Astrocoenia decaturensis Vaughan, 1919
Figure 4.1, 4.2

1919 *Astrocoenia decaturensis* Vaughan, p. 348, pl. 78, figs. 3, 3a, 4, 4a.

Holotype.—USNM M324789, from Chattahoochee Formation, Hales Landing, Georgia, USA. Oligocene.

Occurrence.—Middle Eocene to early Miocene. First record in ?St. Bartholomew Formation, St. Bartholomew Island (Vaughan, 1919). Late Eocene in Gatuncillo Formation, Panama (Budd et al., 1992). Late Oligocene in Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Vaughan (1919, p. 205) also recorded it from the “middle Oligocene” in the “base of Chattahoochee Formation,” Georgia, USA; however, Cooke (1943, p. 81) suggested the name Flint River Formation for this geologic section from the Oligocene. The presence in Siamaná Formation, Colombia, confirms its occurrence in the early Miocene.

Description.—Corallum massive, encrusting or columnar, cerioid in form. Columns oval in transverse section of 5 × 4 cm, which can be covered by encrusting layers. Corallites generally pentagonal or hexagonal, 1.5–1.9 mm in diameter, with fine blunt denticles in the calicular edge. Most calices bear 16 septa in octameral arrangement, eight of which reach the styliform columella. They show a thickening close to the columella, forming a palar crown. Remaining septa one-third to one-half the width of the first cycle. Septal margin with beaded teeth, bearing series of five to six in septa of 0.6 mm width. Fossa shallow.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550012: MUN-STRI-17294, station 550011: MUN-STRI-37858, MUN-STRI-37863. Arroyo Uitpa, station PF0016: MUN-STRI-37869; station 550006: MUN-STRI-37876, MUN-STRI-37878, MUN-STRI-37880, MUN-STRI-37881. SW Ekieps, station PF0018 MUN-STRI-37905.

Remarks.—Although the surfaces of samples are poorly preserved, the denticles in the septa and calicular edge can be distinguished. *Astrocoenia decaturensis* differs from *A. portoricensis* by the presence of a well-developed secondary group of septa and the morphology of the colonies. This species was a component of fringing and patch reefs associated with *Aniguastrea cellulosa* (Duncan, 1863), *Porites* spp., and *Montastraea* spp. in the Siamaná Formation.

Astrocoenia portoricensis Vaughan, 1919
Figures 4.3–4.4

1901 *Astrocoenia ornata*; Vaughan in Spencer, p. 497.
1919 *Astrocoenia portoricensis* Vaughan, p. 350, pl. 76, fig. 4, 4a, pl. 78, fig. 1, 1a.

Holotype.—USNM M324785, from Lares Formation, Puerto Rico. Late Miocene.

Occurrence.—Oligocene to early Miocene. Oldest occurrences from early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Late Oligocene to early Miocene in Browns Town and Newport formations, Jamaica (Steman, 2003). Early Miocene in Culebra Formation, Panama (Johnson and Kirby, 2006); Castillo Formation, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia.

Description.—Corallum branching and cerioid. Branches circular to oval in shape, 1.5–2.0 cm in diameter. Corallites polygonal in shape, 1.5–2.0 mm in diameter. Calicular edges with blunt denticles. Regular calices bear 16 septa in octameral arrangement, eight of them extend to the columella, whereas the rest are poorly developed or rudimentary. Sporadically, bigger corallites, 2.52 mm in diameter, are present with 15–16 septa well developed that reach the columella, while in others the 15–16 are rudimentary. Septal edges with beaded teeth, the last one forming a ?palar crown encircling the styliform columella. Fossa shallow.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-17628. Arroyo Ekieps, station 550012: MUN-STRI-17311.

Remarks.—Samples consist of poorly preserved, broken branches. In the Siamaná Formation, *Astrocoenia portoricensis* was a component of fringing and patch reefs, occurring with *Aniguastrea cellulosa*, *Goniopora hilli* Vaughan, 1919, and *Porites* spp.

Table 4. Species occurrences from the Oligocene–Miocene in the Caribbean formations. Species with (*) are recorded in the Cocinetas Basin. Additional information on the geologic formations is listed in Table 3. O–M = Oligocene–Miocene.

	Oligocene						O–M			Miocene															
Species	Rancho Berlín	Tabera	Anahuac	La Quinta	Antigua	Lares	Newport	Browns Town	Arcadia (Tampa Mem.)	Siamaná	Pedregoso	Agua Clara (Cauderalito Mem.)	San Luis	Culebra	Anguilla	Castillo	Santa Ana	Providencia Island	Chipola	Jimol	Baitoa	Tamana	San Andrés	Valiente	Seroe Domi (Salina)
Astrocoenia d'achiardi	X																								
Astrocoenia incrustans														X											
*Acropora panamensis**			X	X	X	X	X			X				X										X	X
Acropora saludensis					X	X	X	X	X			X		X	X	X	X						X		X
Actinacis alabamensis					X	X																			
Agaricia lamarcki																									X
Agaricia undata																						X			X
*Agathiphyllia antiguensis**	X				X	X		X		X			X			X									
Agathiphyllia browni					X																				
Agathiphyllia gabbi				X		X		X																	
Agathiphyllia hilli	X			X	X		X	X							X		X							X	
Agathiphyllia splendens					X																				
*Agathiphyllia tenuis**					X	X				X			X			X									
Alveopora chiapanecae				X	X	X		X																	
*Alveopora tampae**							X		X	X			X			X									
*Antiguastrea cellulosa**	X		X	X	X	X	X		X	X			X		X	X			X						
Antillia gregorii									X																
Antillophyllia sawkinsi															X		X					X		X	
Astreopora antiguensis				X	X	X								X											
Astreopora goethalsi						X		X			X			X											
*Astrocoenia decaturensis**					X	X				X															
Astrocoenia guantanamensis													X												
Astrocoenia incrustans					X		X																		
Astrocoenia meinzeri						X																			
*Astrocoenia portoricensis**					X	X	X	X		X						X									
Caulastraea dendroidea					X	X																			
Caulastraea portoricensis																						X			
Cladocora recrescens					X	X		X																	
*Colpophyllia willoughbiensis**	X			X	X	X	X			X						X	X								
Dichocoenia tuberosa																									X
*Diploastrea crassolamellata**	X			X	X	X	X	X		X			X			X							X		
*Diploastrea magnifica**										X			X												
Diploria clivosa																									X
Diploria dumblei						X																			
Diploria portoricensis						X	X																		
Diploria zambiensis																						X			
Favia dominicensis																	X	X			X	X		X	
Favia macdonaldi					X	X																			
Favites mexicana			X			X	X																		
Favites polygonalis				X	X	X	X	X																	
Galaxea excelsa									X																

