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Corals and bryozoans from the early Miocene coral reefs in La Guajira (northern Colombia)

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To Julia

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Extended abstract

Shallow-water coral reefs are one of the most diverse environments on Earth, its play important ecosystem roles, interacting physically, biologically and geochemically with adjacent marine and terrestrial ecosystems. Reef corals thriving in the tropical regions of the planet, where thanks to the permanent light intensity and their association with symbionts algae they form the magnificent structural frameworks that we know.

To know the resilience of reef fauna to diverse environmental and geological changes under natural, non-anthropized conditions, as well as the evolutionary processes of such fauna over time, provides baseline information for forecasting short-, medium-, and long-term scenarios, useful in decision-making for the sustainable management of these important ecosystems.

The La Guajira Peninsula, located in the Caribbean basin at northeastern of Colombia, despite of being geographically in the tropic region, currently exhibit atypical environmental conditions that limit the optimal development of the coral reefs. However, the geological record tells a different story. The Siamaná Formation, of early Miocene age (ca. 20-23 Ma), outcrops in the northern peninsula, at foothills of the Cosinas, Jarara and Macuira ranges. There, abundant fossiliferous deposits rich in coral and malacofauna have been reported in the scarce geological studies carry out in the area. However, studies on the spatial-temporal distribution and sedimentology of the reef deposits, attempts at detailed paleoenvironmental interpretations, as well as comprehensive taxonomic studies of their components have not been carried out to date.

Therefore, it is necessary to provide information that increase the knowledge of the reefs in the Colombian Caribbean and, it is of interest to answer the following questions:

1. What types of reef existed during the early Miocene in the Siamaná Formation?

2. How are these reefs distributed temporally and spatially?

3. What are the basic sedimentological features of these reefs?

4. What species of scleractinian corals, hydrocorals and bryozoans build them?

5. What role did these organisms play in the reef framework?

6. According to the assemblages observed, how were the paleoenvironmental conditions in the La Guajira coral reefs?

Our observations indicate that during the early Miocene (ca. 23-20 Ma) there was a reef system in optimal development conditions on the southeastern margin of the

Jarara range (current position). The landscape was dominated by two types of reefs that had a contemporary growth: 1. Patch-type reefs, distributed in a shallow lagoon area, with reduced inputs of terrestrial material from the Jarara paleoisland and, 2. Discontinuous barrier reefs, surround the same paleoisland. In both cases the scleractinian corals were the main bioconstructors. Both types of reefs were dominated by colonies of massive (domestones), erect (pillarstones) and their combinations (mixstones) forms, in clear and shallow water environments. Within bioclastic sediments surrounding the coral colonies (rudstone), rubble of mollusks, coral algae, benthic foraminifera and echinoderms are the most common.

Of the studied fauna, a total of 32 morphospecies of corals belonging to 2 orders (Scleractinia and Anthoathecata), 12 families, and 15 genera have been described. Most of these species became extinct in two later pulses, the first one during the early Miocene and the second one during the transition from the Pliocene to the Pleistocene, and only three species continue to exist in modern Caribbean reefs.

On the other hand, 32 morphospecies belonging to 2 orders (Cyclostomata and Cheilostomata), integrated in 20 families, and 28 genera, of which two genera and eight species are new to science, have been described in the fauna of bryozoans associated with coral reefs. The fauna found reveals that there could have been a faunal connection during the early Miocene with the Mediterranean Sea and the American Pacific, favored by the high capacity of some of the species to grow in various types of substrate and subsist in different types of environments. Although due to their small size the bryozoans did not play a priority role in the construction of reefs in the Siamaná Formation, their encrusting and erect colonies of cryptic habits contributed to the filling of cavities, cementation and accretion of structures.

The species richness in both phyla suggests greater diversity in the barrier reefs than in the lagoon patch reefs.

The Siamaná Formation still holds valuable information to be revealed. Future studies exploring new localities within the formation will contribute to improve the knowledge of the early Miocene reefs, as well as to discover new paleoenvironments and species of corals and bryozoans, which will help to clarify the evolutionary history of these two important groups. In addition, to understand the subsequent collapse of the reef communities in the Colombian La Guajira, it is necessary to extend the paleontological and sedimentary studies spatially and temporally.

Resumen amplio

Los arrecifes de coral de aguas someras se caracterizan por ser uno de los ambientes más diversos de la Tierra y cumplir con importantes roles ecosistémicos, interactuando de forma física, biológica y geoquímica con los ecosistemas marinos y terrestres adyacentes. Los corales arrecifales prosperan especialmente en la franja tropical del planeta, donde gracias a la permanente intensidad lumínica y a su asociación con las algas simbiontes forman los impresionantes marcos estructurales que conocemos.

Entender la capacidad de respuesta de la fauna arrecifal ante los diversos cambios ambientales y geológicos bajo condiciones naturales no antropizadas, así como los procesos evolutivos de dicha fauna a lo largo del tiempo, proporciona información de línea base para pronosticar escenarios a corto, medio y largo plazo, útiles en la toma de decisiones para la gestión sostenible de estos importantes ecosistemas.

La Península de La Guajira, ubicada en la cuenca del Caribe, al nordeste de Colombia, pese a estar geográficamente en el trópico, actualmente presenta condiciones ambientales atípicas que limitan el desarrollo óptimo de arrecifes de coral. No obstante, el registro geológico narra una historia diferente. La Formación Siamaná, de edad Mioceno temprano (ca. 20-23 Ma), aflora en al norte de la península, en las estribaciones de las serranías de Cosinas, Jarara y Macuira. En ella, abundantes depósitos fosilíferos, ricos en corales y malacofauna, han sido reportados en los escasos trabajos geológicos realizados en el área. Sin embargo, estudios acerca de la distribución espacio-temporal y la sedimentología de los depósitos arrecifales, intentos de interpretaciones paleoambientales detalladas, así como estudios taxonómicos exhaustivos de sus componentes no han sido efectuados hasta la fecha.

Por ello, es importante aportar información que fortalezca el conocimiento de los arrecifes en el Caribe colombiano y es de interés responder a las siguientes cuestiones:

1. ¿Qué tipo de estructuras arrecifales existieron en el Mioceno temprano en la Formación Siamaná?

2. ¿Cómo están distribuidas dichas estructuras temporal y espacialmente?

3. ¿Cuáles son los rasgos sedimentológicos básicos de estos arrecifes?

4. ¿Qué especies de corales escleractinios, hidrocorales y briozoos los constituían?

5. ¿Que papel desempeñaban estos organismos en la estructura arrecifal?

6. Según las asociaciones observadas, ¿cómo eran las condiciones paleoambientales de los arrecifes de La Guajira?

Nuestras observaciones indican que durante el Mioceno temprano (ca. 23–20 Ma) existió un sistema arrecifal en óptimas condiciones de desarrollo en el margen sureste de la serranía de Jarara (posición actual). El paisaje estuvo dominado por dos tipos de arrecife que tuvieron un crecimiento coetáneo: 1) Arrecifes de tipo parche, distribuidos en una zona lagunar poco profunda, con aportes reducidos de material terrígeno proveniente de la paleoisla de Jarara y, 2) Arrecifes de barrera discontinua, rodeando la misma paleoisla. En ambos casos los corales escleractinios fueron los principales organismos bioconstructores. Ambos tipos de arrecifes estuvieron dominados por colonias de formas masivas ("domestone"), erectas ("pillarstone") y sus combinaciones ("mixstone"), en ambientes de aguas claras y poco profundas. En los sedimentos bioclásticos que rodean las colonias de coral ("rudstone") son comunes los restos de moluscos, algas coralinas, foraminíferos bentónicos y equinodermos.

De la fauna estudiada, en total se han descrito 32 morfo-especies de corales perteneciente a 2 órdenes (Scleractinia y Anthoathecata), 12 familias, y 15 géneros. La mayoría de estas especies se extinguieron en dos pulsos posteriores, el primero de ellos en el transcurso del Mioceno temprano y el segundo en la transición del Plioceno al Pleistoceno, y solo tres especies continúan existiendo en los arrecifes modernos del Caribe.

Por otra parte, en la fauna de briozoos asociados a los arrecifes de coral se han descrito 32 morfo-especies pertenecientes a 2 órdenes (Cyclostomata y Cheilostomata), integrados en 20 familias, y 28 géneros, de los cuales dos géneros y ocho especies son nuevas para la ciencia. La fauna hallada revela que podría haber existido una conexión faunística durante el Mioceno temprano con el Mar Mediterráneo y el Pacifico americano, favorecida por la alta capacidad de algunas de las especies para crecer en varios tipos de sustrato y subsistir en diferentes tipos de ambientes. Aunque por su reducido tamaño los briozoos no cumplieron un papel prioritario en la construcción de arrecifes en la Formación Siamaná, sus colonias incrustantes y erectas de hábitos crípticos contribuyeron al relleno de cavidades, cementación y acreción de las estructuras.

La riqueza de especies en ambos phyla sugiere una mayor diversidad en los arrecifes de barrera que en los parches de la laguna.

La Formación Siamaná aún alberga información valiosa por ser desvelada. Futuros estudios que exploren nuevas localidades dentro de la formación contribuirán a mejorar el conocimiento de los arrecifes del Mioceno temprano, así como a descubrir nuevos paleoambientes y especies de corales y briozoos, que contribuyan a esclarecer la historia evolutiva de estos dos importantes grupos de organismos. Adicionalmente, para entender el posterior colapso de las comunidades arrecifales en La Guajira colombiana se hace necesario ampliar los estudios paleontológicos y sedimentarios espacial y temporalmente.

1. Introduction

1.1 Objectives

The general objectives of this PhD Thesis are to determine the composition and distribution of fossil coral and bryozoan assemblages in the Miocene reefs of the Siamaná Formation in the La Guajira peninsula (northeastern Colombia), to identify their spatial-temporal changes, and to infer the possible regional environmental and geological events that influenced the variations in the reef communities.
Specific objectives to reach these general ones are:

1. To identify the scleractinian corals, hydrocorals and bryozoans to the lowest possible taxonomic level.
2. To determine the species richness of corals and bryozoans in the different stratigraphic units, and to examine whether there are significant spatial-temporal variations in the composition and structure of reef assemblages.
3. To identify coral growth patterns and geometry of coral frameworks to interpret the paleoenvironments of reef development in combination with additional sedimentological information.
4. To identify the paleobiogeographic patterns of the bryozoan fauna during the early Miocene in the southern Caribbean.
5. To compare the results with those published in other locations in the Caribbean and other regions of the Earth.

1.2 Background

1.2.1 Reef Corals

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).

The main architects of these buildings in shallow-waters of tropical regions are the stony corals (Phylum Cnidaria: Class Anthozoa: Order Scleractinia and Class Hydrozoa: Order Anthoathecata –hydrocorals–). Their building capacity is due to calcification of their skeletons, helped by the symbiotic relationship that they have with zooxanthellae (dinoflagellate algae) living in their endodermal tissues, which ultimately provide the energy necessary for rapid processes of calcification and growth of coral colonies (Hutchings and Hoegh-Guldberg, 2009). Consequently, reef coral communities mainly occur in the photic zone in tropical and subtropical regions, where the incidence of light is permanent throughout the year, and the water temperature remains warm without substantial annual variations. Additionally, they require oligotrophic waters with low turbidity needed for optimal development of the photosynthetic symbionts. These and other environmental factors, such as water salinity, regulate the distribution of shallow-water scleractinian corals and thus make them accurate indicators of the environmental conditions in which they grow (Diaz et al., 2000; Veron, 2000; Reyes et al., 2010).

About 1300 species of Scleractinian corals have been described to date (Cairns, 1999); among them, 656 are zooxanthellate, or hermatypic corals, i.e., builder species (Daly et al., 2007). According to fossil evidence, scleractinian corals appear in the Middle Triassic, around 240 Ma ago (Stanley, 2003; Daly et al., 2007). However, Stolarski et al. (2011) remark that there are no significant morphological differences with current species, and suggest, based on molecular analysis, that the origins of the order date back to the Paleozoic, 425 Ma ago. According to some authors these organisms have not had notable variations, either morphological or in their ecological roles over time. This make them excellent tools for paleoenvironmental interpretations in the tropical regions (Budd et al., 1996; Stolarski et al., 2011). Species composition variations and changes in the structure of reef communities provide information about the paleogeographic and paleoceanographic events that influenced the existence of coral reefs and the changes that experienced.

Three big episodes of extinction, diversification and species turnover of marine benthic communities took place in the Caribbean region during the Cenozoic at: 1. Eocene–Oligocene boundary (ca. 34 Ma), 2. Oligocene–Miocene transition (ca. 23 Ma) and 3. Pliocene–Pleistocene passage (ca. 2.6 Ma). Among them, the second episode was one of the most significant for scleractinian corals, with a loss of up to 50% of Oligocene diversity (Budd et al., 1994, 1996, 2011; Budd, 2000; Johnson et al., 2008, 2009; Wallace, 2012). This loss of species generated a residual gap in ecological niches that was occupied by new species (turnover), favoring diversification processes. In addition to the faunal turnover, there was a change in the type of reef. While barrier and fringing reefs were dominant during the Oligocene in the Caribbean region, later in the early and middle Miocene patch reefs predominate, and a proliferation of solitary and free-living corals was recorded in adjacent ecosystems, such as seagrass meadows (Vaughan, 1919; Edinger and Risk, 1994, 1995; Johnson, 2009).

Another important event during the Oligocene–Miocene was the division of the circumtropical fauna of the Paleogene into separate paleobiogeographic regions, making the western Atlantic and the Caribbean an independent biogeographic province (Perrin, 2000; Perrin and Bosellini, 2012).

The fossil record suggests that the extinction and species turnover of scleractinian corals in the Oligocene-Miocene transition may have been promoted by an increase in productivity and a decrease in water temperature, probably caused by the appearance of upwelling in the area, due to paleogeographic variations that altered the ocean current patterns (Johnson, 2007, 2009). A marine transgression at the end of the Oligocene followed by a regression during the Miocene may have driven sinking and subsequent emergence of the coral reefs (Johnson, 2009).

The surviving genera (e.g., *Montastraea*, *Porites*, *Siderastrea* and *Solenastrea*, among others) are characterized by their tolerance to relatively low temperatures, high sedimentation rates and by their capacity to inhabit different reef zones, and different reef types. Thus, the surviving genera are more cosmopolitan and were even able to change their usual ecological niches (Budd, 2000; Edinger and Risk, 1994).

Paleontological studies of zooxanthellate corals in Caribbean shallow waters date back to the beginning 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 systematics 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 characters for the classification of fossil and recent specimens. 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 works have updated the 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).

Although these studies have provided insights into the coral diversity during important periods of speciation and extinction, few of them 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 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 these collections that will serve for future work on the Cenozoic corals of the Southern Caribbean.

1.2.2 Bryozoans

The bryozoans are a phylum of the animal kingdom, mostly marine (except the class Phylactolaemata). Also known as moss animals, sea mats, or lace corals, these colonial invertebrates are widely distributed in the oceans of the world, from the shorelines of tropical and polar latitudes to the deep sea (Gordon et al., 2009). Around 6000 living species and 15000 fossil species have been recognized; however, estimations suggest that thousands of species have yet to be described (Bock and Gordon, 2013; Taylor and Waeschenbach, 2015). Together with brachiopods and phoronids, the bryozoans conform the lophophorata "group", characterized by a feeding structure formed by a crown of ciliated tentacles around the mouth, called lophophore, which can protrude or retract. They have a U-shaped digestive tube, with an anus open outside the tentacular crown (Gordon et al., 2009).

The phylum has a rich fossil record back to the Tremadocian, Early Ordovician (Xia et al., 2014). Its oldest members belong to the order Stenolaemata, which is characterized by the morphological simplicity of the zooids; this order underwent major periods of diversification during the course of the Ordovician and Cretaceous. Although they were deeply affected by the mass extinctions of the late Permian and Cretaceous–Paleogene boundary, 20% of living species of bryozoans belong to this order (Taylor and Waeschenbach, 2015). On the other hand, the order Cheilostomata, the most diverse nowadays, appeared during the Late Jurassic and began its rapid diversification during the Cretaceous, also interrupted by the massive extinction at the Cretaceous–Paleogene boundary. It had a rapid recovering during the Paleogene and its diversity continued relatively stable until now. This taxon is characterized by a huge increase in morphological features. The polymorphism of its members includes regular feeding zooids, structures of support or anchoring, nutrient-storage chambers, space fillers, sexual polymorphs and organs of defense and mobility (Gordon et al., 2009).

Bryozoans have a good fossil record due to their calcareous skeletons, commonly calcitic, although are occasionally aragonitic or bimineralitic (Taylor et al., 2009). Thanks to their skeletons, they are significant contributors to marine carbonate sediments, and hence to the formation of limestones (Taylor and James, 2013); even they have the capacity to build structural frameworks, or bioherms, under appropriate environmental conditions (Cocito et al., 2000, Bastos et al., 2018).

Cenozoic bryozoan diversity in tropical latitudes was very high (Di Martino et al., 2015, 2017, 2019), within a generally high marine biodiversity (Jackson and Johnson, 2001; Buzas et al., 2002). In the Caribbean, a notable increase of the bryozoan species richness since the Burdigalian (ca. 18 Ma) has been recorded (Cheetham and Jackson, 1996; Cheetham et al., 1999; O'Dea et al., 2004; Di Martino et al., 2017; Di Martino et al., 2018). However, reports of fossil bryozoans in tropical regions, especially in continental South America remain sparse (Taylor et al., 2009; Zágoršek et al., 2014; Taylor and Waeschenbach, 2015; Ramalho et al., 2019). Diagenetic processes, which mainly affect bryozoans with aragonitic skeletons (Taylor et al., 2009; Taylor and Di Martino, 2014), and several other factors have undoubtedly biased against the fossil record of bryozoans in the Cenozoic tropics. In addition, the limited collection efforts have tended to overlook small bryozoan colonies in the field and inventories are therefore largely incomplete.

Despite their small size, bryozoans are a diverse group of invertebrates within marine benthic communities. Their distribution and species richness are related, in part, to the availability of hard substrata and habitat heterogeneity (Clarke and

Lidgard, 2000). Coral reefs provide diverse surfaces for the settlement and growth of bryozoans, including cryptic habitats, such as caves, crevices, areas under coral colonies, rubble and sand grains (Jackson and Winston, 1982; Choi, 1984; Kobluk et al., 1988; Ramalho et al., 2108). In addition, a high diversity of macroinvertebrates (e.g., sponges, crabs, and mollusk shells) are susceptible to colonization by bryozoans (Almeida et al., 2017; Di Martino et al., 2019). Although in terms of biomass, bryozoans are not the most abundant organisms in these tropical ecosystems, their species diversity is relatively high (Novak et al., 2103; Santodomingo et al., 2015).

Commonly, the bryozoans are hidden encrusters (Cuffey, 2011), growing on the undersides of coral colonies, or in grooves of the framework, filling the cavities and hence reinforcing the structural framework and contributing its accretion (Winston and Jackson, 1984; Cuffey, 2011).

Several studies have focused on the characterization of bryozoans associated with modern coral reefs in the Western Central Atlantic region, and have addressed the ecological roles they play in these ecosystems (Cuffey and Kissling, 1973; Schopf, 1974; Cuffey and Fonda, 1977; Jackson, 1979; Jackson and Winston, 1982; Choi, 1984; Winston, 1984, 1986; Winston and Jackson, 1984; Jackson et al., 1985; Gischler, 1997). However, comprehensive taxonomic studies of bryozoan faunas on ancient coral reefs remain scarce in this region.

The most representative taxonomic works on Caribbean Miocene bryozoans were carried out by Canu and Bassler (1919, 1923) in the islands of Jamaica, Hispaniola and Cuba, as well as in Costa Rica and the US states of Maryland, Virginia, North Carolina and Florida; by McGuirt (1941) in Louisiana; by Scolaro (1968) and Di Martino et al. (2017) in Florida; and by Cheetham et al., (1999) in the Dominican Republic and Panama. In Colombia, studies on fossil bryozoans are almost non-existent. Some works have been made on Devonian and Cretaceous samples (McNair, 1940; Jerez-Jaimes et al., 2013), and there are isolated mentions of "*Sertella* sp." and "*Acanthodesia savartii* form *texturata*" from the Miocene reefs in the oceanic island of Providencia (Buge in Geister, 1992).

1.3 Study Area and Geological Setting

The La Guajira Peninsula is located at the northern end of Colombia, in the south of the Caribbean Sea (Fig. 1). In the marine realm, the continental shelf ranges between 10 and 40 km across, and is characterized by sandy-muddy bottoms and turbid waters, despite the low sediment input. The coastline is generally of a high energy, except in some protected bays. A seasonal event (December-February) of upwelling increases the input of nutrients from deep waters and activates high biological productivity and decrease of water temperature, which restrict the development of coral species (Díaz and Gómez, 2000; Rueda-Roa and Muller-Karger, 2013). On land, the peninsula exhibit deserts and tropical dry forest ecosystems, with large flat areas and five isolated mountain ranges of pre-Cenozoic rocks, which do not exceed 865 m of altitude (Fig. 2). Climatologically, it has rainy and dry seasons, which are regulated in part by trade winds from the NE (Zapata, 2010). The so-called Alta Guajira, the northern part of the peninsula, has no developed roads or civil infrastructures, which makes it a remote area with difficult access, where isolated Wayúu indigenous communities live in small villages called rancherías.

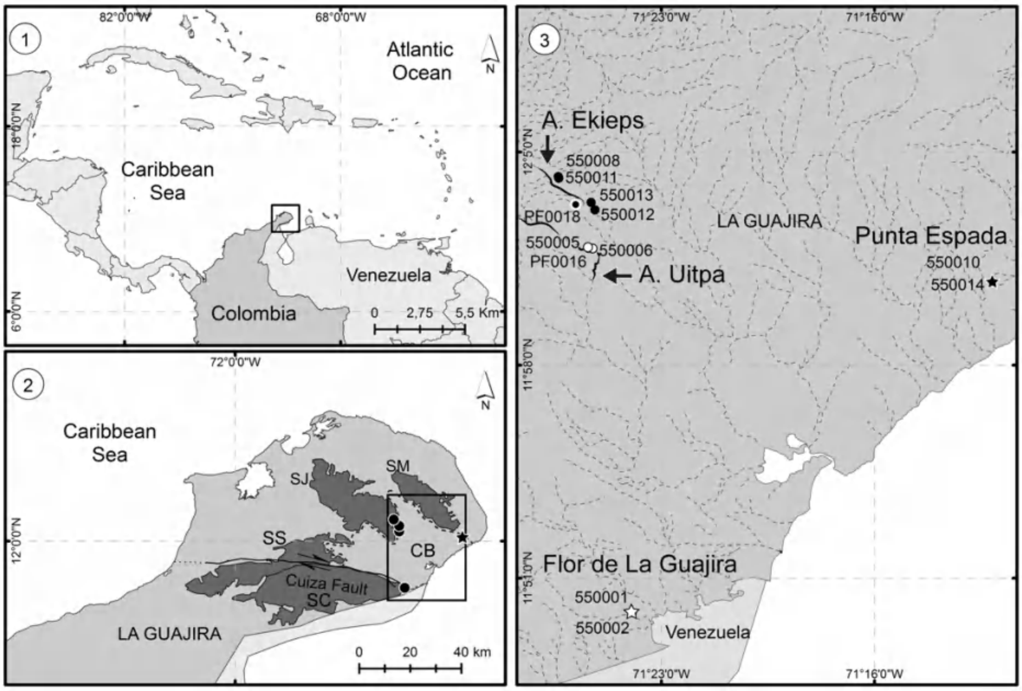

Figure 1. General location of the Guajira Peninsula along the southern margin of the Caribbean Sea. (2) Location of Cocinetas Basin (CB), flanked by the Serranía de la Macuira (SM), Serranía de Jarara (SJ), Serranía de Simarua (SS), Serranía de Cocinas (SC) and Cuiza fault; the black circles indicate stations from the Siamaná Formation (early Miocene) and the black star indicate 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.

Tectonically, La Guajira is part of the South American plate, near the contact zone with the Caribbean plate. Both plates are influenced by the thrust of the Cocos plate under the Caribbean plate, which has determined the current structure and geological configuration of the peninsula (Pindell and Kennan, 2001). Although the tectonic evolution of the Caribbean in general is complex to interpret, studies suggest that it began in the late Jurassic (170 Ma) when North and South America began to separate. Later, during the Cretaceous (110-65 Ma), the South American continent spun counterclockwise, pushing the Caribbean plate in a NE direction. From the early Cenozoic (66 Ma) to the present day, there has been a reverse rotation. In parallel, northern South America was affected by a strong tectonic activity, generated by the interaction of the South American plate with the Caribbean plate, which determined tectonics and sedimentation during the Paleocene–Oligocene in the La Guajira peninsula (Gómez, 2001; Pindel and Kennan, 2001; Pindell and Dewey, 1982).

A marine transgression began in the early Oligocene and the conglomerates, marls and limestones of the Siamaná Formation were deposited over a large area in the peninsula. This transgression continued until the late Miocene (Lockwood 1965; Rollins 1965).

Figure 2. On land ecosystems in the La Guajira Peninsula. (1) Desertic area in the La Flor de La Guajira locality, picture Edwin Cadena; (2) tropical dry forest in Arroyo Ekieps locality, picture Lina Perez.

The Siamaná Formation ranges from the late Oligocene to the early Miocene (Fig. 3) (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; Rollins, 1965; Lockwood, 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), to 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. 3) (Moreno et al., 2015). The Uitpa Formation is composed of deep-water 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.

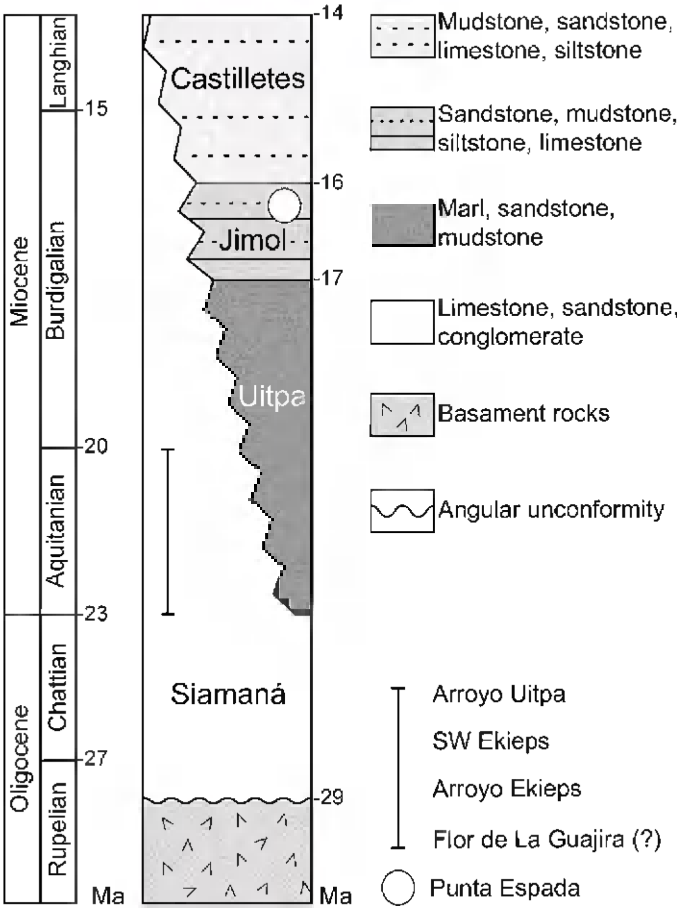

Figure 3. The Cocinetas Basin general stratigraphy showing the stratigraphic range of the localities studied (A–E). Ages and lithological characteristics of the Siamaná, Uitpa, Jimol and Castilletes formations following Moreno et al. (2015) and Silva-Tamayo et al. (2017).

2. Materials and Methods

Field work on the Siamaná and Jimol formations was carried out in two expeditions in 2011 and 2014, both campaigns was developed by the Smithsonian Tropical Research Institute, Universidad de los Andes (Bogotá, Colombia), Universidad del Norte (Barranquilla, Colombia) and the ARES Geological Corporation. Sediment and fossil samples were collected at five localities in the Cocinetas Basin: Arroyo Uitpa, Arroyo Ekieps, SW Ekieps, Flor de La Guajira and Punta Espada (Fig. 1; Table 1).

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°00'37.65"	71°50'58.9"	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?

2.1 Sedimentology and Stratigraphy

Four sections of reef deposits were studied in well-exposed outcrops of the Siamaná Formation. Two sections were logged in Arroyo Uitpa, one in SW Ekieps, and another one in Arroyo Ekieps. Field data collected included lithology, lithofacies, major components, and geometry and distribution of coral buildups at outcrop scale. Seventy-seven thin sections of selected rock samples were prepared to analyze the petrography and to identify coralline algae and larger benthic foraminifers. Carbonate content was estimated with a CM5240 Total Inorganic 207 Carbon autoanalyzer in 26 of samples. The age of the Siamaná Formation was estimated by Silva et al. (2017) through ^{87}Sr/^{86}Sr values in fossil coralline algae. The numerical dating was assessed in the logged sections 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.

2.2 Coral fauna

Coral samples were collected along 10 m horizontal transects in each station of each locality (Fig. 1; Table 1). To increase sampling of taxa, some additional specimens were obtained outside of linear transects. 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 (Fig. 4.1) 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) at the "Centro de Instrumentación Científica, Universidad de Granada", 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 of the corals is presented in alphabetical order, both at family and genus levels. References for the occurrence information provided on each species for the Caribbean region, such as formation, depositional age and country was actualized and compiled in Annex 1 and 2. A list of collected specimens included in this study with catalog numbers, locality names, station numbers are provided in Annex 3.

