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Early Miocene shallow-water corals from La Guajira, Colombia: Part II, Mussidae–Siderastreidae and Milleporidae

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Abstract.—In this contribution we describe and illustrate 14 coral morphospecies collected from the early Miocene Siamaná (Aquitanian–Burdigalian) and Jimol (late Burdigalian) formations of the Cocinetas Basin in La Guajira Peninsula, northern Colombia. Eleven were identified as already established species including seven genera belonging to the families Mussidae, Pocilloporidae, Poritidae, Siderastreidae, and Milleporidae; the other three remain in open nomenclature. Nine of the 11 species identified (81%) are extinct. The remaining two living species, *Siderastrea siderea* and *Millepora alcicornis*, are common on modern Caribbean reefs. Their presence in the Siamaná Formation extends their temporal range in the Caribbean region to the early Miocene. Most of the taxa described here were hermatypic and zooxanthellate corals of the order Scleractinia, with the exception of the fire coral *Millepora alcicornis*, of the order Anthothecata, family Milleporidae. The coral fauna recorded in the Siamaná and Jimol formations is typical of shallow and calm waters of the Oligocene–Miocene transition.

Introduction

The early Miocene was a major epoch in the faunal transition in Caribbean coral species and their capacity for reef-building (Budd et al., 1994; Edinger and Risk, 1994; Budd, 2000; Johnson et al., 2009), in which a loss of coral species diversity of 40% is estimated (Johnson et al., 2008). The transition from prominent and diverse Oligocene reefs to depauperate and poorly developed middle Miocene reefs has been loosely tied to a combination of tectonic events (Hoorn et al., 1995; Iturralde-Vinent and McPhee, 1999; Iturralde-Vinent, 2006), changes in ocean circulation due to the closing or narrowing of gateways (e.g., the emergence of the Isthmus of Panama and Drake passage) (von der Heydt and Dijkstra, 2005, 2006; Newkirk and Martin, 2009), variations in sea level (Iturralde-Vinent, 2006) and temperature (Mutti et al., 2005), increased regional productivity (Hoorn et al., 1995; Mutti et al., 2005; von der Heydt and Dijkstra, 2005, 2006), and enhanced upwelling events (Edinger and Risk, 1994). Understanding the relative importance of these factors requires a better understanding of coral species distribution through time and across the Caribbean region.

This paper represents a second contribution to the first comprehensive taxonomical work on fossil coral reefs in the continental formations in Colombia. We provide descriptions and classifications according to recent revisions to order Scleractinia (Fukami et al., 2004; Budd and Stolarski, 2009, 2011), as well as updates to the age and nomenclature of the Caribbean coral-bearing formations. The first part of this research included the descriptions of 18 morphospecies of the families Acroporidae, Agathiphylliide, Astrocoeniidae, Caryophylliidae, Diploastraeidae, Merulinidae, and Monstastraeidae (Flórez et al., 2018). Here, 14 morphospecies of the families Mussidae, Pocilloporidae, Poritidae, Siderastreidae, and Milleporidae are described and illustrated in detail. We integrate the findings of both studies to summarize paleoenvironmental interpretations of the Siamaná and Jimol formations and assess reef-building capacity in the early Miocene of the southern Caribbean.

Geological setting

The Cenozoic formations of the Cocinetas Basin show fossiliferous horizons from diverse paleoenvironments (Hendy et al., 2015; Moreno et al., 2015; Carrillo-Briceño et al., 2016; Silva-Tamayo et al., 2017). The Siamaná Formation is a diachronic unit with shallow marine carbonates ranging from the late Oligocene to late early Miocene (Silva-Tamayo et al., 2017). It is unconformably overlain by deep marine siliciclastic sediments of the Uitpa Formation, Aquitanian–Burdigalian in age (Silva-Tamayo et al., 2017, p. 228, fig. 12). The Uitpa Formation is in turn overlain the by the Jimol Formation, with shallow marine mixed carbonate and siliciclastic deposits dating to the Burdigalian (Moreno et al., 2015; Silva-Tamayo et al., 2017). An extended description of the geological setting is provided in Flórez et al. (2018).

Materials and methods

The samples studied were collected at the Arroyo Uitpa, Arroyo Ekieps, SW Ekieps, and Flor de La Guajira localities of the

Siamaná Formation, and Punta Espada locality of the Jimol Formation (Fig. 1, Appendix 1) (Flórez et al., 2018, fig. 2). The samples were analyzed using a combination of stereo microscopy, scanning electron microscopy, and thin section microscopy. A list of the collected samples with associated catalog numbers, station numbers, and geologic formations is provided in Appendix 2.

The systematic paleontology, including key morphometric data (Table 1), is presented in alphabetical order. Sources of occurrence information are compiled in Flórez et al. (2018, table 3). Taxonomic classifications were based on literature descriptions of the type material, and through comparisons with specimens housed at Rosenstiel School of Marine and Atmospheric Science.

Repositories and institutional abbreviations.—The samples are deposited at the Mapuka Museum of the Universidad del Norte, with the acronym MUN-STRI. Other abbreviations: PIU, Paleontologiska Institutionene Uppsala, Uppsala, Sweden; NHMUK, The Natural History Museum, London, United Kingdom; USNM, U.S. National Museum of Natural History, Washington, D.C., USA, numbers preceded by 'M' are from Mollusk series.

Systematic paleontology

Class Anthozoa Ehrenberg, 1834
Subclass Hexacorallia Haeckel, 1896
Order Scleractinia Bourne, 1900
Family Mussidae Ortmann, 1890
Genus *Colpophyllia* Milne-Edwards and Haime, 1848

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

Colpophyllia willoughbiensis (Vaughan, 1919)
Figure 2.1, 2.2

1919 *Manicina willoughbiensis* Vaughan, p. 422, pl. 104, figs. 2, 2a, pl. 105.
1974 *Colpophyllia willoughbiensis*; Frost and Langenheim, p. 248, pl. 88, figs. 1–6, pl. 89, figs. 1–7.
1992 *Colpophyllia willoughbiensis*; Budd et al., p. 585, fig. 7.1–7.3.

Holotype.—USNM M325006, from Willoughby Bay, Antigua. Oligocene.

Occurrence.—Late Eocene to Miocene. First occurrences from Gatuncillo Formation, Panama (Budd et al., 1992). Early and late Oligocene in Rancho Berlín and La Quinta formations, respectively, Mexico (Frost and Langenheim, 1974). Late Oligocene in Antigua Formation, Antigua and Barbuda (Johnson, 2007); Lares Formation, Puerto Rico (Frost et al., 1983). Early Miocene in Castillo Formation, Venezuela (Johnson et al., 2009). Middle Miocene in Santa Ana Formation, Mexico (Frost and Langenheim, 1974).

Description.—Corallum massive to relatively flattened, meandroid, with intracalicular budding. Corallum attached to substrate by a central peduncle. Large and sinuous valleys, 10 mm wide and 0.5–10.0 mm deep. Walls usually single, but series could be separated by a furrow. Collines bear 12 or 13 septa per centimeter. Septa equally thick, 0.37–0.40 mm in width; septal face finely granulated. Trabecular columella discontinuous and poorly developed to absent. Endothecal dissepiments well developed and abundant.

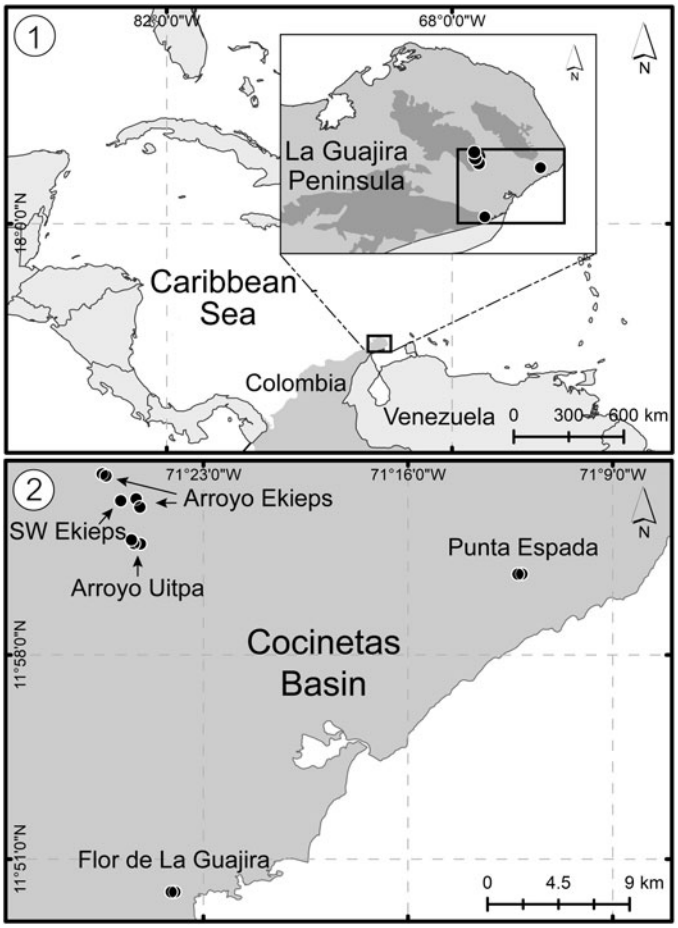

Figure 1. (**1**) Location of La Guajira Peninsula and the study area in the Caribbean region. (**2**) Position of the localities and stations in the Cocinetas Basin: Arroyo Ekieps, SW Ekieps, Arroyo Uitpa and Flor de La Guajira from Siamaná Formation, and Punta Espada from Jimol Formation.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-17276; station 550012: MUN-STRI-17301, MUN-STRI-43515, MUN-STRI-17310, MUN-STRI-17314, MUN-STRI-17318, MUN-STRI-17320, MUN-STRI-17300, MUN-STRI-37864; station 550013: MUN-STRI-43526. Arroyo Uitpa, station PF0016: MUN-STRI-37867. SW Ekieps, station PF0018: MUN-STRI-37924, MUN-STRI-37927.

Remarks.—The samples from the Siamaná Formation are moderately preserved. Although the lower surface does not conserve the epitheca, the septal distribution, collines, and valleys are easily recognizable. They are building components of well-developed framework reefs and patch reefs. According to Frost and Langenheim (1974), specimens from different localities, from the same locality, and even in the same colony

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Table 1. Morphometric data of the corals recorded in this work. Colony growth: B, branching; M, massive; P, platy; K, knobby. CD: calicular diameter (*dactilopore in *Millepora alcicornis*). ICD: Intercalicular distance. Coenosteum: Tb, tubercles; Sp, spongy; Sm, smooth. Kind of columella: St, styliform; L, lamellar; T, trabecular. In all items (—) 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): PE, Punta Espada locality.

		Morphologic characters							Formations	
Family	Species	Colony	CD (mm)	ICD (mm)	Coenosteum	No. septa	No. cycles	Columella	Siamaná EM	Jimol LEM
Mussidae	*Colpophyllia willoughbiensis*	M	—	—	—	12–13/cm	—	L	AE, SWE, AU	
Pocilloporidae	*Pocillopora* sp. indet.	B	1.0–2.0	0.5–1.0	Sm	?12	?2	—		PE
	Stylophora affinis	B	1.0–1.2	0.4–0.8	Tb	12	2	St	AE, SWE, AU	
	Stylophora minor	B	0.6–0.8	0.8–1.8	Tb	?6	?1	St	AE	
	Stylophora sp. indet.	B	0.1–0.5	0.4–0.8	Tb	—	—	—	FG	
Poritidae	*Goniopora hilli*	B, M	2.0–3.8	0.7–1.4	Sp	24	3	T	AE	
	Porites anguillensis	P, K	1.5–2.0	—	Sp	12	2	T	AE	
	Porites baracoaensis	B	1.3–1.4	0.3–0.7	Sp	12	2	T	AE	
	Porites portoricensis	B	1.3–2.0	0.5–0.9	Sp	12	2	T	AE, SWE, AU	
	Porites waylandi	M, K	1.3–1.8	0.50	Sp	12	2	T	AE, SWE, AU, FG	PE
	Porites sp. indet.	B	1.3–2.0	0.6–0.8	—	12	2	—		PE
Siderastreidae	*Siderastrea conferta*	M	4.0–10.0	—	—	54–67	5	T	AE	
	Siderastrea siderea	M	3.5–5.0	—	—	45–50	4	T	AE	PE
Milleporidae	*Millepora alcicornis*	B	0.2–0.5*	0.7–1.0	Sp	—	—	—	AE	

could show morphological variations. The genus *Colpophyllia* was traditionally included in the family Faviidae (Wells, 1956), however, in accordance with recent genetic and morphologic studies, Budd et al. (2012) transferred it into the family Mussidae.