Gardineroseris planulata		X																							
*Goniastrea canalis**	X			X		X			X	X				X		X									
Goniopora calhounensis																			X						
*Goniopora hilli**	X	X		X	X	X			X	X				X	X						X	X			
Goniopora imperatoris					X	X	X		X		X			X	X		X				X			X	X
Goniopora panamensis							X							X											
Goniopora regularis			X	X	X																				
Hydnophora reussi					X	X																			
Leptoria spenceri					X	X																			
Leptoseris anguillensis							X							X	X										
Leptoseris gardineri																						X			X
Leptoseris glabra																									X
Leptoseris portoricensis			X	X	X	X	X																		
Leptoseris walli							X							X								X			
Madracis decactis																									X
Madracis mirabilis																						X			
Meandrina antiguensis	X				X	X		X																	
Meandrina meandrites		X																							
Montastraea brevis																						X			
*Montastraea canalis**		X			X	X	X		X	X	X	X		X	X	X	X		X		X	X		X	X
*Montastraea cavernosa**		X								X						X					X			X	X
Montastraea cylindrica							X															X		X	X
*Montastraea endothecata**	X		X	X	X	X	X			X				X	X		X	X	X			X	X	X	X
Montastraea tampaensis							X		X						X		X								
Montastraea trinitatis							X										X				X	X		X	X
Mycetophyllia bullbrooki	X							X						X								X			X
*Orbicella imperatoris**			X		X	X			X	X	X	X		X	X	X		X		X				X	X
*Orbicella limbata**										X	X	X	X					X				X	X		X
Pavona pennyi																						X			
Pavona modeloensis																	X								
Pavona panamensis														X											
Pavona trinitatis					X												X	X				X			X
Pironastrea anguillensis						X								X	X			X						X	X
Pironastrea antiguensis				X	X	X	X											X							
Placocyathus trinitatis																						X			
Placocyathus variabilis																					X				
Pocillopora arnoldi							X					X		X		X		X				X			
Pocillopora crassoramosa		X																			X				
Pocillopora guantanamensis						X																			
Pocillopora portoricensis																									X
*Porites anguillensis**				X						X				X	X										
*Porites baracoaensis**			X		X	X	X	X		X		X		X	X	X	X	X				X	X	X	X
Porites chipolanum							X												X						
Porites douvillei	X			X		X								X											
Porites macdonaldi				X	X	X	X							X	X										
*Porites portoricensis**		X		X	X	X	X		X	X		X		X	X	X						X		X	X
Porites trinitatis							X									X	X					X			
*Porites waylandi**		X	X	X	X	X	X	X	X	X		X	X	X	X	X		X		X	X	X		X	X
Psammocora trinitatis																	X	X			X	X		X	X
*Siderastrea conferta**	X		X	X	X	X	X			X		X	X	X	X	X		X					X		

Table 4. (Continued)

	Oligocene						O–M			Miocene															
Species	Rancho Berlín	Tabera	Anahuac	La Quinta	Antigua	Lares	Newport	Browns Town	Arcadia (Tampa Mem.)	Siamaná	Pedregoso	Agua Clara (Cauderalito Mem.)	San Luis	Culebra	Anguilla	Castillo	Santa Ana	Providencia Island	Chipola	Jimol	Baitoa	Tamana	San Andrés	Valiente	Seroe Domi (Salina)
Siderastrea mendenhalli																					X				
*Siderastrea siderea**										X							X			X	X	X		X	
Siderastrea silecensis									X												X				
Solenastrea bournoni		X				X	X		X												X	X			X
Solenastrea hyades									X												X				
Stephanocoenia decaseptata																			X						
Stephanocoenia duncani		X										X			X	X								X	X
Stephanocoenia intersepta																						X			
Stephanocoenia spongiformis														X											X
Stylangia panamensis														X											
Stylocoeniella pumpellyi			X		X	X																			
*Stylophora affinis**							X			X	X	X		X		X		X			X	X			X
Stylophora canalis									X					X					X						
Stylophora granulata		X												X		X	X					X		X	X
Stylophora imperatoris														X	X		X		X			X	X		X
*Stylophora minor**		X					X		X	X				X							X	X		X	X
Stylophora monticulosa																		X			X		X		X
Stylophora panamensis																									X
Stylophora ponderosa				X	X	X		X															X		
Stylophora undata							X				X		X						X			X		X	X
Thysanus corbicula																			X						
Thysanus excentricus																							X		
Trachyphyllia bilobata						X		X	X								X	X	X			X			
Undaria crassa																						X			
*Millepora alcicornis**										X															

Astrocoenia sp. indet.
Figure 4.5, 4.6

Occurrence.—Early Miocene in the Siamaná Formation, Colombia.

Description.—Corallum massive, ?encrusting, and plocoid. Corallites circular to oval in shape, 2–3 mm in diameter, spaced 1–2 mm apart. They show 20 septa in decameral arrangement; 10 of them reach the columella and the rest extend to half or more of the width of the first cycle. Columella ?styliform. Calicular edges with blunt denticles and spinose coenosteum.

Material.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-43497.

Remarks.—The sample is a poorly preserved colony fragment. Although the sample resembles its congenerics, it differs from *Astrocoenia portoricensis* and *A. decaturensis* by have a wider intercalicular space and from *A. portoricensis* by the corallum morphology, which is massive in the sample reviewed. *Astrocoenia* sp. indet. occurs with *Antiguastrea cellulosa*, *Diploastrea magnifica* (Duncan, 1863), and *Porites waylandi* Foster, 1986.