2.3 Bryozoan fauna

The bryozoan specimens were obtained from the surfaces of coral colonies and in the cemented sediment. These were washed and scrubbed with a soft brush; the residual sediment was sieved in meshes of 250 µm and 63 µm. In some cases, the sediment was gently removed from corals with a needle and paintbrush to preserve erect bryozoan fragments. Encrusting bryozoans were detached from coral surfaces. The remaining sediment on bryozoan specimens was removed using an ultrasonic cleaner. All specimens were analyzed with a stereomicroscope under 2x and 4x magnification; among them, the best preserved were analyzed with scanning electron microscopy (SEM). Coated and uncoated specimens were examined at the "Centro de Instrumentación Científica, Universidad de Granada", using FEI Quanta 400 and FEI Quemscan 650F microscopes at low and high-vacuum modes using backscattered and secondary electron detectors. Measurements of zooidal characters (Fig. 4.2) were made from SEM images using the image-processing program ImageJ (National Institutes of Health, USA; https://imagej.nih.gov/ij) and are given in mm in the tables for each species. They include average (X), observed range (R), standard deviation (SD) and the number of measurements (N). The systematic paleontology section of Cheilostomata follows the interim classification compiled by D.P. Gordon for the Treatise on Invertebrate Paleontology (2014). A list of collected specimens included in this study with catalog numbers, locality names, station numbers, type of colony and substrate and number of specimens available is provided in Annex 4.

The samples described and illustrated and the type specimens of corals and bryozoans will be stored in the reference collection of the Mapuka Museum of the Universidad del Norte, Barranquilla-Colombia (MUN-STRI). Type material used for comparative purposes is housed in the U.S. National Museum of Natural History, Washington, USA (USNM), numbers preceded by 'M' are from Mollusk series; Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH); Natural History Museum, London, United Kingdom (NHMUK); and Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ).

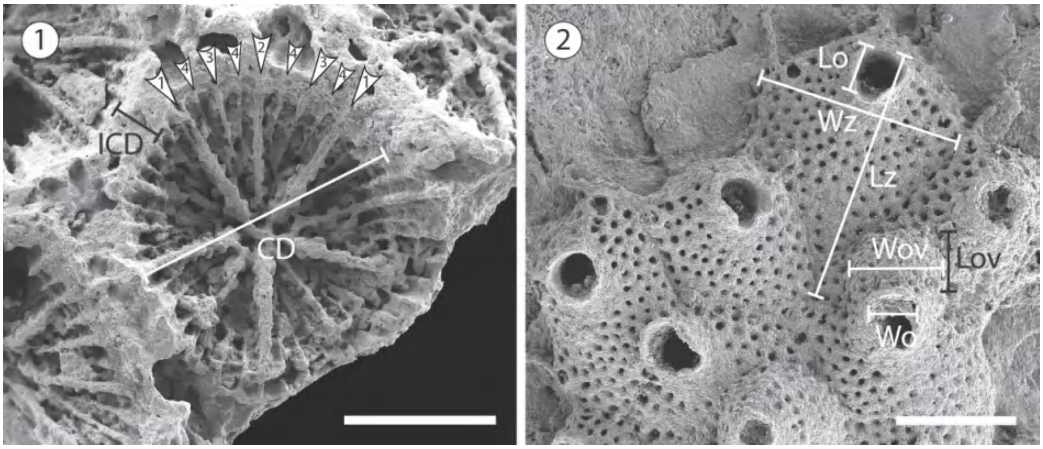

Figure 4. Main morphological features measured: (1) *Antiguastrea cellulosa* (Duncan, 1863), in scleractinian corals the calicular diameter (CD), intercalicular diameter (ICD) and number of cycles (arrowed) were measured. (2) *Marcusadorea* n. sp., in bryozoans length and width of zooids (Lz, Wz), orifices (Lo, Wo) and ovicells (Lov, Wov) were measured.

3. Reefs in the Siamaná Formation

3.1 Age of the studied sections

Two larger benthic foraminifer (LBF) assemblages were identified in thin sections from the four logged sections. One includes *Miogypsina* sp., occasional *Amphistegina* sp., rare *Operculinoides* sp., and Archaiasinae (Renema com. pers.). This assemblage commonly appears in the early Miocene in the Caribbean region, although it can be found in the late Oligocene as well (Mitchell, 2004; Robinson, 2004; Serra-Kiel et al., 2007). A second assemblage consisting of *Amphistegina* sp. and large members of Archaiasinae also suggests an early Miocene age. The absence in the analysed samples of species characteristic of the late Oligocene, such as *Heterostegina antillea*, *Nummulites antiguaensis*, and *Eulepidina* sp. (Serra-Kiel et al., 2007) supports an early Miocene age of the study sections. The LBF assemblages indicate that the reef deposits in Arroyo Uitpa, SW Ekieps, and Arroyo Ekieps localities are roughly coeval. The presence of the coral species *Siderastrea siderea* in the Arroyo Ekieps section (Flórez et al., 2019 a, b) is also consistent with an early Miocene age of these reefs. All previous records of the species occur in Miocene formations (Santa Ana Formation from Mexico, ca. 22-15 Ma, Frost and Langenheim, 1974; Tamana Formation from Trinidad and Tobago, ca. 16-11 Ma, Johnson, 2001).

These biostratigraphic results are relatively compatible with the Sr-isotope ages obtained for the Ekieps and Arroyo de Ekieps sections by Silva-Tamayo et al. (2017), although they contradict the late Oligocene to early Miocene age assigned by these authors to the Arroyo de Uitpa sections. However, the type of samples (coralline algae and rhodalgal rock) analysed by Silva-Tamayo et al. (2017) makes questionable any precise age model based on the Sr-isotopic composition of carbonates.

3.2 Lithofacies

Based on field observations and petrographic analyses, four lithofacies were distinguished in the studied sections: mixstone, pillarstone (sensu Insalaco, 1998), rudstone, and cross-bedded grainstone to packstone (Dunham, 1962). In accordance with the scheme of Insalaco (1998) mixstones are deposits built by aggregated in situ corals mainly comprising massive and branching colonies, whereas pillarstones are dominated by branching colonies with vertical growth.

Rudstones mainly consist of poorly sorted, angular bioclasts with low sphericity and a micrite matrix. Micrite can be locally abundant (floatstone). Coral fragments are the main components with secondary coralline red algae (crustose and geniculate), bivalves (mainly pectinids and oysters), gastropods, echinoids, bryozoans, small and larger benthic foraminifers, and serpulids. Sponge spicules, crab claws, ostracods and shark teeth are minor constituents. Originally aragonitic skeletal particles were dissolved and are partially to totally filled by sparry calcite, which also occurs in some intraskeletal voids.

Cross-bedded grainstones to packstones are well sorted with medium-sized, rounded bioclastic grains. These deposits show low angle parallel cross bedding and lamination. Echinoids, small and larger benthic foraminifers, bivalves, coralline algae, and corals are the main grain components. A few planktonic foraminifers can also be identified. As in rudstones, originally aragonitic grains were dissolved and are partially to totally filled by sparry calcite.

3.1 Arroyo Uitpa sections

The Arroyo Uitpa 1 section is 22 m thick and includes rudstones interbedded with mixstones, and pillarstones of variable thickness, overlain by grainstone (Fig. 5, section 1; Fig. 6). The basal unit is a 2-m thick, well cemented, poorly sorted rudstone with large coral fragments encrusted by coralline red algae (Fig. 7.1). Mixstones appear as discontinuous patches separated laterally and vertically by rudstone, forming domal to lens-shaped structures, ~2−3 m wide and 1.50−2 m high. Massive morphologies in mixstones range from massive colonies with knobs (*Porites waylandi*) to dome-shaped colonies, such as the ones of *Antiguastrea cellulosa*, *Astrocoenia decaturensis* and *Agathiphyllia tenuis*. Branched colonies comprise *Porites portoricensis*. A 25-cm thick bed at 6.75 m from the base contains terrigenous clasts, mainly pebbles (Fig. 7.2), in a sandy matrix with bioclasts. At 15 m from the base a pillarstone bed about 1 m thick, comprises the same branching species of the mixstones. Colonies range from a few centimeters to ~45 cm across. Grainstones with low angle parallel cross bedding and lamination, up to 3 m in thickness, overlie all these facies. The carbonate content average in this section is 89%; the lowest value corresponds to the sandy bed with terrigenous clasts (79%). The values increase at the top of the section (ranging 79-94%, n=7).

The Arroyo Uitpa 2 section is 15 m thick and consists of rudstones, with patches of mixstones and pillarstone (Fig. 5, section 2). The rudstone bed, 2 m thick, at the base includes isolated large massive colonies of *Montastraea* sp. and *Colpophyllia* sp., as well as branching colonies of *Porites* sp., up to 40 cm high. It is overlain by a pillarstone, 1 m thick, composed of branching colonies of *Stylophora* sp. and *Astrocoencia decaturensis*. The section continues with mixstones in lens-shaped, laterally and vertically discontinuous patches, about 6 m wide and up to 3 m high. Mixstones comprise the massive species *Montastraea canalis*, *Colpophyllia willoughbiensis* and *Porites waylandi*, and branching species, such as *Stylophora affinis*, *Astrocoenia decaturensis* and *Porites portoricensis*. Colony size ranges from few centimetres up to 60 cm. The carbonate content average in this section is 84%, (ranging 70-93%, n=4).

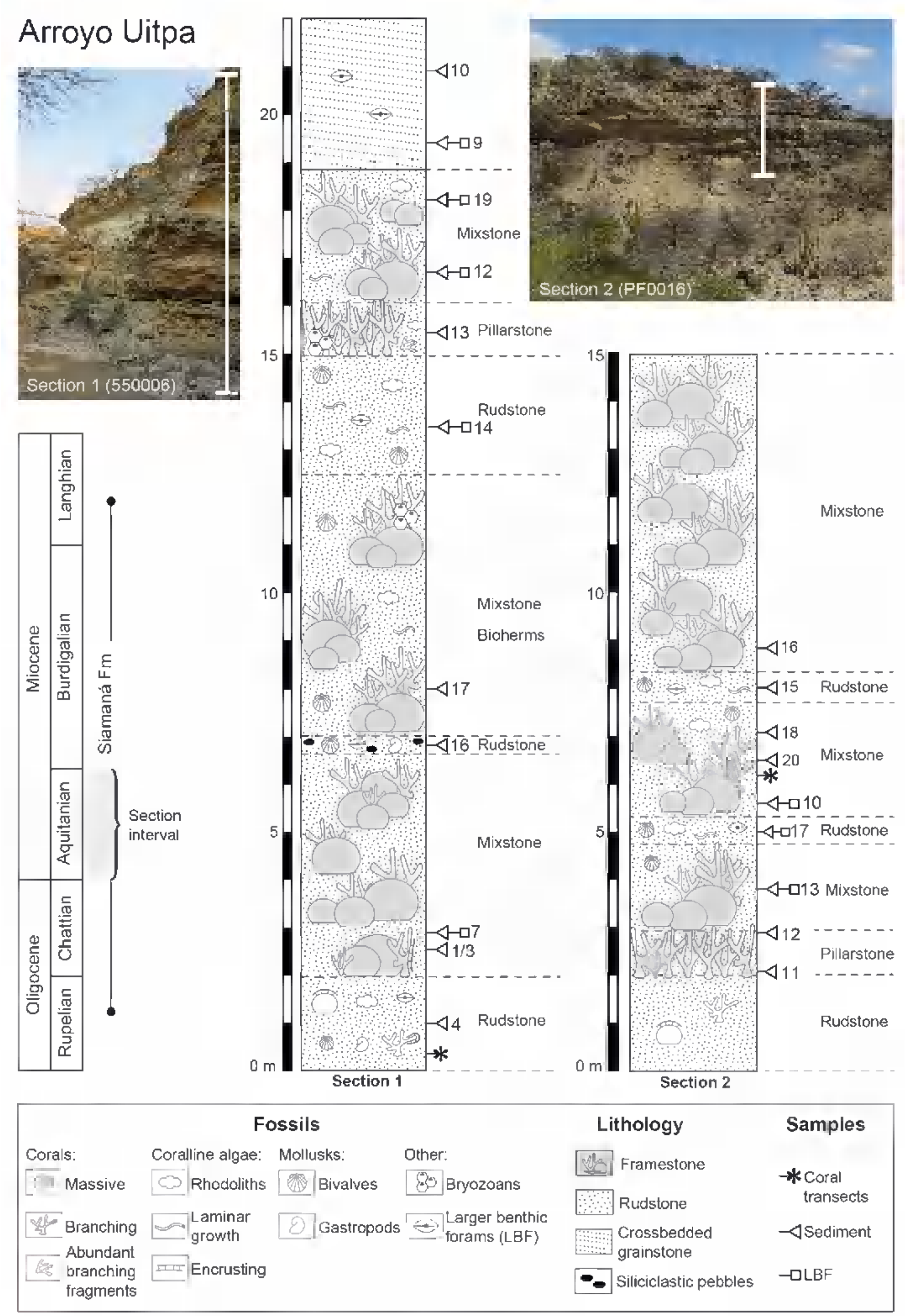

Figure 5. Columns of sections logged in Arroyo Uitpa stations (Siamaná Formation).

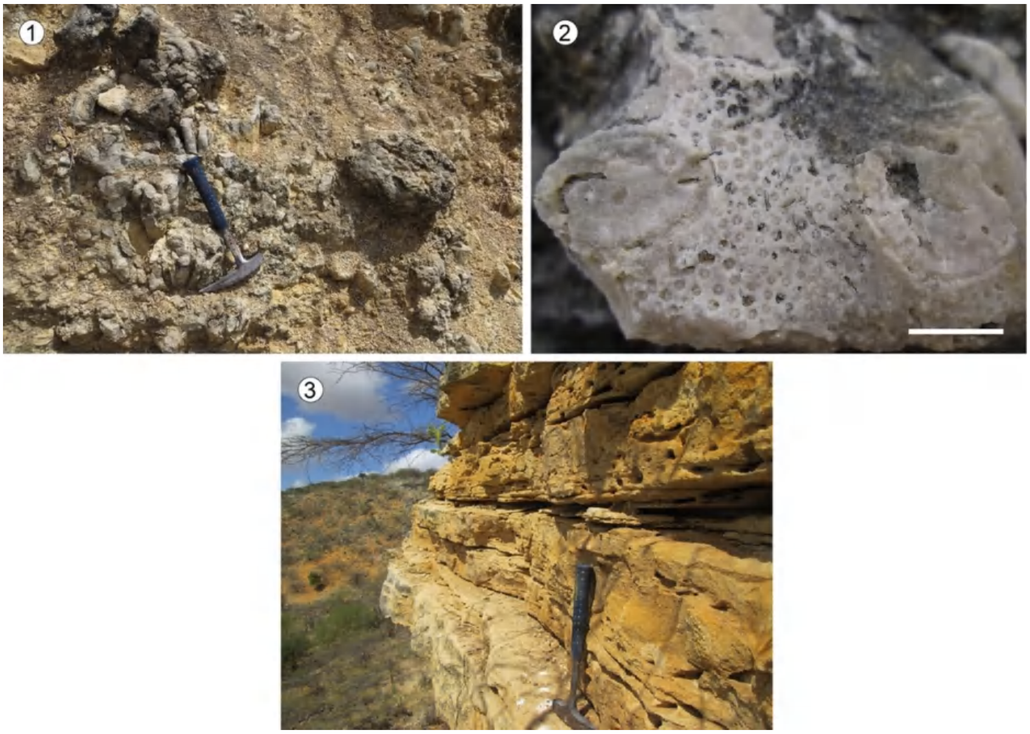

Figure 6. Arroyo Uitpa, section 2. (1) Mixstone. Hammer is 28 cm long. (2) Detail of a branching colony of *Stylophora* sp., dominant component of pillarstone. Scale bar: 1 cm. (3) Grainstones with low-angle parallel cross-bedding at the section top. Hammer is 28 cm long.

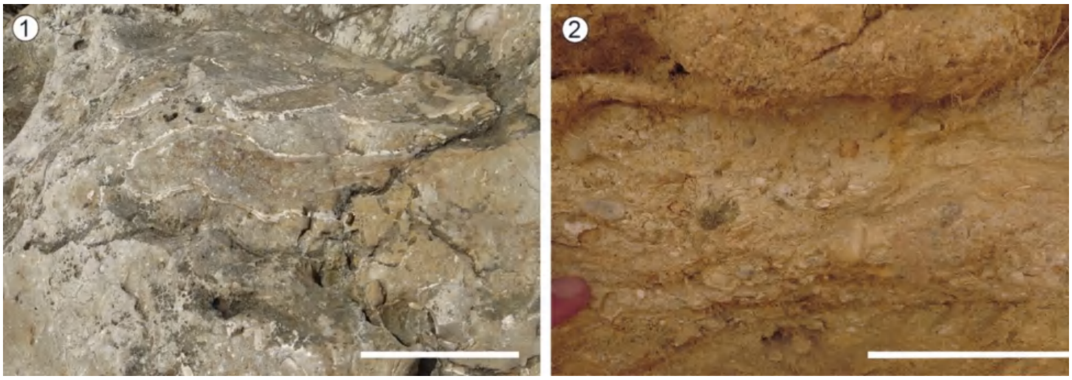

Figure 7. Arroyo Uitpa rudstones, (1) Basal rudstone with coral fragments encrusted by coralline algae. Scale bar: 5 cm. (2) Terrigenous pebbles in the second rudstone bed. Scale bar: 5 cm.

3.2 SW Ekieps section

This section is 14 m thick (Fig. 8, section 3) and consists of rudstones with patches of mixstones. The basal unit is a well cemented rudstone, 3.5 m thick. The overlying reef deposits are mainly poorly cemented lens-shaped mixstones, 1 to 3 m thick, separated by rudstones, with coralline red algae, mainly as rhodoliths (Fig. 9.1), as well as pectinids, and gastropods (Turritellidae) (Fig. 9.2). Branching coral species, such as *Acropora panamensis*, *Alveopora tampae*, and *Astrocoenia* sp., as well as massive colonies of *Montastraea endothecata*, occur together with the species found in the Uitpa sections. Single massive colonies are between 4 and 60 cm wide and branching colonies between 20 and 60 cm wide, with branches up to 4 cm in diameter. This section has the highest carbonate content (average 94%, ranging 89-99%, n=10).

3.3 Arroyo Ekieps section

Reef deposits, about 14 m thick, unconformably overlie the Macuira Gneiss basement. The basal unit of the section consists of a 2 m thick rudstone rich in bivalve fragments. The size of coral fragments gradually increases from bottom to top within the unit. The rest of the section is composed of mixstones interbedded with minor, poorly cemented rudstones (Fig. 8, section 4). Mixstones are laterally continuous, between 1 and 3 m in thickness, with a development degree (sensu Insalaco, 1998, p. 179) of 90%. The mixstone and rudstone beds can be traced for about hundred meters along strike, parallel to the contact with the underlying basement, gently dipping to the NE. Exposures perpendicular to the strike reveal that mixstones and rudstones occur as offlapping clinobeds prograding to the NE. Arroyo Ekieps has the highest species richness of the four study sections (Table 2). In addition to the species recorded in the other localities, the diversity in this site increases due to the presence of massive species, such as *Agathiphyllia antiguensis*, *Goniastrea canalis*, *Goniopora hilli*, *Siderastrea conferta*, and *S. siderea*, branching species such as *Acropora* sp., and platy forms with knobs of *Porites anguillensis*. As in Arroyo Uitpa and SW Ekieps, species such as *Montastraea* spp., *Porites* spp., *Astrocoenia* spp., *Stylophora afinis* and *Antiguastrea cellulosa* are common components of the assemblages. Massive colonies range in width between 10 and 45 cm, and branching colonies are up to 50 cm wide and up to 60 cm high, with branches up to 6 cm in diameter. The carbonate content average is 86% (ranging 76-93%, n=6).

3.4 Paleoenvironmental interpretation

The Siamaná Formation in the study area accumulated on a carbonate platform surrounding a paleo-island of metamorphic basement that was the antecedent relief of the Jarara range (Bloch et al., 2016) (Figs. 1 and 10).

In Arroyo Uitpa 1 and 2 sections, the geometry of small flat lenses or flat domes (small bioherms) and the lateral and vertical discontinuity of mixstones and pillarstones indicate that they were generated by small coral patch reefs. These buildups grew on bioclastic gravels, represented by the rudstones surrounding them. The gravels derived from the destruction of corals building the patches and the accumulation of skeletal debris from organisms living in and around the coral growths. The poor sorting, high angularity, low sphericity of bioclasts and the abundance of micrite suggest that the rudstone is an in situ accumulation of debris with no or negligible transport.

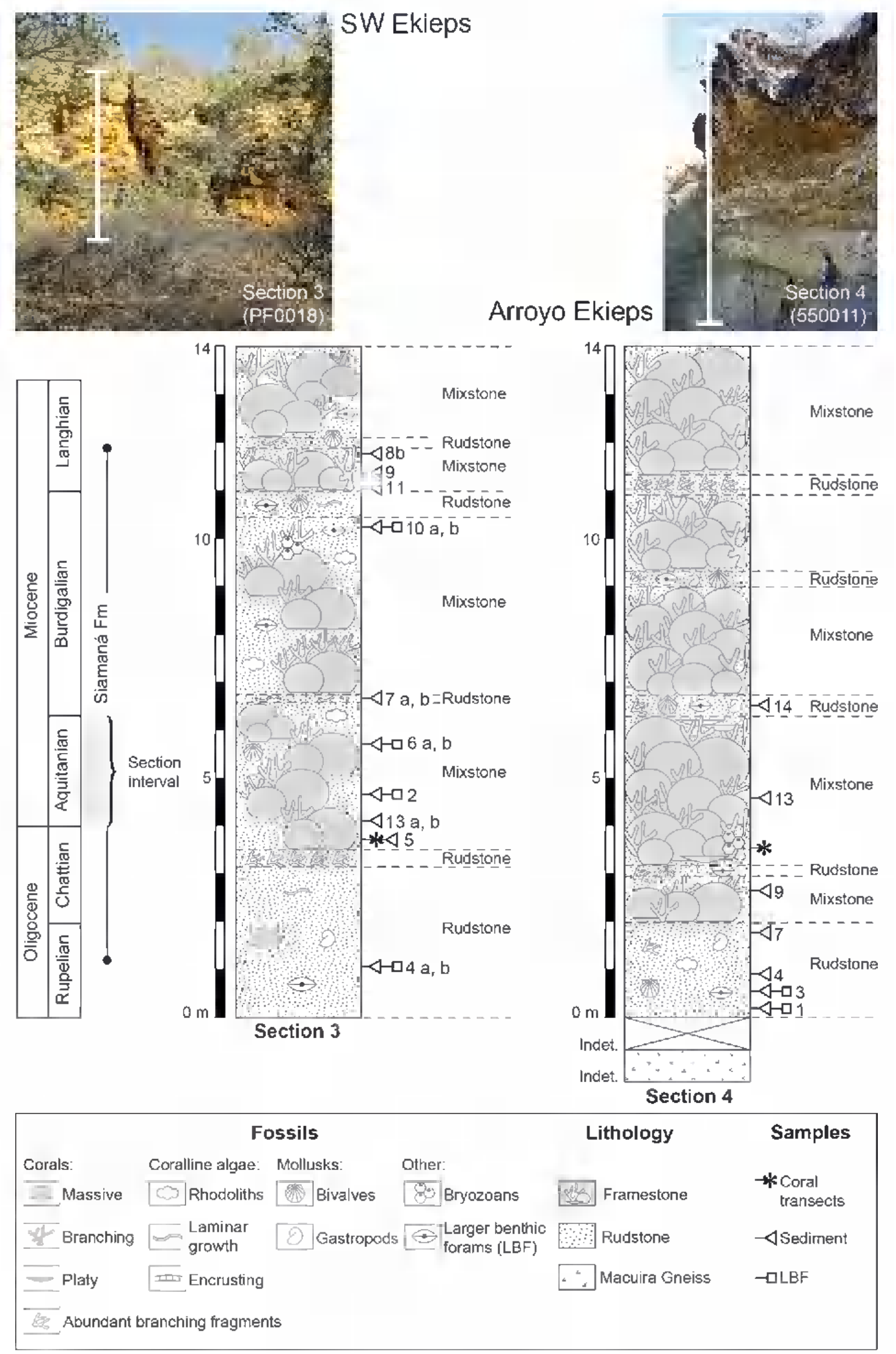

Figure 8. Columns of sections logged in SW Ekieps and Arroyo Ekieps stations (Siamaná Formation).

Figure 9. Rudstones of SW Ekieps, (1) Fruticose coralline algae. Scale bars: 2 cm. (2) Mold of a turritellid gastropod. Scale bar: 3 cm.

The low angle parallel cross-bedding and lamination of the grainstones at the top of the section Arroyo de Uitpa 1 indicate that they formed in a beach foreshore. A dominance of echinoid bioclasts, such as the one observed in the grainstones in Arroyo Uitpa 1, has been reported in carbonate beach deposits in the Miocene of southeastern Spain (Brachert et al., 1998). The beach deposits prograded directly on the reef sediments (Fig. 5, Section 1), suggesting that the growth of the coral patches took place close to the paleoshoreline. In this setting there was episodic influx of coarse-grained siliciclastics from the emergent basement (Jarara paleo-island) represented by the bed with pebbles in a sandy matrix (Figs., 7.2 and 10).

The zooxanthellate coral species, their colony morphology, mainly massive and branching, together with the absence of platy forms, indicate that despite the sporadic siliciclastic input, the patch reefs grew in shallow waters with low turbidity. The scarce fragmentation degree of pectinid shells and other bioclasts, and the characteristics of rudstones suggest a low-energy paleoenvironment, probably a lagoon, in which clusters of coral colonies grew on and surrounded by gravels derived from them due to or favored by bioerosion (Glynn and Manzello, 2015) (Fig. 11.1).

The mixstone lithofacies of SW Ekieps also occur as discontinuous lenses in rudstones, suggesting they also formed in patch reefs that developed on bioclastic gravels. The species richness increases in relation to Arroyo de Uitpa sections due to the appearance of thick branching species, such as *Alveopora tampae* and *Acropora panamensis* (Fig. 11.2). Although the latter was found in the early Miocene Culebra Formation growing in the reef crest and forereef (Johnson and Kirby, 2006), species with thick branches and lobate columns, and massive colonies can grow both in the reef front with rough waters, and in protected environments (Geister, 1983). The patch reefs in SW Ekieps developed in calm waters, as indicated by the characteristics of the surrounding rudstone and low degree of fragmentation of shells of fossil dwellers, probably in the same lagoon setting as the Arroyo Uitpa deposits (Fig. 10). The high carbonate content values in this section suggest an environment far from the coarse siliciclastic input from the Jarara paleo-island.

The mixstones in the Arroyo Ekieps section have lateral extensions up to 100 m parallel to the contact of Miocene deposits with the basement, indicating they formed laterally continuous buildups roughly parallel to the paleoshoreline. The mixstones exhibit a subtle basinwards (NE) progradation marked by low-angle clinobeds (Fig. 12.1–12.2). The reefs in Arroyo Ekieps have the highest species richness, 92% (22 species) of the total builder species found in the studied sections. By contrast, only 54% (13 species) occur in Arroyo Uitpa, and 50% (12 species) in SW Ekieps.

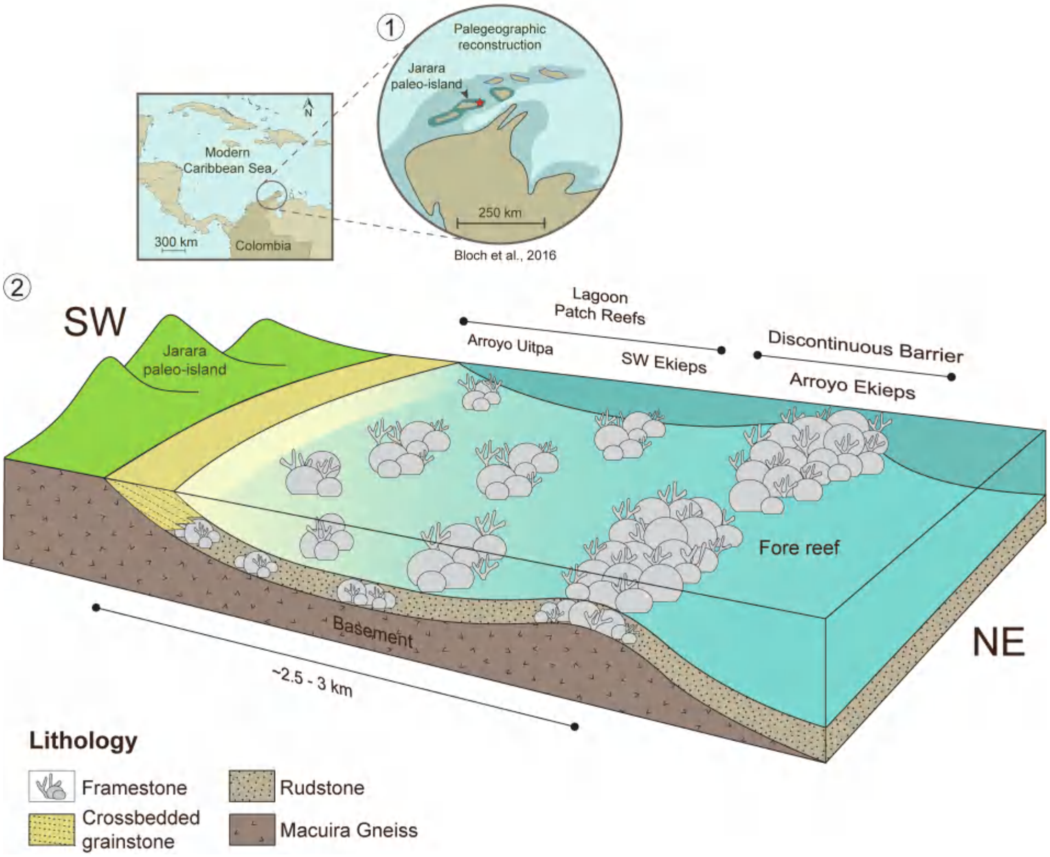

Figure 10. (1) Paleogeographic reconstruction (Bloch et al., 2016) showing shallow-water carbonates (Siamaná Formation) surrounding palaeo-islands (dark green). The red star indicates the hypothetical location of the study area. (2) Depositional model for the early Miocene reef interval of the Siamaná Formation. A discontinuous barrier enclosed a lagoon in which patch reefs developed. SW-NE direction refers to the present-day position of reef deposits.

The reef-framework geometry, stratigraphic patterns and highest species richness indicate that reefs in Arroyo Ekieps formed a barrier, which probably enclosed the lagoon where the patch reefs of Arroyo de Uitpa and SW Ekieps sections developed.