Family Pocilloporidae Gray, 1840
Genus *Pocillopora* Lamarck, 1816

Type species.—*Pocillopora acuta* Lamarck, 1816; by original designation.

Pocillopora sp. indet.
Figure 2.3–2.5

Occurrence.—Early Miocene in Jimol Formation, Colombia.

Description.—Corallum branching and plocoid. Branches are thick and flattened in shape, 2.8 cm in minor diameter, up to 9 cm in major diameter. Corallites circular to oval, 1–2 mm in diameter, spaced 0.5–1.0 mm apart. Calices bear ~12 septa. Calicular fossa moderately deep. Columella absent or reduced. Tabulae present, spaced at 0.7–1.6 mm. Coenosteum covered by granules and circular perforations ~0.2 mm in diameter.

Materials.—Jimol Formation, Punta Espada, station 550014: MUN-STRI-17345, MUN-STRI-43542.

Remarks.—Samples are highly crystallized and poorly preserved; however, specimens resemble *Pocillopora guantanamensis* described by Vaughan (1919, p. 344). Both have robust and flat branches, as well as verrucae absent; nevertheless, the corallites in *Pocillopora* sp. indet. are bigger than those in *P. guantanamensis*. Samples also differ from other species of *Pocillopora* recorded for the Oligocene–Miocene, such as *P. crassoramosa* Duncan, 1864 and *P. portoricensis* (Vaughan, 1919), which bear well-developed verrucae, as well as from *P. arnoldi* Vaughan, 1919, which has thin branches and smaller corallites than *Pocillopora* sp. indet. (Vaughan, 1919, p. 343). Most of the surface features were lost, which limited their identification at the genus level. In addition, the boundaries between *Pocillopora* species are overlapping, due to the high phenotypic plasticity and capacity of hybridization of the colonies (Schmidt-Roach et al., 2014). Nevertheless, based on branch size and morphology, the presence of tabular dissepiments, as well as irregularity of the coenosteum, which suggests the presence of verrucae, we assign these specimens to the genus *Pocillopora*. The thick branches indicate a robust builder of patch reefs from the Jimol Formation, in occurrence with *Orbicella imperatoris* Vaughan, 1919 and *Porites waylandi* Foster, 1986.

Genus Stylophora Schweigger, 1819

Type species.—*Madrepora pistillata* Esper, 1797; by unknown designation.

Stylophora affinis Duncan, 1863
Figure 2.6–2.8

1863 *Stylophora affinis* Duncan, p. 436, pl. 16, fig. 4.
1919 *Stylophora panamensis* Vaughan, p. 335, pl. 75, figs. 1, 1a.

Holotype.—NHMUK R28788, from Nivajè Shale Formation, Dominican Republic. Neogene.

Occurrence.—Late Oligocene to Pleistocene. First occurrences from Newport Formation, Jamaica (Stemann, 2003). Early Miocene in Siamaná Formation, Colombia; Pedregoso, Castillo and Agua Clara (Cauderalito Member) formations, Venezuela (Johnson et al., 2009); Culebra Formation, Panama (Johnson and Kirby, 2006). Early–middle Miocene in Providencia Island, Colombia (Geister, 1992); Tamana Formation, Trinidad and Tobago (Johnson, 2001). Middle Miocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene and early Pliocene in Cercado and

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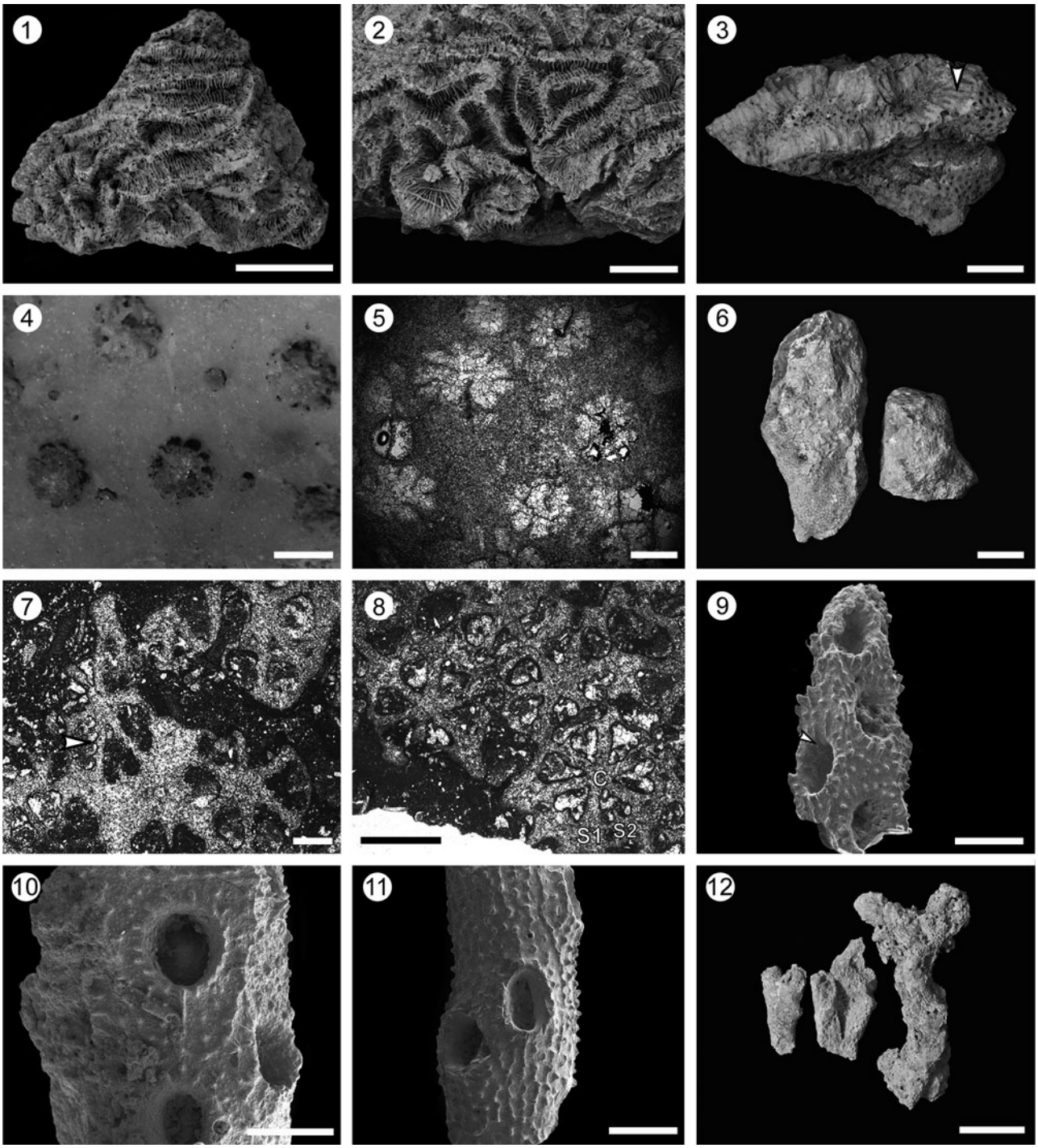

Figure 2. *Colpophyllia willoughbiensis* (Vaughan, 1919) from the Siamaná Formation, Arroyo Ekieps: (**1**) colony fragment (MUN-STRI-17310); (**2**) detail of the septa and sinuous valleys (MUN-STRI-17318). *Pocillopora* sp. indet. from the Jimol Formation, Punta Espada: (**3**) transversal view of the branch fragment showing the trabecular dissepiments (white arrow) (MUN-STRI-43542); (**4**) detail of the surface of the colony and corallites (MUN-STRI-17345); (**5**) transverse thin section showing the septal arrangement (MUN-STRI-43542). *Stylophora affinis* Duncan, 1863 from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-17608): (**6**) branching fragments; (**7**) transverse thin section showing the septal granules (white arrow); (**8**) transverse thin section showing the septal arrangement (S1, S2), and styliform columella location (c). *Stylophora minor* Duncan, 1863 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-43797): (**9**) pointed tip of branch, showing the granulated coenosteum and poorly developed septa (white arrow); (**10**) detail of the corallites and their costae, (**11**) coenosteum with rows of granules. *Stylophora* sp. indet. from the Siamaná Formation, Flor de La Guajira (MUN-STRI-43535): (**12**) branch fragments. Scale bars are (**1**) 3 cm; (**2, 3, 6**) 2 cm; (**4, 9, 10, 11**) 1 mm; (**5**) 500 μ; (**7**) 200 μ; (**8**) 400 μ; (**12**) 2 cm.

Gurabo formations, Dominican Republic (Klaus et al., 2008). Pliocene in Mao Formation, Dominican Republic (Klaus et al., 2008); Quebrada Chocolate Formation, Costa Rica (Budd et al., 1999). Pliocene–early Pleistocene in Tamiani Formation, Florida, USA (Klaus et al., 2017). Late Pliocene–early Pleistocene in La Cruz and Matanzas formations, Cuba

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(Budd et al., 1999). Early Pleistocene in Old Pera Formation, Jamaica (Budd and McNeill, 1998); Curaçao Highest Terrace (Budd et al., 1998); Isla Colón and Urracá formations, Panama (Klaus et al., 2012).

Description.—Corallum branching and plocoid. Branches robust, cylindrical to slightly compressed in shape, 3.0–3.5 cm in diameter. Branch tips blunt or flattened. Corallites circular, 1.0–1.2 mm in diameter, spaced 0.4–0.8 mm apart. Calices bear ~12 septa, hexamerally arranged in two cycles. S1 reach the columella, while S2 does not extend too far away from calicular wall. Fossa shallow and styliform columella. Coenosteum covered with granules.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550005: MUN-STRI-17608, MUN-STRI-17609; station PF0016: MUN-STRI-37873. Arroyo Ekieps, station 550011: MUN-STRI-37932. SW Ekieps, station PF0018: MUN-STRI-37921.

Remarks.—Specimens of *Stylophora affinis* resemble *Stylophora imperatoris* Vaughan, 1919 because both are branched species of large size recorded in the Oligocene and Miocene units. However, these can be differentiated because *S. imperatoris* exhibits contorted and lamellate branches, commonly ending in plates. *Stylophora imperatoris* also bears nodules in the older branches, as well as larger corallites and more prominent walls than *S. affinis* (Vaughan, 1919, p. 334). In addition, in well-preserved specimens of *S. affinis*, a characteristic polygonal calicular margin is visible in the intercalicular space (Vaughan, 1919, p. 336). The colonies from the Siamaná Formation are poorly preserved and highly recrystallized. They were associated with shallow patch reefs in occurrence with *Antiguastrea cellulosa* (Duncan, 1863) and *Diploastrea crassolamellata* (Duncan, 1863).

Stylophora minor Duncan, 1863
Figure 2.9–2.11

1863 *Stylophora affinis* var. *minor* Duncan, p. 436, not pl. 16, fig. 4.
1900 *Stylophora minutissima* Vaughan, p. 131, pl. 13, figs. 13–15.
1919 *Stylophora goethalsi* Vaughan, p. 338, pl. 75, figs. 2–4.
1973 *Stylophora* cf. *minutissima*; Weisbord, p. 18, pl. 1, fig. 1–5, pl. 4, fig. 1.

Holotype.—NHMUK R28788, from Nivajè Shale Formation, Dominican Republic. Neogene.