Family Caryophylliidae Dana, 1846
Caryophylliidae gen. indet. sp. indet.
Figure 4.7, 4.8

Occurrence.—This family has a wide record in the world, from the Upper Jurassic to Recent (Kitahara and Cairns, 2005).

Description.—Corallum ahermatypic, dendroid to irregularly shaped. Elongated corallites, trochoid in shape, sometimes free. Asexual reproduction by budding, with one or two daughter corallites rising from the outer margins of parent corallites; parricidal budding may also be present. Calices oval in shape, 6–8 mm in the largest calicular diameter, and 4.5–5.6 mm in the smallest. About 48 septa hexamerally arranged in four cycles, sometimes with additional S5. S1–S2 extended to the calicular center, S3 half or more the width of S1–2, S4 similar to S3, and when present, S5 poorly developed. Septal faces bear rounded granules. Pali and paliform lobes absent. Columella absent or poorly developed, composed by a single blunt element. Granular costae present along the corallite.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550012: MUN-STRI-17305; station 550013: MUN-STRI-17327 (*Acropora panamensis*), MUN-STRI-43525, MUN-STRI-43528; station 550013: MUN-STRI- 37865.

Remarks.—Samples are recrystallized or with the skeleton partially dissolved by diagenetic processes, with only the internal mold remaining. Better-preserved specimens with shades of purple. Caryophylliidae samples resemble genus *Anomocora* in the extracalicular budding, morphology of the corallites, and septal arrangement. The colonies from the Siamaná Formation, however, differ from these because they have up to four generations in a single colony, while in *Anomocora* the budded corallites detach from the parent before the third generation (Cairns, 2000, p. 127). In addition, the specimens of *Anomocora* present paliform lobes and trabecular columella (Cairns, 2000). The morphology of the corallites also has a resemblance to the family Flabellidae in the septal arrangement, absence of pali, and rudimentary columella, but this group is exclusively solitary (Wells, 1956, p. 432). In the Siamaná Formation, Caryophylliidae colonies are a few centimeters in length and are found in fringing reefs with *Acropora panamensis*, *Alveopora tampae*, *Astrocoenia decaturensis*, *Colpophyllia willoughbiensis*, and *Porites baracoaensis.*

Family Diploastraeidae Chevalier and Beauvais, 1987
Genus *Diploastrea* Matthai, 1914

Type species.—*Orbicella minikoiensis* Gardiner, 1904; by original designation.

Diploastrea crassolamellata (Duncan, 1863)
Figure 4.9

1863 *Astraea crassolamellata* Duncan, p. 412, pl. 13, figs. 1–7.
1866 *Heliastraea crassolamellata*; Duchassaing and Michelotti, p. 180.
1901 *Orbicella crassolamellata*; Vaughan in Spencer, p. 497.
1919 *Diploastrea crassolamellata*; Vaughan, p. 470, pl. 135, figs. 1–5b, pl. 136, fig. 1, 1b, pl. 137, figs. 1–5.
1919 *Diploastrea crassolamellata* var. *nugenti*; Vaughan, p. 477, pl. 138, fig. 3, 3a.

Holotype.—NHMUK R28616, from Marl Formation, Antigua. Miocene.

Occurrence.—Oligocene to early Miocene. First occurrences from early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003). Early Miocene in the southern Caribbean in Castillo and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation in Colombia; until middle Miocene in San Andrés Formation, Colombia (Geister, 1975).

Description.—Corallum massive and plocoid, with extratentacular budding. Calices slightly exsert and circular in shape, 5–7 mm in diameter, spaced 1–2 mm apart. Calices bear 18–21 septa hexamerally arranged in three cycles; all septa reach the columella and are exsert; the principal septa thicken abaxially. Coenosteum costate. Columella trabecular and wide, 1–2 mm in diameter, occupying one-third of calicular diameter.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-43488, MUN-STRI-17614, MUN-STRI-17617,

MUN-STRI-17631, MUN-STRI-17634, MUN-STRI-17635, MUN-STRI-17638, MUN-STRI-43499; Flor de La Guajira, station 550001:MUN-STRI-17187.

Remarks.—*Diploastrea crassolamellata* has a wide morphological variation and can be easily confused with members of Montastraeidae and other species of the genus. It differs from montastraeids by the presence of a synapticulothecal wall at the calices level and synapticulothecate and septothecate below these (Frost and Langenheim, 1974, p. 268). Despite the Siamaná samples being poorly preserved, and it not being possible to observe characteristics such as their large septal teeth, *D. crassolamellata* can be distinguished from *D. magnifica* by the calicular size, which is usually smaller in *D. crassolamellata*, as well as by the thickness of the septocostae, which are wider in *D. crassolamellata*. The species occurs with *D. magnifica*, *Antiguastrea cellulosa*, and *Porites waylandi.*

Diploastrea magnifica (Duncan, 1863)
Figure 4.10, 4.11

1863 *Astraea crassolamellata* var. *magnifica* Duncan, p. 417, pl. 13, fig. 3.
1919 *Diploastrea crassolamellata* var. *magnifica*; Vaughan, p. 476, pl. 138, figs. 1, 2, 2a.

Hypotype.—USNM M325277, from Chattahoochee Formation, Georgia, USA. Early Miocene (Vaughan, 1919).

Occurrence.—Late Oligocene to early Miocene. Oldest occurrence from late Oligocene in Antigua Formation, Antigua and Barbuda (Johnson, 2007). Early Miocene in the southern Caribbean in San Luis Formation, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia. *Diploastrea magnifica* is globally extinct, and the only living species of the genus is *D. heliopora* (Lamarck, 1816) of Indo-Pacific waters (Veron, 2000).

Description.—Corallum massive and plocoid, with extratentacular budding. Calices circular in shape, 7–10 mm in diameter, spaced 3–5 mm apart. Calices bear 42–48 septa, hexamerally arranged in four incomplete cycles, which extend to the columella. Septocostae thickened close to calicular edge. Trabecular columella, 3–4 mm in diameter, occupying about one-third of calicular diameter.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-17616, MUN-STRI-17618, MUN-STRI-43496; Arroyo Ekieps, station 550013: MUN-STRI-17322; Flor de La Guajira, station 550001: MUN-STRI-17182.