The rudstones at the base of the Arroyo Ekieps section probably are forereef deposits derived from the destruction of barrier builders and downslope accumulation of their fragments together with skeletal particles of fore-reef inhabitants such as bivalves. This is suggested by the gradual upwards increase in coral-fragment size from the base of the rudstone to the overlying mixstone and by the occurrence of these rudstones at the lower part of prograding clinoforms. These grain-size and stratigraphic patterns are common in modern and Pleistocene Caribbean reefs (Ginsburg, 1956; Mesolella et al., 1970; James et al., 1977; James and Macintyre, 1985; Díaz de Neira et al., 2015).

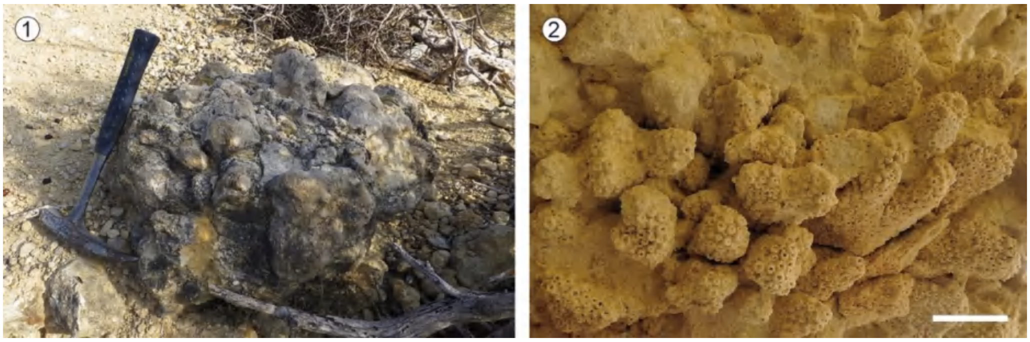

Figure 11. (1) Isolated massive colony of *Montastraea* sp. in the lagoon deposits in Arroyo Uitpa. Hammer is 28 cm long. (2) *Acropora panamensis* in a patch reef at SW Ekieps. Scale bar: 4 cm.

In general, the maintenance of shallow coral assemblages throughout the sections, the low-relief morphology of the reef bodies, as well as the lateral progradation in Arroyo Ekieps (Fig. 12.1) suggest they were keep-up reefs (sensu Newmann and Macintyre, 1985), growing in a stable relative sea level.

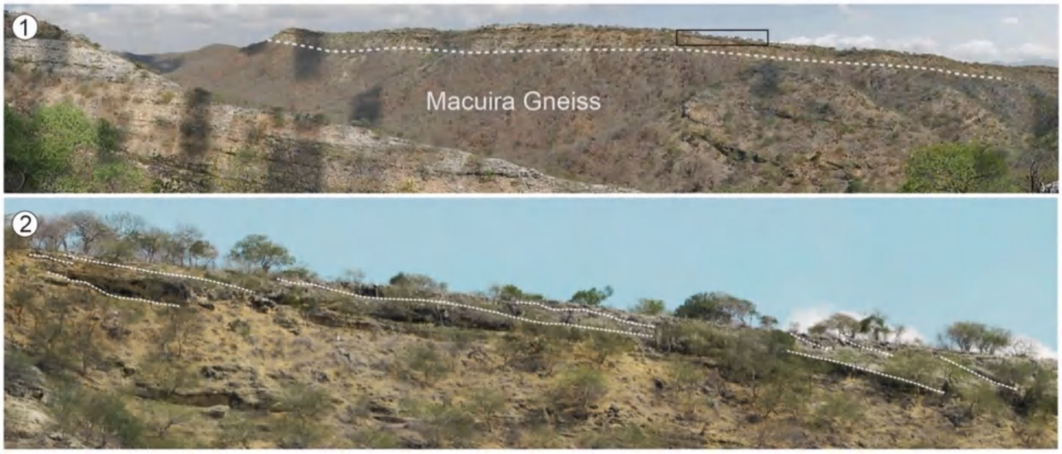

Figure 12. (1) Ekieps barrier reef on basement rocks. The inset area is zoomed in 2. (2) Reef progradation in Arroyo Ekieps. Photos by L. Pérez and C. Montes, GigaPan system.

A modern analogue of Siamaná reefs can be the reef complex of the Caribbean Providencia island, in which patch reefs in the lagoon are mainly composed of 2 species, which change according to wave exposure (Geister, 1992, p. 22). In the Providencia reef complex, while the fringing reefs are built by 4 species, species richness increases up to 14 in the seawards outer slope (Geister, 1992, p. 22, 24). In a similar way, in the Belize shelf, patch reefs in the lagoon have species richness from 1 to

10 (Burke, 1982; Rützler and Macintyre, 1982; Burke et al., 1998; McNeill et al., 2010), whereas the barrier is built by up to 24 species (Rützler and Macintyre, 1982, p. 18). The richness increases up to 42 species of scleractinian corals and 3 hydrozoans in the outer edge of the barrier (Cairns, 1982).

4. Corals

4.1 Systematic Paleontology of Corals

Published in the Journal of Paleontology, v. 93 (1), p. 1–24, and 93(3), p. 416–436. Authors Paola Flórez, Paula Zapata-Ramírez and James Klauss (Appendix 1 and 2).

Phylum Cnidaria Hatschek, 1888
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 13.1, 13.2; Table 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.

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.

Discussion.—*Acropora panamensis* could be easily confused with *A. saludensis*, 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*; e.g., 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, Montastraea canalis, Montastraea cavernosa* and *Colpophyllia willoughbiensis*, among others.

Acropora sp. indet.

Figure 13.3; Table 2

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, 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.

Discussion.—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.

Genus *Alveopora* Blainville, 1830

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

Alveopora tampae Weisbord, 1973

Figure 13.4–13.6; Table 2

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.

Discussion.—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*, *Millepora alcicornis*, *Porites anguillensis*, *P. portoricensis*, *Siderastrea siderea* and *Goniastrea canalis.*

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

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

Discussion.—*Agathiphyllia*, *Montastraea* and *Antiguastrea* show several similar external morphological characters, for which they are often confused, in particular when samples are poorly preserved by effects of diagenetic processes (Neil-Champagne, 2011). 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 than in *Agathiphyllia*, and the columella is also larger and usually trabecular to spongy (Frost and Langenheim, 1974; Neil-Champagne, 2001). The genus *Agathiphyllia* is globally extinct (Budd, 2000).

Agathiphyllia antiguensis (Duncan, 1863)
Figure 13.7–13.9; Table 2

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 1/4 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 1/3 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.

Discussion.—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 tenui*s (Duncan, 1863)

Figure 13.10–13.12; Table 2

1863 *Astraea tenuis* Duncan, p. 421, pl. 13, fig. 11.
1919 *Cyathomorpha tenuis*; Vaughan, p. 467, pl. 132, figs. 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 1/3 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.

Discussion.—*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.

Table 2. Species list and summary of the main characters used to identify taxa from the Siamaná and Jimol formations. Colony growth: B, branching; M, massive; D, dendroid; P, platy; K, knobby. CD: calicular diameter; (*dactilopore in *Millepora alcicornis*). ICD: Intercalicular distance. Coenosteum: Cos, costae present; Sp, spinose; Tb, tubercles; Sp, spongy; Sm, smooth. No. cycles: inc., incomplete. Kind of 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	
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	

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

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

Discussion.—Within the family Astrocoenidae, the specimens of *Astrocoenia* resemble species of *Madracis* recorded from the Caribbean Oligocene–Miocene (Annex 2), 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 14.1, 14.2; Table 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", Georgioa, 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 x 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 1/3–1/2 width of first cycle. Septal margin with beaded teeth, bearing series of 5–6 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.

Discussion.—Although the surface of samples is 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*, *Porites* spp., and *Montastraea* spp. in the Siamaná Formation.

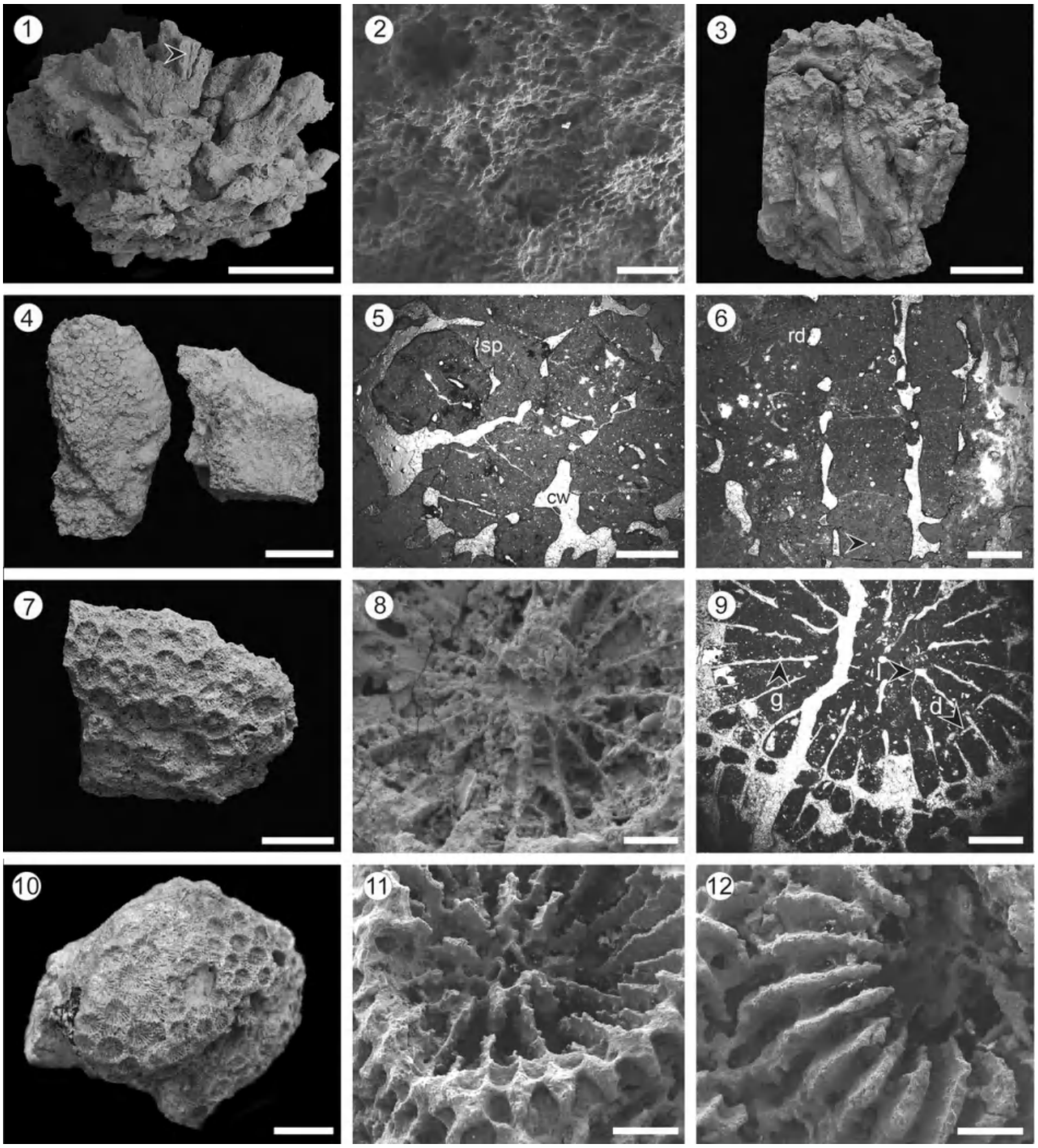

Figure 13. *Acropora panamensis* Vaughan, 1919: (1) morphology of the colony (MUN-STRI-17331), showing an axial corallite 1.4 cm in length (black arrow) cut laterally; (2) detail of the corallites, showing the septal arrangement and coenosteum reticulo-costate (MUN-STRI-17327). (3) Colony of *Acropora* sp. indet. (MUN-STRI-43531). *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). *Agathiphyllia antiguensis* (Duncan, 1863) (MUN-STRI-17309): (7) morphology of the colony; (8) detail of the corallites; (9) transverse thin section showing the endothecal dissepiments (d), septal granules (g) and paliform lobes (l). *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. Scale bars are (1, 7) 3 cm; (2, 8, 11, 12) 1 mm; (3) 4 cm; (4) 2 cm; (5) 800 µ; (6, 9) 600 µ; (10) 1 cm.

Astrocoenia portoricensis Vaughan, 1919

Figure 14.3, 14.4; Table 2

1901 *Astrocoenia ornata*; Vaughan [*in* Spencer], p. 497.

1919 *Astrocoenia portoricensis* Vaughan, p. 350, pl. 76, figs. 4, 4a, pl. 78, figs. 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 others 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.

Discussion.—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*, and *Porites* spp.

Astrocoenia sp. indet.

Figure 14.5, 14.6; Table 2

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.

Discussion.—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, as well as from *A. portoricensis* by the corallum morphology, which is massive in the sample reviewed. *Astrocoenia* sp. indet. occurs with *Antiguastrea cellulosa*, *Diploastrea magnifica* and *Porites waylandi.*

Family Caryophylliidae Dana, 1846

Caryophylliidae sp. indet.

Figure 14.7, 14.8; Table 2

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 one. 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 are 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.

Discussion.—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 the 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 14.9; Table 2

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, figs. 1, 1b, pl.137, figs. 1–5.
1919 *Diploastrea crassolamellata* var. *nugenti*; Vaughan, p. 477, pl. 138, figs.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 1/3 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.

Discussion.—*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 14.10, 14.11; Table 2

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* 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 1/3 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.

Discussion.—*Diploastrea crassolamellata* var. *magnifica* was described by Duncan (1863) and accepted by Vaughan (1919), based on a larger size of corallites, less exsert calices, as well as 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.*

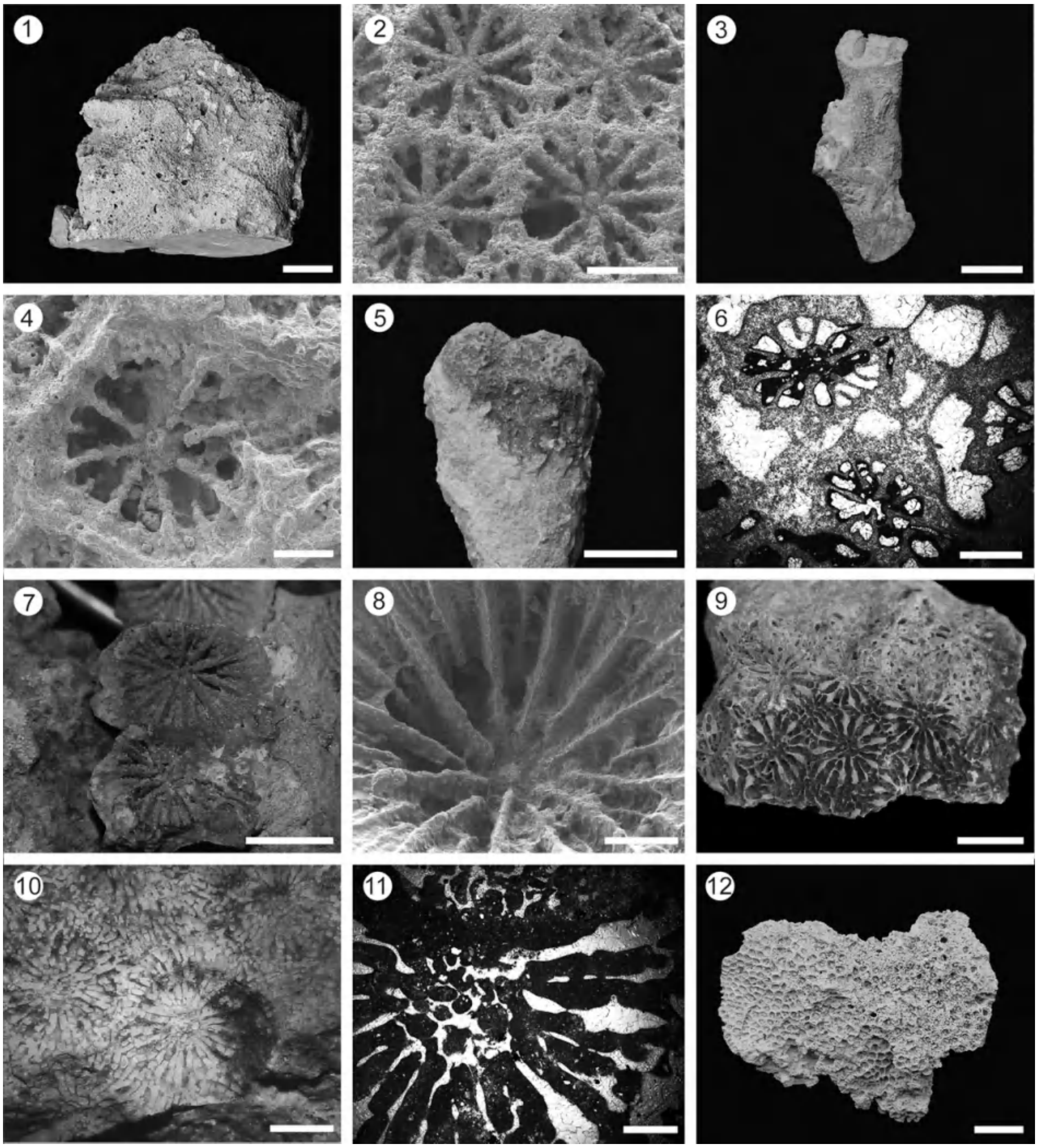

Figure 14. *Astrocoenia decaturensis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17294): (1) general view of the colony; (2) detail of the corallites. *Astrocoenia portoricensis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17311): (3) morphology of the colony; (4) detail of the corallites, septa and granules. *Astrocoenia* sp. indet. from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-43497): (5) morphology of the colony; (6) transverse thin section. Caryophylliidae sp. indet. from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-43528): (7) phaceloid corallites; (8) detail of the rudimentary columella, and septal granules. *Diploastrea crassolamellata* (Duncan, 1863) from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-17635): (9) detail of corallites. *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. *Antiguastrea cellulosa* (Duncan, 1863) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17224): (12) colony morphology. Scale bars are (1, 12) 2 cm; (2, 8) 1 mm; (3) 2.5 cm; (4) 0.5 mm; (5) 3.5 cm; (6, 11) 600 μ; (7) 4 mm; (9) 7 mm; (10) 5 mm.

Family Merulinidae Verrill, 1865

Genus *Antiguastrea* Vaughan, 1919

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

Antiguastrea cellulosa (Duncan, 1863)

Figures 14.12, 15.1; Table 2

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, figs. 2, 2a.
1919	*Antiguastrea cellulosa* var. *curvata*; Vaughan, p. 408, pl. 98, figs. 4, 4a.
1919	*Antiguastrea cellulosa* var. *silicensis* Vaughan, p. 408, pl. 101, figs. 1, 1a.
1929	*Antiguastrea cellulosa* var. *curvata*; Coryell and Ohlsen, p. 193, pl. 27, fig. 5.
1992	*Antiguastrea cellulosa*; Budd et al., p. 585, figs. 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.

Discussion.—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*.

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 15.2, 15.3; Table 2

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 and S2 reach the columella, depending upon development of S2, S3 half to 2/3 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 1/3 of calicular diameter.

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

Discussion.—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 15.4, 15.5; Table 2

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 extracalicular 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.

Discussion.—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, as well as the extension of secondary and tertiary septa, cannot be observed. However, the size and shape of raised corallites, development of the first septal cycle, as well as the 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 15.6, 15.7; Table 2

1863 *Phyllocoenia limbata* Duncan, p. 433.
1863 *Phyllocoenia sculpta* var. *tegula* Duncan, p. 432.
1864 *Plesiastraea ramea* Duncan, p. 39, pl. 5, figs. 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.

Discussion.—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).

Discussion.—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 Discussion under genus *Agathiphyllia*.

Montastraea canalis (Vaughan, 1919)
Figure 15.8, 15.9; Table 2

1919 *Orbicella canalis* Vaughan, p. 389, pl. 94, figs. 1, 1a, 3, 3a, not pl. 94, figs. 2, 2a, pl. 97, figs. 4, 4a.
1919 *Orbicella tampaensis* Vaughan, p. 390, pl. 95, figs. 1, 3, 3a, not pl. 95, figs. 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 1/3 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.

Discussion.—The *Monstastraea* species with four cycles in their septal arrangement show a high morphological similarity; however *M. canalis* can be differentiated from *M. endothecata* 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.*

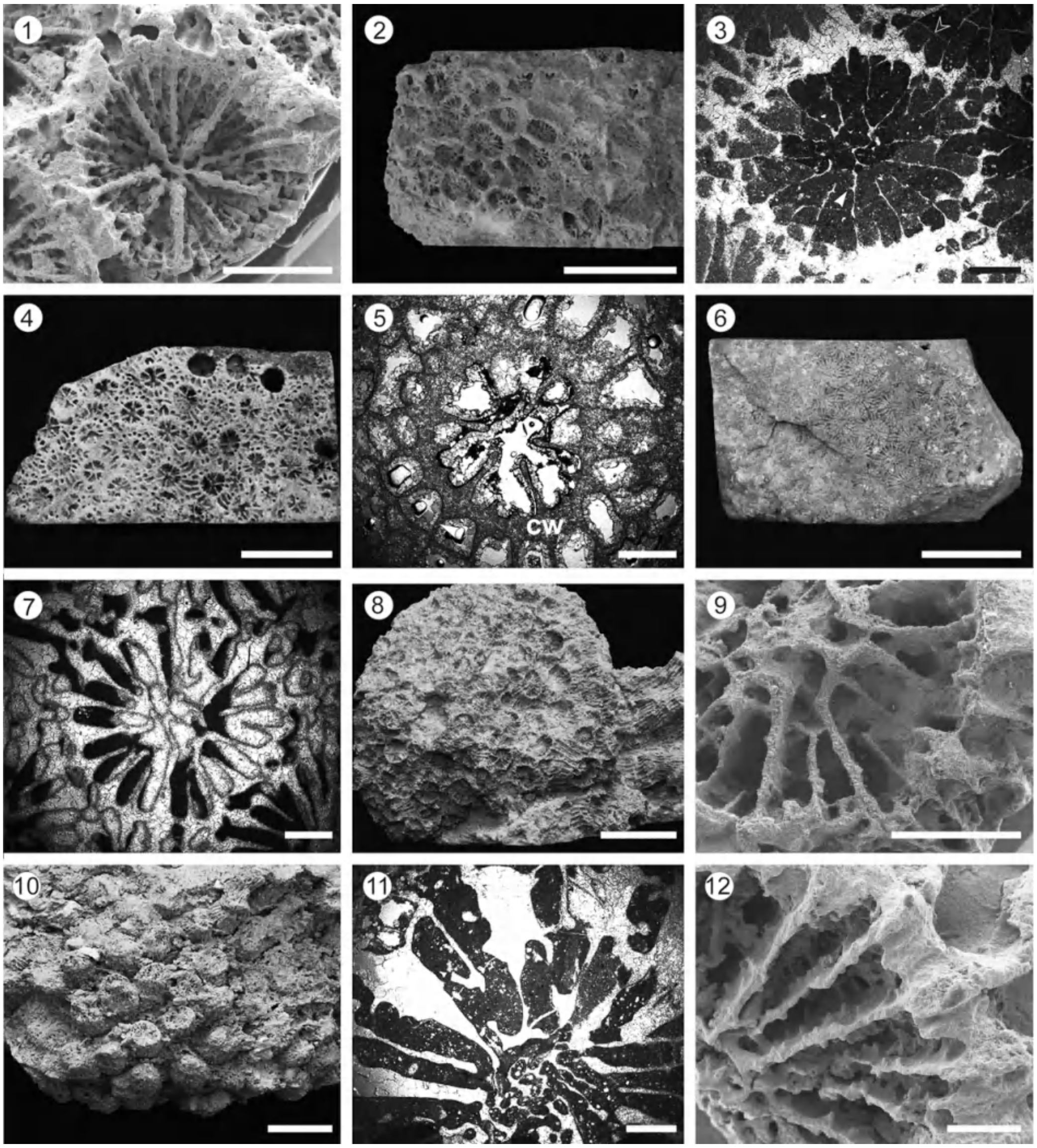

Figure 15. *Antiguastrea cellulosa* (Duncan, 1863) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17224): (1) detail of corallite. *Goniastrea canalis* Vaughan, 1919 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17332): (2) fragment of the colony; (3) transverse thin section, showing the septal arrangement, dissepiments (black arrow), and septal granules (white arrow). *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). *Orbicella limbata* (Duncan, 1863) from Siamaná Formation, Flor de La Guajria (MUN-STRI-17185): (6) colony; (7) transverse thin section showing the septal arrangement. *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. *Montastraea cavernosa* (Linnaeus, 1767) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17306): (10) morphology of the colony; (11) transverse thin section. *Montastraea endothecata* Duncan, 1863 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17225): (12) detail of the columella and septal granules. Scale bars are (1, 9) 2 mm; (3, 7, 11) 500 μ; (2, 4, 6) 1.5 cm; (5) 600 μ; (8, 10) 2 cm; (12) 1 mm.

Montastraea cavernosa (Linnaeus, 1767)

Figure 15.10, 15.11; Table 2

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, figs. 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, 1/4 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.

Discussion.—*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 15.12; Table 2

1863 *Astraea endothecata* Duncan, p. 434, pl. 14, fig. 9, pl. 15, figs. 7a, b.
1919 *Orbicella cavernosa* var. *endothecata*; Vaughan, p. 384, pl. 63, figs. 1, 1a.
1919 *Orbicella bainbridgensis* Vaughan, p. 386, pl. 90, figs. 1, 1a–c.
1919 *Cyathomorpha roxboroughi* Vaughan, p. 461, pl. 129, figs. 1, 1a, b.
1919 *Orbicella canalis* Vaughan, p. 389, pl. 94, figs. 2, 2a, pl. 97, figs. 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 (Setemann, 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 1/3 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.

Discussion.—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).

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 16.1, 16.2; Table 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, figs. 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.

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.

Discussion.—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 fringing and patch reefs. According to Frost and Langenheim (1974), specimens from different localities, from the same locality, and even in the same colony 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 16.3–16.5; Table 2

Occurrence.—Early Miocene in Jimol Formation, Colombia.

Description.—Corallum branching and plocoid. Branches are thick and flattened in shape, 2.8 cm in a minor diameter, until 9 cm great diameter. Corallites circular to oval, 1–2 mm in diameter, spaced 0.5–1.0 mm apart. Calices bear approximately 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 around 0.2 mm in diameter.

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

Discussion.—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* and *P. portoricensis*, which bear well developed verrucae, as well as from *P. arnoldi*, 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* and *Porites waylandi*.

Genus *Stylophora* Schweigger, 1819

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

Stylophora affinis Duncan, 1863

Figure 16.6–16.8; Table 2

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 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 (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 around 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.

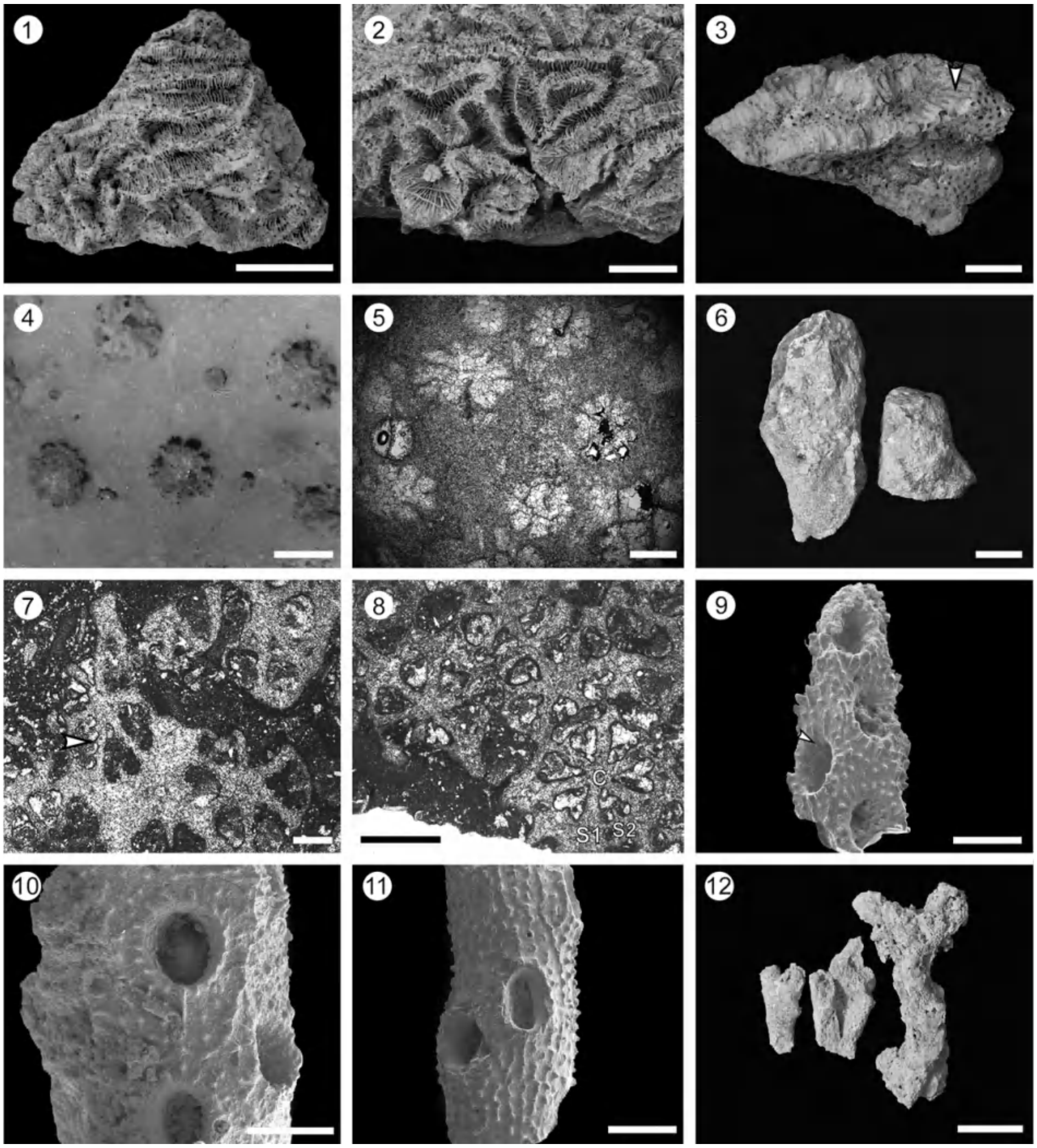

Figure 16. *Colpophyllia willoughbiensis* (Vaughan, 1919) from the Siamaná Formation, Arroyo Ekieps: (1) colony fragment (MUN-STRI-17310); (2) detail of the septa and sinuous valleys (MUN-STRI-17318). *Pocillopora* sp. indet. from the Jimol Formation, Punta Espada: (3) transversal view of the branch 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.