Occurrence.—Late Oligocene to early Pleistocene. First occurrences from Tabera Formation, Dominican Republic (Budd et al., 1994). Late Oligocene–early Miocene in Arcadia Formation (Tampa Member), Florida, USA (Budd et al., 1994). Early Miocene in Siamaná Formation, Colombia; Culebra Formation, Panama (Johnson and Kirby, 2006). Early–middle Miocene in Baitoa Formation, Dominican Republic (Budd et al., 1994); Tamana Formation, Trinidad and Tobago (Johnson, 2001); reaching the Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene in Cercado Formation, Dominican Republic; Old Bank Formation, Panama (Klaus et al., 2008, 2012). Late Miocene–early Pliocene in Gurabo Formation, Dominican Republic (Klaus et al., 2008). Early Pliocene in Río Banano Formation (Brazo Seco), Costa Rica (Budd et al., 1999); Mao Formation, Dominican Republic (Klaus et al., 2008). Late Pliocene in Quebrada Chocolate Formation, Costa Rica (Budd et al., 1999); Layton Formation (Bowden Member), Jamaica (Budd and McNeill, 1998). Early Pleistocene in Old Pera and Hope Gate formations, Jamaica (Budd and McNeill, 1998); Isla Colón Formation, Panama (Klaus et al., 2012).

Description.—Corallum branching and plocoid. Branches thin with pointed tips, fragments 6.43–10.80 mm long, circular to slightly flat in cross-section, 1.6–3.7 mm in diameter. Corallites rounded to slightly oval, 0.64–0.65 mm in the smallest calicular diameter and 0.75–0.80 mm in the largest one. Corallites distributed irregularly at branch surface, sometimes in rows. Intercalicular space of 0.8–1.8 mm, which decreases in the branch tips. S1 are not preserved and S2 are poorly developed, formed by rows of granules. Fossa moderately deep, containing a styliform columella, which does not reach the height of the calicular edge. Calicular wall slightly exsert, bearing 18–24 blunt costae, from which project rows of round-pointed granules that cover the coenosteum, sometimes forming ridges along the branches.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-43797, MUN-STRI-43798, MUN-STRI-43799, MUN-STRI-43800, MUN-STRI-43801; station 550012: MUN-STRI-43802, MUN-STRI- 43881; station 550013: MUN-STRI-43803; station 550008: MUN-STRI-43879, MUN-STRI- 43880.

Remarks.—Samples from the Siamaná Formation are branch fragments that are recrystallized and poorly preserved. Despite the loss of septa, the size of corallites and characters of corallite rims and coenosteum allow specimen identification. *Stylophora minor* closely resembles *S. granulata*, but differs from it by the granule arrangement in the coenosteum, which in the latter species is rarely organized forming continuous ribs (Vaughan, 1919, p. 340). In addition, *S. granulata* Duncan and Wall, 1865 shows a mostly smooth coenosteum and branches with blunt tips. In the Siamaná Formation, *S. minor* occurs in a well-developed reef with *Siderastrea conferta* (Duncan, 1863), *Porites portoricensis*, *P. baracoaensis* Vaughan, 1919, *Montastraea canalis* (Vaughan, 1919), *Agathiphyllia tenuis* (Duncan, 1863), and a member of the family Caryophylliidae.

Stylophora sp. indet.
Figure 2.12

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

Description.—Corallum branching and plocoid. Branches thin, terete to slightly compressed in shape, 7.4–14.0 mm in diameter. Corallites circular to slightly irregular of variable

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size, 0.1–0.5 mm in diameter, irregularly arranged in the coenosteum, spaced 0.4–0.8 mm apart. Septa and columella are not preserved. Coenosteum covered with granules or spines, and with frequent circular perforations of 0.20–0.42 mm in diameter.

Materials.—Siamaná Formation, Flor de La Guajira, station 550002: MUN-STRI-43535.

Remarks.—The sample consists of poorly preserved colony fragments with many characters missing. The specimen differs from *Stylophora affinis* and *S. minor* by the morphology and size of the branches, which in *S. affinis* are more robust, and in *S. minor* more slender and small. In addition, the specimen differs from *S. minor* by the irregular distribution of the corallites. However, the general pattern of corallum and coenosteum, as well as corallite size, indicate that it belongs to *Stylophora*. It was found in a patch reef with *Montastraea cavernosa* (Linnaeus, 1767) and *Orbicella imperatoris*.

Family Poritidae Gray, 1840
Genus *Goniopora* Blainville, 1830

Type species.—*Goniopora pedunculata* Quoy and Gaimard, 1833; by subsequent designation. Holotype lost.

Goniopora hilli Vaughan, 1919
Figure 3.1–3.3

1919 *Goniopora hilli* Vaughan, p. 488, pl. 142, figs. 1, 1a.
1919 *Goniopora jacobiana* Vaughan, p. 492, pl. 144, figs. 1, 1a, 2, 2a, 3, 3a.
1919 *Goniopora canalis* Vaughan, p. 494, pl. 146, figs. 1–3.
1973 *Goniopora aucillana* Weisbord, p. 30, pl. 33, fig. 1, pl. 34, fig. 1, pl. 35, fig. 1.
1973 *Goniopora tampaensis* Weisbord, p. 36, pl. 15, figs. 1, 2.

Holotype.—USNM M325058, from La Boca Formation, Panama. Middle Miocene.

Occurrence.—Early Oligocene to early Pleistocene. Early Oligocene in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in Tabera Formation, Dominican Republic (Budd et al., 1994); La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Arcadia Formation (Tampa Member), Florida, USA (Budd et al., 1994). Early Miocene in Siamaná Formation, Colombia; Culebra Formation, Panama (Johnson and Kirby, 2006); Anguilla Formation, Anguilla (Budd et al., 1995). Early–middle Miocene in Tamana Formation, Trinidad and Tobago (Johnson, 2001); reaching the Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene–early Pliocene in Gurabo Formation, Dominican Republic (Klaus et al., 2008). Early Pleistocene in Matanzas and La Cruz formations, Cuba (Budd et al., 1999).

Description.—Corallum massive, sometimes with columnar projections or growing in contorted plates. Colonies subplocoid with extracalicular budding. Corallites hexagonal in shape, sometimes compressed, 2.9–3.8 mm in diameter. Calices bear 24 septa, hexamerally arranged in three cycles. Dorsal and ventral septa are free. S1 and S2 reach the columella, while S3 fuse to adjacent S2 close to the columella. Septal margins and faces with denticles. Columella trabecular, matted and wide, around 1.0 mm in diameter. Wall is synapticulothecal and prominent. Fossa is moderately deep.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-43511; station 550012: MUN-STRI-17312, MUN-STRI-17297, MUN-STRI-43521.

Remarks.—Frost and Langenheim (1974) described a crown of six paliform knots circling the columella, at the fused end of S1 and S2. This character is not observed in the samples from the Siamaná Formation due to the preservation of the samples. This species is often confused with members of *Porites*, but they can be separated by corallite size and columella width, which are larger in the species of *Goniopora*, which also show three septal cycles instead of two, as occur in the species of *Porites* (Kitano et al., 2014).

Genus *Porites* Link, 1807

Type species.—*Porites polymorphus* Link, 1807 (= *Madrepora porites* Pallas, 1766 [in part]); by original designation.

Remarks.—Although the morphology of the colonies helps to identify the samples at the species level, the Neogene *Porites* species can often be confused, in particular if the samples are not well preserved. Several morphological characters of corallites could overlap or show high variability even in the same colonies. The genus has been an important building component of reefs since the early Miocene (Foster, 1986). *Porites* diversified and thrived in clear and turbid shallow waters around the world (Foster, 1986; Braga et al., 1990; Santodomingo et al., 2015a), inhabiting all reef zones, from near shore, to reef crest, to deep forereef (Goreau, 1959; Geister, 1983; Foster, 1986).

Porites anguillensis Vaughan, 1919
Figure 3.4–3.6

1919 *Porites anguillensis* Vaughan, p. 504, pl. 149, figs. 1a, 1b (type), pl. 150, fig. 5.

Holotype.—PIU WI43, from Anguilla Formation, Anguilla. Early Miocene.

Occurrence.—Late Oligocene to early Miocene. First occurrence in La Quinta Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene–early Miocene in Browns Town Formation, Jamaica (Stemann, 2003). Early Miocene in Siamaná Formation, Colombia; Culebra Formation, Panama (Johnson and Kirby, 2006); and Anguilla Formation, Anguilla (Budd et al., 1995).

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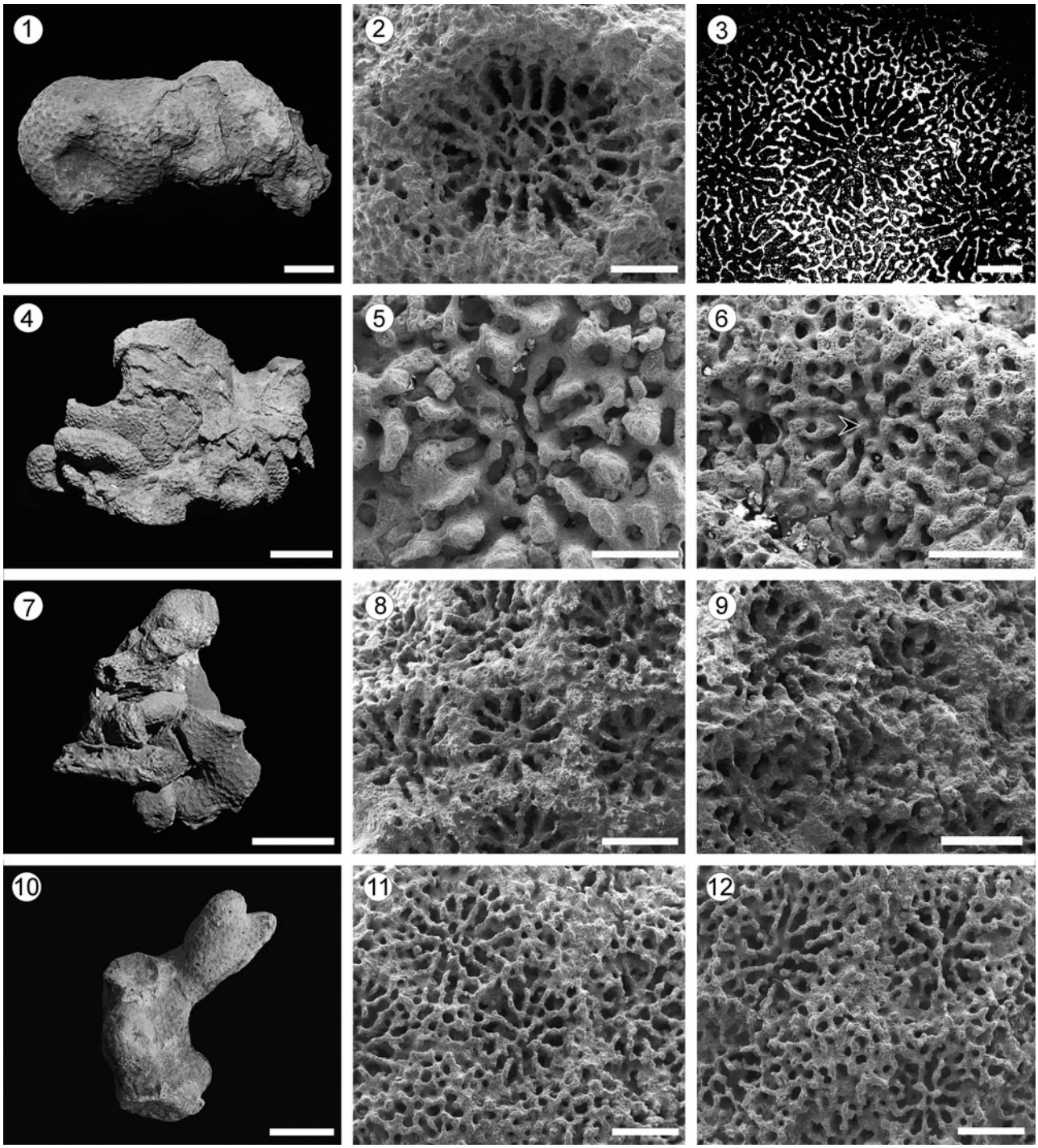

Figure 3. *Goniopora hilli* Vaughan, 1919 (MUN-STRI-43521): (**1**) morphology of the colony; (**2**) detail of a corallite, showing the septal arrangement and columella; (**3**) transverse thin section showing the denticles in the septal faces and calicular wall. *Porites anguillensis* Vaughan, 1919: (**4**) morphology of the colony (MUN-STRI-17285); (**5**) detail of the corallite (MUN-STRI-17240); (**6**) septal arrangement and columella (black arrow) surrounded by five elements of the palar crown. *Porites baracoaensis* Vaughan, 1919 (MUN-STRI-43527): (**7**) branch fragments; (**8, 9**) detail of corallites showing septal arrangements, the fusion of triplets and lateral pairs, columella, palar crown, and calicular wall. *Porites portoricensis* (Vaughan, 1919) (MUN-STRI-43486): (**10**) branch tip morphology; (**11, 12**) septal arrangement and columella of corallites, and coenosteum reticulate. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are (**1, 4**) 2 cm; (**2, 6, 8, 9, 11, 12**) 1 mm; (**3, 5**) 500 μ; (**7**) 1.5 cm; (**10**) 1.8 cm.