Remarks.—*Diploastrea crassolamellata* var. *magnifica* was described by Duncan (1863) and accepted by Vaughan (1919) based on a larger size of corallites, less exsert calices, and smaller thickness of the septocostae in the wall. Frost and Langenheim (1974), however, considered the variety indistinguishable from *D. crassolamelata*. Subsequently, Johnson (2007) and Johnson et al. (2009) recovered the taxon as *Diploastrea magnifica*. The Colombian samples are poorly preserved and do not have the external calicular structures. However, they can be identified by the small septal thickness in the wall and the larger corallites. The species was collected in patch and fringing reefs associated with *D. crassolamellata*, *Antiguastrea cellulosa*, *Porites waylandi*, *P. baracoaensis*, and *Alveopora tampae.*

Family Merulinidae Verrill, 1865
Genus *Antiguastrea* Vaughan, 1919

Type species.—*Astraea cellulosa* Duncan, 1863; by original designation (Vaughan, 1919).

Antiguastrea cellulosa (Duncan, 1863)
Figures 4.12, 5.1

1863 *Astraea cellulosa* Duncan, p. 417, pl. 13, fig. 10.
1919 *Antiguastrea cellulosa*; Vaughan, p. 402, pl. 98, figs. 3–4a, pl. 99, figs. 1–3a, pl. 100, figs. 1–4a, pl. 101, fig. 2, 2a.
1919 *Antiguastrea cellulosa* var. *curvata*; Vaughan, p. 408, pl. 98, fig. 4, 4a.
1919 *Antiguastrea cellulosa* var. *silicensis*; Vaughan, p. 408, pl. 101, fig. 1, 1a.
1929 *Antiguastrea cellulosa* var. *curvata*; Coryell and Ohlsen, p. 193, pl. 27, fig. 5.
1992 *Antiguastrea cellulosa*; Budd et al., p. 585, fig. 7.4–7.6.
2006 *Antiguastrea cellulosa*; Baron-Szabo et al., p. 1037, fig. 4.2.

Holotype.—USNM M324936, from Chattahoochee Formation, Hales Landing, Georgia, USA. Late Miocene.

Occurrence.—Upper Cretaceous to early Miocene. Oldest occurrences from Maastrichtian in Cardenas Formation, Mexico (Baron-Szabo et al., 2006). Early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003); Arcadia Formation (Tampa Member), Florida, USA (Weisbord, 1973). Early Miocene in Anguilla Formation, Anguilla Island (Budd et al., 1995); Castillo and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia. Middle Miocene in Chipola Formation, Florida, USA (Budd et al., 1996).

Description.—Corallum massive and subplocoid, with extracalicular budding. Corallites rounded to polygonal in shape, 3–4 mm in diameter, separated by a furrow of 0.5–1.0 mm. Calices bear about 48 septa hexamerally arranged in four complete cycles. S1 and S2 are thick and reach the columella.

S3 about half width of S1–2, S4 half width of S3 or does not extend away from calicular wall. Parathecal wall, formed by dissepiments. Columella lamellar and thin, rises from a shallow fossa.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-17603, MUN-STRI-43490, MUN-STRI-43493, MUN-STRI-17610, MUN-STRI-17615, MUN-STRI-43494, MUN-STRI-17619, MUN-STRI-17620, MUN-STRI-17622, MUN-STRI-17625, MUN-STRI-17629, MUN-STRI-17637, MUN-STRI-17640, MUN-STRI-17600, MUN-STRI-17602, MUN-STRI-43498; station 550006: MUN-STRI-17197, MUN-STRI-17199, MUN-STRI-43500, MUN-STRI-17201, MUN-STRI-43501, MUN-STRI-17202, MUN-STRI-17203, MUN-STRI-37886. Arroyo Ekieps, station 550008: MUN-STRI-17230, MUN-STRI-17224; station 550011: MUN-STRI-17287, MUN-STRI-17261, MUN-STRI-17296. SW Ekieps, station PF0018: MUN-STRI-37902, MUN-STRI-37906, MUN-STRI-37922.

Remarks.—Samples moderately preserved, generally with the calicular margin covered by red algae. Several morphologic characters are variable in this taxon: diameter of the corallites ranges between 2 and 6 mm (Baron-Szabo et al., 2006), corallites can be plocoid to cerioid and circular to oval in shape in the same colony, and the corallum can be flat to dome-shaped in the same population (Frost and Langenheim, 1974). In the Siamaná Formation, it was found in patch and fringing reefs with *Astrocoenia portoricensis*, *Diploastrea* spp., *Montastraea* spp., *Porites* spp., and *Stylophora affinis* Duncan, 1863.

Genus *Goniastrea* Milne-Edwards and Haime, 1848

Type species.—*Astrea retiformis* Lamarck, 1816; by original designation (Milne-Edwards and Haime, 1848).

Goniastrea canalis Vaughan, 1919
Figure 5.2, 5.3

1919 *Goniastrea canalis* Vaughan, p. 416, pl. 91, fig. 4.
1973 *Favites yborensis* Weisbord, p. 38, pl. 16, figs. 1–3.

Holotype.—USNM M324996, from La Boca Formation, Panama. Middle Miocene.

Occurrence.—Middle Eocene to middle Miocene. First occurrences from middle Eocene in St. Bartholomew Formation, St. Bartholomew (Vaughan, 1919). Late Eocene in Gatuncillo Formation, Panama (Budd et al., 1992). Early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Until early Miocene in Arcadia Formation (Tampa Member), Florida, USA (Weisbord, 1973). Early Miocene in Culebra Formation, Panama (Johnson and Kirby, 2006); Castillo Formation, Venezuela (Johnson et al., 2009); Siamaná Formation in Colombia.