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.

Discussion.—Specimens of *Stylophora affinis* resemble *Stylophora imperatoris*, as 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* and *Diploastrea crassolamellata*.

Stylophora minor Duncan, 1863

Figure 16.9–16.11; Table 2

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 between 18 and 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.

Discussion.—Samples from the Siamaná Formation are branch fragments 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* shows a mostly smooth coenosteum and branches with blunt tips. In the Siamaná Formation *S. minor* occurs in a fringing reef with *Siderastrea conferta*, *Porites portoricensis*, *P. baracoaensis*, *Montastraea canalis*, *Agathiphyllia tenuis* and a member of the family Caryophylliidae.

Stylophora sp. indet.

Figure 16.12; Table 2

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 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.

Discussion.—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* 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 17.1–17.3; Table 2

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.

Discussion.—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 could 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.

Discussion.—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 was 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 17.4–17.6; Table 2

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).

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.

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.

Discussion.—*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*, *Agathiphyllia tenuis*, *Colpophyllia willoughbiensis*, *Porites waylandi*, *P. portoricensis*, *P. baracoaensis*, *Montastraea canalis*, *M. endothecata* and *Siderastrea conferta* in fringing reefs environments.

Porites baracoaensis Vaughan, 1919
Figure 17.7–17.9; Table 2

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 5 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.

Discussion.—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 fringing reefs with *Acropora panamensis*, *Antiguastrea cellulosa*, *Agathiphyllia tenuis*, *Colpophyllia willoughbiensis*, *Porites waylandi*, *P. portoricensis*, *P. anguillensis*, *Alveopora tampae*, *Montastraea canalis*, *M. cavernosa*, *Siderastrea siderea* and Caryophylliidae.

Porites portoricensis (Vaughan, 1919)

Figure 17.10–17.12; Table 2

non 1859 *Alveopora fenestrata*; Dana, p. 98.
1863 *Alveopora fenestrata*; Duncan, p. 437.
1919 *Goniopora portoricensis* Vaughan, 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.

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.

Discussion.—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 fringing and patch reefs with *Alveopora tampae, Antiguastrea cellulosa, Colpophyllia willoughbiensis, Montastraea endothecata, Porites waylandi, P. baracoaensis* and *P. anguillensis.*

Porites waylandi Foster, 1986

Figure 18.1, 18.2; Table 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-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.

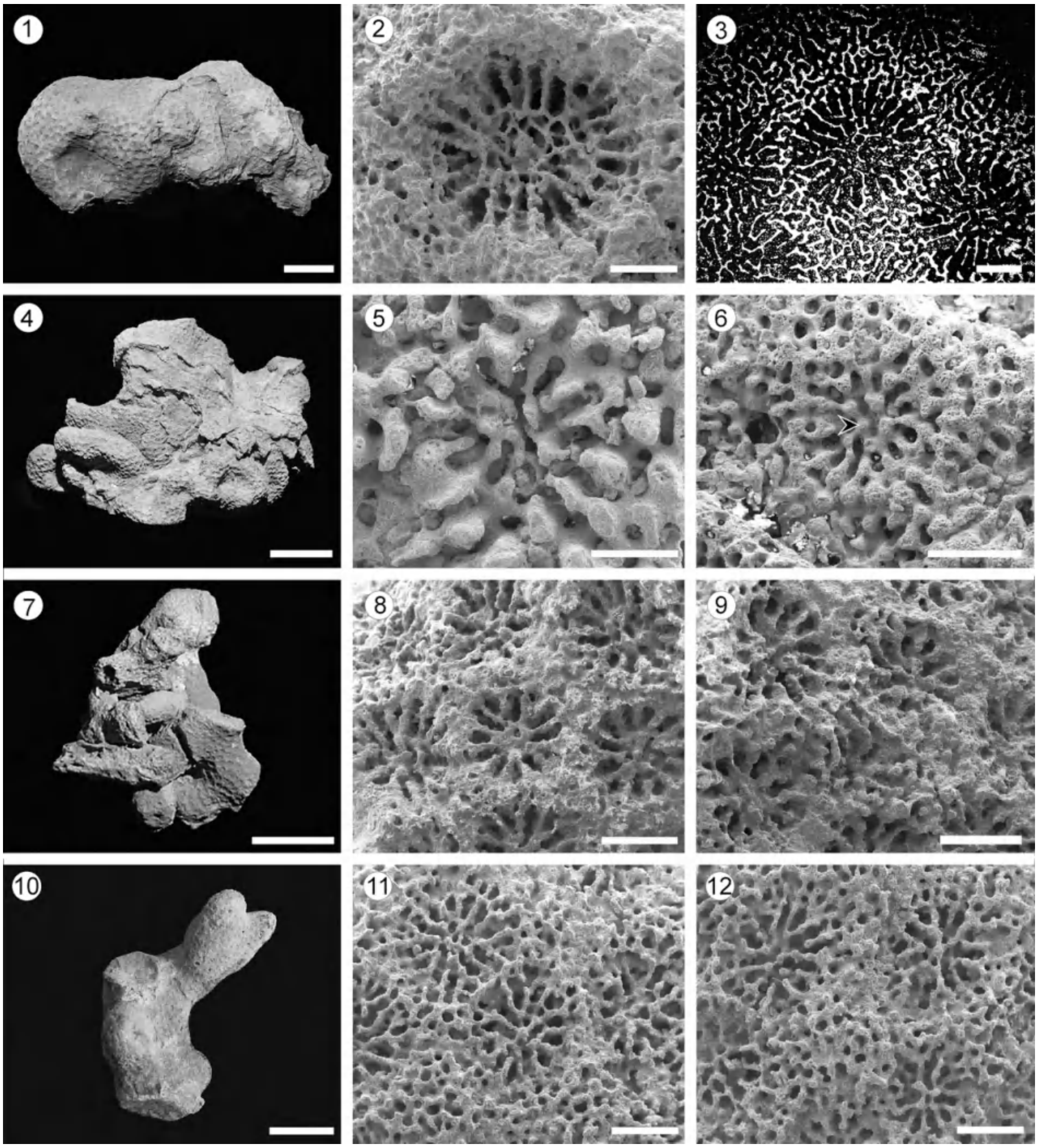

Figure 17. *Goniopora hilli* Vaughan, 1919 (MUN-STRI-43521): (1) morphology of the colony; (2) detail of a corallite, showing the septal arrangement and columella; (3) transverse thin section showing the denticles in the septal faces and calicular wall. *Porites anguillensis* Vaughan, 1919: (4) morphology 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.

Discussion.—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 fringing and patch reefs with *Antiguastrea cellulosa, Colpophyllia willoughbiensis, Diploastrea crassolamellata, D. magnifica, Porites anguillensis, P. portoricensis, Montastraea canalis, M. cavernosa* and *Orbicella limbata.* In the Jimol Formation it was found with *Orbicella imperatoris, Siderastrea siderea* and *Pocillopora* sp. indet.

Porites sp. indet.

Figure 18.3, 18.4; Table 2

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 to 2.0 mm in diameter, spaced 0.6 to 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.

Discussion.—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 18.5–18.7; Table 2

1863	*Isastrea conferta* Duncan, p. 25.
1919	*Siderastrea conferta*; Vaughan, p. 451, 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.

Discussion.—*Siderastrea conferta* could 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 fringing 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 18.8–18.10; Table 2

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.

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 penta- 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.

Discussion.—See Discussion 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 fringing 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 imperatori*s and *Porites* sp. indet.

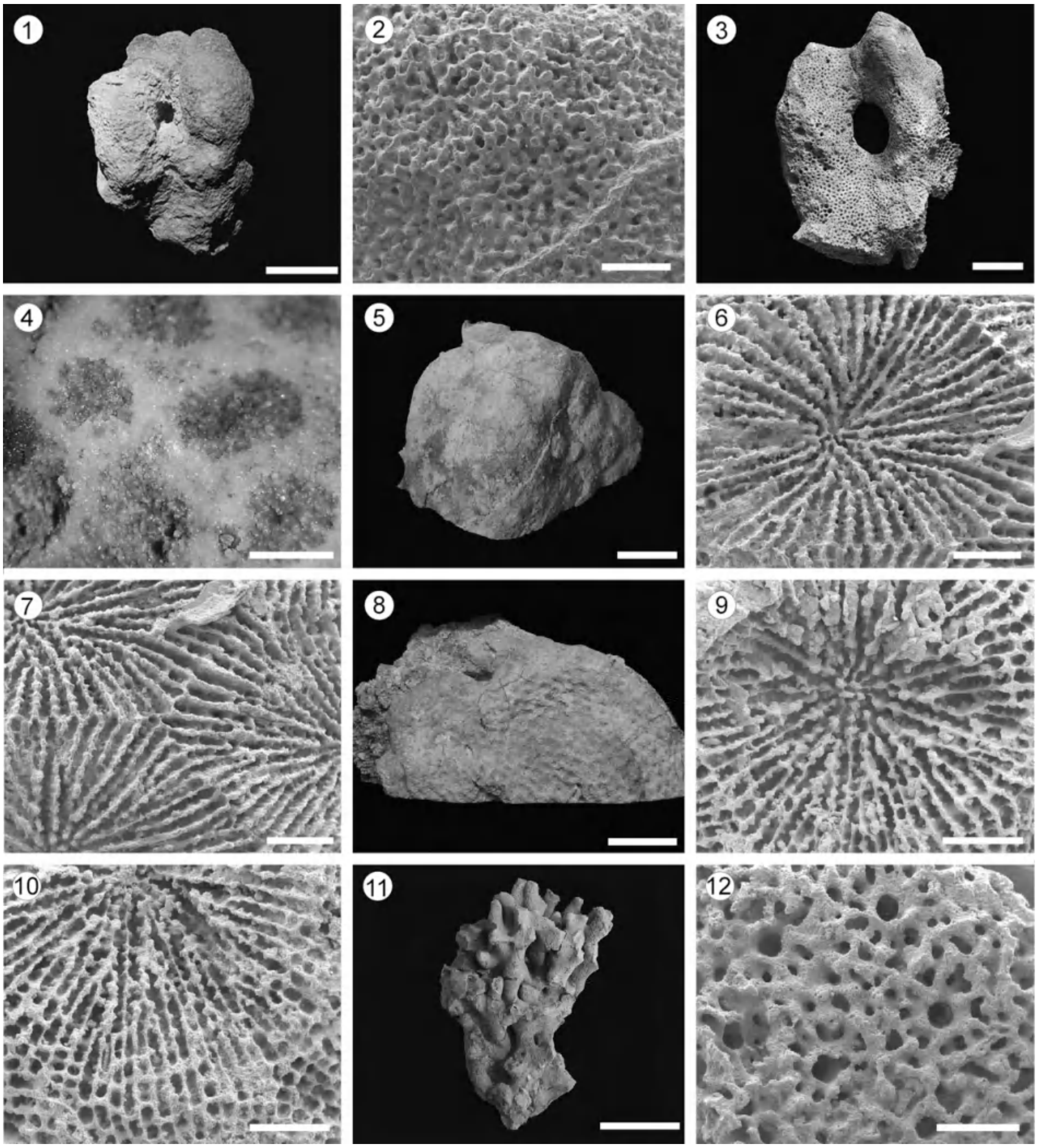

Figure 18. *Porites waylandi* Foster, 1986 from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-17222): (1) morphology of the colony; (2) detail of the corallites, showing the septal arrangement, columella, palar crown and calicular wall. *Porites* sp. indet. from the Jimol Formation, Punta Espada (MUN-STRI-17254): (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.

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 18.11, 18.12; Table 2

1758 *Millepora alcicornis* Linnaeus, p. 791.
1834 *Palmipora alcicornis*; Blainville, p. 391, pl. 58, fig. 2.
1948 *Millepora alcicornis*; Boschma, p. 18, 23, 79, 86, 100, 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) did not describe specimens of this genus, or record 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 to 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.

Discussion.—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* 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 fringing reefs with *Porites* spp.

4.2 Paleoecologic and paleobiogeographic significance of coral assemblages

A total of 272 lots of fossil corals were collected from the Siamaná (239 lots) and Jimol (33 lots) formations (Annex 3). The specimens were classified into two orders (Scleractinia and Anthoathecata), 12 families, 15 genera and 26 species. Of the total of 32 morphospecies, the 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, from 2 to 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).

Although, 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). 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.

Despite of the most species found in the Siamaná Formation 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.

From the Siamaná Formation (Aquitanian–Burdigalian), the Arroyo Ekieps locality exhibited the highest number of morphospecies (25) (Table 2). 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 (Annex 2), while *Alveopora tampae*, *Diploastrea magnifica*, *Montastraea cavernosa*, *Orbicella limbata*, *Porites anguillensis*, *Siderastrea siderea*, *Stylophora affinis*, *Stylophora minor* and *Millepora alcicorni*s 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 (Annex 2), and *Acropora panamensis*, *Astrocoenia decaturensis*, *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 (Annex 2). 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 first appeared in the Eocene and Oligocene (Fig. 19). Possible exceptions are *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. 19).

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. 19, box 1); nine persisted until the Pliocene and the Quaternary (Fig. 19, box 2); and the remaining three, the scleractinians *Montastraea cavernos*a and *Siderastrea siderea*, and the hydrocoral *Millepora alcicornis* (Fig. 19, 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 the 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 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.

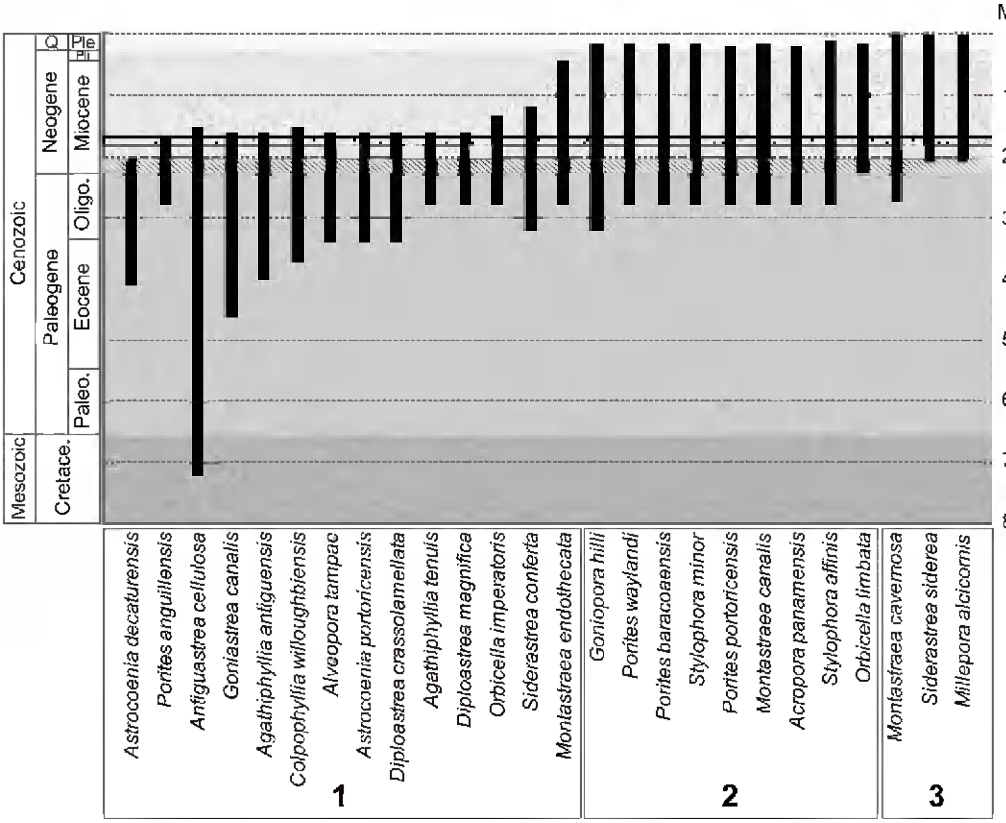

Figure 19. Range chart of first and last occurrence in the Greater Caribbean of species recorded in this study. The striped interval indicates the estimated stratigraphic range for the reef units studied in the Siamaná Formation, ca. 23–20.5 (Silva et al., 2017), and the dotted interval indicates the Jimol Formation, ca. 16.5–18 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 Annex 1.

5. Bryozoans

5.1 Systematic Paleontology of Bryozoans

Part of these results was submitted to the Journal of Paleontology, and a second part will be submitted at the same magazine. Authors Paola Flórez, Emanuela Di Martino and Lais Vieira Ramalho (Appendix 3).

Phylum Bryozoa Ehrenberg, 1831
Class Stenolaemata Borg, 1926
Order Cyclostomata Busk, 1852a
Suborder Tubuliporina Milne-Edwards, 1838
Family Entalophoridae Reuss, 1869
Genus *Mecynoecia* Canu, 1918

Type species.—*Entalophora proboscidea* Milne-Edwards, 1838 from the Mediterranean Sea, Recent; by original designation.

Mecynoecia sp. indet.
Figure 20.1, 20.2; Table 3

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony erect with branches circular in cross section, about 0.46 mm in diameter. Zooids cylindrical with openings arranged in somewhat alternating whorls all around the branch, zooidal boundaries marked by narrow, thread-like, grooves. Peristomes not preserved. Frontal surface smooth, undulose, covered by moderately spaced, rounded pseudopores. Axial lumen absents. Gonozooids not observed.

Table 3. Measurements of *Mecynoecia* sp. indet.

Character	X	R	SD	N
Autozooid width	0.15	0.15	0	3
Aperture diameter	-	0.13	-	1
Pseudopore diameter	0.01	0.01	0	10

Discussion.—Canu and Bassler (1920, p. 734) proposed using the genus *Entalophora* Lamouroux, 1821 to classify erect cyclostomes with cylindrical branches and zooids arranged in all directions and lacking gonozooids. However, Walter (1970) showed that species of the genus *Entalophora* were characterized by branches with a narrow axial lumen and subtriangular gonozooids. Based on the absence of the axial lumen, we place this poorly preserved, single branch fragment in *Mecynoecia* sp. indet. The lack of preserved gonozooids means that both genus- and species-level identification is problematic. *Mecynoecia* sp. indet. was found in the sediment cemented to the scleractinian coral *Goniopora hilli* Vaughan, 1919.

Family Oncousoeciidae Canu, 1918
Genus *Oncousoecia* Canu, 1918

Type species.—*Oncousoecia lobulata* Canu, 1918 from British Isles, Recent; by subsequent designation (Taylor and Zatoń, 2008).

?*Oncousoecia* sp. indet.
Figure 20.4, 20.5; Table 4

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting with large zooids, arranged in uni- to biserial alternating rows. Branches straight to slightly curved. Zooids tubular (mean L/W 1.66), little visible. Zooidal surface densely perforated by rounded pseudopores, sometimes with transverse striations. Peristomes rising almost perpendicularly to the zooidal surface with circular to oval apertures. Branch apparently bifurcated. Gonozooids not observed.

Discussion.—Based on the encrusting colony form with apparent bifurcation, autozooids relatively spaced arranged oligoserially and with circular apertures (Taylor and Zatoń, 2008), we tentatively attribute this specimen to *Oncousoecia*. The specimen from Siamaná Formation is an incomplete, poorly preserved colony. The broken peristomes and the absence of the gonozooid prevent further identification. *Oncousoecia* has a wide fossil record from the Early Jurassic to the Recent (Taylor and Zatoń, 2008). Five fossil species are known from North America: ?*Oncousoecia nonomologabili* Taylor and McKinney, 2006 and *O. khirar* Martha, Taylor and Rader, 2019 from the Cretaceous of New Jersey and Texas, respectively; *O. contortilis* (Lonsdale, 1845) and *O. bifurcata* (Ulrich and Bassler, 1907) from the Paleocene of New Jersey, and *O. quinqueseriata* Canu and Bassler, 1920 from the Oligocene of Alabama. In addition, three Recent species are also known: *O. abrupta* and *O. ovoidea* both described by Osburn (1953) from California, and *O. arcuata* Canu and Bassler, 1928 from Gulf of Mexico. Among them, *O. ovoidea*, *O. khirar* and ?*O. nonomologabili* differ from ?*Oncousoecia* sp. indet. in having fan-shaped colonies; *O. bifurcata* differs in having wider encrusting branches (1.2 mm vs. 0.66 mm), while *O. quinqueseriata* has narrower branches (0.5 mm), becomes erect, and has five longitudinal rows of autozooids. ?*Oncousoecia* sp. indet. resemble the astogenetic stages of both *O. contortilis* and *O. abrupta*, but differs from the former species in having branches slightly curved instead of contorted, and from the latter species in having wider branches (0.66 vs. 0.45 mm). Furthermore, it resembles *O. arcuata* in the shape of the branch and autozooid arrangement, but differs in having larger peristome diameter. ?*Oncousoecia* sp. indet. was found, along with the ascophoran-grade cheilostome bryozoan *Poricella* n. sp., encrusting a fragment of the scleractinian coral *Alveopora tampae* Weisbord, 1973.

Table 4. Measurements of ?*Oncousoecia* sp. indet.

Character	X	R	SD	N
Branch width	0.66	0.62–0.77	0.10	3
Autozooid length	0.78	0.67–0.9	0.12	4
Autozooid width	0.47	0.39–0.55	0.11	2
Aperture diameter	0.19	0.17–0.23	0.03	6
Pseudopore diameter	0.01	0.01	0.00	10

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852a
Superfamily Calloporoidea Norman, 1903
Family Calloporidae Norman, 1903
Genus *Copidozoum* Harmer, 1926

Type species.—*Membranipora plana* Hincks, 1880 from Australia, Recent; by original designation.

Copidozoum sp. indet.
Figure 20.5, 20.6; Table 5

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, unilaminar and multiserial. Zooids oval to irregular, distinct by deep grooves (mean L/W 1.49). Opesia occupying most of the frontal surface, same shape as the zooids. Gymnocyst reduced, visible only in some zooids proximally. Cryptocyst narrow, forming a thin and elevated mural rim. A single interzooidal avicularium observed, lozenge-shaped with narrow, rounded triangular rostrum, proximolaterally directed, seemingly with pivotal condyles. Spines absent. Ancestrula and ovicells not observed.

Discussion.—Based on the characters of the interzooidal avicularium and autozooids, we place this specimen in *Copidozoum*. Other species of *Copidozoum* recorded in Miocene American deposits include *C. parvirostris* (Canu and Bassler, 1923) and *C. tenuirostris* (Hincks, 1880). *Copidozoum* sp. indet. differs from these species in having a thicker mural rim, in the orientation of the avicularia, which is distal both in *C. parvirostris* (Di Martino et al., 2019, p. 14, fig. 12) and *C. tenuirostris* (Osburn, 1950, pl. 7, fig. 4). *Copidozoum* sp. indet. also resembles *Aplousina* Canu and Bassler, 1927, in the general appearance of the autozooids; however, *Aplousina* lacks avicularia (Canu and Bassler, 1927, p. 3). *Copidozoum* sp. indet. was found growing on the basal surface of the scleractinian coral *Colpophyllia willoughbiensis*, along with the microporid *Calpensia nobilis* and the phidoloporid *Rhynchozoon* sp.

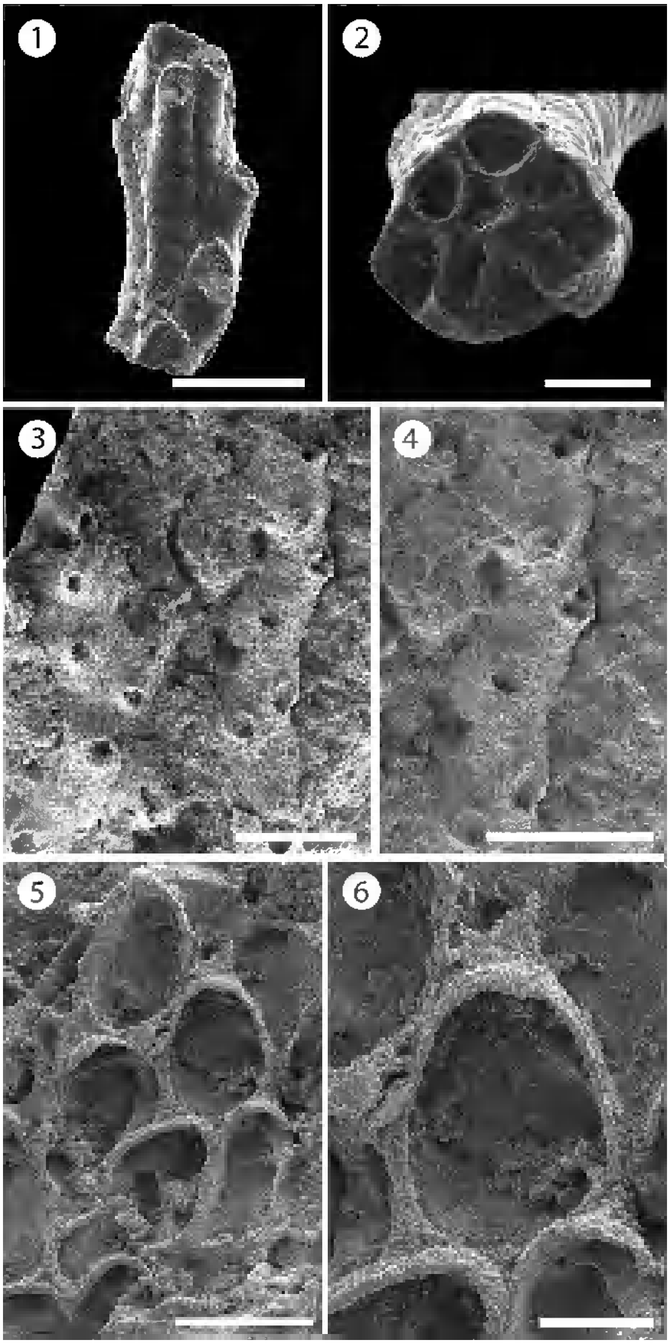

Figure 20. *Mecynoecia* sp. indet. (MUN-STRI-47623): **(1)** branch fragment; **(2)** view of the base of the branch fragment showing the absence of the lumen in cross-section; ?*Oncousoecia* sp. indet. (MUN-STRI-47625): **(3)** general view, **(4)** detail of the bifurcate branch; *Copidozoum* sp. indet. (MUN-STRI-47627): **(5)** general view of the colony, **(6)** detail of the zooid and avicularium. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are **(1, 5)** 0.5 mm;

(2, 6) 0.2 mm; **(3, 4)** 1 mm.

Table 5. Measurements of *Copidozoum* sp. indet.

Character	X	R	SD	N
Opesia length	0.49	0.46–0.55	0.04	4
Opesia width	0.28	0.19–0.34	0.08	3
Autozooid length	0.51	0.39–0.56	0.08	4
Autozooid width	0.34	0.25–0.4	0.08	3
Avicularium length	-	0.21	-	1
Avicularium width	-	0.08	-	1
Ooecium length	0.05	0.04–0.05	0.01	3
Ooecium width	0.2	0.2–0.2	0	3

Family Antroporidae Vigneaux, 1949
Genus *Antropora* Norman, 1903

Type species.—*Membranipora granulifera* Hincks, 1880 from Madeira, Recent; by subsequent designation (Tilbrook, 1998).

Antropora typica (Canu and Bassler, 1928)
Figure 21; Table 6

1926 *Antropora granulifera* Harmer, p. 232 (in part), pl. 14, figs. 12–14.
1928 *Dacryonella typica* Canu and Bassler, p. 57, pl. 5, figs. 4–8, pl. 32, figs. 11, 12, text figs. 8a, not the specimen from the Pliocene of Panama (USNM 70838).
1928 *Membrendoecium strictorostris* Canu and Bassler, p. 23, pl. 2, fig. 7.
1940 *Canua* (*Membrendoecium*) *strictorostris* Osburn, p. 358.
1967 *Antropora typica* Rucker, p. 817, fig. 12b.
1988 *Crassimarginatella cookae* Hayward, p. 277, figs. 2c–e.

Holotype.—USNM 7484, from North of Cuba, Caribbean, Recent.

Occurrence.—Early Miocene to Recent. Earliest occurrence is at Arroyo Uitpa, Colombia in the Siamaná Formation. Pleistocene of Venezuela in continental shelf sediments (Rucker, 1967). Recent occurrences in Cuba, Jamaica, Brazil, Malaysia, Mauritius and Japan (Winston, 1986; Tilbrook, 1998).

Description.—Colony encrusting, multiserial and unilaminar. Zooids distinct by deep grooves, oval to elliptical in shape (mean L/W 1.37), sometimes polygonal when the proximal gymnocystal area is more extensive. Opesia oval to subtriangular with rounded corners, occupying half to two-thirds of the frontal surface. Gymnocyst smooth, more developed proximally and surrounding the cryptocyst. Cryptocyst granular extended proximally, narrowing progressively laterally, tapering distally. Avicularia interzooidal, elliptical to drop-shaped with rounded rostrum, oriented distolaterally and arranged randomly within the colony, cross-bar not seen. Ovicells endozooidal. Intramural reparative budding common. Large vicarious avicularia not observed.

Discussion.—Although the single specimen analyzed has smaller autozooids than the holotype of *Antropora typica*, Canu and Bassler (1928) and Tilbrook (1998) noted that zooid size varies greatly within colonies and between geographic localities. Based on the extensive development of the gymnocyst, and the presence of the typical drop-shaped interzooidal avicularia, we attribute this specimen to *A. typica.* Canu and Bassler (1917, p. 17, 28) introduced the genera *Membrendoecium* and *Dacryonella* for some American fossil species; however, both genera have been regarded as junior synonyms of *Antropora* (Bassler, 1953; Tilbrook, 1998). Among species of American *Antropora*, the late Pliocene *Antropora parvicapitata* (Canu and Bassler, 1923) differs from *A. typica* in having small rounded kenozooids between the zooids and a single median tubercle in the proximal gymnocyst (Taylor and Foster, 1998, p. 66, figs. 5, 6; Di Martino et al., 2017, p. 108, figs. 8b–c). *Antropora lowei* (Canu and Bassler, 1920) from the Oligocene differs in having small, but frequent, indistinct "avicularia"; which in fact could be "interopesial cavities" between the zooids (Canu and Bassler, 1920, p. 121, pl. 81, fig. 1). *Antropora typica* was previously recorded in modern coral reef environments (Winston, 1986). In the Siamaná Formation, it was found growing on the rubble of *Porites sp.*, and co-existing with the bryozoans Steginoporellidae n. gen. n. sp., and ?*Hippomenella* sp.