Description.—Corallum encrusting and multilaminar with knobs. Laminae flat and undulate, 1.0–2.5 mm thick, separated by spaces filled with sediment or cryptic fauna. Colonies subplocoid in form. Corallites circular to polygonal in shape, 1.5–2.0 mm in diameter, spaced 0.3–0.5 mm apart. Corallites bear 12 septa comprising a free dorsal directive, a fused ventral triplet, and four lateral pairs. Well-developed trabecular columella, formed by a single trabecular blunt, at the same level of the palar crown. Palar crown of five or six pali. Wall formed by one or two trabecular rings. Coenosteum reticulate.

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Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-17237, MUN-STRI-17239, MUN-STRI-17240, MUN-STRI-17241, MUN-STRI-17244; station 550011: MUN-STRI-17256, MUN-STRI-43506, MUN-STRI-43507, MUN-STRI-17271, MUN-STRI-17277, MUN-STRI-17278, MUN-STRI-17279, MUN-STRI-17285, MUN-STRI-17288, MUN-STRI-17289; station 550012: MUN-STRI-17308, MUN-STRI-17313, MUN-STRI-43520, MUN-STRI-17315, MUN-STRI-17316, MUN-STRI-43523.

Remarks.—*Porites anguillensis* can be differentiated from other poritids from the Siamaná Formation by the morphology of the colonies, which are flexed laminar plates, the relatively large size of the corallite and a robust and well-developed columella and palar crown. Within the Siamaná Formation *P. anguillensis* was associated with *Antiguastrea cellulosa*, *Alveopora tampae* Weisbord, 1973, *Agathiphyllia tenuis*, *Colpophyllia willoughbiensis*, *Porites waylandi*, *P. portoricensis*, *P. baracoaensis*, *Montastraea canalis*, *M. endothecata* Duncan, 1863, and *Siderastrea conferta* in well-developed reefs.

Porites baracoaensis Vaughan, 1919
Figure 3.7–3.9

1919 *Porites baracoaensis* Vaughan, p. 499, pl. 147, figs. 1, 1a.
1919 *Porites baracoäensis* var. *matanzasensis* Vaughan, p. 500, pl. 147, figs. 2–4.
1919 ?*Porites douvillei* Vaughan, p. 501, pl. 149, figs. 2, 2a, pl. 151, figs. 1, 1a.
1919 *Porites toulai* Vaughan, p. 501, pl. 150, figs. 1–4.
1986 *Porites baracoaensis*; Foster, p. 75, pl. 16, figs. 1–13, pl. 17, figs. 1–7, pl. 18, figs. 1–4, text-figs. 2–5, 10, 12, 14, 16, 17.

Holotype.—USNM M325069, from Baracoa, Cuba. Miocene.

Occurrence.—Late Oligocene to early Pleistocene. First records from late Oligocene in Tabera Formation, Dominican Republic (Budd et al., 1994); Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); Antigua Formation, Antigua and Barbuda (Johnson, 2007); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003). Early Miocene in Siamaná Formation, Colombia; Agua Clara (Cauderalito Member) and Castillo formations, Venezuela (Johnson et al., 2009); Culebra Formation, Panama (Johnson and Kirby, 2006); Anguilla Formation, Anguilla (Budd et al., 1995); Santa Ana Formation, Mexico (Frost and Langenheim, 1974). Early–middle Miocene in Providencia Island, Colombia (Geister, 1992); Tamana Formation, Trinidad and Tobago (Johnson, 2001). Middle Miocene in Valiente Formation, Panama (Klaus et al., 2012). Middle–late Miocene in San Andrés Formation, Colombia (Geister, 1975). Middle Miocene–early Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene in Cercado Formation, Dominican Republic; Old Bank Formation, Panama (Klaus et al., 2008, 2012). Late Miocene–early Pliocene in Gurabo Formation, Dominican Republic (Klaus et al., 2008). Early Pliocene in Río Banano Formation (Brazo Seco), Costa Rica (Budd et al., 1999); Mao Formation, Dominican Republic (Klaus eta al., 2008). Late Pliocene in Quebrada Chocolate Formation, Costa Rica (Budd et al., 1999); Layton Formation (Bowden Member), Jamaica (Budd and McNeill, 1998). Late Pliocene–early Pleistocene in Matanzas and La Cruz formations, Cuba; Moin Formation, Costa Rica (Budd et al., 1999). Early Pleistocene in Old Pera Formation, Jamaica (Budd and McNeill, 1998); Isla Colón Formation, Panama (Klaus et al., 2012).

Description.—Corallum branching and cerioid. Branches thin, circular to flattened. Circular branches 5.7–8.9 mm in diameter, and flat branches 11.0–17.0 mm in maximum dimension, by 5.0–6.0 mm in width. Corallites polygonal in shape, 1.3–1.4 mm in diameter, spaced 0.3–0.5 mm apart. Corallites bear 12 septa including a free dorsal directive, a fused ventral triplet, and four lateral pairs. Columella poorly developed or absent; when present, constituted by a small trabecula. Palar crown prominent, bearing five pali. Wall formed by one trabecular ring.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-43505; station 550011: MUN-STRI-43510, MUN-STRI-43514; station 550012: MUN-STRI-17302, MUN-STRI-43516, MUN-STRI-43519, MUN-STRI-17299, MUN-STRI-43522, MUN-STRI-17324, MUN-STRI-43527, MUN-STRI-17326, MUN-STRI-43530.

Remarks.—According to Foster (1986), *Porites baracoaensis* is characterized by small colonies, with thin branches, and their corallites have shallow fossa, solid walls, and conspicuous pali. In the Simaná Formation, *P. baracoaensis* was found building well-developed reefs with *Acropora panamensis* Vaughan, 1919, *Antiguastrea cellulosa*, *Agathiphyllia tenuis*, *Colpophyllia willoughbiensis*, *Porites waylandi*, *P. portoricensis*, *P. anguillensis*, *Alveopora tampae*, *Montastraea canalis*, *M. cavernosa*, *Siderastrea siderea* (Ellis and Solander, 1786), and Caryophylliidae.

Porites portoricensis (Vaughan, 1919)
Figure 3.10–3.12

non 1859 *Alveopora fenestrata*; Dana, p. 98.
1863 *Alveopora fenestrata*; Duncan, p. 437.
1919 *Goniopora portoricensis* Vaughan, p. 495, pl. 146, figs. 4, 5.
1919 *Goniopora clevei* Vaughan, p. 496, pl. 145, figs. 1, 3–6a, ?pl. 145, figs. 2, 2a.
1919 *Goniopora cascadensis* Vaughan, p. 497, pl. 146, figs. 6–9.
1919 ?*Portites* (*Synaraea*) *howei* Vaughan, p. 505, pl. 151, figs. 2–4.
1973 *Goniopora ballistensis* Weisbord, p. 32, pl. 10, figs. 4, 5, pl. 11, figs. 1–3, ?pl. 12, figs. 1, 2.
1973 *Goniopora matsoni* Weisbord, p. 34, pl. 12, fig. 3–6, ?pl. 14, figs. 1–3.
1986 *Porites portoricensis*; Foster, p. 79, pl. 24, figs. 1–15, pl. 25, figs. 1–6, pl. 26, figs. 1–6, pl. 27, figs. 1–4, pl. 28, figs. 1–4, text-figs. 2–5, 10, 12, 14, 16–19.

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Holotype.—USNM M325061, from Lares Formation, Puerto Rico. Late Miocene.

Occurrence.—Late Oligocene to early Pleistocene. Oldest occurrences in La Quinta Formation, Mexico (Frost and Langenheim, 1974); Antigua Formation, Antigua and Barbuda (Johnson, 2007); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003); Arcadia Formation (Tampa Member), Florida, USA (Budd et al., 1994). Early Miocene in Siamaná Formation, Colombia; Agua Clara (Cauderalito Member) and Castillo formations, Venezuela (Johnson et al., 2009); Culebra Formation, Panama (Johnson and Kirby, 2006); Anguilla Formation, Anguilla (Budd et al., 1995). Middle Miocene in 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 Cercado Formation, Dominican Republic; Old Bank Formation, Panama (Klaus et al., 2008, 2012). Late Miocene–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 Formation, Costa Rica (Budd et al., 1999). Late Pliocene–early Pleistocene in Moin Formation, Costa Rica (Budd et al., 1999). Early Pleistocene in Old Pera Formation, Jamaica (Budd and McNeill, 1998).

Description.—Corallum branching to columnar and cerioid. Branches are thick oval to flattened. Oval branches 1.5–2.5 cm in major diameter; flat branches 2.5–3.0 cm long and 1.0–2.0 cm wide. Corallites polygonal in shape, 1.3–2.0 mm in diameter, spaced 0.5–0.9 mm apart. Corallites bear 12 septa arranged with a free dorsal directive, a fused ventral triplet, and four lateral pairs. Trabecular columella well developed, formed by a single trabecular blunt, at the same level of the palar crown. Palar crown of six pali. Wall formed by one or two trabecular rings. Coenosteum reticulate.

Materials.—Siamaná Formation, Arroyo Uitpa, station 550006: MUN-STRI-17200, MUN-STRI-43485, MUN-STRI-37880; station PF0016: MUN-STRI-37868. Arroyo Ekieps, station 550008: MUN-STRI-17226, MUN-STRI-17220, MUN-STRI-17223; station 550011: MUN-STRI-17272, MUN-STRI-17273, MUN-STRI-43484, MUN-STRI-43486, MUN-STRI-17258, MUN-STRI-17259, MUN-STRI-37857, MUN-STRI-37862; station 550012: MUN-STRI-43487. SW Ekieps, station PF0018: MUN-STRI-37898, MUN-STRI-37899.

Remarks.—This species shows high morphological variability. For this reason, several authors have established numerous younger synonyms (Foster, 1986). The specimens from the Siamaná Formation can be separated from other *Porites* by having branching colonies and large corallites. *Porites portoricensis* was found building well-developed framework reefs and patch reefs with *Alveopora tampae, Antiguastrea cellulosa, Colpophyllia willoughbiensis, Montastraea endothecata, Porites waylandi, P. baracoaensis*, and *P. anguillensis*.

Porites waylandi Foster, 1986
Figure 4.1, 4.2

non 1843 *Porites collegniana* Michelin, p. 65, pl. 13, fig. 9.
1863 *Porites collegniana*; Duncan, p. 437.
non 1866 *Porites panamensis* Verrill, p. 329.
1919 *Porites panamensis* Vaughan, p. 503, pl. 148, figs. 1–3a.
1986 *Porites waylandi* Foster, p. 81, pl. 29, figs. 1–4, pl. 30, figs. 1–7, pl. 31, figs. 1–4, text-figs. 2–5, 10, 12, 14, 16, 17.

Holotype.—USNM M325063, from La Boca Formation, Panama. Middle Miocene.

Occurrence.—Late Oligocene to early Pleistocene. First records from late Oligocene in Tabera Formation, Dominican Republic (Budd et al., 1994); Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); La Quinta Formation, Mexico (Frost and Langenheim, 1974); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003); Arcadia Formation (Tampa Member), Florida, USA (Budd et al., 1994). Early Miocene in Siamaná Formation, Colombia; Agua Clara (Cauderalito Member), San Luis and Castillo formations, Venezuela (Johnson et al., 2009); Culebra Formation, Panama (Johnson and Kirby, 2006); Anguilla Formation, Anguilla (Budd et al., 1995). Early–middle Miocene in Providencia Island, Colombia (Geister, 1992); Tamana Formation, Trinidad and Tobago (Johnson, 2001). Latest early Miocene in Jimol Formation, Colombia. Middle Miocene in Valiente Formation, Panama (Klaus et al., 2012). Middle Miocene–early Pleistocene in Seroe Domi Formation, Curaçao (Budd et al., 1998). Late Miocene in Cercado Formation, Dominican Republic; Old Bank Formation, Panama (Klaus et al., 2008, 2012). Late Miocene–early Pliocene in Gurabo Formation, Dominican Republic (Klaus et al., 2008). Early Pliocene in Mao Formation, Dominican Republic (Klaus eta al., 2008). Late Pliocene in Quebrada Chocolate Formation, Costa Rica (Budd et al., 1999). Early Pleistocene in Moin Formation, Costa Rica (Budd et al., 1999).