Description.—Corallum massive and cerioid, with intercalicular budding. Calices highly irregular in shape, polygonal to oval, 2.2–5.6 mm in diameter, spaced 0.8–1.5 mm apart. Calices bear 28–33 septa hexamerally arranged in three cycles. S1 reach the columella, S2 equal to S1 or slightly smaller, S3 half to two-thirds width of S2, sometimes fused to them. Septal faces finely granulated with small rounded granules. Septothecal wall. Paliform lobes developed before ?S1 and S2. Columella trabecular and wide, occupying about one-third of calicular diameter.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550013: MUN-STRI-17332.

Remarks.—The sample is a single colony fragment recrystallized and poorly preserved. However, the septothecal wall and well-developed paliform lobes are characteristic of *G. canalis*. In the Caribbean fossil record, *Goniastrea* can be confused with *Favites* spp., but the two genera differ by the presence of abortive septa in *Goniastrea* and a double wall or fused walls in *Favites* (Frost and Langenheim, 1974; Huang et al., 2014). In the Siamaná Formation, it was found in a fringing reef with *Acropora panamensis*, *Acropora* sp., and *Alveopora tampae*.

Genus *Orbicella* Dana, 1846

Type species.—*Madrepora annularis* Ellis and Solander, 1786; by subsequent designation (Vaughan, 1919).

Orbicella imperatoris Vaughan, 1919
Figure 5.4, 5.5

1919 *Orbicella imperatoris* Vaughan, p. 378, pl. 86, figs. 2–5.
1973 *Montastrea annularis*; Weisbord, p. 39, pl. 17, figs. 1–3, pl. 18, figs. 1–3, pl. 19, figs. 1, 2.
1974 *Montastrea limbata*; Frost and Langenheim, p. 258, pl. 93, figs. 3–6, pl. 94, fig. 1.

Syntype.—USNM M324884, from La Boca Formation, Panama. Middle Miocene.

Occurrence.—Late Oligocene to Miocene. Oldest occurrences in Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); Lares Formation, Mexico (Frost et al., 1983). Until early Miocene in Arcadia Formation (Tampa Member), Florida, USA (Weisbord, 1973). Early Miocene in Anguilla Formation, Anguilla Island (Budd et al., 1995); Culebra Formation, Panama (Johnson and Kirby, 2006); Agua Clara and Castillo formations, Venezuela (Johnson et al., 2009); Siamaná and Jimol formations, Colombia. Middle Miocene in Valiente Formation, Panama (Klaus et al., 2012); Providencia Island, Colombia (Geister, 1992); Pedregoso Formation, Venezuela (Johnson et al., 2009). Middle to late Miocene in San Andrés, Colombia (Geister, 1975). Latest occurrences from middle Miocene–late Pliocene in Seroe Domi Formation, Curaçao (Budd et al., 1998).

Description.—Corallum massive and plocoid, with extra-calicular budding. Corallites moderately raised and circular in shape, 3.2–4.0 mm in diameter, spaced 1.7–4.2 mm apart. Calices bear 24 septa, hexamerally arranged in three cycles, sometimes incomplete. A well-developed S1 reaches the columella. ?Trabecular columella, formed by the union of the primary septa. Well-developed costae corresponding to all or almost all cycles. Well-developed endothecal and exothecal dissepiments.

Materials.—Siamaná Formation, Flor de La Guajira, station 550002: MUN-STRI- 43534. Jimol Formation, Punta Espada, station 550010: MUN-STRI-17246, MUN-STRI-17247, MUN-STRI-17252, MUN-STRI-17253, MUN-STRI-43536, MUN-STRI-43537, MUN-STRI-17255; station 550014: MUN-STRI-17337, MUN-STRI-17338, MUN-STRI-17339, MUN-STRI-43538, MUN-STRI-17340, MUN-STRI-17341, MUN-STRI-17342, MUN-STRI-17343, MUN-STRI-17344, MUN-STRI-43539, MUN-STRI-17346, MUN-STRI-43540, MUN-STRI-43541, MUN-STRI-17347, MUN-STRI-17350, MUN-STRI-17351.

Remarks.—The samples of *O. imperatoris* from the Siamaná and Jimol formations are poorly preserved and highly recrystallized. Many characters, such as the morphology of the columella, the presence of paliform lobes, and the extension of secondary and tertiary septa, cannot be observed. However, the size and shape of raised corallites, development of the first septal cycle, and number of cycles are diagnostic of the species. This species appears in patch reefs with *Pocillopora* sp. indet. and *Porites waylandi*.

Orbicella limbata (Duncan, 1863)
Figure 5.6, 5.7

1863 *Phyllocoenia limbata* Duncan, p. 433.
1863 *Phyllocoenia sculpta* var. *tegula* Duncan, p. 432.
1864 *Plesiastraea ramea* Duncan, p. 39, pl. 5, fig. 1a, b.
1929 not *Orbicella limbata*; Coryell and Ohlsen, p. 197, pl. 2, fig. 3.
1974 not *Montastrea limbata*; Frost and Langenheim, p. 258, pl. 93, figs. 3–6, pl. 94, fig. 1.
1991 *Montastraea limbata*; Budd, p. 41, pl. 18, figs. 1–7, 9, pl. 19, figs. 1–6, pl. 20, figs. 1, 2, 4–6, pl. 21, figs. 1–6, pl. 24, fig. 4, text figs. 3–5, 10, 11, 14, 17.

Holotype.—NHMUK R28780, from Yellow Shale, Dominican Republic. Neogene.

Occurrence.—Early Miocene to early Pleistocene. First records from early Miocene in Agua Clara, Pedregoso, and San Luis formations, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia. Until the middle Miocene in Tamana Formation, Trinidad and Tobago (Johnson, 2001); San Andrés Formation and Providencia Island, Colombia (Geister, 1975, 1992; Budd et al., 1994). Middle Miocene–late Pliocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). From late Miocene in Cercado Formation, Dominican Republic (Budd et al., 1994; Budd and Klaus 2001; Klaus et al., 2008), Old Bank Formation, Panama (Klaus et al., 2012). From late Miocene–early Pliocene in Gurabo Formation and early Pliocene in Mao Formation, both in Dominican Republic (Budd et al., 1994; Budd and Klaus 2001; Klaus et al., 2008). Late Pliocene in Quebrada Chocolate Formation, Costa Rica, and until early Pleistocene in Moin Formation, Costa Rica (Budd et al., 1999). Latest occurrences from early Pleistocene in Old Pera Formation, Jamaica (Budd and McNeill, 1998); Isla Colón Formation, Panama (Klaus et al., 2012).