Table 6. Measurements of *Antropora typica*.

Character	X	R	SD	N
Autozooid length	0.36	0.31–0.43	0.04	10
Autozooid width	0.26	0.25–0.28	0.01	12
Opesia length	0.15	0.13–0.16	0.01	14
Opesia width	0.12	0.11–0.13	0.01	10
Avicularium length	0.09	0.08–0.12	0.01	11
Avicularium width	0.05	0.05–0.05	0	10
Ooecium length	0.035	0.03–0.04	0.007	2
Ooecium width	0.16	0.15–0.17	0.014	2

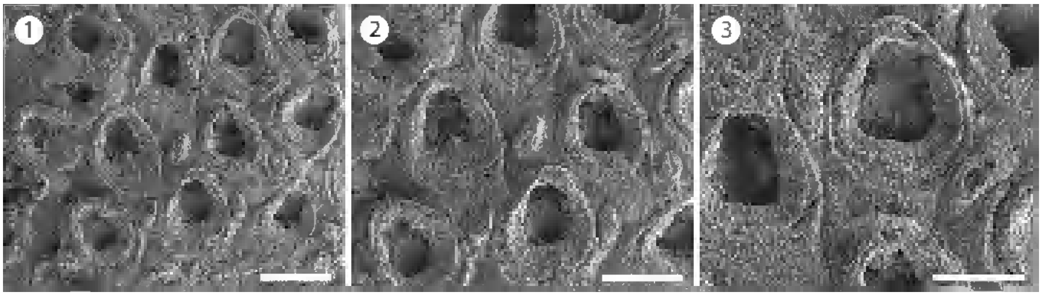

Figure 3. *Antropora typica* (Canu and Bassler, 1928) from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-47628): (1) general view (2) detail of the autozooids with intramural reparative budding, and drop shaped interzooidal avicularia (3) close-up of two autozooids and interzooidal avicularia. Scale bars are **(1)** 0.25 mm; **(2)** 0.2 mm; **(3)** 0.15 mm.

Family Quadricellariidae Gordon, 1984
Genus *Nellia* Busk, 1852b

Type species.—*Cellaria tenella* (Lamarck, 1816) from Austral seas?, Recent; by subsequent designation (Busk, 1852b).

Nellia tenella (Lamarck, 1816)
Figure 22.1–22.3; Table 7

1816	*Cellaria tenella* Lamarck, p. 135.
1851	*Cellaria quadrilatera* d'Orbigny, p. 29.
1852b	*Nellia oculata* Busk, p. 18, pl. 64, fig. 6, pl. 65, fig. 4.
1920	*Nellia oculata*; Canu and Bassler, p. 196, pl. 82, figs. 6–10.
1966	*Nellia tenella*; Cheetham, p. 48, text fig. 28.
1984	*Nellia tenella*; Winston and Cheetham, p. 257, figs. 1–2.
2017	*Nellia tenella*; Di Martino et al., p. 109, fig. 9.
2019	*Nellia tenella*; Ramalho et al., p. 111, figs. 2a–c.

Lectotype.—NHMUK 1854.11.15.256, from Australia, Recent.

Occurrence.—Late Cretaceous to Recent. The oldest record is from the Maastrichtian of Jamaica (Cheetham, 1968). Eocene Crystal River Formation, Florida, USA and Oligocene Chickasawhay Formation, Alabama, USA (Winston and Cheetham, 1984). Early Miocene Pirabas Formation, Pará State, Brazil (Ramalho et al., 2019) and Arroyo Ekieps, Siamaná Formation, Colombia. Late Miocene Cercado Formation, Dominican Republic (Winston and Cheetham, 1984). Recent, widespread in tropical and warm-temperate waters (Cheetham, 1966).

Description.—Colony erect, articulated. Branches narrow, quadriserial, squared in cross-section. Zooids arranged in four longitudinal rows, in alternate position with the lateral neighbors. Zooids distinct, delimited by a slender groove, all similar in size, elongate and sub-rectangular in shape. Opesia sub-rectangular, occupying most of the frontal surface. Gymnocyst smooth, extended proximally and reduced laterally and distally. Mural rim slightly raised. Two small, elliptical avicularia placed in the proximal corners of the gymnocyst of each zooid, with a circular rootlet pore below the raised rostrum. Autozooids located at the tip of the internode tapering proximally. Ooecium and cryptocyst not observed.

Other material examined.—*Nellia tenella* (syntype) MNHN IB-2008-4546.

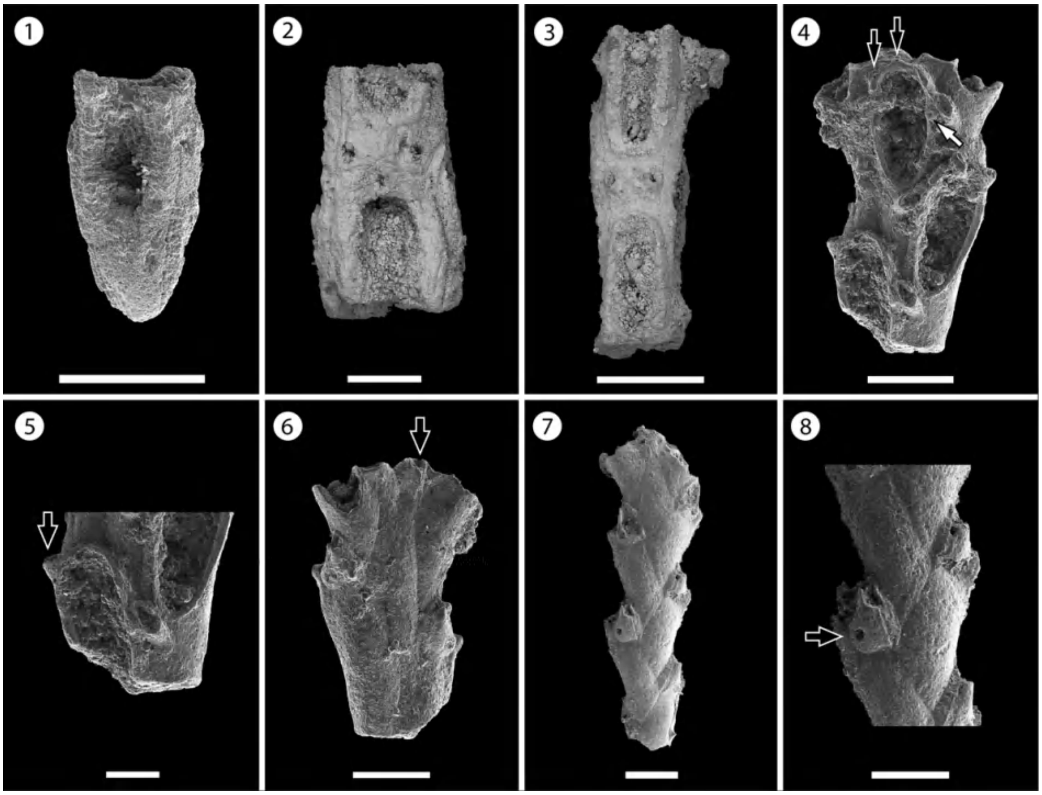

Figure 22. *Nellia tenella* (Lamarck, 1816) (MUN-STRI-47630): (1) part of a tapering zooid at the tip of the branch, (2) paired elliptical avicularia, (3) branch fragment with incomplete zooids; *Licornia* sp. indet. (MUN-STRI-47632): (4) frontal view of the branch at bifurcation showing the joint point cross, two distal spine bases (black arrows), and the insertion of the scutum (white arrow), (5) frontal view of the branch with the lateral (arrowed) and frontal avicularia, (6) abfrontal view of the branch at bifurcation showing the single axial vibraculum (arrowed); (MUN-STRI-47633): (7) abfrontal view of a branch fragment showing the vibracular chambers, (8) detail of the vibracular chamber showing the straight setal groove and the rhizoidal pore (black arrow). All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are (1, 3, 4, 6) 0.2 mm; (2, 8) 1 mm; (5) 0.1 mm; (7) 0.25 mm.

Discussion.—The internode fragments available in our material are poorly preserved. However, *Nellia tenella* is distinguishable by the characteristic arrangement and shape of the autozooids and avicularia. The specimens from the Siamaná Formation resemble those from the Miocene of the Dominican Republic figured by Winston and Cheetham (1984, fig. 2D). However, the size of the opesia of the analyzed fragments is smaller than that of the Dominican specimens, as well as the syntype, and other specimens from different regions and ages (Cheetham, 1963, 1966; Winston et al., 2014; Di Martino et al., 2017). A statistical analysis performed by Winston and Cheetham (1984, p. 260) on specimens ranging from the Late Cretaceous to the Recent suggested that the variation in size is, however, not significant. *Nellia tenella*, which is considered a living fossil among bryozoans, is also very common in the Miocene, with a circumtropical to subtropical distribution in shelf sediments, but also present in deep and cold waters (Rucker, 1967; Flórez et al., 2007), as well as on Recent coral reefs (Winston, 1986). In the

Siamaná Formation, *N. tenella* was found in the sediment cemented to the scleractinian coral *Goniopora hilli*, co-occurring with the bryozoan *Poricellaria* sp., *Margaretta* sp. (as also observed in other fossil localities and environments by Winston and Cheetham, 1984), *Ditaxiporina* n. sp. and *Mecynoecia* sp.

Table 7. Measurements of *Nellia tenella*.

Character	X	R	SD	N
Autozooid width	0.14	0.12–0.16	0.016	4
Opesia width	0.07	0.06–0.08	0.009	5
Avicularium length	0.05	0.04–0.06	0.008	4
Avicularium width	0.04	0.03–0.04	0.005	4

Superfamily Buguloidea Gray, 1848
Family Candidae d'Orbigny, 1851
Genus *Licornia* van Beneden, 1850

Type species.—*Acamarchis jollaisii* Audouin, 1826 from Red Sea, Recent; by original designation.

Licornia sp. indet.
Figure 22.4–22.8, Table 8

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony erect, articulated. Branches flat, elliptical in cross-section. Zooids distinct, biserial, alternately arranged, sub-rectangular in shape (mean L/W 2.97). Opesia wide, oval, with a raised mural rim, occupying two-thirds of the frontal surface. ?Two distal spine bases. Base of the scutum arising from the distal third of the inner side of the opesia, next to the frontal avicularia of the adjacent zooid. Gymnocyst smooth, developed proximally, tapering laterally and distally around the opesia. Avicularia adventitious, frontal and lateral; frontal avicularia placed proximally immediately below the rim of the opesia, monomorphic, frequent, with a proximally raised, rounded rostrum, proximolaterally directed towards the exterior; lateral avicularia smaller than frontal avicularia, located on the outer distal corner of each autozooid, triangular. Abfrontal surface smooth. Vibracular chamber trapezoidal with rhizoidal pore and straight setal groove, directed obliquely to the internodal axis, occupying two-thirds of the length of the vibracular chamber. Joints crossing the proximal opesia of the outer zooids and below the opesia of the inner zooids at the bifurcation. Single axial vibraculum, with straight setal groove and lacking a rhizoidal pore. Ooecium not observed. Scutum and spines not preserved.

Discussion.—We place the specimens analyzed in the genus *Licornia* based on the position of the joint crossings, the straight rostrum of the lateral avicularia, the oblique setal groove of the vibracular chambers and the single axial vibraculum. The closest allied genus, *Paralicornia* Vieira et al., 2014, differs in having an opesia occupying only half of the total length of the zooids and a shorter setal groove. North American Cenozoic species of *Licornia* include Canu and Bassler's (1920) *L. cookei*, *L. milneri*, and *L. resseri*, all known from the Oligocene. *Licornia* sp. indet. differs from these species in the morphology and size of the frontal and lateral avicularia: *L. cookei* has rounded lateral avicularia, *L. milneri* has very large and acuminate frontal avicularia, and *L. resseri* has very large lateral avicularia. *Licornia regularis* (Osburn, 1940), known in the Caribbean region from the Pleistocene to Recent, differs in having larger vibracular chambers reaching half of the total length of the zooids, frontal avicularia with triangular rostrum, lateral avicularia with serrated rostrum, and squatter zooids (Winston, 2005, p. 27, figs. 63–68). Other Recent Tropical Western Atlantic species, such as *L. drachi* (Marcus, 1955) and *L. micheli* (Marcus, 1955), differ from *Licornia* sp. indet. in having larger opesia that covers almost the whole frontal surface of the zooids, and lateral avicularia of variable size, sometimes as long as the opesia. The scarcity of material, as well as the absence of diagnostic features such as ooecia, spines and scuta, prevent species-level identification. In the Siamaná Formation, the fragments of *Licornia* sp. indet. were found in the sediment cemented to the coral *Acropora panamensis* Vaughan, 1919, co-occurring with other erect bryozoans including *Ditaxiporina colombiana* n. sp., *Catenicella* sp., and *Margaretta* sp.

Table 8. Measurements of *Licornia* sp. indet.

Character	X	R	SD	N
Autozooid length	0.50	0.47–0.52	0.026	3
Autozooid width	0.17	0.16–0.2	0.016	6
Opesia length	0.27	0.26–0.28	0.012	3
Opesia width	0.11	0.1–0.11	0.006	4
Avicularium frontal length	0.07	0.07	0.000	3
Avicularium frontal width	0.04	0.03–0.05	0.008	4
Avicularium lateral length	0.05	0.04–0.05	0.007	2
Avicularium lateral width	0.02	0.02–0.03	0.006	3
Vibracular chamber length	0.17	0.14–0.2	0.019	10
Rhizoidal pore diameter	0.03	0.03	0.000	6

Superfamily Microporoidea Gray, 1848

Family Microporidae Gray, 1848

Genus *Calpensia* Jullien, 1888

Type species.—*Membranipora calpensis* Busk, 1854 from Mediterranean Sea, Recent; by original designation.

Calpensia nobilis (Esper, 1797)

Figure 23.1–23.3; Table 9

1797	*Cellepora nobilis* Esper, p. 145, pl. 7, figs. 1–3.
1803	*Eschara impressa* Moll, p. 51, pl. 2, figs. 9a–i.

1848 *Eschara nobilis*; Michelin, p. 329, p. 79, fig. l.
1907 *Micropora impressa*; Norman, p. 207, pl. 9, figs. 1–3.
1923 *Calpensia impressa*; Canu and Bassler, p. 83, pl. 1, fig. 4.
1930 *Calpensia impressa*; Canu and Bassler, p. 26, pl. 1, figs. 13–16.
1957 *Calpensia nobilis*; Buge, p. 174.

Holotype. – Unknown.

Occurrence.—Late Oligocene to Recent. Earliest occurrences in Antigua Formation, Antigua and Barbuda (Canu and Bassler, 1923). Early Miocene at Arroyo Ekieps, Colombia in the Siamaná Formation. Middle Miocene of Hungary (Moissette et al., 2007), Marmarica Formation, Egypt (Ziko et al., 2000), Italy and Algeria (Moissette, 1988). Pliocene of Greece and Italy (Pouyet and Moissette, 1992) and Tunis (Moissette, 1988). Pleistocene of Greece (Moissette et al., 2010). Recent occurrences in the Mediterranean Sea and east Atlantic (Madeira), Gulf of Biscay and southern England in the Channel Islands (Canu and Bassler, 1930; Buge, 1957; Pouyet and Moissette, 1992; Hayward and Ryland, 1998).

Description.—Colony encrusting, multiserial, unilaminar. Zooids distinct with a raised mural rim, elongate and sub-rectangular in shape (mean L/W 1.58), widening at about mid-length and arranged in alternating, longitudinal rows. Orifice terminal, semicircular with a straight proximal margin; peristome slightly developed. Frontal wall flat proximally, depressed in correspondence of the opesiular area at about two-thirds of zooidal length, and raised distally. Cryptocyst granular, densely perforated, except in the area surrounding the opesia and between the opesia and the opesiules; pseudopores circular, about 5 µm in diameter. Mural rim raised and crenulated. Two elliptical opesiules, longer than wide, equal in size, located proximolaterally at about two-thirds of zooidal length, about 0.14 mm below the opesia. Ovicells and avicularia absent.

Table 9. Measurements of *Calpensia nobilis*.

Character	X	R	SD	N
Autozooid length	0.67	0.62–0.75	0.046	11
Autozooid width	0.43	0.38–0.49	0.034	16
Orifice length	0.09	0.08–0.1	0.006	10
Orifice width	0.15	0.14–0.18	0.011	13
Opesiule length	0.08	0.05–0.11	0.02	11
Opesiule width	0.05	0.04–0.06	0	11

Discussion.—The specimens of *Calpensia nobilis* found in the Siamaná Formation are similar in morphology and size to those described by Canu and Bassler (1930) from Recent Mediterranean samples. In the Siamaná Formation, *C. nobilis* was found encrusting coralline algae covering the coral *Alveopora tampae* and on the basal surface of the coral *Colpophyllia willoughbiensis* (Vaughan, 1919), while small detached fragments were scattered in the sediment associated with *Goniopora hilli*. In our material, *Calpensia nobilis* co-occurs with *Copidozoum* sp., *Gemelliporidra* sp., and *Rhynchozoon* sp.

Family Onychocellidae Jullien, 1882

Onychocellidae new genus

Type species.—Onychocellidae n. gen. sp., from Arroyo Ekieps, Colombia, early Miocene, Siamaná Formation.

Diagnosis.—Colony encrusting, multiserial. Zooids distinct, defined by a raised thread distally and a deep groove proximally and laterally. Opesia terminal, occupying one-third of the total length of the zooid; opesiular indentations present. Cryptocyst extensive, granular, flat to slightly convex. Gymnocyst absent. Putative vicarious avicularia present, opesia poorly preserved. Ovicells unknown.

Discussion.—We place Onychocellidae n. gen. in the family Onychocellidae because of its extensive cryptocyst, the bell-shaped opesia with opesiular identations, and the absence of a gymnocyst, spines, and visible ovicells (Taylor et al., 2018). Onychocellidae n. gen. resembles in general appearance the genus *Steraechmella* Lagaaij, 1952 belonging to the family Microporidae Gray, 1848, which is commonly allied with Onychocellidae (Taylor et al., 2018). It differs in having wider opesia and, and as from remaining genera of this family, in lacking a raised mural rim. The poor preservation of the single specimen available prevents a detailed description of the morphology of the putative vicarious avicularia (i.e. opesia and rostrum), which could alternatively be narrower autozooids placed at row bifurcations where two regular zooids sometimes occupy the same width of the one preceding them in the row. However, studies carried out by Cook (1968) on the Recent genus *Crassimarginatella* Canu, 1900, and by Cheetham et al. (2006) in the fossil genus *Wilbertopora* Cheetham, 1954 suggest that the morphology of avicularia is variable, some involving only slight modifications of the autozooids. In some onychocellids, e.g., *Euritina* Canu, 1900, interzooidal avicularia are similar to autozooids, although smaller (Taylor et al., 2018, p. 1676, fig. 10).

Onychocellidae new species

Figure 23.4–23.6; Table 10

Holotype.—MUN-STRI-47637, from the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting, multiserial, uni- to multilaminar. Zooids rhomboidal to elliptical, defined by a thread distally and a deep groove proximolaterally. Opesia terminal, triangular to bell-shaped, as long as wide, occupying one-third of the frontal surface; opesiular indentations shallow; proximal edge projected, straight to slightly curved. Cryptocyst extensive, granular, flat to slightly convex. Putative vicarious avicularia, narrower than regular zooids; rounded triangular, commonly located at row bifurcations; opesia poorly preserved. Ovicells unknown.

Description.—Colony encrusting, multiserial, uni- to multilaminar. Early astogenetic stages apparently fan-shaped. Zooids distinct, elongate, rhomboidal to elliptical (mean L/W 1.74), separated distally by a thread, commonly not preserved, and a fine and deep groove proximo-laterally. Opesia terminal, wide, triangular to bell-shaped, as long as wide; borders raised, a furrow forming between the distal opesia margin and the distal thread; opesiular indentations located at the proximolateral corners, slightly constricted laterally, proximal edge projecting distally with straight to slightly convex margin. Cryptocyst granular, occupying two-thirds of the frontal surface, flat to slightly convex, narrow laterally to the opesia. Putative vicarious avicularia narrower and slightly shorter than ordinary feeding zooids, rounded triangular, commonly located at longitudinal row bifurcations; opesia poorly preserved, ?oval, occupying more than half of the frontal surface, rostrum extended but broken observed in only two avicularia, probably rounded (Fig. 23.4). Ovicells not observed.

Discussion.—The single colony found in the Siamaná Formation is poorly preserved, with clear signs of cryptocyst dissolution. The raised distal borders may have originally extended around the entire zooidal outline or, conversely, dissolution may have occurred, giving the false impression that the frontal wall was depressed, as occurs in some bimineralic species. Onychocellidae n. gen. n. sp. resembles species of *Aechmella* Canu and Bassler, 1917 and *Aechmellina* Taylor, Marta and Gordon, 2018. *Aechmella* differs in having smaller interzooidal avicularia, about half the width of the zooids with acutely triangular rostrum, while *Aechmellina* differs in having frequent, small interzooidal avicularia with a pointed rostrum. The new genus and species also resembles *Floridinella vicksburgica* Canu and Bassler, 1917 in having a wide opesia, but differs in having kenozooids and avicularia with triangular rostrum oriented laterally (Cook and Bock, 2001, p. 547). In the Siamaná Formation, Onychocellidae n. sp. was found encrusting a mollusk shell, sharing the substrate with '*Lepralina*' sp. indet. and a poorly preserved cyclostome.

Table 10. Measurements of Onychocellidae n. gen. n. sp.

Character	X	R	SD	N
Autozooid length	0.74	0.57–0.93	0.095	19
Autozooid width	0.43	0.31–0.83	0.125	17
Opesia length	0.22	0.16–0.28	0.029	15
Opesia width	0.20	0.17–0.23	0.020	11
Interzooidal avicularium length	0.63	0.49–0.72	0.081	11
Interzooidal avicularium width	0.32	0.26–0.4	0.045	10
Avicularian opesia length	0.37	0.35–0.38	0.017	3
Avicularian opesia width	0.23	0.22–0.24	0.012	3

Genus *Smittipora* Jullien, 1882

Type species.—Vincularia abyssicola Smitt, 1873 from Cuba and Florida, USA, Recent; by original designation.

Smittipora elongata (Canu and Bassler, 1923)

Figure 23.7–23.9; Table 11

1923 *Velumella elongata* Canu and Bassler, p. 58, pl. 14, fig. 5.

Holotype. – USNM 68479, from Duplin marl, North Carolina, USA. Miocene.

Occurrence.—Miocene. Early Miocene, Siamaná Formation, Arroyo Uitpa, Colombia. Late Miocene, Duplin Marl, North Carolina, USA (Canu and Bassler, 1923).

Description.—Colony encrusting, multiserial, unilaminar. Zooids defined by a raised rim, sub-hexagonal, rounded distally (mean L/W 1.32). Opesia subterminal, bell-shaped, with proximolateral indentations outlining a tongue-like process medially, occupying half to one-third of the total length of the zooid. Cryptocyst extensive, depressed, flat, and coarsely granular. Vicarious avicularia symmetrical, similar in length to autozooids but about half of their width, rounded rhomboidal; opesia reversed pear-shaped; cryptocyst granular. Ovicells immersed.

Table 11. Measurements of *Smittipora elongata*.

Character	X	R	SD	N
Autozooid length	0.57	0.5–0.65	0.035	17
Autozooid width	0.43	0.36–0.51	0.049	18
Opesia length	0.21	0.18–0.25	0.021	7
Opesia width	0.23	0.2–0.26	0.022	13
Interzooidal avicularium length	0.53	0.51–0.55	0.028	2
Interzooidal avicularia width	0.28	0.25–0.31	0.030	3
Avicularian opesia length	-	0.3	-	1
Avicularian opesia width	-	0.16	-	1

Discussion.—We identify the specimen from the Siamaná Formation as *Smittipora elongata* because of the symmetrical and rounded rostrum of its avicularia. Three other species of *Smittipora* have been previously described from the North American Oligocene: *S. fusiformis* (Canu and Bassler, 1917), *S. lineata* (Canu and Bassler, 1920) and *S. tenuis* (Canu and Bassler, 1920), but all differ from *S. elongata* in having exclusively fusiform avicularia. Our sample also resembles the Cretaceous species *Reptolunulites zipfi* Taylor and McKinney, 2006 in having a bell-shaped opesia and symmetrical vicarious avicularia, but it differs in having a longer rostrum, and in the proportion between the length of the opesia and the length of the zooid, which is higher. In the Siamaná Formation, *S. elongata* was found encrusting coralline algae covering the coral

Porites sp., co-occurring with the ascophoran-grade cheilostome ?*Hippopleurifera* sp. and an undetermined cheilostome.

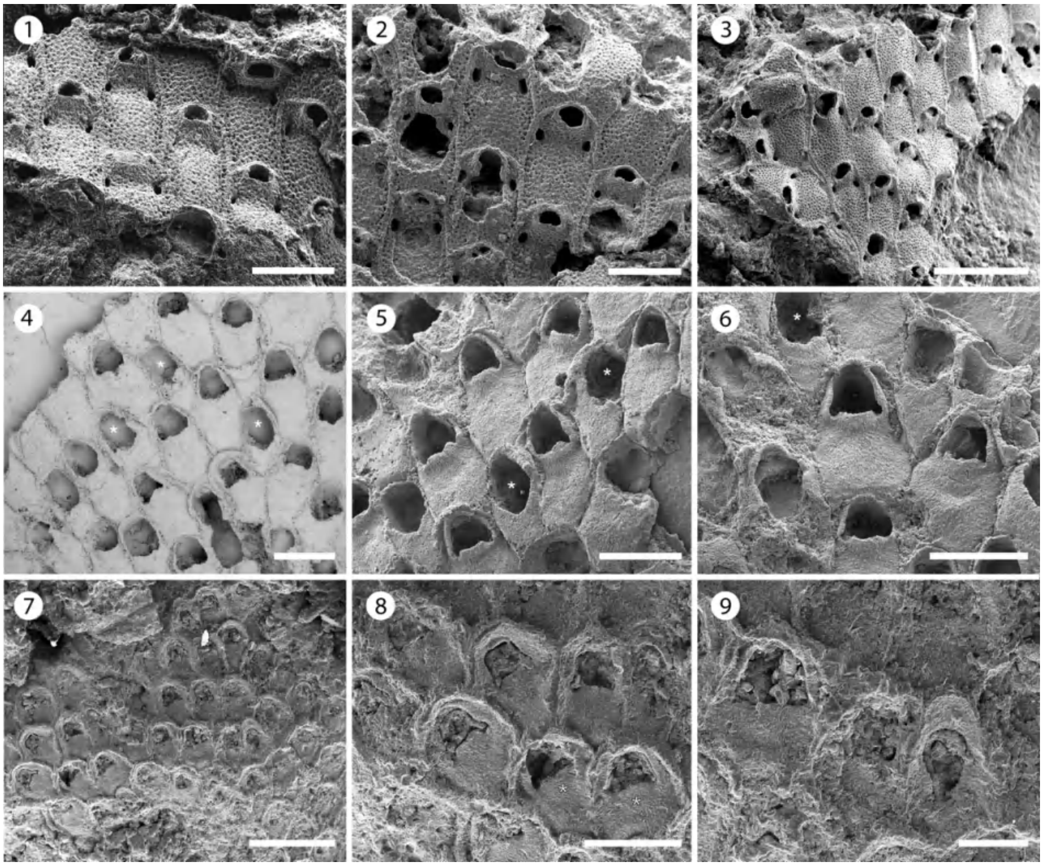

Figure 23. *Calpensia nobilis* (Esper, 1797) from the Siamaná Formation, Arroyo Ekieps (MUN-STRI-47635): (1) autozooids showing the semicircular opesia and the proximal raised peristome, (2) close-up of autozooids showing paired opesiules (3) general view of the colony. Onychocellidae n. gen. n. sp. from the Siamaná Formation, Arroyo Ekieps (holotype MUN-STRI-47637): (4) group of autozooids, (5) oblique view showing the development and shape of the cryptocyst, (6) zooids showing well-preserved opesia with opesiular indentations. Asterisks indicate putative avicularia. *Smittipora elongata* (Canu and Bassler, 1923) from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-47638): (7) general view of the colony, (8) close-up of autozooids and a fertile zooids (asterisk), (9) two zooids and a vicarious avicularium with round rostrum. Scale bars are (3, 7) 1 mm; (9) 0.25 mm; (1, 2, 4, 5, 6, 8) 0.5 mm.

Family Steginoporellidae Hincks, 1884
Steginoporellidae new genus

Type species.—Steginoporellidae n. sp., from Arroyo Uitpa, Siamaná Formation, Colombia, early Miocene; by monotype.

Diagnosis.—Colony encrusting, unilaminar, uni- to multiserial. Zooids oval, distinct laterally by a fine groove. Opesia terminal, trifoliate with deep opesiular indentations outlining a tongue-like process medially and sided by two conspicuous tubercles. Cryptocyst extensive, granular, slightly concave, occupying three-quarters of the zooidal length, surrounded by a raised rim. Gymnocyst smooth, surrounding the cryptocyst, more extended proximally. B-zooids either present or absent. Polypide tube not calcified. Kenozooids frequent in the multiserial stages.