Description.—Corallum columnar to massive with knobs. Colonies subplocoid. Corallites polygonal in shape, 1.3–1.8 mm in diameter, spaced 0.5 mm apart. Corallites bear 12 septa comprising a free dorsal directive, a fused ventral triplet, and four lateral pairs. When present, the columella is trabecular, formed by a single trabecular blunt, at the same or lower level of the palar crown. Wide palar crown of four or five pali. Wall formed by one or two trabecular rings. Coenosteum reticulate.

Materials.—Siamaná Formation, Flor de La Guajira, station 550001: MUN-STRI-17183, MUN-STRI-17184, MUN-STRI-17186. Arroyo Uitpa, station 550005: MUN-STRI-17604, MUN-STRI-43492, MUN-STRI-43495, MUN-STRI-17639, MUN-STRI-17601; station 550006: MUN-STRI-43502, MUN-

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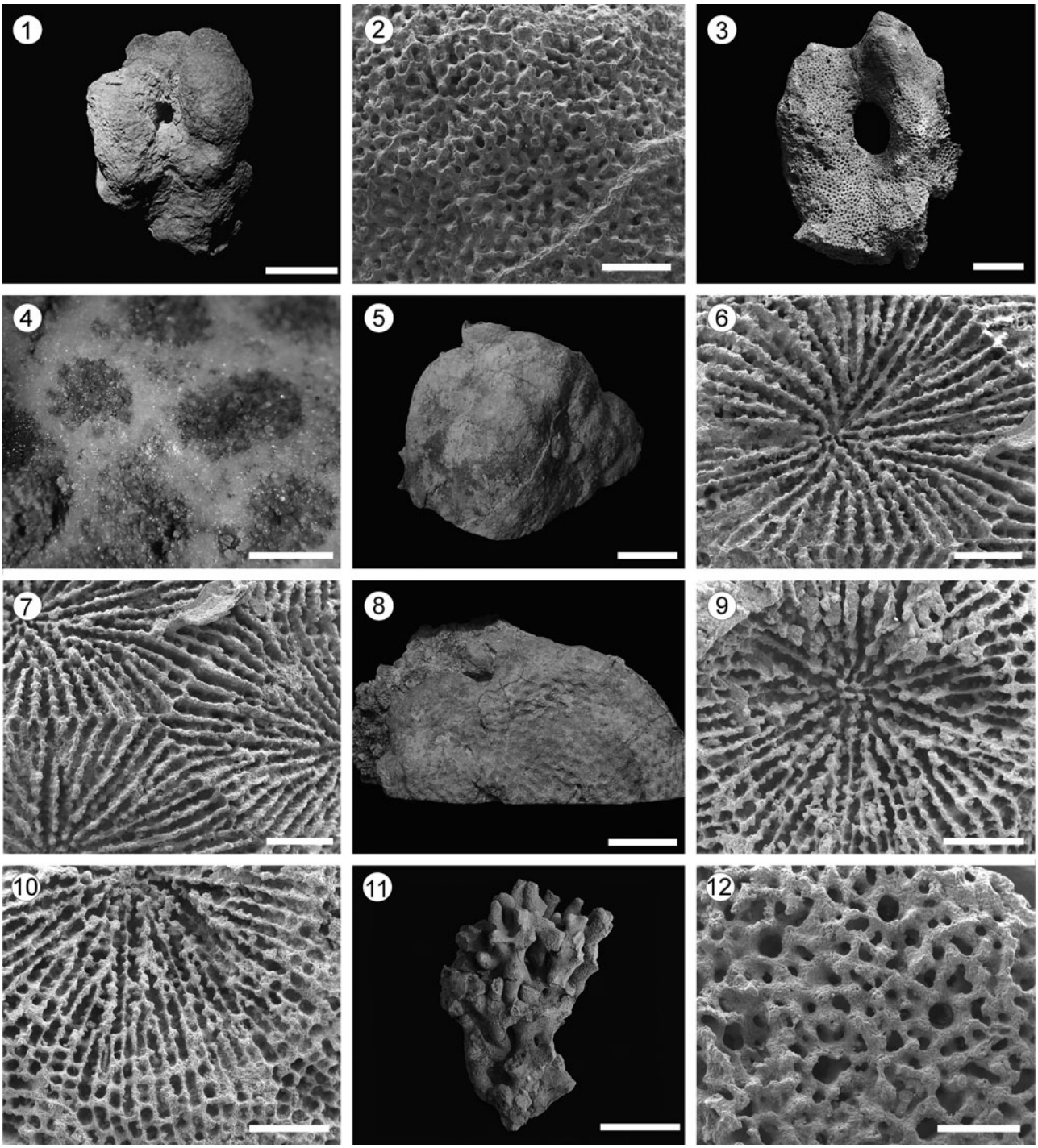

Figure 4. *Porites waylandi* Foster, 1986 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17222): (**1**) morphology of the colony; (**2**) detail of the corallites, showing the septal arrangement, columella, palar crown, and calicular wall. *Porites* sp. indet. from the Jimol Formation, Punta Espada (MUN-STRI-17254): (**3**) branch fragment; (**4**) crystallized corallites. *Siderastrea conferta* (Duncan, 1863) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17270): (**5**) morphology of the colony; (**6**) detail of the corallites showing septal arrangement, ornamentation, and the columella elements; (**7**) detail of the calicular walls and the fusion with the adjacent septa. *Siderastrea siderea* (Ellis and Solander, 1786) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17269): (**8**) morphology of the colony; (**9, 10**) detail of the corallite and calicular walls, respectively. *Millepora alcicornis* Linnaeus, 1758 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17286): (**11**) morphology of the colony; (**12**) detail of the dactilopores and coenosteal texture. Scale bars in (**1**) 2 cm; (**2, 4, 6, 7, 9, 10, 12**) 1 mm; (**3, 5**) 3 cm; (**8**) 2.5 cm; (**11**) 4 cm.

STRI-43503; station PF0016: MUN-STRI-37871, MUN-STRI-37872. Arroyo Ekieps, station 550008: MUN-STRI-17242, MUN-STRI-17245, MUN-STRI-17221, MUN-STRI-17222; station 550011: MUN-STRI-37857, MUN-STRI-37860, MUN-STRI-37861; station 550012: MUN-STRI-17317, MUN-STRI-17319. SW Ekieps, station PF0018: MUN-STRI-37889, MUN-STRI-37891, MUN-STRI-37896. Jimol Formation, Punta Espada, station 550010: MUN-STRI-17248, MUN-STRI-17249; station 550014: MUN-STRI-17336, MUN-STRI-17348, MUN-STRI-17349.

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Remarks.—The samples from the Siamaná Formation can be differentiated from other *Porites* species by their massive colonies, small calicular diameters, and palar crown at a low level. In the Simaná Formation *Porites waylandi* built well-developed framework reefs and patch reefs with *Antiguastrea cellulosa*, *Colpophyllia willoughbiensis*, *Diploastrea crassolamellata*, *D. magnifica*, *Porites anguillensis*, *P. portoricensis*, *Montastraea canalis*, *M. cavernosa*, and *Orbicella limbate* (Duncan, 1863). In the Jimol Formation it was found with *Orbicella imperatoris*, *Siderastrea siderea*, and *Pocillopora* sp. indet.

Porites sp. indet.
Figure 4.3, 4.4

Occurrence.—Middle Miocene from the Jimol Formation.

Description.—Corallum branching, plocoid to subplocoid. Branches much compressed, 23.0–29.0 mm wide, 37.0–110.0 mm in length, and 155 mm high, with anastomosing growth pattern. Corallites rounded to slightly compressed, 1.3–2.0 mm in diameter, spaced 0.6–0.8 mm apart. Septa arranged in two complete cycles. Fossa deep. Columella not evident. Coenosteum with circular perforations, 0.3–0.4 mm in diameter.

Materials.—Jimol Formation, Punta Espada, station 550010: MUN-STRI-17254.

Remarks.—The preservation is very poor. The sample consists of two recrystallized broken branches, whereby several characters cannot be observed, such as coenosteum characters, presence of tertiary septa, as well as differences between primaries and secondary. *Porites* sp. indet. differs from *P. baracoaensis* and *P. portoricensis*, the other branching species of *Porites* found in the Siamaná Formation, by its robust branches, which exceed the dimensions of *P. portoricensis*, the larger of the two. The sample was found in a patch reef with *Orbicella imperatoris*, *Porites waylandi*, and *Siderastrea siderea.*

Family Siderastreidae Vaughan and Wells, 1943
Genus *Siderastrea* Blainville, 1830

Type species.—*Madrepora radians* Pallas, 1766; by original description.

Siderastrea conferta (Duncan, 1863)
Figure 4.5–4.7

1863 *Isastrea conferta* Duncan, p. 422.
1919 *Siderastrea conferta*; Vaughan, p. 451, pl. 117, fig. 3, pl. 120, figs. 1–4, pl. 121, figs. 1–2a.
1929 *Siderastrea conferta*; Coryell and Ohlsen, p. 213, pl. 38, fig. 2.
1974 *Siderastrea* (*Siderastrea*) *conferta*; Frost and Langenheim, p. 206, pl. 66, figs. 1–6.

Holotype.—NHMUK R28740, from Antigua Formation, Antigua. Late Oligocene.

Occurrence.—Early Oligocene to late Miocene. First records in Rancho Berlín Formation, Mexico (Frost and Langenheim, 1974). Late Oligocene in Anahuac Formation, Texas, USA (Frost and Schafersman, 1978); La Quinta Formation, Mexico (Frost and Langenheim, 1974); Antigua Formation, Antigua and Barbuda (Johnson, 2007); Lares Formation, Puerto Rico (Frost et al., 1983). Late Oligocene–early Miocene in Browns Town and Newport formations, Jamaica (Stemann, 2003). Early Miocene in Siamaná Formation, Colombia; Agua Clara (Cauderalito Member), San Luis and Castillo formations, Venezuela (Johnson et al., 2009); Culebra Formation, Panama (Johnson and Kirby, 2006); Anguilla Formation, Anguilla (Budd et al., 1995). Early–middle Miocene in Providencia Island, Colombia (Geister, 1992). Late Miocene in San Andrés Formation, Colombia (Geister, 1975).

Description.—Corallum massive and cerioid, with extratentacular budding. Corallites tetra-, penta- or hexagonal in shape, 4.0–10 mm in diameter. Calices bear 54–67 septa, which could be confluent or not with adjacent corallites. Septa hexamerally arranged in five cycles always incomplete. Septa uniformly spaced, S1 are free and reach the columella, while the rest are fused to adjacent systems. S3 fused to adjacent S2 close to the columella, S4 fused to S3 at a half or 3/4 of the width of S1, and, when present, S5 fused to S4 close to the calicular wall. Septal margins curving and falling gently towards the columella, which bear acute teeth, 6–7 per millimeter. Septal faces granulate with thick trabeculae, generally fused to the adjacent septa. Fossa shallow. Paliform lobes absent. Trabecular columella with few elements or weakly developed. Synapticulothecal wall.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-17265, MUN-STRI-17270, MUN-STRI-43512, MUN-STRI-17291.

Remarks.—*Siderastrea conferta* can be differentiated from *S. siderea* by the size of the corallites, which are greater in *S. conferta*, and despite both having a septal arrangement of four cycles with additional elements of S5, *S. conferta* bears more septa than *S. siderea*. The samples from the Siamaná Formation are well preserved and built well-developed reefs in association with *Alveopora tampae*, *Agathiphyllia tenuis*, *Montastraea canalis*, *Porites anguillensis*, and *P. portoricensis*. This species is common in Oligocene and Miocene reefs and lagoons.

Siderastrea siderea (Ellis and Solander, 1786)
Figure 4.8–4.10

1786 *Madrepora siderea* Ellis and Solander, p. 168, pl. 49, fig. 2.
1919 *Siderastrea siderea*; Vaughan, p. 443, pl.114, figs. 2, 3, pl. 122, figs. 1–3a.
1974 *Siderastrea* (*Siderastrea*) *siderea*; Frost and Langenheim, p. 208, pl. 67, figs. 1–6.