Description.—Corallum massive and plocoid. Corallites circular in shape, 3.5–4.2 mm in diameter, spaced 0.4–1.3 mm apart. Calices bear 24 septa, hexamerally arranged in three complete cycles. S1 and S2 reach the columella; S3 half width of S2 or little more, occasionally reaching the columella. Paliform lobes present before S1, S2, and S3, in the latter just when they reach the columella. Columella trabecular, 0.7–1.0 mm in diameter. Well-developed costae corresponding to all septa.

Material.—Siamaná Formation, Flor de La Guajira, station 550001: MUN-STRI-17185.

Remarks.—The sample is a highly recrystallized colony fragment and it is not possible to observe characters typical of the species, such as costae and endothecal and exothecal dissepiments. Despite their similitude in corallite size and number of septal cycles, *O. limbata* differs from *O. imperatoris* by the well-developed septal of cycles one and two, the wider trabecular columella, and reduced distance between corallites. According to Budd (1991), the samples described by Frost and Langenheim (1974) as *O. limbata* from Central Chiapas actually belong to *O. imperatoris*. In the Siamaná Formation, *O. limbata* was a component of patch reefs in association with *Porites waylandi* and *Diploastrea* spp.

Family Montastraeidae Yabe and Sugiyama, 1941
Genus *Montastraea* Blainville, 1830

Type species.—*Astrea guettardi* Defrance, 1826; by subsequent designation (Lang and Smith, 1935).

Remarks.—Poorly preserved colonies could be confused with *Antiguastrea* spp. and *Agathiphyllia* spp. However, corallites in *Montastraea* spp. are usually more exsert and have bigger calices and columella. See Remarks under genus *Agathiphyllia*.

Montastraea canalis (Vaughan, 1919)
Figure 5.8, 5.9

1919 *Orbicella canalis* Vaughan, p. 389, pl. 94, figs. 1, 1a, 3, 3a, not pl. 94, fig. 2, 2a, pl. 97, fig. 4, 4a.
1919 *Orbicella tampaensis* Vaughan, p. 390, pl. 95, figs. 1, 3, 3a, not pl. 95, fig. 2, 2a.
1919 *Orbicella tampaensis* var. *silecensis* Vaughan, p. 390, pl. 96.
1971 *Montastrea* cf. *costata*; Weisbord, p. 31, pl. 7, figs. 1–4.
1973 *Montastrea* cf. *tampaensis silecensis*; Weisbord, p. 50, pl. 22, figs. 1, 2, pl. 23, fig. 1.

1974 *Montastrea tampaensis*; Frost and Langenheim, p. 253, pl. 91, figs. 1, 2, pl. 92, figs. 1, 2, 4, 6, pl. 93, figs. 1, 2, pl. 94, fig. 2.
1991 *Montastraea canalis*; Budd, p. 36, pl. 5, figs. 1–8, pl. 6, figs. 1–6, pl. 7, figs. 1–6, pl. 8, fig. 2, pl. 9, fig. 2, pl. 14, fig. 2, text figs. 3–5, 7, 10, 11, 14, 17.

Holotype.—USNM M324862, from La Boca Formation, Panama. Middle Miocene.

Occurrence.—Late Oligocene to early Pleistocene. Oldest occurrences from late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Until early Miocene in Arcadia Formation (Tampa Member), Florida, USA (Weisbord, 1973). Early Miocene in Tamana Formation, Trinidad and Tobago (Johnson, 2001); Anguilla Formation, Anguilla Island (Budd et al., 1995); Culebra Formation, Panama (Johnson and Kirby, 2006); Castillo Formation, Venezuela (Johnson et al., 2009); Siamaná Formation, Colombia. Middle Miocene–late Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene in Cercado Formation, Dominican Republic (Budd et al., 1994); Old Bank Formation, Panama (Klaus et al., 2012); and until early Pliocene in Gurabo Formation, Dominican Republic (Budd et al., 1994). Late Pliocene in Quebrada Chocolate Formation, Costa Rica (Budd et al., 1999); Mao Formation, Dominican Republic (Budd et al., 1994). Youngest occurrences in Isla Colón Formation, Panama (Klaus et al., 2012).

Description.—Corallum massive and plocoid, with extracalicular budding. Corallites circular to slightly oval in shape, moderately raised, 4–8 mm in diameter, spaced 3–6 mm apart. Calices bear 42–49 septa, hexamerally arranged in four cycles, generally complete. S1, S2, and some S3 reach the columella, S4 half width of S3 or less. Septal faces granulate with spaced pointed granules. Paliform lobes present before S1, S2, and S3, in the latter just when they reach the columella. Trabecular, wide, and raised columella occupies about one-third of corallite diameter. Well-developed costae, mainly in S1, S2, and S3. Dissepiments endothecal and exothecal developed.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-17243; station 550011: MUN-STRI-17283, MUN-STRI-17290; station 550012: MUN-STRI-17307, MUN-STRI-17293, MUN-STRI-17298; station 550013: MUN-STRI-43529. Arroyo Uitpa, station 550016: MUN-STRI-37866, MUN-STRI-37874. SW Ekieps, station PF0018: MUN-STRI-37923, MUN-STRI-37925.

Remarks.—The *Monstastraea* species with four cycles in their septal arrangement show a high morphological similarity; however, *M. canalis* can be differentiated from *M. endothecata* Duncan, 1863 and *M. cavernosa* by its smaller calices and equal costae. In addition, it can be differentiated from *M. cavernosa* because *M. canalis* has thicker walls and more closely spaced corallites (Budd, 1991, p. 37, 39). *Montastraea canalis* is a common framework component in reefs. In the Siamaná Formation, it was found in patch reef environments with *Porites* spp., *Siderastrea conferta*, *Agathiphyllia tenuis*, and other *Montastraea.*

Montastraea cavernosa (Linnaeus, 1767)
Figure 5.10, 5.11

1767 *Madrepora cavernosa* Linnaeus, p. 1276.
1901 *Orbicella cavernosa*; Vaughan, p. 27.
1901 *Orbicella braziliana* Verrill, p. 101.
1901 *Orbicella cavernosa* var. *hirta* Verrill, p. 102, 189, pl. 33, fig. 2, 2a.
1991 *Montastraea cavernosa*; Budd, p. 37, pl. 8, figs. 1, 4, 6, 7, pl. 9, figs. 1, 3–6, pl. 10, figs. 1–6, text figs. 3–5, 7, 10, 11, 14, 17, 19.