Discussion.—Specimens of Steginoporellidae n. gen. from the Siamaná Formation are almost identical to the fossil morphospecies aff. "*Steginoporella*" *cornuta* (Osburn, 1950), recorded by Cheetham et al. (1999) in the Dominican Republic (ca. 7.1 Ma) and Panamanian Caribbean (ca. 3.5 Ma), as well as "*S.*" *cornuta* from the Recent Panamanian Pacific (figured in Cheetham and Jackson, 2000, fig. 2; NMiTA Database, 1996–2016; STRI Database, 2017), in having a narrow band of gymnocyst, more developed proximally, surrounding the cryptocyst and the opesia, in the morphology of the opesia and opesiular indentations, and in having a pair of conspicuous tubercles placed at the distal corners of the opesia. However, in the original description of *S. cornuta*, Osburn (1950, p. 108, pl. 12, figs. 3–6), made no mention of the presence of a gymnocyst, which is effectively absent in the type material (SBMNH 635758, Fig. 6.1, 6.2), but is present in a paratype (SBMNH 636427, Fig. 6.4, 6.3). In addition, Osburn described B-zooids, also present in "*Steginoporella*" *cornuta* from the Pliocene of Panama (Cheetham and Jackson, 2000), but not observed or preserved in the material from the Siamaná Formation. The family Steginoporellidae includes to date six genera, of which only *Siphonoporella* Hincks, 1880 develops a narrow gymnocyst, e.g., *S. nodosa* Hincks, 1880 and *S. delicatissima* (Busk, 1861). However, this genus differs from Steginoporellidae n. gen. in having a lightly calcified skeleton and very obvious polypide tube (Cook et al., 2018, p. 96). Because *Steginoporella* sensu stricto lacks a gymnocyst (Harmer, 1926, p. 268; Gordon, 1984, p. 56), we introduce this new genus, and we place it in the family Steginoporellidae owing to its close resemblance with *Steginoporella cornuta* and other species in this family.

Steginoporellidae new species

Figures 24.5–24.10; Table 12

1950 in part *Steganoporella cornuta* Osburn, p. 108, pl. 12, figs. 3–6.

Holotype.—MUN-STRI-47640. Paratypes: MUN-STRI-47641, MUN-STRI-47644, MUN-STRI-47642, MUN-STRI-47643, MUN-STRI-43526. From the early Miocene Siamaná Formation, Arroyo Uitpa, La Guajira, Colombia.

Diagnosis.– Colony encrusting, uni- to multiserial. Zooids oval, distinct laterally by a narrow groove. Opesia terminal, trifoliate with deep opesiular indentations outlining a tongue-like process medially. Tubercles prominent placed at each side of the opesia. Cryptocyst extensive, granular, slightly concave, occupying three-quarters of the zooidal length, surrounded by a raised rim. Gymnocyst smooth, slightly convex, surrounding the cryptocyst and the opesia, without edges between distal and proximal zooids, more extended in the early astogeny. Arrangement uni- and biserial in early astogeny. Kenozooids frequent in multiserial colonies.

Description.—Colony encrusting, unilaminar, uni- to biserial in early astogeny and multiserial in the advanced stages. Bifurcation of the bi- and triserial sections at angles of ca. 45°. Zooids oval to elliptical separated laterally by a fine groove (mean L/W 1.68). Opesia terminal, trifoliate, with large opesiular indentations proximally outlining a tongue-shaped process placed medially. Tubercles prominent, blunt, oval to elliptic in cross-section, placed laterodistally on each side of the opesia. Cryptocyst extensive and granular, slightly concave, surrounded by a raised mural rim, commonly with intramural buds, occupying three-quarters of the zooid length. Gymnocyst smooth, slightly convex surrounding the cryptocyst and the opesia, extending continually between zooids of the same row, except in some bifurcations, more extended in the early astogeny and proximally. Kenozooids frequent in the multiserial stages: triangular, elliptical, or similar in shape to the zooids. Polypide tube and rosette-plates not observed.

Other material examined.—*Steginoporella cornuta* (Osburn, 1950) Holotype: Recent, Acapulco, Mexico, 27 m depth, SBMNH 635758; Paratypes: Recent, Acapulco, Mexico SBMNH-636426, Recent, Isla Rancheria, Panama SBMNH-636427.

Table 12. Measurements of Steginoporellidae n. gen. n. sp.

Character	X	R	SD	N
Autozooid length	0.68	0.56–0.86	0.082	33
Autozooid width	0.40	0.35–0.46	0.031	25
Cryptocyst length	0.38	0.32–0.46	0.053	7
Cryptocyst width	0.29	0.24–0.33	0.029	14
Opesia length	0.11	0.09–0.12	0.015	4
Opesia width	0.12	0.09–0.17	0.028	8
Kenozooecium length	0.51	0.37–0.66	0.121	4
Kenozooecium width	0.34	0.21–0.47	0.108	4
Opesiule length	0.08	0.07–0.08	0.006	3
Opesiule width	0.04	0.03–0.04	0.007	2

Discussion.—Steginoporellidae n. gen. n. sp. resembles *Steginoporella tuberculata* David and Pouyet, 1974, from the Miocene of Austria in having two conspicuous distolateral tubercles; however, *S. tuberculata* differs in having a granular cryptocyst that is finely perforated, undeveloped gymnocyst, and both erect and encrusting colonies. The uni- and biserial early stages of Steginoporellidae n. sp., resemble members of the family Cymuloporidae Winston and Vieira, 2013, which also have a gymnocyst; however, those differ from Steginoporellidae n. sp. in having colonies that are exclusively uniserial, opesia occupying the distal half of the zooid total length, and in the absence of opesiules. Electridae d'Orbigny, 1852 (e.g., *Pyripora* d'Orbigny, 1852) also have gymnocyst and may have uni- to multiserial growth patterns (e.g., *P. magna* Larwood, 1973, p. 467, fig. 1) but differ in having a reduced cryptocyst and larger opesia lacking opesiular indentations. In the Siamaná Formation, Steginoporellidae n. sp. was found growing over coral rubble of *Porites* sp., covered by coralline algae, and sharing the substrate with *Antropora typica, Cribrilaria* sp., ?*Hippomenella* sp., and *Escharoides* aff. *martae*.

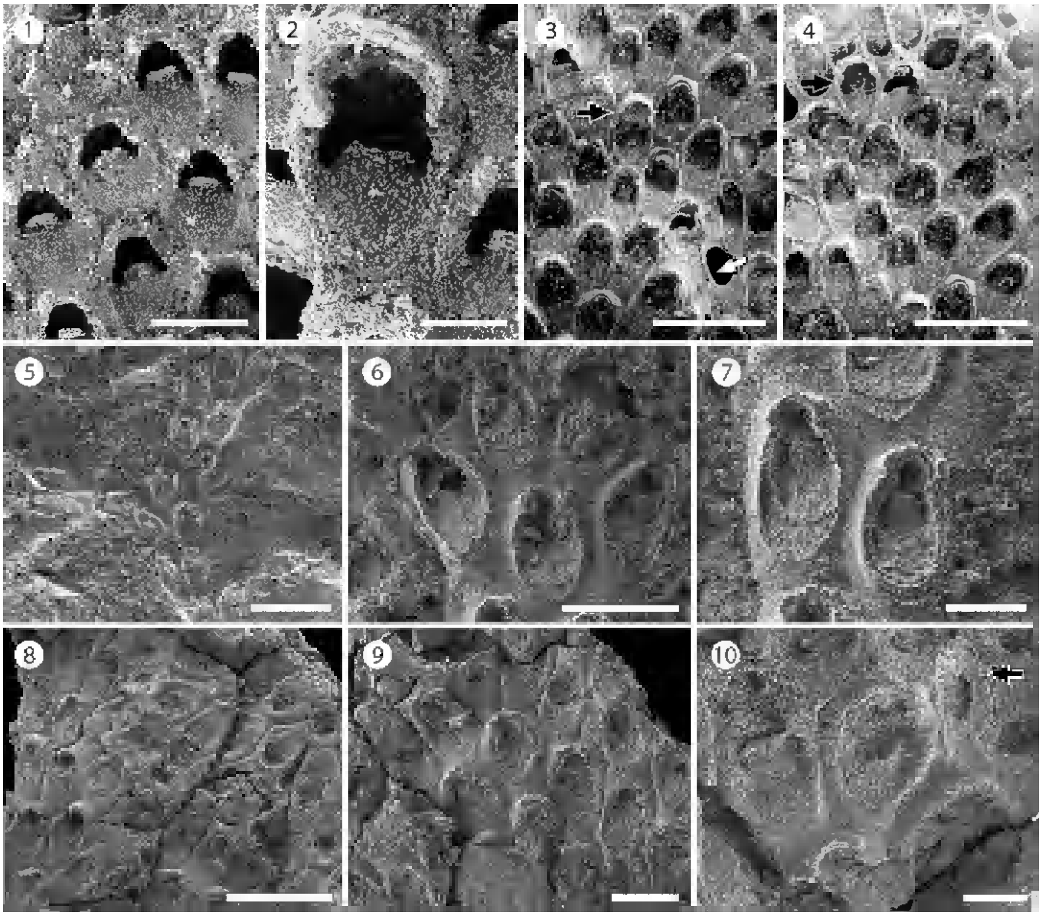

Figure 24. *Steginoporella cornuta* (Osburn, 1950), Recent, Acapulco, Mexico, Pacific Ocean (holotype SBMNH 635758) (photos courtesy of V. Delnavaz): (1) detail of the autozooids, note the absence of gymnocyst, (2) detail of a B-zooid; from Recent, Isla Rancheria, Panama, Pacific Ocean (paratype SBMNH 636427): (3) group of autozooids with reduced gymnocyst in the proximal area, kenozooids (white arrow) and B-zooid (black arrow), (4) autozooid with uncalcified polypide tube (arrowed). Steginoporellidae n. gen. n. sp. from the Siamaná Formation, Arroyo Uitpa (paratype MUN-STRI-47643): (5) general view of the uni- and biserial stages, note the extended, proximal gymnocyst; (holotype MUN-STRI-47640): (6) detail of the regular autozooids, (7) detail of two autozooids with intramural buds and opesia showing opesiular indentations; (paratype MUN-STRI-47641): (8, 9) general view of the multiserial stage; (10) close-up of autozooids and a kenozooid (arrowed). Scale bars are (1, 6, 9) 0.5 mm; (2, 7, 10) 0.25 mm; (3, 4, 5, 8) 1 mm.

Family Poricellariidae Harmer, 1926
Genus *Poricellaria* d'Orbigny, 1854

Type species.—*Poricellaria alata* d'Orbigny, 1854 from vicinity of Paris, France, Eocene; by original designation.

Poricellaria sp. indet.
Figure 25.1, 25.2; Table 13

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony erect. Branches slender and circular in cross-section. Zooids pyriform (mean L/W 1.80), curved distally, arranged in ?three longitudinal, alternated rows. Orifice terminal, semi-circular, oblique, tilted at an angle of 50–60° respect to the branch axis, facing in all directions, borders raised. Cryptocyst well-developed, oval, smooth, flat, with raised borders, perforated by a single slit-like opesiule, lying adjacent to the raised edge. Gymnocyst well-developed, smooth, covering the proximal area. Avicularia adventitious, small, placed on the proximal gymnocyst of each autozooid, rostrum acute and rounded, proximolaterally directed, pivotal bar absent or not preserved. Ovicells not observed.

Table 13. Measurements of *Poricellaria* sp. indet.

Character	X	R	SD	N
Autozooid length	0.25	0.24–0.25	0.006	3
Autozooid width	0.14	0.13–0.14	0.006	3
Orifice length	0.06	0.05–0.06	0.007	2
Orifice width	0.08	0.07–0.08	0.006	3
Avicularium length	-	0.07	-	1
Avicularium width	-	0.04	-	1
Opesiule length	0.07	0.06–0.07	0.007	2
Branch width	0.21	0.2–0.21	0.007	2

Discussion.—Only two broken and recrystallized fragments were found in the samples. However, the inclined zooids with the oblique opesia and slit-like opesiule, and the avicularia placed on the gymnocyst of each autozooid are features diagnostic of the genus *Poricellaria*. Nine species of this genus are known worldwide; among these, only *Poricellaria vernoni* Cheetham, 1963 is known from North America. This species from the Oligocene of Florida differs from *Poricellaria* sp. indet. in having a finely perforate cryptocyst. Cheetham (1973) found a specimen of *Poricellaria* in the Caribbean Miocene, which he identified as *P.* aff. *ratoniensis*; subsequently, Cheetham et al. (1999) reported it as *Poricellaria* new species 1 (figured in NMiTA Database, 1996–2016) from the Miocene (ca. 15.7–3.9 Ma) of the Dominican Republic. Although the Siamaná material resembles the species found by Cheetham et al. (1999), even in the size of the zooids, the poor preservation and scarcity of specimens preclude any further comparison and the description of a new species. In the Siamaná Formation, *Poricellaria* sp. indet. was found in the sediment attached to the coral *Goniopora hilli*, co-occurring with the bryozoan *Nellia tenella*, as is common in other fossil localities and environments (Winston and Cheetham, 1984), as well as with *Margaretta* sp., *Ditaxiporina* n. sp., and *Mecynoecia* sp.

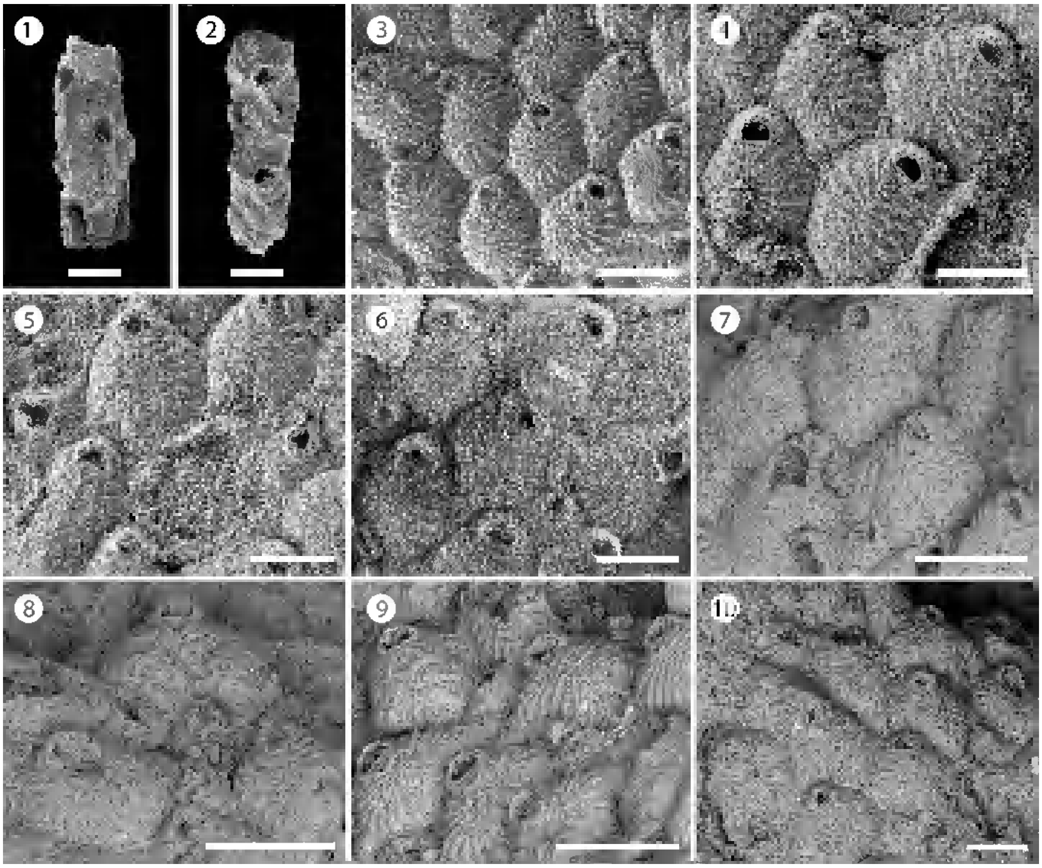

Figure 25. *Poricellaria* sp. indet. (MUN-STRI-47645): **(1, 2)** branch fragments showing the oblique orifice and the slit-like opesiule on the cryptocyst. *Cribrilaria* n. sp. 1 (holotype MUN-STRI-47650): **(3)** general view of the autozooids, **(4)** autozooids showing the orifice shape, spine bases and suboral lacunar pore, **(5)** detail of the avicularium with flared rostrum; (paratype MUN-STRI-47651): **(6)** fertile zooid with type A ovicell. *Cribrilaria* n. sp. 2 (holotype MUN-STRI-47657): **(7, 8, 9)** autozooids (showing the orifice shape, spine bases and suboral lacunar pore) and interzooidal avicularia, **(10)** fertile zooid with type B ovicell. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are **(1)** 0.15 mm; **(2, 4, 5, 6)** 0.2 mm; **(3, 10)** 0.25 mm; **(7, 8, 9)** 0.3 mm.

Superfamily Cribrilinoidea Hincks, 1879
Family Cribrilinidae Hincks, 1879
Genus *Cribrilaria* Canu and Bassler, 1929

Type species.—Eschara radiata Moll, 1803 from the Mediterranean Sea, Recent; by original designation.

Cribrilaria sp. 1 new species

Figure 25.3–25.6; Table 14

Holotype.—MUN-STRI-47650. Paratypes: MUN-STRI-47651, MUN-STRI-47652, MUN-STRI-47653, MUN-STRI-47654, MUN-STRI-47655, MUN-STRI-47656. From the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting, unilaminar. Zooids oval to rhomboidal. Orifice D-shaped bearing five spine bases. Lacuna broad, placed in a triangular area between the orifice and the first pair of costae. Frontal shield formed by 13–17 slender costae. Gymnocyst narrow surrounding the costate shield and the orifice. Interzooidal avicularia with flared rostrum, and rhombic cystid. Ooecium hyperstomial, subglobular, laying on the distal zooid (type A Bishop and Househam, 1987), smooth, imperforate and with a medial umbo.

Description.—Colony unilaminar, forming extensive and irregular incrustations. Zooids oval to rhomboidal, distinct by deep grooves, longer than wide (mean L/W 1.17). Orifice transversely D-shaped, bearing five spine bases in non-ovicellate zooids and four in ovicellate zooids, proximal border thick and straight. Frontal shield extensive and convex formed by 13–17 slender costae; first pair of costae forming a 'V'-area with a large lacuna visible in some zooids, obliterated by sediment in others; five to six intercostal pores. Gymnocyst narrow. Interzooidal avicularia frequent, large, placed over a rhombic cystid with a gymnocyst well developed; rostrum flared at the tip with slightly narrow middle portion, oriented distally. Ovicell type A of Bishop and Househam (1987), wider than long; ooecium surface smooth, not punctate and with a median umbo or keel.

Discussion.—Two fossil species from North America are known, *Cribrilaria anaticula* Canu and Bassler, 1920 and *Cribrilaria carolinensis* Gabb and Horn, 1862, both from the early Oligocene. They resemble *Cribrilaria* n. sp. 1 in having five oral spines, and large interzooidal avicularia. However, *Cribrilaria* n. sp. 1 differs from both in having avicularia with flared rostrum. Nine Recent *Cribrilaria* morphospecies are described in the literature having avicularia with flared mandibles (Harmelin, 2006), seven of them at species level: *C. flabellifera* (Kirkpatrick, 1888) and *C. vaceleti* (Harmelin, 2006) from Indo-Pacific; *C. arrecta* Bishop and Househam, 1987, *C. atlantis*, *C. macaronensis*, *C. mikelae* (Harmelin, 2006) from central Atlantic and Mediterranean Sea, and *C. smitti* (Winston, 2005) from Florida and the Caribbean. *Cribrilaria* n. sp. 1 is distinguishable from all of them by having a greater number of costae, up to 17 instead than 5–12, and five oral spines instead of six or seven (except in *C. mikelae* which also bears five). *Cribrilaria smitti*, the congener geographically closer, differs also in having the first pair of costae more pronounced, letting a wider space between it and the orifice, where it develops a bifid median umbo. In the Siamaná Formation, *Cribrilaria* n. sp. 1 was found encrusting the surface of the coral *Acropora panamensis*, co-occurring with the bryozoans *Cribrilaria* n. sp. 2, *Poricella* sp., *Hippoporina* sp., and *Hippomenella* sp.

Table 14. Measurements of *Cribrilaria* n. sp. 1.

Character	X	R	SD	N
Autozooid length	0.34	0.28–0.44	0.033	29
Autozooid width	0.29	0.25–0.4	0.037	29
Orifice length	0.04	0.03–0.06	0.008	17
Orifice width	0.07	0.06–0.1	0.01	12
Avicularium length	0.29	0.25–0.36	0.061	3
Avicularium width	0.15	0.11–0.17	0.024	9
Ooecium length	0.14	0.12–0.17	0.019	5
Ooecium width	0.16	0.15–0.19	0.015	6

Cribrilaria sp. 2 new species

Figure 25.7–25.10; Table 15

Holotype.—MUN-STRI-47657. Paratype: MUN-STRI-47658. From the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting. Zooids oval to elliptical. Orifice D-shaped bearing five spine bases. Lacuna broad and elliptical. Frontal shield formed by 17–22 costae. Gymnocyst narrow. Interzooidal avicularia with ?flared to slender rostrum, cystid rhombic with extensive gymnocyst. Ovicell hyperstomial, ooecium laying on the distal zooid or on a kenozooid (type A and B, Bishop and Househam, 1987), smooth, imperforate and with a medial keel.

Description.—Colony encrusting, multiserial, unilaminar. Zooids oval to elliptical distinct by shallow grooves (mean L/W 1.21). Orifice semicircular, wider than long; proximal border straight formed by a thin bar. Five oral spine bases in non-ovicellate zooids and four in ovicellate zooids. Frontal shield extensive, slightly convex to flat, formed by 17–22 slender costae, tapering up at the distal end, and fusing in the middle line. Costae separated by two to five circular intercostal pores. Suboral lacuna broad, elliptic, flanked by the first pair of costae forming a 'V'. Gymnocyst very narrow. Interzooidal avicularia frequent, rostrum short, ?flared to slender, cystid rhombic with a well developed gymnocyst, oriented distally, sometimes laying on the frontal shield of the distal zooid, opesia oval. Ooecium type A and B (Bishop and Househam, 1987), longer than wide, surface smooth, not punctate, and with a median keel. Kenozooids present.

Discussion.—A single, poorly preserved colony is available for this species. It differs from *Cribrilaria* n. sp. 1, in the number of costae, length of the zooids, type of ovicell budding from a kenozooid (type B), and in the size of the avicularian opesia which is wider. In the Siamaná Formation, *Cribrilaria* n. sp. 2 was found encrusting the surface of the coral *Acropora panamensis*, co-occurring with the bryozoans *Cribrilaria* n. sp. 1, *Poricella* n. sp., *Hippoporina* sp., and *Hippomenella* sp.

Table 15. Measurements of *Cribrilaria* n. sp. 2.

Character	X	R	SD	N
Autozooid length	0.45	0.36–0.6	0.056	12
Autozooid width	0.37	0.32–0.52	0.068	7
Orifice length	0.06	0.05–0.07	0.007	9
Orifice width	0.08	0.06–0.08	0.007	12
Avicularium length	-	0.34	-	1
Avicularium width	0.23	0.17–0.31	0.063	4
Ooecium length	-	0.16	-	1
Ooecium width	-	0.17	-	1

Genus *Figularia* Jullien, 1886

Type species.—*Lepralia figularis* Johnston, 1847 from Cornwall, United Kingdom, Recent; by original designation.

Figularia new species

Figure 26.1–26.5; Table 16

Holotype.—MUN-STRI-47647. Paratypes: MUN-STRI-47648, MUN-STRI-47649. From the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting. Gymnocyst smooth, developed laterally and proximally. Frontal shield formed by 19–24 costae with a pelmatidium located at two-thirds of the total length of each costa. Orifice semi-circular with a centered, suboral pore. Interzooidal avicularia infrequent, with spoon-shaped rostrum. Ooecium ovoidal with two drop-shaped or slit-like fenestrae, and a longitudinal suture medially.

Description. – Colony encrusting, multiserial, uni- to multilaminar. Zooids large (mean L/W 1.68), rhomboidal to elliptical, flat to slightly convex, distinct by fine and shallow furrows. Gymnocyst smooth, slightly convex, developed laterally and proximally, occupying one-quarter of the frontal length of the zooid. Frontal shield oval, flat to slightly convex, a little raised above the level of the gymnocyst, formed by 19–24 adjacent costae, fused in the median line. Costae broad, bar-shaped in the central and distal area, tapering proximally, apparently separated by one to three slit-like intercostal lacunae; each costa bears a circular pelmatidium placed close to the fusion line of the costae. Orifice terminal, wide, semi-circular, straight proximally, with a suboral, small, centered pore. Interzooidal avicularia infrequent, narrow, almost half of the zooid width but similar in length; rostrum spoon-shaped, foramen rounded and narrow with complete pivotal bar, oriented proximodistally. Ovicell hyperstomial, ovoidal; ectooecium smooth, with a longitudinal suture in the median line; two drop-shaped or slit-like fenestrae, oriented transversally, exposing a smooth endooecium. Ancestrula unknown. Kenozooids absents.

Discussion.—?*Figularia crassicostulata* (Canu and Bassler, 1920) was recorded in the late Eocene of North America, but the absence of a pelmatidium and proximal and lateral gymnocyst in the specimen described and figured by Canu and Bassler (1920, p. 316, pl. 43, fig. 9) suggests that the specimen does not belong to the genus *Figularia*. *Figularia* n. sp. resemble the Miocene species from Indonesia ?*Filaguria kalimantanensis* Di Martino and Taylor, 2015 in the size of zooids, number of costae, position of the pelmatidium, and the morphology of the ooecium; however, the latter species also has putative vicarious avicularia similar to autozooids, and two lateral oral spine bases, which are diagnostic of the genus *Filaguria* Moyano, 1991 and absent in the Colombian material. *Figularia bragai* also differs from the Recent species, recorded from the Gulf of Mexico, ?*Figularia ampla* Canu and Bassler, 1928 and *Figularia contraria* Lagaaij, 1963 in the number of costae and size of the zooids and opesiae; the former species has six pairs of costae, and larger zooids (1.5 mm long by 1.0 mm wide); while the latter species has 8–11, more commonly nine, costae and a distinctly smaller opesia in ovicellate zooids. In the Siamaná Formation, *Figularia* n. sp. was found encrusting the underside of the coral *Colpophyllia willoughbiensis* as well as the lateral surface of *Porites baracoaensis* and *Acropora* sp., sharing the substrate with an undetermined Cribrilinidae, ?*Hippopleurifera* sp., *Gemelliporidra* sp., and ?*Hippomenella* sp.

Table 16. Measurements of *Figularia* n. sp.

Character	X	R	SD	N
Autozooid length	0.72	0.59–0.88	0.103	10
Autozooid width	0.43	0.34–0.52	0.051	10
Orifice length	0.14	0.11–0.17	0.019	9
Orifice width	0.20	0.17–0.23	0.023	9
Cryptocyst length	0.39	0.29–0.46	0.058	10
Cryptocyst width	0.30	0.25–0.35	0.034	11
Pelmatidium diameter	0.01	0.01–0.01	0.000	2
Avicularium length	-	0.72	-	1
Avicularium width	-	0.2	-	1
Ooecium length	0.21	0.2–0.22	0.010	3
Ooecium width	0.35	0.34–0.35	0.006	3
Fenestra length	0.16	0.12–0.18	0.032	3
Fenestra width	0.03	0.02–0.04	0.014	2

Genus *Lepralina* Kühn, 1925

Type species.—*Lepralina auriculata* Kühn, 1925 from Eggenburg, Austria, Miocene; by original designation.

‘*Lepralina*’ sp. indet.

Figure 26.6–26.10; Table 17

Occurrence.—Early Miocene, Arroyo Ekieps, Siamaná Formation, Colombia.

Description.—Colony encrusting, unilaminar. Zooids oval and small (mean L/W 1.36). Orifice terminal, transversely D-shaped, bearing six to seven spine bases in non-ovicellate zooids. Gymnocyst very narrow developed proximally and laterally. Frontal shield formed by 13–15 costal ridges fused in the middle line, without forming a median suture or umbo. Between the costae, five or six lacunae are visible. A pair of small avicularia, adventitious, triangular located on each side of the orifice of the ovicellate zooids, oriented distally; rostrum small, raised at its distal end, crossbar not observed. Ovicell hyperstomial, formed from the maternal zooid (type C, Bishop and Househam, 1987), apparently with a proximo-medial umbo or keel. Kenozooids present. Ancestrula not preserved.

Discussion.—'*Lepralina*' sp. indet. shares mixed features with three other genera of the family Cribrilinidae: *Puellina* Jullien, 1886, *Glabrilaria* Bishop and Househam, 1987, and *Cribrilina* (Gray, 1848). However, it is distinguishable from all three genera because *Puellina* has perforated ooecium type C and lacks avicularia (Rosso et al., 2018); *Glabrilaria* may have adventitious avicularia associated with an imperforated ooecium, of the types A or B and often bears pedunculate avicularia (Rosso et al., 2018); *Cribrilina* sensu stricto has ooecium always perforated (Yang et al., 2018), in addition to oral avicularia in all zooids. We place our sample provisionally in the genus '*Lepralina*' following Kühn's (1925) diagnosis, which indicates "...not avicularia interzooidal and avicularia at least in the fertile zooids". '*Lepralina*' sp. indet. resembles the type species *L. auriculata* in having paired oral avicularia in ovicellate zooids, and in the size of both autozooids and orifices. However, *L. auriculata* differs in having ear-shaped avicularia, which reach the border of the zooids, in both ovicellate and non-ovicellate zooids. On the other hand, the diagnosis of the species *Lepralina galeata* Bobies, 1956 includes a perforated ooecium, which suggests that it could belong to another genus and needs revision. Despite this is the first record of the genus in the American continent, some specimens of the genus '*Puellina*' described by Canu and Bassler, 1920, e.g., '*Puellina*' *simulator* (p. 298, pl. 41, fig. 21; not pl. 84, fig. 14), might belong to *Lepralina*. In the Siamaná Formation '*Lepralina*' sp. indet. was found encrusting a mollusk shell, sharing the substrate with *Atoichos magnus* and a poorly preserved cyclostome.

Table 17. Measurements of '*Lepralina*' sp. indet.