Holotype.—Lost.

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Occurrence.—Early Miocene to present. First occurrences from early Miocene in Siamaná Formation, Arroyo Ekieps locality, Colombia. Late early Miocene in Jimol Formation, Colombia. Early–middle Miocene in Santa Ana Formation, Mexico (Frost and Langenheim, 1974); Tamana Formation, Trinidad and Tobago (Johnson, 2001). Middle Miocene in Valiente Formation, Panama (Klaus et al., 2012). Middle Miocene–early Pleistocene in Seroe Domi, Curaçao (Budd et al., 1998). Late Miocene in Cercado Formation, Dominican Republic; late Miocene–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 Formation, Costa Rica (Budd et al., 1999); Layton Formation (Bowden Member), Jamaica (Budd and McNeill, 1998). Late Pliocene–early Pleistocene in Matanzas and La Cruz formations, Cuba; Moin Formation, Costa Rica (Budd et al., 1999). Early Pleistocene in Old Pera, Hope Gate and Manchioneal formations, Jamaica (Budd and McNeill, 1998); Caloosahatchee and Glades formations, Florida, USA (Budd et al., 1994); Isla Colón and Urracá formations, Panama (Klaus et al., 2012). Middle–late Pleistocene in San Luis Formation (San Andrés Terraces), Colombia; Key Largo Formation, Florida, USA; Santo Domingo Terraces, Dominican Republic; late Pleistocene in Falmouth Formation, Jamaica (Budd and McNeill, 1998). At present this species is widespread in the Caribbean and remains as a "secondary contributor" of reef building in the region (Foster, 1980, p. 442). In La Guajira Peninsula (Colombia) it inhabits patch reefs in protected bays (Díaz et al., 2000; Reyes et al., 2010).

Description.—Corallum massive and cerioid, with extracalicular budding. Corallites pentagonal or hexagonal in shape, 3.5–5.0 mm in diameter. Calices bear 45–50 septa, which could be confluent or not with adjacent corallites. Septa hexamerally arranged in four cycles. Septa uniformly spaced, which go down into the fossa in a gentle slope. S1 are free and usually reach the columella, while the rest are fused to adjacent systems, generally S4 to S3 and S3 to S2, forming trident patterns. Septal margins bear acute teeth, about six per millimeter. Septal faces granulate with thick trabeculae, sometimes fused to the adjacent septa. Paliform lobes absent. Trabecular columella with several and robust elements. Synapticulothecal wall.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550011: MUN-STRI-17260, MUN-STRI-17269, MUN-STRI-17263; station 550012: MUN-STRI-17292. Jimol Formation, Punta Espada, station 550010: MUN-STRI-17250, MUN-STRI-17251.

Remarks.—See Remarks under *Siderastrea conferta*. Despite the inside recrystallization of most of the colonies, the surface of the corallites is preserved. In the Siamaná Formation, *S. siderea* was found in well-developed reefs with *Porites baracoaensis*, *P. anguillensis*, *Alveopora tampae*, *Agathiphyllia tenuis*, *Montastraea canalis*, and *M. cavernosa*. This species was in a patch reef in the Jimol Formation with *Porites waylandi*, *Orbicella imperatoris*, and *Porites* sp. indet.

Class Hydrozoa Owen, 1843
Order Anthoathecata Cornelius, 1992
Family Milleporidae Fleming, 1828
Genus *Millepora* Linnaeus, 1758

Type species.—*Millepora alcicornis* Linnaeus, 1758; by subsequent designation (Apstein, 1915).

Millepora alcicornis Linnaeus, 1758
Figure 4.11, 4.12

1758 *Millepora alcicornis* Linnaeus, p. 791.
1834 *Palmipora alcicornis*; Blainville, p. 391, pl. 58, fig. 2.
1948 *Millepora alcicornis*; Boschma, p. 18, fig. 6, pl. 14, fig. 3.
1974 *Millepora alcicornis*; Weisbord, p. 276, pl. 21, fig. 1.
1988 *Millepora alcicornis*; Calder, p. 73, figs. 53–55.

Holotype.—Lost.

Occurrence.—Early Miocene to present. First occurrences in Siamaná Formation, Arroyo Ekieps, Colombia. Pleistocene in Buckingham (Petuch, 1986) and Key Largo (Weisbord, 1974) formations, Florida, USA; Dominican Republic (Vaughan et al., 1921; Weisbord, 1974). At present this species is widespread in the shallow waters of the Caribbean region (Weisbord, 1974; Weerdt, 1984, 1990).

According to Woodring (1957, p. 21), J.W. Wells identified samples from the Gatuncillo Formation (late Eocene) as *Millepora* aff. *alcicornis*. However, further studies conducted by Budd et al. (1992) neither described specimens of this genus nor recorded it in the species-list of the middle to late Eocene from the Caribbean region.

Description.—Corallum ramose. Branches cylindrical to flattened, with anastomosis, 8.0–16.0 mm in diameter at the middle of the branch. Branch tips rounded and bifurcated, 6.0–9.0 mm in diameter. Corallum surface reticulate, composed of a meshwork of rods with 25–37 rounded pores per cm^2. One or two gastropores per cm^2, 0.4 mm in diameter. Dactylopore diameters are 0.29–0.30 mm. Ampullae and arrangements of cyclosystems cannot be distinguished.

Materials.—Siamaná Formation, Arroyo Ekieps, station 550008: MUN-STRI-17218; station 550011: MUN-STRI-17286.

Remarks.—Poorly preserved samples could be confused with species of *Porites*, and the octocoral *Heliopora* sp., due to the similarity of the coenosteum surface, which is a meshwork. *Millepora alcicornis*, however, can be distinguished by its branching growth form, which could range from coarse to fine, by the smooth texture of the surface, as well as by the size and density of the dactylopores (Weerdt, 1984). In modern samples, the morphology of *M. alcicornis* is highly variable, from branching, to encrusting, to hemispheric colonies (Amaral et al., 2008). According to Weerdt (1984), at present, *M. alcicornis* and *Millepora complanata* Lamarck,

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1816 are closely related species, sometimes difficult or impossible to differentiate from one another. The robust colonies of *M. alcicornis* could be easily confused with the delicate forms of *M. complanata*. However, *M. complanata* is not yet known from the fossil record. The samples found in the Siamaná Formation have a characteristic upright and delicate form that differs from the honeycombed form of *M. complanata*. Samples from the Siamaná Formation occur in well-developed reefs with *Porites* spp.

Discussion

Integrating the information of Flórez et al. (2018) (species list Appendix 3) and that reported in this study, 272 total lots were collected from the Siamaná (239 lots) and Jimol (33 lots) formations (Appendix 2). The specimens were classified into two orders (Scleractinia and Anthoathecata), 12 families, 15 genera, and 26 species. Of the 32 total morphospecies, 81% were identified at the species level with the remainder left unidentified due to recrystallization and poor preservation of the coral skeleton.

Overall, the faunal composition was dominated by species of *Porites*, *Montastraea*, *Orbicella*, and *Antiguastrea*. They were common species in shallow-water paleoenvironments, 2–30 m of depth, in protected and low-energy environments, during the late Oligocene to early Miocene in the Caribbean region (Budd et al., 1995; Budd, 2000; Johnson et al., 2009).

From the Siamaná Formation (Aquitanian–Burdigalian), the Arroyo Ekieps locality, one of the youngest (Flórez et al., 2018, fig, 2), exhibited the highest number of morphospecies (25) (Table 1, Appendix 3). The assemblages were made up by species of massive colony shapes such as *Porites*, *Montastraea*, *Siderastrea*, and *Agathiphyllia*, which built extensive structures, often accompanied by *Colpohyllia willoughbiensis* and *Alveopora tampae*. In addition, there were other non-frame-building species, such as Caryophylliidae sp. indet. and *Stylophora minor*. Flor de La Guajira, the oldest locality studied in the Siamaná Formation, had the lowest species richness of the formation, and was constituted by the species *Orbicella limbata*, *O. imperatoris*, *Diploastrea crassolamellata*, *D. magnifica*, *Montastraea cavernosa*, *Porites waylandi*, and *Stylophora* sp. Within the Jimol Formation (Burdigalian), low-diversity patch reefs were common, with assemblages dominated by the species *O. imperatoris*, *Siderastrea siderea*, *Porites* sp. indet., *P. waylandi*, and *Pocillopora* sp. indet.

Coral species from the Siamaná Formation show affinities with Caribbean late Oligocene formations, such as the Antigua Formation of Antigua (Johnson, 2007) and the Lares Formation of Puerto Rico (Frost et al., 1983). Sixteen species were common in the three formations (Flórez et al., 2018, table 4), while *Alveopora tampae*, *Diploastrea magnifica*, *Montastraea cavernosa*, *Orbicella limbata*, *Porites anguillensis*, *Siderastrea siderea*, *Stylophora affinis*, *Stylophora minor*, and *Millepora alcicornis* were exclusive to the Siamaná Formation. Other units with similar coral composition include the early Miocene Castillo and San Luis formations of the Falcón Basin in Venezuela (Johnson et al., 2009), in which seven species were common (Flórez et al., 2018, table 4). *Acropora panamensis*, *Astrocoenia decaturensis* Vaughan, 1919, *Goniopora hilli*, *Montastraea endothecata*, *Porites anguillensis*, *Siderastrea siderea*, *Stylophora minor*, and *Millepora alcicornis* were only present in the Siamaná Formation. In addition, despite the geographic and temporal proximity of the Culebra Formation from Panama (Johnson and Kirby, 2006), the species composition differs (Flórez et al., 2018, table 4). Although both have 13 species in common, 19 were exclusive to the Culebra Formation, and 13 to the Siamaná Formation. Only a few similarities can be found at the species level with early Miocene shallow-water corals from the Indo-Pacific and the Mediterranean Sea. Only *Porites* cf. *baracoaensis* is reported in the Indo-Pacific (Bromfield, 2013, p. 21), while at the genus level, *Porites* and *Acropora* occur in the Mediterranean and in the Indo-Pacific (Bromfield, 2013; Santodomingo et al., 2015b).

The low diversity in the Jimol Formation is in part due to scant sampling. More collections of this formation are needed in order to improve the data of the late early Miocene. This will help to increase understanding of the patterns of the faunal change during the early Miocene.

The majority of identified species of the Siamaná and Jimol formations appeared in the Eocene and Oligocene (Fig. 5), with the possible exception of *Antiguastrea cellulosa*, which is reported from the late Cretaceous (Baron-Szabo et al., 2006), and *Orbicella limbata*, *Siderastrea siderea*, and *Millepora alcicornis*, which first occurred in the early Miocene (Jung, 1971; Frost and Langenheim, 1974; Weisbord, 1974; Geister, 1975; Johnson et al., 2009), and were components of the coral fauna turnover after the extinction of the late Oligocene. The finding of *Siderastrea siderea* and *Millepora alcicornis* in the Siamaná Formation extends their temporal record to early Miocene, as well as confirms their presence in the southern Caribbean. In general, the species of the Siamaná and Jimol formations were common in the Caribbean region during the Oligocene to Miocene transition, and most of them are now extinct (Budd et al., 1994) (Fig. 5).

Fourteen of the 26 species identified in the Siamaná and Jimol formations (Fig. 5) became extinct at the end of the early Miocene (Burdigalian) and in the middle Miocene (Fig. 5, box 1), nine persisted until the Pliocene and the Quaternary (Fig. 5, box 2), and the remaining three, the scleractinians *Montastraea cavernosa* and *Siderastrea siderea*, and the hydrocoral *Millepora alcicornis* (Fig. 5, box 3), are extant and widespread in the Caribbean (Foster, 1980; Calder, 1988; Budd et al., 1994). These peaks of extinction were highly significant to the coral biodiversity in the Caribbean region during the Cenozoic (Budd, 2000; Johnson et al., 2008; Budd et al., 2011). Johnson et al. (2008) estimated reductions of 40% of species during the early Miocene, and 50% in the Pliocene–Pleistocene transition. According to Edinger and Risk (1994) and von der Heydt and Dijkstra (2006), the causes of the earlier extinction were changes in water quality, such as a drop in temperature and increased turbidity and nutrients, due to increased upwellings. The second peak coincides with changes in oceanic circulation patterns and climate in the Caribbean, promoted by the uplift and closing of the Central American Isthmus, which caused a rise in surface productivity, and the inception of the Northern Hemisphere glaciation (Jackson et al., 1996; Allmon, 2001; Budd et al., 2011), as well as new events of upwelling (Prange and Schulz, 2004).