Holotype.—USNM 36669, from North Rocks, Bermuda. Recent.

Occurrence.—Late Oligocene to Recent. Earliest occurrences in Antigua Formation, Antigua and Barbuda (Johnson, 2007). Early Miocene in Castillo Formation, Venezuela (Johnson et al., 2009); Siamaná and Jimol formations, Colombia. Until middle Miocene in Chipola Formation, Florida, USA (Budd et al., 1996); Baitoa Formation, Dominican Republic (Budd et al., 1994); Valiente Formation, Panama (Klaus et al., 2012). Middle Miocene–early Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene in San Andrés Formation, Colombia (Geister, 1975); Old Bank Formation, Panama (Klaus et al., 2012); Cercado Formation, Dominican Republic (Klaus et al., 2008). Between late Miocene and early Pliocene in Gurabo Formation, Dominican Republic (Klaus et al., 2008). Early Pliocene in Mao Formation, Dominican Republic (Klaus et al., 2008). Late Pliocene in Quebrada Chocolate and Moin formations, Costa Rica (Budd et al., 1999). Early Pleistocene in Isla Colón and Urracá formations, Panama (Klaus et al., 2012); Hope Gate and Manchioneal formations, Jamaica (Budd and McNeill, 1998). Recent occurrences in the Greater Caribbean and Brazil.

Description.—Corallum massive and plocoid. Corallites circular to oval in shape, 6–7 mm in diameter, spaced apart 2.5–4.5 mm. Calices bear 38–48 septa, hexamerally arranged in four cycles. Primary, secondary, and tertiary septa reach the columella; S4 thin, one-fourth width of S3 or less. Trabecular and wide columella, 1–2 mm in diameter. Paliform lobes absent. Costae developed in all cycles. Endothecal and exothecal dissepiments present.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-43489, MUN-STRI-43491, MUN-STRI-17607. Arroyo Ekieps, station 550012: MUN-STRI-17306, MUN-STRI-17295; station 550013: MUN-STRI-17329. SW Ekieps, station PF0018: MUN-STRI-37907. Flor de La Guajira, station 550001: MUN-STRI-17190; station 550002: MUN-STRI-17192, MUN-STRI-17193.

Remarks.—*Montastraea cavernosa* is similar to *M. endothecata* and *M. canalis* but can be differentiated by its calicular diameters, which are of intermediate size. It also differs from *M. canalis* by having subequal costae, and usually the colonies present a wide variation of intercalicular spaces, even in the same colony, especially at their edges (Budd, 1991, p. 39). The samples from the Siamaná Formation are poorly preserved and recrystallized. This species was found in patch reef environments with *Porites* spp., *Siderastrea conferta*, *Agathiphyllia tenuis*, and other *Montastraea*. At present, *M. cavernosa* is a common species in the Caribbean, Bahamas, and Florida, living up to 90 m depth, but usually from 12 to 30 m depth.

Montastraea endothecata Duncan, 1863
Figure 5.12

1863 *Astraea endothecata* Duncan, p. 434, pl. 14, fig. 9, pl. 15, fig. 7a, b.
1919 *Orbicella cavernosa* var. *endothecata*; Vaughan, p. 384, pl. 63, fig. 1, 1a.
1919 *Orbicella bainbridgensis* Vaughan, p. 386, pl. 90, fig. 1, 1a–c.
1919 *Cyathomorpha roxboroughi* Vaughan, p. 461, pl. 129, fig. 1, 1a, b.
1919 *Orbicella canalis* Vaughan, p. 389, pl. 94, fig. 2, 2a, pl. 97, fig. 4, 4a, not pl. 94, figs. 1, 1a, 3, 3a.
1991 *Montastraea endothecata*; Budd, p. 40, pl. 1, fig. 4, pl. 5, fig. 7, pl. 8, fig. 5, pl. 14, figs. 1, 3–5, pl. 15, figs. 1–4, pl. 16, figs. 1–6, pl. 17, figs. 1–6, text figs. 3–5, 7, 10, 11, 14, 17.

Holotype.—NHMUK R28791, from Nivajè Shale Formation, Dominican Republic. Neogene.

Occurrence.—Oligocene to Pliocene. First occurrences from early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983); Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); Antigua Formation, Antigua and Barbuda (Johnson, 2007). Until early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003); Providencia Island, Colombia (Geister, 1992). Early Miocene in Anguilla Formation, Anguilla (Budd et al., 1995); Chipola Formation, Florida, USA (Budd et al., 1996); Culebra Formation, Panama (Johnson and Kirby, 2006); Siamaná Formation, Colombia. Until middle Miocene in Tamana Formation, Trinidad and Tobago (Johnson, 2001); Seroe Domi Formation, Curaçao (Budd et al., 1998); San Andrés Formation, Colombia (Geister, 1975); Santa Ana Formation, Mexico (Frost and Langenheim, 1974). Late Miocene in Old Bank Formation, Panama (Klaus et al., 2012). Latest occurrences from early Pliocene in Gurabo and Mao formations, Dominican Republic (Budd et al., 1994; Klaus et al., 2008).

Description.—Corallum massive and plocoid. Corallites circular to oval in shape, moderately raised, 5.3–10.0 mm in diameter, spaced 1.4–6.0 mm apart. Calices bear around 48 septa, hexamerally arranged in four cycles. Primary, secondary, and tertiary septa reach the columella; S4 thin and one-third width of S3 or less. Septal faces granulate with spaced and irregularly arranged rounded or pointed granules. Trabecular and wide columella, 2–3 mm in diameter. Septothecal theca. Well-developed dentate costae in S1, S2, and S3, ornate with pointed granules. Endothecal and exothecal dissepiments present.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-17229, MUN-STRI-17225; station 550011: MUN-STRI-17284; station 550011: MUN-STRI-17303. SW Ekieps, station PF0018: MUN-STRI-37926.