Character	X	R	SD	N
Autozooid length	0.38	0.34–0.41	0.033	4
Autozooid width	0.28	0.25–0.33	0.039	4
Orifice length	0.04	0.04–0.05	0.005	3
Orifice width	0.06	0.05–0.07	0.008	3
Avicularium length	0.07	0.06–0.07	0.005	4
Avicularium width	0.04	0.04–0.05	0.010	4
Ooecium length	0.11	0.11–0.11	0.000	2
Ooecium width	0.15	0.14–0.15	0.003	2

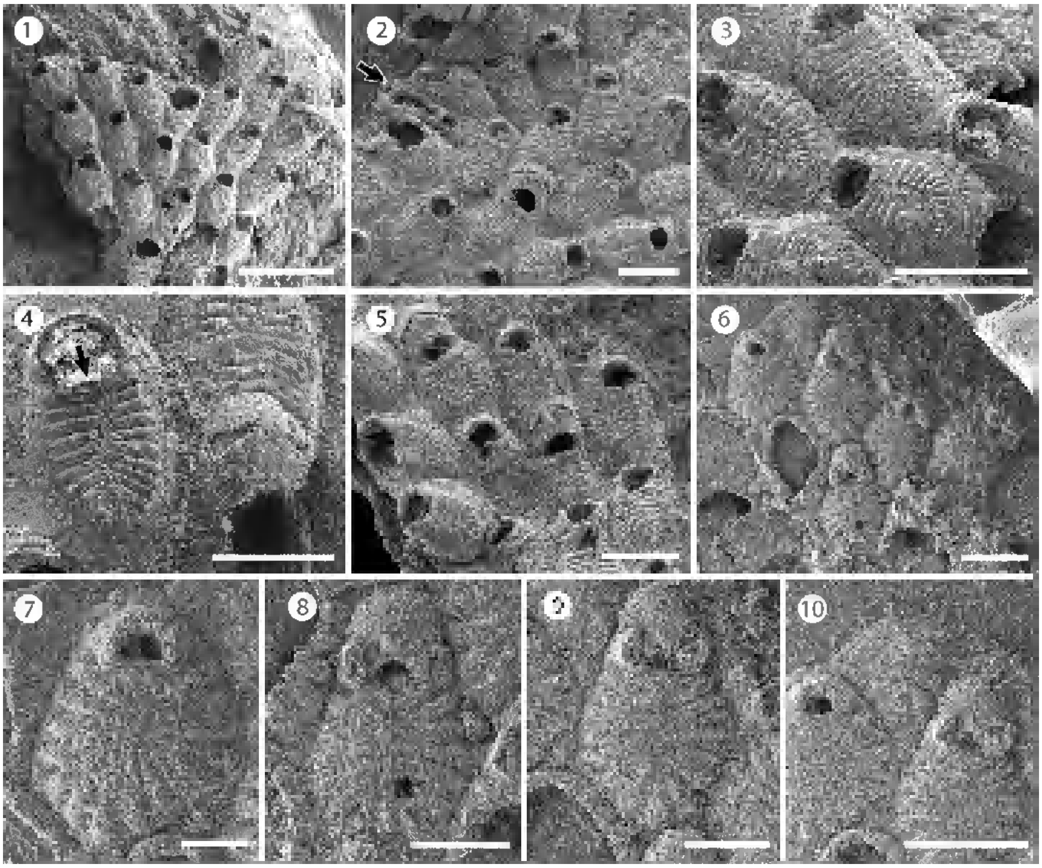

Figure 26. *Figularia* n. sp. (MUN-STRI-47647): (1) general view of the colony, (2) autozooids and interzooidal avicularia (arrowed), (3) close-up of autozooids showing the frontal shield (costae and pelmatidium) and the smooth gymnocyst, (4) close-up of a zooid showing the shape of the orifice and the suboral pore (arrowed), and an ovicell, (5) group of ovicellate and non-ovicellate zooids. '*Lepralina*' sp. indet. (MUN-STRI-47646): (6) group of zooids, (7) close-up of a non-ovicellate autozooid, showing the orifice shape, oral spine bases and pore chamber windows (8, 9) close-up of ovicellate zooids with paired latero-oral avicularia, (10) detail of a kenozooid. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are (1) 1 mm; (2, 3, 5) 0.5 mm; (4) 0.3 mm; (6, 10) 0.25 mm; (8, 9) 0.15 mm; (7) 0.1 mm.

Superfamily Catenicelloidea Busk, 1852b
Family Catenicellidae Busk, 1852b
Genus *Catenicella* de Blainville, 1830

Type species.—*Eucratea contei* Audouin, 1826 from Mediterranean Sea, Egypt and Syria, Recent; by original designation.

Catenicella sp. indet.
Figure 27.1–27.5; Table 18

Occurrence.—Early Miocene, Arroyo Ekieps, Siamaná Formation, La Guajira, Colombia.

Description. – Colony erect, jointed, branched and flexible. Zooids elongate (mean L/W 3.21), pyriform, uniserially arranged, all facing the same side. Gymnocyst smooth and ?finely perforated. Orifice subterminal, semicircular, with a proximal lip slightly raised, forming a shallow sinus and flanked by ?two condyles. Infrascapular chamber with a circular to elliptical pore oriented frontally. Avicularia small with triangular rostrum, placed at the sides of the orifice, oriented frontal to laterofrontally. Suprascapular chamber ?drop-shaped, oriented distally. Vittae long and narrow, placed on both sides of the zooid, bearing 12–13 circular communication pores, beginning next to the joint and ending at the base of the lateral chamber. Abfrontal surface convex and smooth. Rhizooids and ovicells not observed. Giant avicularia unknown.

Other material examined. – *Catenicella uberrima* Recent, Arraial do Cabo (Forno Beach), Rio de Janeiro State, Brazil, 1.5 m depth, MNRJ-136.

Table 18. Measurements of *Catenicella* sp. indet.

Character	X	R	SD	N
Autozooid length	0.41	0.38–0.46	0.028	9
Autozooid width	0.13	0.11–0.15	0.016	8
Orifice length	0.07	0.06–0.08	0.009	5
Orifice width	0.06	0.06–0.07	0.005	4
Lateral pore chamber length	0.02	0.02–0.03	0.005	9
Lateral pore chamber width	0.02	0.02–0.02	0.000	8
Avicularium length	0.06	0.05–0.06	0.005	4
Avicularium width	0.03	0.02–0.03	0.006	3
Vittae length	0.27	0.2–0.32	0.033	11
Pore vittae diameter	-	0.01	-	1

Discussion.—Material from the Siamaná Formation resembles the modern species *Catenicella uberrima* (Harmer, 1957) described from Indonesia, and reported from western Africa (Cook, 1968) and western Atlantic in Florida, Gulf of Mexico, Caribbean, and Brazil (Winston, 1982; Ramalho et al., 2014; Delgadillo-G and Flórez, 2015). Both species have elongate zooids and long vittae. However, *C. uberrima* is slightly larger, the pores of the infrascapular chambers and avicularia are placed laterally in regular zooids, and laterofrontally only in ovicellate zooids; in addition, at bifurcations almost half of the non-articulated budded zooid is fused to the parental zooid (e.g., Ramalho et al., 2014, fig. 2b), while in *Catenicella* sp. indet. the budded zooid is fused just at the base (Fig. 9.1). Cheetham et al. (1999) recorded *Vittaticella* sp. (=*Catenicella*, illustrated in NMiTA Database, 1996–2016) from the Caribbean ca. 5.9–15.7 Ma; however, it differs from *Catenicella* sp. indet. in having the pore of the infrascapular chamber narrow and lanceolate, oriented proximomedially, as well as two small drop-shaped suprascapular pores, oriented almost frontally. The scarcity of the material found in the Siamaná Formation prevents the classification at species level or the description of a new species. In the Siamaná Formation, *Catenicella* sp. indet. was found in the sediment adhering to the coral *Acropora panamensis*, co-occurring with the bryozoans *Licornia* sp., *Ditaxiporina* n. sp., and *Reteporellina* sp. This is the oldest record of the genus *Catenicella* in the American continent (ca. 23–20 Ma) and the first one in coral reefs ecosystems.

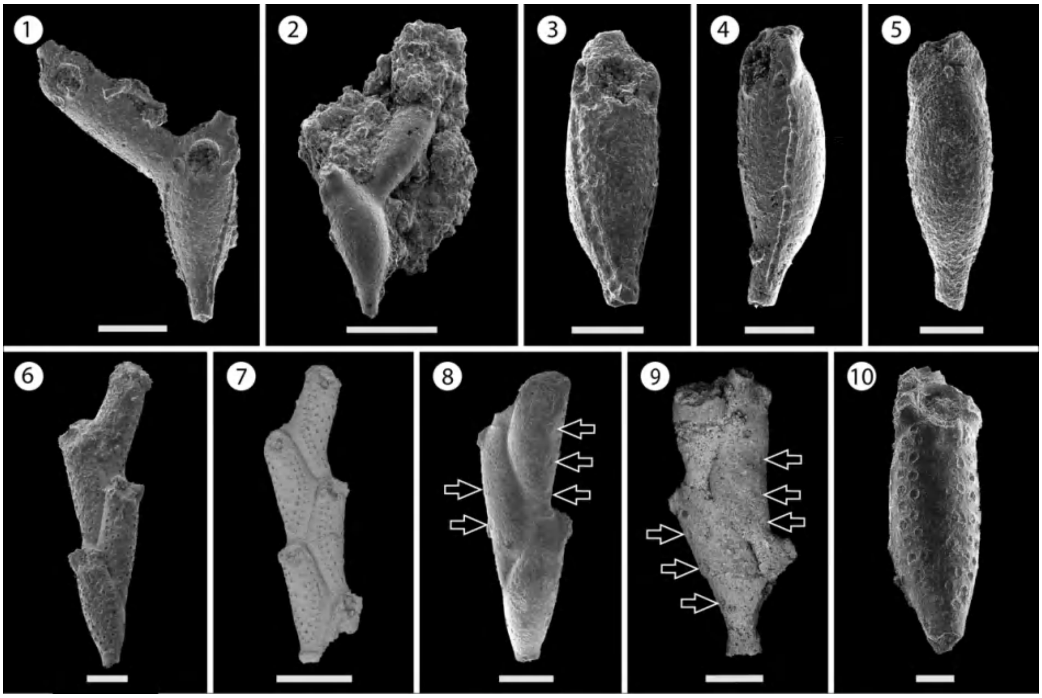

Figure 27. *Catenicella* sp. indet. (MUN-STRI-47666): **(1)** frontal view of zooids at bifurcation, showing orifice shape, latero-oral avicularia, and location of the vittae, **(2)** abfrontal view of the bifurcation, **(3)** detail of a single zooid showing the vittae, the orificial sinus and oral avicularia, **(4)** lateral view of a zooid, **(5)** abfrontal surface of a zooid. *Ditaxiporina* n. sp. (holotype MUN-STRI-47667): **(6)** frontal view of a biserial internode, **(8)** abfrontal view of a biserial internode showing the lateral pores (arrowed), **(10)** detail of the single zooid showing the orifice shape, vestigial subroral costae and arrangement of a frontal pores; (paratype MUN-STRI-47672): **(7)** frontal view of a biserial internode, **(9)** abfrontal view of a biserial internode showing the lateral pores (arrowed). All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are **(1)** 0.15 mm; **(2, 6, 8, 9)** 0.25 mm; **(3, 4, 5, 10)** 0.1 mm; **(7)** 0.5 mm.

Genus *Ditaxiporina* Stach, 1935

Type species.—Catenicella septentrionalis Waters, 1891 from Montecchio Maggiore, Italy, Priaboniano (Eocene); by original designation.

Ditaxiporina new species
Figure 27.6–27.10; Table 19

Holotype.—MUN-STRI-47667. Paratypes: MUN-STRI-47668; MUN-STRI-47669, MUN-STRI-47670, MUN-STRI-47671, MUN-STRI-47672. From the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis. – Colony erect, branching, uni- or biserial. Biserial internodes can be without fertile zooids. Zooids claviform. Orifice semicircular, proximal border forming by two vestigial costae. Frontal shield formed by a smooth gymnocyst, regularly perforated by circular pores arranged in six longitudinal rows. ?Three elliptical pores placed on each side of the zooid. Abfrontal surface smooth, lacking pores. Paired or single oral avicularia with triangular rostrum oriented distomedially and complete crossbar. Ovicells unknown.

Description. – Colony erect, articulated, internodes uni- or biserial. Zooids elongate and claviform (mean L/W 2.76); biserial internodes with up to five zooids, alternated and separated by a narrow groove, all facing the same side. Orifice terminal, semicircular with a broad sinus; proximal rim formed by two short and raised vestigial costae, ?with pelmata and separated by a suture in the middle line. Gymnocyst smooth, convex, perforated by circular and conspicuous pores with a slightly raised rim. Pores aligned forming three curved and concentric 'V'; the outer series bear 23–27 pores; the middle, slightly smaller, have 17–19; and the inner, smaller than latest, seven pores; the central area is generally unperforated, but one small and isolated pore may occur. Three elliptical to oval lateral pores. Abfrontal surface smooth, imperforate and concave. Avicularia small, single or paired, placed at the sides of the orifice; rostrum triangular, short, oriented distomedially; crossbar complete. Ovicells unknown. Oral spines absent.

Discussion.—The analyzed material has characteristics of two close genera of the subfamily Ditaxiporinae Stach, 1935: the fossil genus *Ditaxiporina*, and the recent genus *Vasignyella* Gordon, 1989, the latter genus transferred to the subfamily Vasignyellinae Gordon and Braga, 1994 (Vieira et al., 2007). Both genera have species with unizooidal and multizooidal internodes. In the members of *Vasignyella*, the multizooidal internodes are infrequent and bear ovicellate zooids, the paired avicularia lack crossbar and bear lateral pore chambers (Vieira et al., 2007, p. 51, 56). By contrast, the members of *Ditaxiporina* have internodes multiserial with and without fertile zooids, pelmatidia in the suboral costae, and avicularia single or paired with a complete crossbar (Gordon and Braga, 1994). Despite the scarcity of material and its poor preservation is possible to infer that the specimens belong to *Ditaxiporina* owing to the absence of ovicells or scars in the multizooidal internodes. Two North American congeners are known from the early Oligocene, *Ditaxiporina subseptentrionalis* (Canu and Bassler, 1917), and *Ditaxiporina bifenestrata* Cheetham, 1962. The former species differs from *Ditaxiporina* n. sp. in having tubular frontal pores and in the absence of the suboral vestigial costae, while the latter species differs in having the orifice proportionately much smaller and a single smaller avicularium without crossbar (Cheetham, 1962). The closest congener is *D. septentrionalis* (Waters, 1891), known from the Eocene of Italy (Gordon and Braga, 1994, fig. 10 a–d), which is similar also in the size of the autozooids; however, *Ditaxoporina* n. sp. differs in having lateral pore chambers and three longitudinal series of pores, and in the absence of a pore-chamber in the abfrontal surface, below the avicularia. In the Siamaná Formation, *Ditaxiporina* n. sp. was found in the sediment adhering to the corals *Acropora panamensis*, *Alveopora tampae*, and *Goniopora hilli*, co-occurring with the bryozoans '*Licornia*' sp., *Catenicella* sp., *Reteporellina* sp., *Margaretta* sp., *Mecynoecia* sp. and *Poricellaria* sp.

Table 19. Measurements of *Ditaxiporina* n. sp.

Character	X	R	SD	N
Autozooid length	0.71	0.63–0.76	0.045	7
Autozooid width	0.26	0.22–0.3	0.026	7
Orifice length	0.11	0.08–0.13	0.019	5
Orifice width	0.11	0.1–0.12	0.009	5
Avicularium length	0.10	0.09–0.1	0.005	4
Pore diameter (outer row)	-	0.02	-	12

Superfamily Hippothooidea Busk, 1859
Family Trypostegidae Gordon, Tilbrook and Winston in Winston, 2005
Genus *Trypostega* Levinsen, 1909

Type species.—*Lepralia venusta* Norman, 1864 from English Channel, Guernsey Island, Recent; by original description.

Trypostega sp. indet.
Figure 28.1–28.4; Table 20

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Uitpa, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by narrow and shallow grooves, rhomboidal, longer than wide (mean L/W 1.64), arranged quincuncially. Frontal shield flat, evenly perforated by 46–58 circular pseudopores (diameter 0.01 mm). Orifice subterminal, pyriform to cleithridiate, longer than wide; anter semicircular, condyles seemingly robust and rounded, sinus U-shaped. Basal pore-chamber windows elliptical to circular. Zooeciules placed distally to almost each autozooid, subcircular to oval, similar in size to the primary opening of autozooids; opening small, ?circular, placed in the center or slightly displaced distally; frontal shield flat, evenly covered by circular pseudopores as in autozooids. Suboral umbo absent. Ovicells not observed.

Discussion.—Despite the high recrystallization of the single specimen available, the key features of the genus *Trypostega* are clearly distinguishable. Five fossil species of this genus are known from North America: *T. inornata* (Gabb and Horn, 1862), *T. elongata* Canu and Bassler, 1920 and *T. undulata* (Canu and Bassler, 1920) from the Eocene; *T. vokesi* Di Martino, Taylor and Portell, 2017 from the Miocene (Burdigalian); and *T. composita* Di Martino, Taylor and Portell, 2019 from the Pliocene (Piacenzian). *Trypostega inornata* and *T. elongata* both resemble *T.* sp. indet. in having zooeciules associated to each autozooid, but the former species differs in having an imperforated frontal wall, while the latter species in having elongate and fusiform zooeciules.

Trypostega composita differs in having zooeciules of variable size and shape often forming clusters, in addition to frontal subcolonies. The remaining species differ in having suboral umbo constantly present or at least developed in some areas of the colony (e.g., *T. vokesi*). Among Recent west Atlantic species *T. striatula* (Smitt, 1873), *T. ilhabelae* Winston and Vieira, 2013, and *T. tropicalis* Winston, Vieira and Woollacott, 2014, all differ in having a suboral umbo, and *T. striatula* also longitudinal, conspicuous striations. In the Siamaná Formation *Trypostega* sp. indet. was found growing on *Porites* sp., co-occurring with an indeterminate cheilostome.

Table 20. Measurements of *Trypostega* sp. indet.

Character	X	R	SD	N
Autozooid length	0.47	0.41–0.55	0.041	21
Autozooid width	0.29	0.24–0.35	0.034	21
Orifice length	0.09	0.08–0.11	0.010	13
Orifice width	0.08	0.07–0.09	0.008	13
Zooeciules length	0.09	0.07–0.13	0.014	20
Zooeciules width	0.10	0.07–0.12	0.011	20
Zooeciular opesia length	0.03	0.03–0.04	0.005	4
Zooeciular opesia width	0.03	0.02–0.05	0.014	4

Superfamily Arachnopusioidea Jullien, 1888

Family Arachnopusiidae Jullien, 1888

Genus *Poricella* Canu, 1904

Type species.—Poricella maconnica Canu, 1904 from Tunisia, Eocene; by original description.

Poricella n. sp.

Figure 28.5–28.10; Table 21

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Diagnosis.—Colony encrusting. Autozooids distinct, ovoidal to elliptical. Orifice terminal, elliptical, slightly wider proximally; four to six oral spine bases. Frontal shield smooth, convex, perforated by 3–9 (more often 7) foramina; suboral mucro present or absent. Two prominent, interzooidal avicularia surrounding each autozooid, usually rounded to elliptical, rarely subspatulate. Sparse giant interzooidal avicularia, with elliptical or pyriform opesia and rounded rostrum. All avicularia lacking crossbar. Ovicell hyperstomial, globular.

Description. – Colony encrusting, multiserial, multilaminar. Autozooids distinct by deep furrows, ovoidal to elliptical (mean L/W 1.39), arranged in alternating rows or irregularly. Frontal shield convex, smooth, perforated by 3–9, more often seven, circular or bean-shaped foramina of different sizes; suboral mucro developed in most zooids. Marginal areolar pores few and small. Pore-chamber windows large, circular to elliptical, visible in the lateral and distal walls of the marginal zooids. Orifice terminal, elliptical; two rounded, proximally placed condyles separating a semicircular anter from a slightly wider sinus with straight to slightly concave proximal border; four to six oral spine bases. Two interzooidal avicularia, placed mid-lateral or distolateral to each zooid, variable in shape and size, mainly oval, sporadically subspatulate, prominent, with short rostrum oriented distally to distolaterally. Less frequent, interzooidal, giant avicularia, with long, straight, parallel sided, rounded rostrum and pyriform to elliptical opesia. Crossbar not observed. Ovicell hyperstomial, globular, imperforate.

Discussion.—Three fossil species of *Poricella* are known from southern North America and the Caribbean: *P. horrida* (Canu and Bassler, 1923) from the Miocene of Florida, *P. lidgardi* (Taylor and Foster, 1994) from the Plio-Pleistocene of Tobago, *P. mucronata* (Smitt, 1873) from the Miocene (to Recent) of Gulf of Mexico and Caribbean, and '*Poricella miocenica*' (McGuirt, 1941) originally described from the middle Miocene of Louisiana, and subsequently found in the Middle Miocene of Florida and South Carolina (Cook, 1977). *Poricella horrida* is easily distinguishable from *Poricella* n. sp. in having an elongate orifice with condyles very close to the proximal border, large interzooidal avicularia with triangular rostrum, single foramen, and conspicuous marginal areolar pores. *Poricella lidgardi* differs from the new species in having one to three foramina, adjacent zooids connected by calcified buttresses, and in the lack of condyles, oral spines and mucro. *Poricella mucronata* exhibits a significant variation in the number of frontal foramina and oral spines, in the presence/absence of the suboral mucro, and in the shape and size of avicularia (Powell and Cook, 1967; Cook, 1977; Di Martino et al., 2017). However, some features appear to be more dominant than others, such as avicularia with truncate rostra and distal expansion, reduced number of foramina, generally three and always less than six, and almost equidimensional orifice. Although '*Poricella miocenica*' is closely related to *P. mucronata*, Cook (1977, p. 131) separated this species based on its similarity with Miocene species from Africa and Europe. *Poricella* n. sp. resembles '*P. miocenica*' sensu stricto (Cook, 1977) in having avicularia associated with the ovicell, in the size of the orifice, and the frequency and orientation of oval/elliptical avicularia. However, it differs in the greater number of foramina (3–9 versus 1–2), and in the broader variety of interzooidal avicularia. Among the European congeners, *Poricella* n. sp. shares some features with *P. areolata* (Reuss, 1874) from Austria (on the coral *Porites incrustans*) and *P. pouyetae* (Cook, 1977) from France. However, both these species have elongate orifices. In addition, *P. areolata* bears a single foramen and *P. pouyetae*, despite bearing seven foramina as *Poricella* n. sp., shows conspicuous marginal areolar pores and the foramina are located more centrally on the frontal shield. In the Siamaná Formation, *Poricella* n. sp. was found growing on the corals *Alveopora tampae* Weisbord, 1973; *Acropora panamensis* (Vaughan, 1919); *Millepora* sp. and Caryophylliidae, co-occurring with *Hippopodina* aff. *iririkiensis* Tilbrook, 1999, *Cribrilaria* n. sp. 1, ?*Hippomenella* sp. indet. 1, and an indeterminate cheilostome.

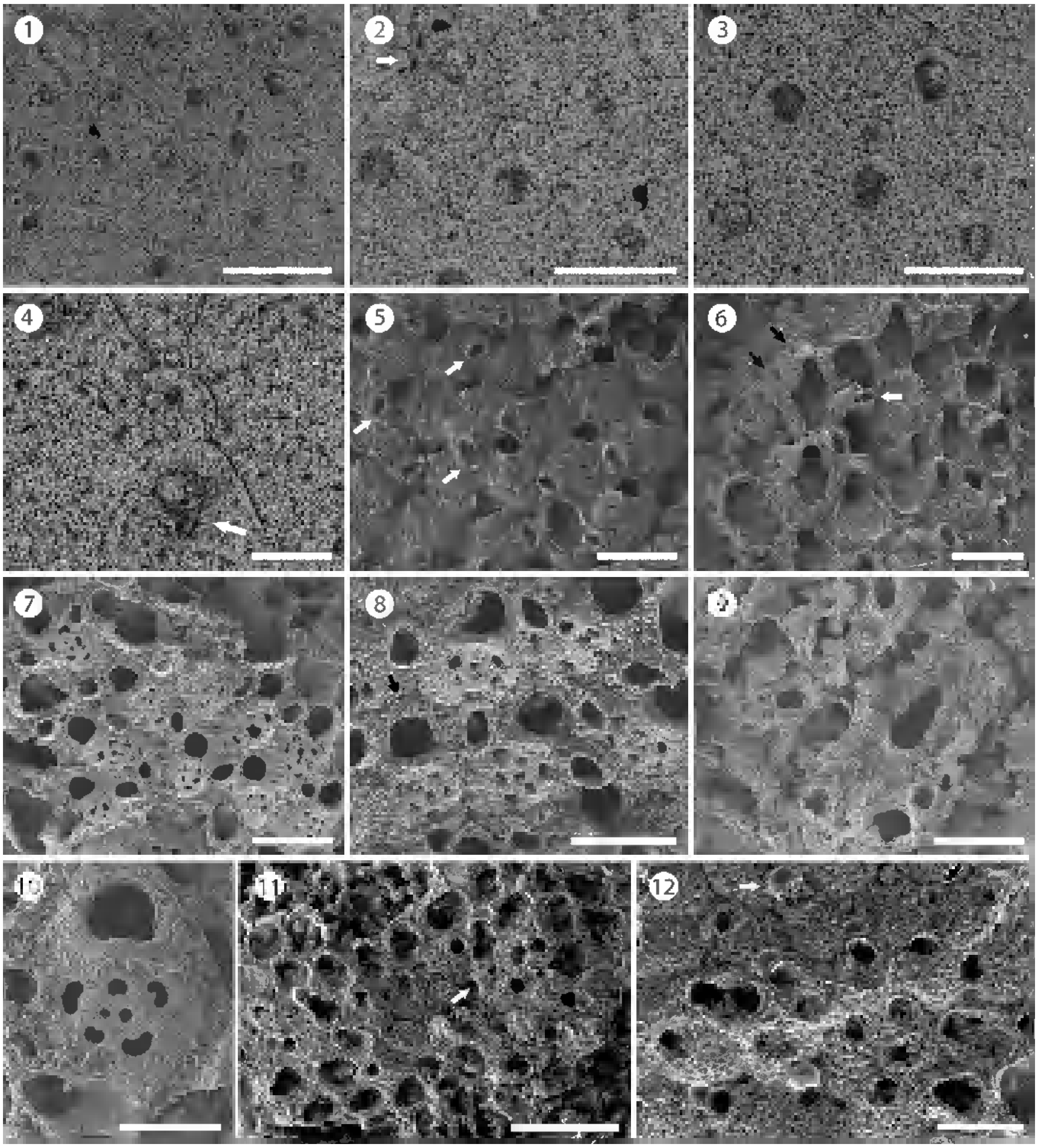

Figure 28. *Trypostega* sp. indet. (MUN-STRI-47675) from the Siamaná Formation, Arroyo Uitpa: (1) general view; (2) detail of the basal pore-chambers (arrowed); (3) detail of the zooids and zooeciules; (4) detail of the orifice, sinus and condyles (arrowed). *Poricella* n. sp. (paratype MUN-STRI-47680) from the Siamaná Formation, Arroyo Ekieps: (5) general view of the colony and subspatulate avicularia (arrowed); (6) detail of the pore-chambers (black arrows) and avicularia associated to the ovicell (white arrow); (holotype MUN-STRI-47676) (7) general view of the zooids and interzooidal avicularia rounded, (8) detail of the orifice and oral spines (arrowed); (9) detail of the interzooidal giant avicularia; (10) detail of the frontal foramina, condyles and interzooidal avicularia. Arachnopusiidae gen. sp. indet. (MUN-STRI-47682) from the Siamaná Formation, Arroyo Ekieps: (11) general view showing the ovicell with a frontal window (arrowed) (12) fertile zooids with incomplete ectooecium (white arrow), and interzooidal avicularia rounded (black arrow). Scale bars are (1, 5, 6, 7, 9) 0.5 mm; (2, 3, 10) 0.3 mm; (4) 0.1 mm; (8) 0.4 mm; (11) 1 mm; (12) 0.25 mm.

Table 21. Measurements of *Poricella* n. sp.

Character	X	R	SD	N
Autozooid length	0.56	0.43–0.72	0.070	36
Autozooid width	0.40	0.24–0.62	0.090	31
Orifice length	0.15	0.11–0.18	0.017	26
Orifice width	0.16	0.14–0.19	0.013	24
Oval avicularium length	0.20	0.16–0.26	0.024	19
Oval avicularium width	0.13	0.1–0.19	0.022	19
Oval avicularian opesia length	0.13	0.1–0.15	0.017	15
Oval avicularian opesia width	0.09	0.07–0.11	0.011	15
Spatulate avicularium length	0.22	0.19–0.24	0.022	4
Spatulate avicularium width	0.14	0.13–0.14	0.005	4
Spatulate avicularian opesia length	0.13	0.11–0.14	0.021	2
Spatulate avicularian opesia width	0.08	0.08–0.08	0.000	3
Large avicularium length	0.40	0.38–0.42	0.028	2
Large avicularium width	0.16	0.14–0.17	0.021	2
Large avicularian opesia length	0.47	0.37–0.64	0.129	4
Large avicularian opesia width	0.21	0.18–0.23	0.024	4
Ooecium length	0.16	0.14–0.17	0.015	4
Ooecium width	0.22	0.18–0.27	0.045	3
Foramen diameter	0.05	0.03–0.1	0.026	12

Arachnopusiidae gen. sp. indet.
Figures 28.11, 28.12, 29.1–29.3; Table 22

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, multiserial, uni- to multilaminar. Autozooids distinct by deep furrows, elliptical to rounded hexagonal, longer than wide (mean L/W 1.34), irregularly arranged. Frontal shield cryptocystal, convex perforated by 16–18 rounded to elliptical pseudopores (0.03 mm); marginal areolar pores subcircular to slit-like, wider at zooidal corners (0.10 x 0.05 mm); one or two large, elliptical to drop-shape, pore-chamber windows. Orifice subcircular; horseshoe-shaped anter separated from a slightly wider, shallow sinus by two blunt condyles; six spine bases in non-ovicellate zooids, four in ovicellate zooids, the proximal most pair seemingly larger in diameter (around 0.03 mm in diameter) Single, adventitious avicularium placed lateral to the orifice, triangular, oriented distally, apparently without crossbar. Interzooidal avicularia infrequent, oval, located lateral to the autozooids. Ovicells hyperstomial, subglobular; ectooecium poorly preserved, endooecium seemingly largely exposed, smooth.