The low species richness, 32 morphospecies and 15 genera found in the Siamaná and Jimol formations, agrees with the low

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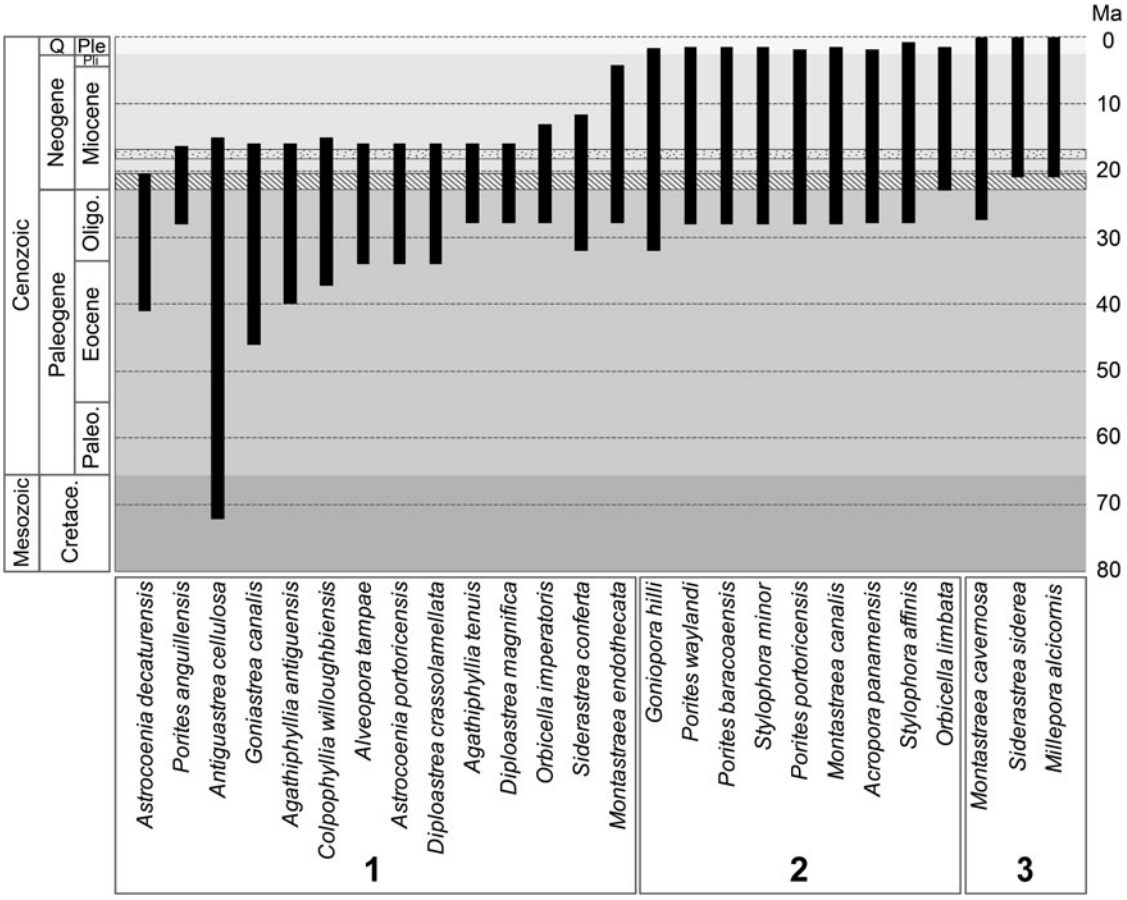

Figure 5. Range chart of first and last occurrence in the Greater Caribbean of species recorded in this study and in Flórez et al. (2018). The interval of sloping lines indicates the estimated stratigraphic range for the reef units studied in the Siamaná Formation, ca. 23.03–20.44 Ma (Silva et al., 2017), and the interval of dotted fill indicates the Jimol Formation, ca. 16.7–17.9 Ma (Hendy et al., 2015; Moreno et al., 2015). Boxes: (**1**) Species extinct at the end of the early Miocene and in the middle Miocene, (**2**) species extinct in the late Pliocene and Pleistocene, and (**3**) extant species. Source references of stratigraphic units, countries and ages are provided in Flórez et al. (2018, table 3).

diversity described by Budd (2000), Budd et al. (1989, 1995), Johnson and Kirby (2006), and Johnson et al. (2008) for the early to middle Miocene interval in the Caribbean. However, the capacity to develop reefs does not depend on high species diversity of reef-building corals (Johnson et al., 2008). As was observed in the Arroyo Ekieps locality, a significant coral framework was developed, built by relict species from the late Oligocene, and the new fauna from the early Miocene.

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Appendix

Appendix 1. Geographical coordinates of the localities and stations studied. Estimation of the age of the Siamaná Formation was carried out by Silva-Tamayo et al. (2017) based on strontium isotopes in coralline algae. Age determination of the Jimol Formation was performed by Hendy et al. (2015) and Moreno et al. (2015) through biostratigraphic analysis and strontium isotopes in mollusk shells. Samples of Flor de La Guajira are reworked material.

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?

Appendix 2. Coral specimens collected in the Siamaná and Jimol formations, from Cocinetas Basin in La Guajira Peninsula, northern Colombia.

Species	Formation	Locality	Station code	Catalog number MUN-STRI
Acropora panamensis	Siamaná	Arroyo Ekieps	550013	17331
Acropora panamensis	Siamaná	Arroyo Ekieps	550013	17325
Acropora panamensis	Siamaná	Arroyo Ekieps	550013	17327
Acropora panamensis	Siamaná	SW Ekieps	PF0018	37928
Acropora sp. indet.	Siamaná	Arroyo Ekieps	550011	43531
Acropora sp. indet.	Siamaná	Arroyo Ekieps	550011	43532
Acropora sp. indet.	Siamaná	Arroyo Ekieps	550013	43533
Agathiphyllia antiguensis	Siamaná	Arroyo Ekieps	550012	17304
Agathiphyllia antiguensis	Siamaná	Arroyo Ekieps	550012	17309
Agathiphyllia antiguensis	Siamaná	Arroyo Ekieps	550013	17328
Agathiphyllia tenuis	Siamaná	Arroyo Ekieps	550011	17275
Agathiphyllia tenuis	Siamaná	Arroyo Ekieps	550011	43509
Agathiphyllia tenuis	Siamaná	Arroyo Ekieps	550011	43513
Agathiphyllia tenuis	Siamaná	Arroyo Ekieps	550012	43518
Agathiphyllia tenuis	Siamaná	Arroyo Uitpa	550006	37877
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37890
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37893
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37894
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37900
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37901
Agathiphyllia tenuis	Siamaná	SW Ekieps	PF0018	37903
Alveopora tampae	Siamaná	Arroyo Ekieps	550008	43504
Alveopora tampae	Siamaná	Arroyo Ekieps	550011	17268
Alveopora tampae	Siamaná	Arroyo Ekieps	550011	43508
Alveopora tampae	Siamaná	Arroyo Ekieps	550011	17274
Alveopora tampae	Siamaná	Arroyo Ekieps	550012	43517
Alveopora tampae	Siamaná	Arroyo Ekieps	550013	43524
Alveopora tampae	Siamaná	Arroyo Ekieps	550013	17323
Alveopora tampae	Siamaná	SW Ekieps	PF0018	37892
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17603
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	43490
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	43493
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17610
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17615
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	43494
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17619
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17620
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17622
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17625
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17629
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17637
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17640
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17600

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Appendix 2. Continued.

Species	Formation	Locality	Station code	Catalog number MUN-STRI
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	17602
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550005	43498
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	17197
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	17199
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	43500
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	17201
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	43501
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	17202
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	17203
Antiguastrea cellulosa	Siamaná	Arroyo Ekieps	550008	17230
Antiguastrea cellulosa	Siamaná	Arroyo Ekieps	550008	17224
Antiguastrea cellulosa	Siamaná	Arroyo Ekieps	550011	17287
Antiguastrea cellulosa	Siamaná	Arroyo Ekieps	550011	17261
Antiguastrea cellulosa	Siamaná	Arroyo Ekieps	550012	17296
Antiguastrea cellulosa	Siamaná	Arroyo Uitpa	550006	37886
Antiguastrea cellulosa	Siamaná	SW Ekieps	PF0018	37902
Antiguastrea cellulosa	Siamaná	SW Ekieps	PF0018	37906
Antiguastrea cellulosa	Siamaná	SW Ekieps	PF0018	37922
Astrocoenia decaturensis	Siamaná	Arroyo Ekieps	550012	17294
Astrocoenia decaturensis	Siamaná	Arroyo Ekieps	550011	37858
Astrocoenia decaturensis	Siamaná	Arroyo Ekieps	550011	37863
Astrocoenia decaturensis	Siamaná	Arroyo Uitpa	PF0016	37869
Astrocoenia decaturensis	Siamaná	Arroyo Uitpa	550006	37876
Astrocoenia decaturensis	Siamaná	Arroyo Uitpa	550006	37878
Astrocoenia decaturensis	Siamaná	Arroyo Uitpa	550006	37880
Astrocoenia decaturensis	Siamaná	Arroyo Uitpa	550006	37881
Astrocoenia decaturensis	Siamaná	SW Ekieps	PF0018	37905
Astrocoenia portoricensis	Siamaná	Arroyo Uitpa	550005	17628
Astrocoenia portoricensis	Siamaná	Arroyo Ekieps	550012	17311
Astrocoenia sp. indet.	Siamaná	Arroyo Uitpa	550005	43497
Caryophylliidae sp. indet.	Siamaná	Arroyo Ekieps	550012	17305
Caryophylliidae sp. indet.	Siamaná	Arroyo Ekieps	550013	43525
Caryophylliidae sp. indet.	Siamaná	Arroyo Ekieps	550013	43528
Caryophylliidae sp. indet.	Siamaná	Arroyo Ekieps	550013	17327
Caryophylliidae sp. indet.	Siamaná	Arroyo Ekieps	550011	37865
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550011	17276
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17301
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	43515
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17310
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17314
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17318
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17320
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550012	17300
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550013	43526
Colpophyllia willoughbiensis	Siamaná	Arroyo Ekieps	550011	37864
Colpophyllia willoughbiensis	Siamaná	Arroyo Uitpa	PF0016	37867
Colpophyllia willoughbiensis	Siamaná	SW Ekieps	PF0018	37924
Colpophyllia willoughbiensis	Siamaná	SW Ekieps	PF0018	37927
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	43488
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17614
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17617
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17631
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17634
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17635
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	17638
Diploastrea crassolamellata	Siamaná	Arroyo Uitpa	550005	43499
Diploastrea crassolamellata	Siamaná	Flor de La Guajira	550001	17187
Diploastrea magnifica	Siamaná	Arroyo Uitpa	550005	17616
Diploastrea magnifica	Siamaná	Arroyo Uitpa	550005	17618
Diploastrea magnifica	Siamaná	Arroyo Uitpa	550005	43496
Diploastrea magnifica	Siamaná	Arroyo Ekieps	550013	17322
Diploastrea magnifica	Siamaná	Flor de La Guajira	550001	17182
Goniastrea canalis	Siamaná	Arroyo Ekieps	550013	17332
Goniopora hilli	Siamaná	Arroyo Ekieps	550011	43511
Goniopora hilli	Siamaná	Arroyo Ekieps	550012	17312
Goniopora hilli	Siamaná	Arroyo Ekieps	550012	17297
Goniopora hilli	Siamaná	Arroyo Ekieps	550012	43521
Millepora alcicornis	Siamaná	Arroyo Ekieps	550008	17218
Millepora alcicornis	Siamaná	Arroyo Ekieps	550011	17286
Montastraea canalis	Siamaná	Arroyo Ekieps	550008	17243
Montastraea canalis	Siamaná	Arroyo Ekieps	550011	17283
Montastraea canalis	Siamaná	Arroyo Ekieps	550011	17290
Montastraea canalis	Siamaná	Arroyo Ekieps	550012	17307

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Appendix 2. Continued.