Remarks.—The samples from the Siamaná Formation are well preserved. *Montastraea endothecata* was found building fringing systems, associated with *Porites* spp. It can be differentiated from *M. canalis* and *M. cavernosa* due to the presence of bigger corallites, subequal costae, and a thick theca in *M. endothecata* (Budd, 1991).

Discussion

The morphospecies reported in this study were common from the late Oligocene to the early Miocene in the Caribbean region (Budd et al., 1994; Budd, 2000) (Fig. 6). Most of them became extinct either at the end of the Burdigalian (Fig. 6, group 1) or in the Pliocene-Pleistocene transition, one of the most critical turnovers for the scleractinian corals in the Caribbean (Budd et al., 1996; Budd, 2000; Klaus and Budd, 2003).

Species such as *Agathiphyllia antiguensis*, *A. tenuis*, *Antiguastrea cellulosa*, *Diploastrea crassollamelata*, and *D. magnifica* were considered typical components of the late Oligocene assemblages in the southern Caribbean (Johnson, 2007; Johnson et al., 2009). However, several studies have reported these species in early Miocene formations, such as Chipola, Antigua, Arcadia, Santa Ana (Budd et al., 1994), and San Andrés (Geister, 1975). In addition, recent stratigraphic studies of the Castillo and San Luis formations of Venezuela, conducted by Rincón et al. (2014) suggest an early Miocene age for these units, previously dated as Oligocene. The occurrence of these species in the Siamaná Formation confirms their presence in the early Miocene of the southern Caribbean region.

Although most of the species described have been previously recorded in the early Miocene, the occurrence of *Astrocoenia decaturensis* in the Siamaná Formation confirms its temporal distribution until the Burdigalian. On the other hand, *Orbicella limbata*, which has been commonly recorded from the early Miocene in other Caribbean formations, was found in the Flor de La Guajira locality from the Aquitanian; however, the uncertainty in age is due to the material being reworked and it could come from the Chattian beds of the Siamaná Formation.

All analyzed species had previous records in other southern Caribbean formations, mainly in the Valiente and Culebra formations of Panama (Johnson and Kirby, 2006; Klaus et al., 2012) and the Pedregoso, Agua Clara (Cauderalito Member), San Luis, and Castillo formations of Venezuela (Johnson et al., 2009).

In addition to the coral fauna described here, in the Siamaná and Jimol formations, morphospecies of the families Mussidae, Pocilloporidae, Poritidae, and Siderastreidae of the order Scleractinia and of the family Milleporidae of the order Anthothecata were found; they will be described in an additional work. However, we can mention the principal patterns observed. Of the total of 116 species of corals from the Oligocene and Miocene recorded in the Caribbean region (Table 4), just 22.4% were observed in the Cocinetas Basin. With the exception of one member of the family Caryophylliidae, the species studied were considered important building components of shallow coral reefs during the late Oligocene in the Caribbean Sea (Johnson et al., 2009; Budd, 2000), most of them with massive and branching morphologies. The species composition in both the Siamaná and Jimol formations suggests shallow and clear-water environments, with moderate physical disturbance. During the early Miocene, Caribbean coral reefs have been predominantly recognized as patch reefs (Budd et al., 1995; Budd, 2000), likely due to environmental changes in the Oligocene–Miocene transition, which inhibited the building capacity of zooxanthellate scleractinian corals (Edinger and Risk, 1994). However, the coral reef structures from the Siamaná Formation (early Miocene) differ from this general pattern in that well-developed coral formations were common, and *Montastraea* spp. and *Porites* spp. were the dominant species in the coral assemblages. By contrast, reefs in the Jimol Formation (late early Miocene) are small structures of low diversity, matching the characteristics of other early Miocene reefs in the region (Budd et al., 1995).

Differences in species composition were also observed in the localities of the Siamaná Formation (Table 2). Arroyo Ekieps was the most diverse in species number and colony morphology, for example, massive and branching to columnar (*Alveopora tampae*). By contrast, Flor de La Guajira had the lowest species richness with mainly massive colonies. Thus, the reef system in Arroyo Ekieps (Aquitanian–Burdigalian) was better developed, while Flor de La Guajira, estimated to be near the lower Aquitanian boundary, is limited to patch reefs of low diversity. Flor de La Guajira, the oldest locality evaluated in this study, has a prevalent Miocene fauna, including *Orbicella limbata* and *O. imperatoris* (Budd, 1991; Budd et al., 1992), as well as *Montastraea cavernosa*, one of the few species to persist through both the Oligocene-Miocene and Pliocene-Pleistocene coral faunal turnover events in the Caribbean.

Here we provide source information for future studies that potentially will help to describe the paleoenvironmental conditions of reef development in the Cocinetas Basin, as well as data to explore morphologic changes in the different species across time and space.

Acknowledgments

This study was supported by Colciencias, project code 7277 569 33195. PF is funded by the scholarship Doctorados en el Exterior 2015-Colciencias. We also acknowledge the partial support of Ecopetrol S.A., Smithsonian Tropical Research Institute, University of Zurich, Universidad del Norte, Universidad de Granada, NSF (Grant EAR 0957679), National Geographic Society, Anders Foundation, 1923 Fund, and G.D. and J. Walston Johnson. Special thanks to J.C. Braga for his guidance, support, and helpful comments on the manuscript and C. Jaramillo for encouraging and supporting the study. We thank T. Stemann and an anonymous reviewer for their valuable comments. We are also grateful to A. Budd for sharing species distribution information, W. Renema for the LBF identifications, V. Pretković for her help in the field, S. Montes for preparing the thin sections, and I. Sanchez for her help with the SEM. Thanks to the ARES team and the Wayúu community for their support and guidance in the field.

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Accepted 16 May 2018