Species	Formation	Locality	Station code	Catalog number MUN-STRI
Montastraea canalis	Siamaná	Arroyo Ekieps	550012	17293
Montastraea canalis	Siamaná	Arroyo Ekieps	550012	17298
Montastraea canalis	Siamaná	Arroyo Ekieps	550013	43529
Montastraea canalis	Siamaná	Arroyo Uitpa	PF0016	37866
Montastraea canalis	Siamaná	Arroyo Uitpa	PF0016	37874
Montastraea canalis	Siamaná	SW Ekieps	PF0018	37923
Montastraea canalis	Siamaná	SW Ekieps	PF0018	37925
Montastraea cavernosa	Siamaná	Arroyo Uitpa	550005	43489
Montastraea cavernosa	Siamaná	Arroyo Uitpa	550005	43491
Montastraea cavernosa	Siamaná	Arroyo Uitpa	550005	17607
Montastraea cavernosa	Siamaná	Arroyo Ekieps	550012	17306
Montastraea cavernosa	Siamaná	Arroyo Ekieps	550012	17295
Montastraea cavernosa	Siamaná	Arroyo Ekieps	550013	17329
Montastraea cavernosa	Siamaná	SW Ekieps	PF0018	37907
Montastraea cavernosa	Siamaná	Flor de La Guajira	550001	17190
Montastraea cavernosa	Siamaná	Flor de La Guajira	550002	17192
Montastraea cavernosa	Siamaná	Flor de La Guajira	550002	17193
Montastraea endothecata	Siamaná	Arroyo Ekieps	550008	17229
Montastraea endothecata	Siamaná	Arroyo Ekieps	550008	17225
Montastraea endothecata	Siamaná	Arroyo Ekieps	550011	17284
Montastraea endothecata	Siamaná	Arroyo Ekieps	550012	17303
Montastraea endothecata	Siamaná	SW Ekieps	PF0018	37926
Orbicella imperatoris	Siamaná	Flor de La Guajira	550002	43534
Orbicella imperatoris	Jimol	Punta Espada	550010	17246
Orbicella imperatoris	Jimol	Punta Espada	550010	17247
Orbicella imperatoris	Jimol	Punta Espada	550010	17252
Orbicella imperatoris	Jimol	Punta Espada	550010	17253
Orbicella imperatoris	Jimol	Punta Espada	550010	43536
Orbicella imperatoris	Jimol	Punta Espada	550010	43537
Orbicella imperatoris	Jimol	Punta Espada	550010	17255
Orbicella imperatoris	Jimol	Punta Espada	550014	17337
Orbicella imperatoris	Jimol	Punta Espada	550014	17338
Orbicella imperatoris	Jimol	Punta Espada	550014	17339
Orbicella imperatoris	Jimol	Punta Espada	550014	43538
Orbicella imperatoris	Jimol	Punta Espada	550014	17340
Orbicella imperatoris	Jimol	Punta Espada	550014	17341
Orbicella imperatoris	Jimol	Punta Espada	550014	17342
Orbicella imperatoris	Jimol	Punta Espada	550014	17343
Orbicella imperatoris	Jimol	Punta Espada	550014	17344
Orbicella imperatoris	Jimol	Punta Espada	550014	43539
Orbicella imperatoris	Jimol	Punta Espada	550014	17346
Orbicella imperatoris	Jimol	Punta Espada	550014	43540
Orbicella imperatoris	Jimol	Punta Espada	550014	43541
Orbicella imperatoris	Jimol	Punta Espada	550014	17347
Orbicella imperatoris	Jimol	Punta Espada	550014	17350
Orbicella imperatoris	Jimol	Punta Espada	550014	17351
Orbicella limbata	Siamaná	Flor de La Guajira	550001	17185
Pocillopora sp. indet.	Jimol	Punta Espada	550014	17345
Pocillopora sp. indet.	Jimol	Punta Espada	550014	43542
Porites anguillensis	Siamaná	Arroyo Ekieps	550008	17237
Porites anguillensis	Siamaná	Arroyo Ekieps	550008	17239
Porites anguillensis	Siamaná	Arroyo Ekieps	550008	17240
Porites anguillensis	Siamaná	Arroyo Ekieps	550008	17241
Porites anguillensis	Siamaná	Arroyo Ekieps	550008	17244
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17256
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	43506
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	43507
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17271
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17277
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17278
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17279
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17285
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17288
Porites anguillensis	Siamaná	Arroyo Ekieps	550011	17289
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	17308
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	17313
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	43520
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	17315
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	17316
Porites anguillensis	Siamaná	Arroyo Ekieps	550012	43523
Porites baracoaensis	Siamaná	Arroyo Ekieps	550008	43505
Porites baracoaensis	Siamaná	Arroyo Ekieps	550011	43510
Porites baracoaensis	Siamaná	Arroyo Ekieps	550011	43514

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Appendix 2. Continued.

Species	Formation	Locality	Station code	Catalog number MUN-STRI
Porites baracoaensis	Siamaná	Arroyo Ekieps	550012	17302
Porites baracoaensis	Siamaná	Arroyo Ekieps	550012	43516
Porites baracoaensis	Siamaná	Arroyo Ekieps	550012	43519
Porites baracoaensis	Siamaná	Arroyo Ekieps	550012	17299
Porites baracoaensis	Siamaná	Arroyo Ekieps	550012	43522
Porites baracoaensis	Siamaná	Arroyo Ekieps	550013	17324
Porites baracoaensis	Siamaná	Arroyo Ekieps	550013	43527
Porites baracoaensis	Siamaná	Arroyo Ekieps	550013	17326
Porites baracoaensis	Siamaná	Arroyo Ekieps	550013	43530
Porites portoricensis	Siamaná	Arroyo Uitpa	550006	17200
Porites portoricensis	Siamaná	Arroyo Uitpa	550006	43485
Porites portoricensis	Siamaná	Arroyo Ekieps	550008	17226
Porites portoricensis	Siamaná	Arroyo Ekieps	550008	17220
Porites portoricensis	Siamaná	Arroyo Ekieps	550008	17223
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	17272
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	17273
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	43484
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	43486
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	17258
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	17259
Porites portoricensis	Siamaná	Arroyo Ekieps	550012	43487
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	37857
Porites portoricensis	Siamaná	Arroyo Ekieps	550011	37862
Porites portoricensis	Siamaná	Arroyo Uitpa	PF0016	37868
Porites portoricensis	Siamaná	Arroyo Uitpa	550006	37880
Porites portoricensis	Siamaná	SW Ekieps	PF0018	37898
Porites portoricensis	Siamaná	SW Ekieps	PF0018	37899
Porites sp. indet.	Jimol	Punta Espada	550010	17254
Porites waylandi	Siamaná	Arroyo Uitpa	550005	17604
Porites waylandi	Siamaná	Arroyo Uitpa	550005	43492
Porites waylandi	Siamaná	Arroyo Uitpa	550005	43495
Porites waylandi	Siamaná	Arroyo Uitpa	550005	17639
Porites waylandi	Siamaná	Arroyo Uitpa	550005	17601
Porites waylandi	Siamaná	Arroyo Uitpa	550006	43502
Porites waylandi	Siamaná	Arroyo Uitpa	550006	43503
Porites waylandi	Siamaná	Arroyo Ekieps	550008	17242
Porites waylandi	Siamaná	Arroyo Ekieps	550008	17245
Porites waylandi	Siamaná	Arroyo Ekieps	550008	17221
Porites waylandi	Siamaná	Arroyo Ekieps	550008	17222
Porites waylandi	Siamaná	Arroyo Ekieps	550012	17317
Porites waylandi	Siamaná	Arroyo Ekieps	550012	17319
Porites waylandi	Siamaná	Arroyo Ekieps	550011	37857
Porites waylandi	Siamaná	Arroyo Ekieps	550011	37860
Porites waylandi	Siamaná	Arroyo Ekieps	550011	37861
Porites waylandi	Siamaná	Arroyo Uitpa	PF0016	37871
Porites waylandi	Siamaná	Arroyo Uitpa	PF0016	37872
Porites waylandi	Siamaná	SW Ekieps	PF0018	37889
Porites waylandi	Siamaná	SW Ekieps	PF0018	37891
Porites waylandi	Siamaná	SW Ekieps	PF0018	37896
Porites waylandi	Siamaná	Flor de La Guajira	550001	17183
Porites waylandi	Siamaná	Flor de La Guajira	550001	17184
Porites waylandi	Siamaná	Flor de La Guajira	550001	17186
Porites waylandi	Jimol	Punta Espada	550010	17248
Porites waylandi	Jimol	Punta Espada	550010	17249
Porites waylandi	Jimol	Punta Espada	550014	17336
Porites waylandi	Jimol	Punta Espada	550014	17348
Porites waylandi	Jimol	Punta Espada	550014	17349
Siderastrea conferta	Siamaná	Arroyo Ekieps	550011	17265
Siderastrea conferta	Siamaná	Arroyo Ekieps	550011	17270
Siderastrea conferta	Siamaná	Arroyo Ekieps	550011	43512
Siderastrea conferta	Siamaná	Arroyo Ekieps	550011	17291
Siderastrea siderea	Siamaná	Arroyo Ekieps	550011	17260
Siderastrea siderea	Siamaná	Arroyo Ekieps	550011	17269
Siderastrea siderea	Siamaná	Arroyo Ekieps	550011	17263
Siderastrea siderea	Siamaná	Arroyo Ekieps	550012	17292
Siderastrea siderea	Jimol	Punta Espada	550010	17250
Siderastrea siderea	Jimol	Punta Espada	550010	17251
Stylophora affinis	Siamaná	Arroyo Uitpa	550005	17608
Stylophora affinis	Siamaná	Arroyo Uitpa	550005	17609
Stylophora affinis	Siamaná	Arroyo Ekieps	550011	37932
Stylophora affinis	Siamaná	Arroyo Uitpa	PF0016	37873
Stylophora affinis	Siamaná	SW Ekieps	PF0018	37921
Stylophora minor	Siamaná	Arroyo Ekieps	550011	43797

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Appendix 2. Continued.

Species	Formation	Locality	Station code	Catalog number MUN-STRI
Stylophora minor	Siamaná	Arroyo Ekieps	550011	43798
Stylophora minor	Siamaná	Arroyo Ekieps	550011	43799
Stylophora minor	Siamaná	Arroyo Ekieps	550011	43800
Stylophora minor	Siamaná	Arroyo Ekieps	550011	43801
Stylophora minor	Siamaná	Arroyo Ekieps	550012	43802
Stylophora minor	Siamaná	Arroyo Ekieps	550013	43803
Stylophora minor	Siamaná	Arroyo Ekieps	550008	43879
Stylophora minor	Siamaná	Arroyo Ekieps	550008	43880
Stylophora minor	Siamaná	Arroyo Ekieps	550012	43881
Stylophora sp. indet.	Siamaná	Flor de La Guajira	550002	43535

Appendix 3. Species list recorded by Flórez et al. (2018) in the Cocinetas Basin, and localities where they were found. Siamaná EM (early Miocene) localities: AE, Arroyo Ekieps; SWE, SW Ekieps; AU, Arroyo Uitpa; FG, Flor de La Guajira. Jimol LEM (late early Miocene): PE, Punta Espada locality.

		Formations	
		Siamaná	Jimol
Family	Species	EM	LEM
Acroporidae	*Acropora panamensis*	AE, SWE	
	Acropora sp. indet.	AE	
	Alveopora tampae	AE	
Agathiphylliidae	*Agathiphyllia antiguensis*	AE	
	Agathiphyllia tenuis	AE, SWE, AU	
Astrocoeniidae	*Astrocoenia decaturensis*	AE, SWE, AU	
	Astrocoenia portoricensis	AE, AU	
	Astrocoenia sp. indet.	AU	
Caryophylliidae	sp. indet.	AE	
Diploastraeidae	*Diploastrea crassolamellata*	AU, FG	
	Diploastrea magnifica	AE, AU, FG	
Merulinidae	*Antiguastrea cellulosa*	AE, SWE, AU	
	Goniastrea canalis	AE	
	Orbicella imperatoris	FG	PE
	Orbicella limbata	FG	
Montastraeidae	*Montastraea canalis*	AE, SWE, AU	
	Montastraea cavernosa	AE, SWE, AU, FG	
	Montastraea endothecata	AE, SWE	

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