Discussion.—We place this specimen in the family Arachnopusiidae because of the relatively large size of the frontal surface pseudopores, the presence of oral spines and basal pore chambers, and the prominent ovicells (Gordon, 1984, p. 68). Among the genera of this family, it resembles *Arachnopusia* Jullien, 1888 in having recumbent ovicells with a frontal window exposing the endooecium; however, it differs in having autozooids with distinct outline, the foramina lacking the ligula, and the absence of suboral avicularia (Hayward and Thorpe, 1988). It also resembles *Briarachnia* Gordon, 1984 in having exposed endooecium. This genus, however, lacks interzooidal avicularia. The poorly preservation of the single specimen found in the Siamaná Formation prevents the description of a new genus or species. Arachnopusiidae sp. indet. was found encrusting the coral *Porites baracoaensis* Vaughan, 1919.

Table 22. Measurements of Arachnopusiidae gen. sp. indet.

Character	X	R	SD	N
Autozooid length	0.49	0.58–0.4	0.040	28
Autozooid width	0.37	0.42–0.31	0.029	26
Orifice length	0.13	0.14–0.13	0.006	3
Orifice width	0.15	0.16–0.14	0.010	3
Oval avicularium length	0.16	0.16–0.16	0.000	2
Oval avicularium width	0.14	0.15–0.13	0.014	2
Triangular vicularium length	-	0.21	-	1
Triangular avicularium length	-	0.1	-	1
Ooecium length	0.13	0.14–0.1	0.015	6
Ooecium width	0.18	0.22–0.15	0.029	6
Pore diameter	0.028	0.03–0.02	0.004	10

Superfamily Lepralielloidea Vigneaux, 1949
Family Romancheinidae Jullien, 1888

Genus *Escharoides* Milne-Edwards, 1836

Type species.—*Cellepora coccinea* Abildgaard, 1806 from Australia, Recent; by original description.

Escharoides aff. *martae* Marcus, 1955

Figure 29.4–29.8; Table 23

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Uitpa, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by deep grooves, oval to polygonal, slightly longer than wide (mean L/W 1.27). Frontal shield slightly convex, smooth, imperforate, surrounded by a single row of circular marginal areolae separated by ridges. Orifice terminal, semicircular distally, proximal border slightly narrower and undulate flanked by two, robust, rounded condyles; peristome shallow with a median notch; six to seven oral spine bases (0.03 mm in diameter). Adventitious avicularia single or paired, similar in size, placed on a raised, well-developed cystid, with marginal areolae at the base, located laterally close to the zooidal margins, at about zooid half length, when paired one placed more proximally than the other, rostrum triangular oriented proximolaterally, crossbar complete. Ovicells not observed.

Discussion.—Canu and Bassler (1920) introduced (as *Peristomella*) the species *Escharoides falcifera* and *E. laticella* from the Eocene, and *E. erecta* from the Oligocene of North America. Cheetham, Sanner and Jackson (2007) described *E. guraboensis* from the late Miocene–early Pliocene, and Osburn (1914) described *E. costifer* from the late Pliocene–Recent of the Caribbean region. All of them differ from *Escharoides* aff. *martae* in the position and orientation of the lateral avicularia which are placed more distally and closer to the orifice laterally, distally or distolaterally directed. Although these fossil specimens closely resemble the Recent *Escharoides martae* Marcus, 1955 from Brazil, in the location, shape and direction of the avicularia, and size of autozooids, the nominal species has a more developed peristome without a central notch, sparse and prominent calcified granules on the frontal shield, and larger avicularia. Even though *E.* aff. *martae* may have lost the ornament of the frontal shield by dissolution or mechanical abrasion, as seen in other *Escharoides* species (Berning, 2006), the preserved morphology of the peristome in the samples from Siamaná Formation differentiate it from *E. martae* sensu stricto. However, the absence of ovicells discouraged the description of a new species. In the Siamaná Formation, *Escharoides* aff. *martae* was found encrusting rubble of *Porites* sp., sharing the substrate with Steginoporellidae n. gen. n sp. and poorly preserved, indeterminate cribrilinids.

Table 23. Measurements of *Escharoides* aff. *martae*.

Character	X	R	SD	N
Autozooid length	0.56	0.49–0.63	0.045	12
Autozooid width	0.44	0.4–0.49	0.027	10
Orifice length	3.09	0.1–12	5.942	4
Orifice width	0.15	0.14–0.16	0.010	4
Avicularium length	0.14	0.12–0.15	0.011	5
Avicularium width	0.09	0.08–0.09	0.006	3
Avicularian cystid length	0.11	0.1–0.11	0.007	2

Genus *Hippomenella* Canu and Bassler, 1917

Type species.—*Lepralia mucronelliformis* Waters, 1899 from Madeira, Atlantic Ocean, Recent; by original description.

Discussion.—The systematic placement (family level) and the definition of this genus were modified several times since its introduction in 1917 (Tilbrook, 2006, p. 257; Berning, 2013, p. 8; Ramalho et al., 2015, p. 126). The absence of ovicell description in the original genus definition allowed the inclusion of species with bifenestrate ectooecium, a diagnostic feature of the genus *Hippopleurifera* (Berning, 2013). This fact has generated confusion between these two genera, which has not yet been resolved as observed in some fossil specimens exhibiting a combination of characters of the two genera (Di Martino and Taylor, 2015, p. 18). Here, we follow, in part, the amended diagnosis of *Hippomenella* performed by Berning (2013) and include the genus into the family Romancheinidae.

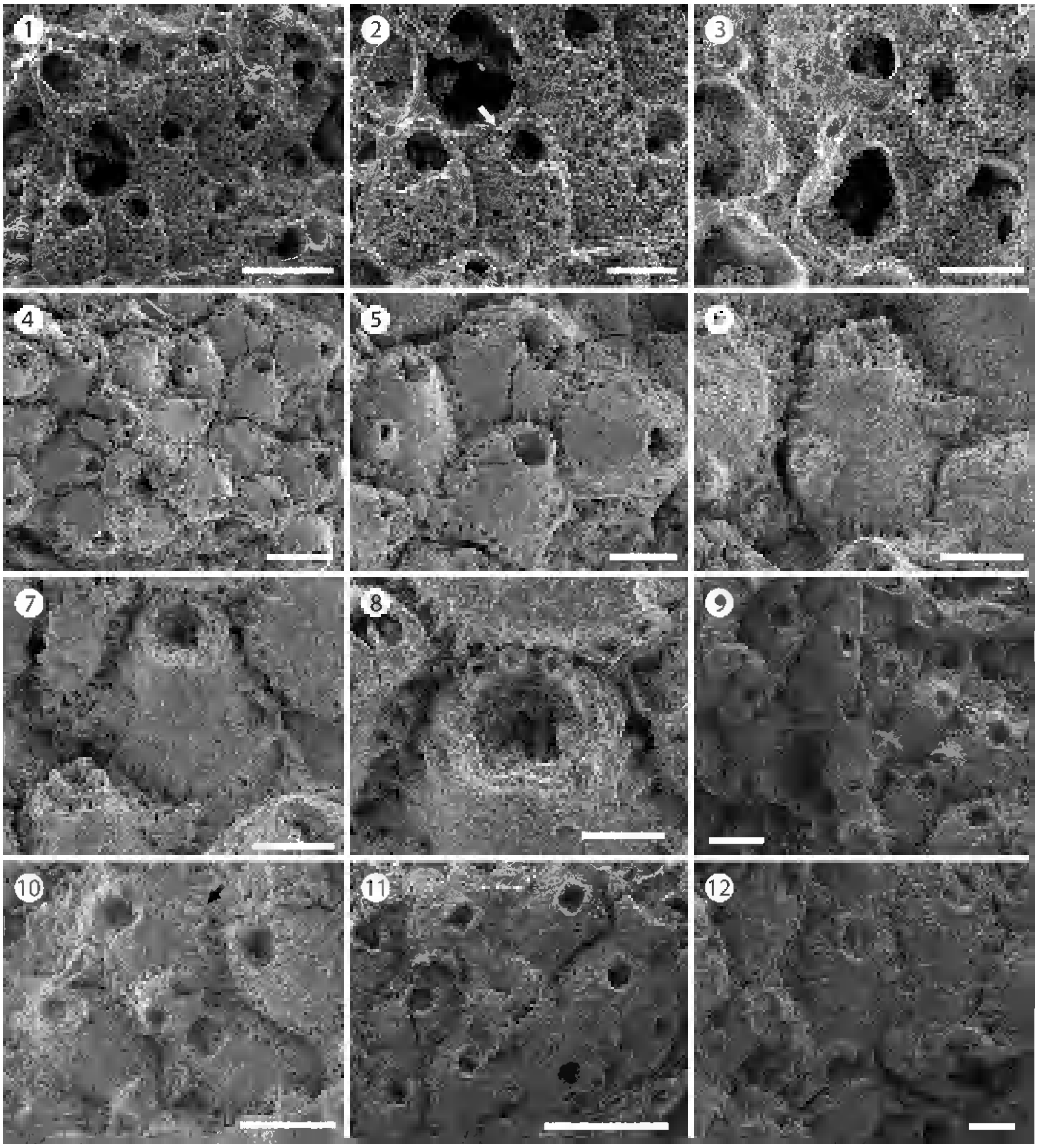

Figure 29. Arachnopusiidae gen. sp. indet. (MUN-STRI-47682) from the Siamaná Formation, Arroyo Ekieps: **(1)** general view of fertile and unfertile zooids; **(2)** detail of the basal pore-chambers (black arrow) and oral spines (white arrow); **(3)** detail of the triangular adventitious avicularia. *Escharoides* aff. *martae* Marcus, 1955 (MUN-STRI-47683) from the Siamaná Formation, Arroyo Uitpa: **(4)** general view; **(5)** detail of the zooids and avicularia arrangement; **(6)** detail of a zooid and its avicularia; **(7)** detail of the orifice; **(8)** detail of the orifice, central notch and oral spines. ?*Hippomenella* sp. indet. 1 from the Siamaná Formation, Arroyo Uitpa: (MUN-STRI-47690): **(9)** general view; **(10)** detail of the fertile zooid, showing ectooecium ridged and bifenestrate, and the elliptical avicularia (arrowed); (MUN-STRI-47689): **(11)** group of autozooids; **(12)** detail of the orifice and suboral peristome, oral spines and marginal pores. Scale bars are **(1, 4, 9, 10)** 0.5 mm; **(2, 3, 5, 12)** 0.25 mm; **(6, 7)** 0.2 mm; **(8)** 0.1 mm; **(11)** 1 mm.

?*Hippomenella* sp. indet. 1

Figure 29.9–29.12; Table 24

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Uitpa and Flor de La Guajira, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by deep grooves, elliptical to subhexagonal, slightly longer than wide (mean L/W 1.22). Frontal shield slightly convex, central U-shaped area imperforate, flanked by three to four rows of circular, elliptical or drop-shaped areolar pores (0.04 mm long by 0.03 wide mm) sloping inwards and separated by ridges. Orifice slightly longer than wide with arched anter separated by two blunt condyles from a smaller concave poster; 8–10 distolateral oral spine bases in non-ovicellate zooids, four in ovicellate zooids; suboral peristome well developed. Adventitious avicularia present or absent, one or two; one placed on the lateral margin of the zooid among the rows of areolar pores, at about the same level of the orifice condyles, with triangular rostrum oriented laterally to proximolaterally, crossbar complete; in about half of the zooids, a second, smaller, oval to elliptical avicularium without crossbar was observed, also placed over the rows of areolar pores but generally on the opposite side of the zooid and more proximally. Ovicell hyperstomial, globular, slightly flattened centrally, surrounded by a row of marginal pores with radial ridges in between; ectooecium surface tubercular, with two large (0.04 mm long by 0.03 mm wide), drop-shaped fenestrae.

Discussion.—Although the features of the ovicells in the specimens studied here differ from the genotype of *Hippomenella*, we place them tentatively into this genus based on the characters of the frontal shield, which is centrally imperforate and surrounded by multiple rows of areolar pores, and the presence of dimorphic adventitious avicularia (Berning, 2013). Canu and Bassler (1920) introduced the species *Hippomenella transversora* and ?*Hippomenella pungens* from the North American Oligocene; ?*Hippomenella* sp. indet. 1 resemble *H. transversora* in the general appearance; however, it differs in having up to 10 oral spines instead of six, ovicells with a single elongate pore, and a larger, triangular avicularium transversally directed. ?*Hippomenella* sp. indet. 1 resembles ?*H. pungens* in having ovicells with radial ridges and ectooecium partially uncalcified leaving two fenestrae, but differs in having two symmetrical avicularia placed below the level of the orifice. In addition, Canu and Bassler (1920) described seven species of ?*Hippomenella* from the North American Eocene, among them ?*Hippomenella* sp. indet. 1 resembles ?*H. transversata* in the shape and location of the avicularia, but differs in having encrusting colonies instead than erect and bilamellar. ?*Hippomenella infratelum* Canu and Bassler, 1919 known from the Caribbean early Miocene lacks oral spines and differs from ?*Hippomenella* sp. indet. 1 also in having an elliptical avicularium, with a complete crossbar, placed more proximally on the autozooid. In the Siamaná Formation ?*Hippomenella* sp. indet. 1 was found encrusting the hydrocoral *Millepora* sp. and coralline algae covering the coral *Porites* sp.

In our material ?*Hippomenella* sp. indet. 1 co-occurs with Steginoporellidae n. gen. n. sp. and *Antropora typica* (Canu and Bassler, 1928).

Table 24. Measurements of ?*Hippomenella* sp. indet. 1.

Character	X	R	SD	N
Autozooid length	0.80	0.77–0.82	0.019	7
Autozooid width	0.65	0.63–0.68	0.020	7
Orifice length	0.20	0.19–0.21	0.007	10
Orifice width	0.16	0.15–0.18	0.013	5
Ooecium length	0.32	0.28–0.35	0.049	2
Ooecium width	0.41	0.39–0.42	0.021	2
Avicularium length	0.22	0.13–0.28	0.065	4

?*Hippomenella* sp. indet. 2

Figure 30.1–30.4; Table 25

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by shallow interzooidal grooves, subhexagonal rounded distally, slightly longer than wide (mean L/W 1.27). Frontal shield almost flat to slightly depressed, granular, central area imperforate except for three to four rows of areolar pores. Orifice longer than wide, anter arched separated from the smaller and narrower poster with proximal border straight to slightly concave by two blunt, rounded condyles; nine distolateral oral spine bases. One or two small, adventitious avicularia with raised, acutely triangular rostrum, oriented proximally to proximolaterally; when paired, avicularia placed symmetrically close to the lateral zooidal margins, almost at zooidal mid-length; occasionally a similar, slightly larger adventitious avicularium, located laterally at the same level of the orifice, oriented lateroproximally; crossbar complete. Ovicells not observed.

Discussion.—Among the fossil species described by Canu and Bassler (1920) from North America, ?*Hippomenella* sp. indet. 2 resembles ?*H. pungens* in the general appearance and in having avicularia small and triangular, symmetrically placed below the aperture; however, it differs in having nine oral spines instead of four. ?*Hippomenella* sp. indet. 2 also resembles the Recent Caribbean species *Hippopleurifera belizae* Winston, 1984 in the shape and location of the avicularia, as well as in its general aspect, but differs in the number of oral spines, nine instead of six to eight, and in the morphology of the orifice. In the absence of ovicells, we place this species tentatively in the genus *Hippomenella* based on the broad, imperforate frontal area. In the Siamaná Formation, ?*Hippomenella* sp. indet. 2 was found encrusting the coral *Acropora panamensis*, co-occurring with ?*Hippopleurifera* sp. indet., *Figularia* n. sp. and other indeterminate cribrilinids.

Table 25. Measurements of ?*Hippomenella* sp. indet. 2.

Character	X	R	SD	N
Autozooid length	0.69	0.59–0.74	0.057	5
Autozooid width	0.54	0.41–0.69	0.101	7
Orifice length	0.17	0.15–0.18	0.021	2
Orifice width	0.16	0.15–0.16	0.007	2
Avicularium length	0.15	0.1–0.2	0.037	8
Avicularium width	0.08	0.06–0.12	0.021	7

Genus *Hippopleurifera* Canu and Bassler, 1925

Type species.—*Eschara biauriculata* Reuss, 1847 from Eisenstadt, Mörbisch and Kroisbach Austria, and Oedenburg Hungary, Miocene; by original description.

Hippopleurifera mucronata (Smitt, 1873)

Figure 30.5–30.9; Table 26

1873	*Hippothoa mucronata* Smitt, p. 45, pl. 8, fig. 169.
1928	*Hippomenella rubra* Canu and Bassler, 1928, p. 108, pl. 10, fig. 7, text fig. 19c.
1947	*Hippomenella mucronata*; Osburn, 1947, p. 33.
2005	*Hippopleurifera mucronata*; Winston, p. 54, figs. 143–145.
2017	*Hippopleurifera mucronata*; Di Martino et al., p. 151, figs. 41a–d.
2019	*Hippopleurifera mucronata*; Di Martino et al., p. 31, fig. 26.

Occurrence.—Early Miocene to Recent. Earliest occurrences: Aquitanian, Siamaná Formation, Arroyo Uitpa, Colombia; Burdigalian, Chipola Formation, Florida, USA (Scolaro, 1968; Di Martino et al., 2017); Pliocene, Duplin Formation, North Carolina, USA (Canu and Bassler, 1923); Pliocene (Piacenzian), lower Tamiami Formation, Florida, USA (Di Martino et al., 2019). Recent records are from the central American Atlantic (Osburn, 1947; Winston, 2005) and the Central American Pacific (Osburn, 1952; Soule, 1961).

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by narrow and deep grooves, rhomboidal, claviform or hexagonal, almost as long as wide (mean L/W 1.05). Frontal shield convex, ribbed, with two to three rows of marginal areolar pores, evenly spaced, subcircular (0.02–0.03 mm in diameter), imperforate central area reduced. Orifice with semielliptical anter and narrow, U-shaped sinus; condyles not preserved; pointed suboral umbo poorly preserved; six distolateral oral spine bases. Adventitious avicularia infrequent, placed at about the same level of the orificial sinus, near and parallel to zooidal margins; rostrum triangular, narrow, oriented proximolaterally; crossbar not preserved. Ovicells not observed.

Discussion.—Despite the poor preservation of the specimens available, the key morphological features of *Hippopleurifera mucronata*, i.e. orifice shape, number of oral spines, multiple rows of marginal areolar pores, the position and shape of the avicularia, are distinguishable. Canu and Bassler (1920) introduced the species *H. capitimortis* and *H. ampla* from the North American Oligocene; *H. mucronata* differs in having frontal shield with a reduced imperforate central area. In the Siamaná Formation, *H. mucronata* was found encrusting rubble of the coral *Porites* sp. as well as coralline algae, co-occurring with *Smittipora elongata* (Canu and Bassler, 1923) and *Trypostega* sp. indet.

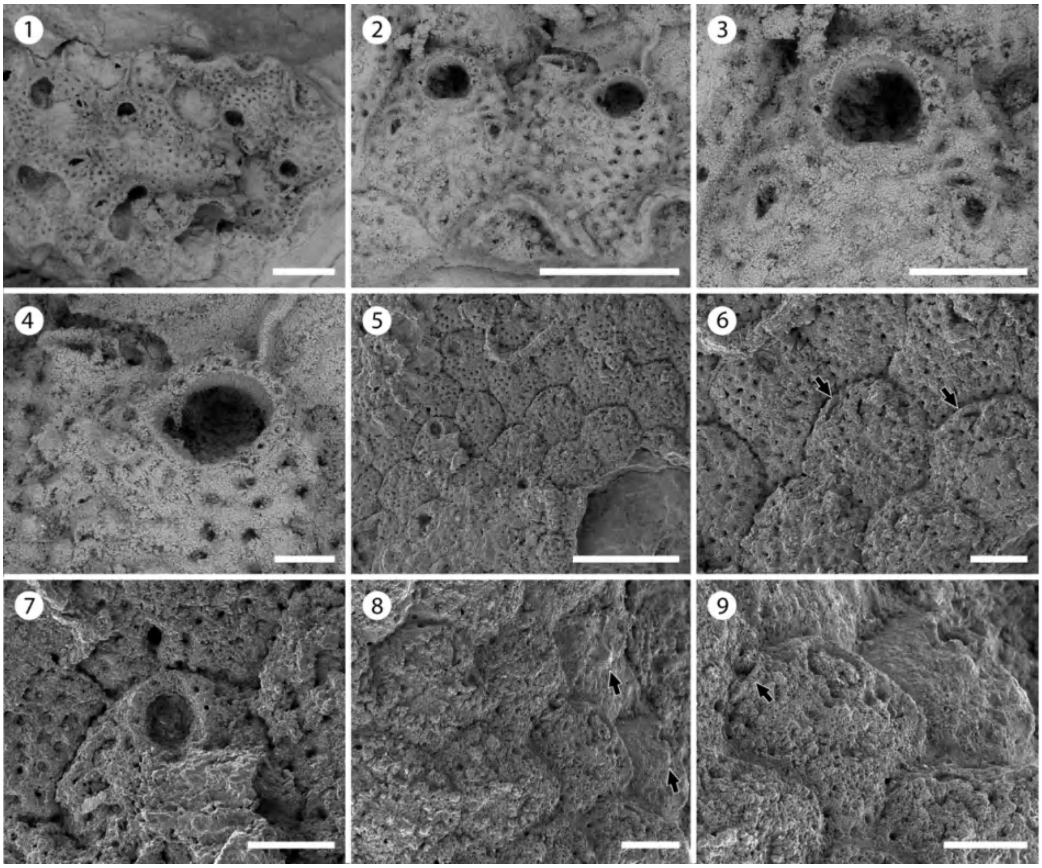

Figure 30. ?*Hippomenella* sp. indet. 2 (MUN-STRI-47691) from the Siamaná Formation, Arroyo Ekieps: **(1)** general view; **(2)** detail of two zooids showing the arrangement of the areolar pores; **(3)** detail of the orifice, oral spines and paired avicularia; **(4)** detail of the orifice showing a condyle and oral spines, detail of the avicularia lateral. *Hippopleurifera mucronata* (Smitt, 1873) (MUN-STRI-47693) from the Siamaná Formation, Arroyo Uitpa: **(5)** general view; **(6)** detail of the zooids and avicularia (arrowed); **(7)** detail of the orifice showing the U-shaped sinus and oral spines; **(8)** zooids showing the suboral umbo (arrowed); **(9)** zooid showing the avicularia (arrowed) and orifice with sinus. Scale bars are **(1, 2)** 0.5 mm; **(3, 7, 9)** 0.2 mm; **(4)** 0.1 mm; **(5)** 1 mm; **(6, 8)** 0.25 mm.

Table 26. Measurements of *Hippopleurifera mucronata*.

Character	X	R	SD	N
Autozooid length	0.59	0.46–0.69	0.060	13
Autozooid width	0.56	0.45–0.65	0.065	10
Orifice length	0.16	0.15–0.16	0.007	2
Orifice width	0.12	0.11–0.13	0.009	8
Avicularium length	0.20	0.19–0.21	0.014	2

?*Hippopleurifera* sp. indet.

Figure 31.1–31.4; Table 27

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, multiserial, uni- to multilaminar. Autozooids distinct by deep grooves, rhomboidal to claviform, longer than wide (mean L/W 1.35). Frontal shield slightly depressed marginally, raised suborally, imperforate except for two to three rows of elliptical marginal areolar pores (0.03–0.04 mm in length) with radially arranged ridges in between. Orifice subcircular with straight to slightly convex proximal border; four distal oral spine bases in non-ovicellate zooids, at least two visible in ovicellate zooids. Adventitious avicularia dimorphic; a small avicularium, generally poorly preserved, placed suborally on a raised umbo; larger, distolateral avicularia placed slightly above the orifice proximal half-length, with triangular rostrum, oriented distolaterally and inwards, sometimes bending over the orifice. Ovicells hyperstomial, globular; ectooecium seemingly bifenestrate, surface granular.

Table 27. Measurements of ?*Hippopleurifera* sp. indet.

Character	**X**	**R**	**SD**	**N**
Autozooid length	0.83	0.65–1	0.097	14
Autozooid width	0.61	0.43–0.89	0.122	20
Orifice length	0.20	0.19–0.22	0.015	3
Orifice width	0.22	0.2–0.23	0.014	4
Avicularium lateral length	0.29	0.19–0.34	0.060	5
Avicularium lateral width	0.15	0.15–0.15	0	3
Ooecium length	-	0.36	-	1
Ooecium width	0.43	0.42–0.44	0.014	2

Discussion.—Our specimens consist of small colony fragments with few autozooids each and poorly preserved. Based on the general appearance of the frontal shield, the presence of suboral and lateral avicularia and oral spines, we tentatively placed them into the genus *Hippopleurifera*. Six species of *Hippopleurifera* are known from the American continent, four are fossil (Oligocene–Miocene) and two are Recent. Ramalho et al. (2015) introduced *H. confusa* and *H. barbosae* from the Miocene of Brazil; Canu and Bassler (1920) described *H. ampla* and *H. capitimortis* from Alabama, USA; *H. mucronata* (Smitt, 1873) and *H. belizae* are known from the Gulf of Mexico and the Caribbean. Among them ?*Hippopleurifera* sp. indet. mostly resembles *H. confusa* in the size and locations of the avicularia; however, it differs in having four oral spines instead of 6–8, larger zooids, smaller marginal areolar pores and a wider imperforate frontal area. In the Siamaná Formation, ?*Hippopleurifera* sp. indet. was found on the corals Caryophylliidae and *Acropora* sp., co-occurring with *Figularia* n. sp. and an indeterminate cribrilinid.

Superfamily Schizoporelloidea Jullien, 1883
Family Schizoporellidae Jullien, 1883
Genus *Gemelliporidra* Canu and Bassler, 1927

Type species.—*Gemelliporidra typica* Canu and Bassler, 1927 from North of Cuba, Caribbean Sea, Recent; by original description.

Gemelliporidra aff. *magniporosa* Canu and Bassler, 1923
Figure 31.5–31.7; Table 28

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by a narrow groove or a thin thread, subrectangular to irregularly pentagonal, almost as long as wide (mean L/W 1.07). Frontal shield flat to slightly depressed, granular, evenly perforated by regularly spaced, circular pseudopores (diameter 0.2–0.4 mm), except for a reduced imperforate area below the orifice. Orifice terminal, anter semielliptical, sinus V-shaped, condyles rounded triangular. Small, triangular structures seemingly oriented proximolaterally and placed at the distal zooidal margins interpreted as putative adventitious avicularia. Ovicell hyperstomial, globular, occupying most of the frontal surface of the next distal zooid, up to the proximal margin of the orifice; apparently perforated by closely spaced pseudopores, smaller than those of the frontal shield.

Discussion.—Eight of the nine species of *Gemelliporidra* known at date are extant and recorded off the American continent: *G. colombiensis* Osburn, 1952 and *G. lata* Osburn, 1952 from the Pacific coast of Colombia and California, respectively; *G. aculeata* Canu and Bassler, 1928, *G. pertusa* (Smitt, 1873) from the Gulf of Mexico; *G. multilamellosa* Canu and Bassler, 1923, *G. typica* Canu and Bassler, 1927, and *G. belikina* Winston, 1984 from the Caribbean Sea; and *G. magniporosa* Canu and Bassler, 1923 from both the Gulf of Mexico and the Caribbean Sea. The size, shape and position of the putative adventitious avicularia distinguish *Gemelliporidra* aff. *magniporosa* from all these congeners: *G. typica*, *G. multilamellosa* and *G. aculeata* have larger, straight or curved avicularia; *G. belikina* and *G. colombiensis* have small, rounded to drop-shaped avicularia placed proximolateral to the orifice; avicularia are proximolateral to the orifice in *G. lata*, and oval, placed on the peristome in *G. pertusa*. We tentatively assigned our specimens to *G.* aff. *magniporosa* based on the morphology of the autozooids, orifice and ovicells, as well as the calcification of the frontal shield and the pattern of perforation. However, *G.* aff. *magniporosa* differs from the nominal specie in having larger autozooids (i.e., Lz 0.75 mm, Wz 0.70 mm vs. Lz 0.65 mm, Wz 0.50–0.55 mm) and orifices. In addition, although avicularia can be inconstant, *G. magniporosa* commonly bears a pair of small, triangular avicularia placed at the sides of the orifice oriented distomedially, which were not observed in our specimens. *Gemelliporidra magniporosa* and *G. multilamellosa* were also reported from the Pleistocene of Panama, while *G. magniporosa*, *G. belikina* and *G. multilamellosa* were also recorded in coral reef environments of the Caribbean region (Jackson et al., 1985; Winston, 1986). In the Siamaná Formation, *Gemelliporidra* aff. *magniporosa* was found encrusting the corals *Porites baracoaensis*, *Alveopora tampae* and *Acropora* sp. sharing the substrate with *Calpensia nobilis* (Esper, 1796), *Figularia* n. sp., ?*Hippomenella* sp. indet. 2, ?*Hippopleurifera* sp. indet., and indeterminate cribrilinids.

Table 28. Measurements of *Gemelliporidra* aff. *magniporosa*.

Character	X	R	SD	N
Autozooid length	0.75	0.65–0.87	0.079	6
Autozooid width	0.70	0.56–0.88	0.135	7
Orifice length	0.22	0.2–0.23	0.015	3
Orifice width	0.18	0.16–0.19	0.011	7
Ooecium length	-	0.52	-	1
Ooecium width	-	0.54	-	1

Family Margarettidae Harmer, 1957
Genus *Margaretta* Gray, 1843

Type species.—*Cellaria cereoides* Ellis and Solander, 1786 from Algeria, Mediterranean Sea, Recent; by original description.

Margaretta buski Harmer, 1957
Figure 31.8–31.10; Table 29

1928 *Tubucellaria cereoides*; Canu and Bassler, 1928, p. 113, pl. 15, fig. 6.
1957 *Margaretta buski* Harmer, 1957, p. 194, pl. 55, fig. 29, text fig. 91.
2019 *Margaretta* cf. *buski*; Ramalho et al., 2019, p. 112, fig. 3.

Occurrence.—Miocene to Recent. Earliest occurrences: early Miocene (Aquitanian), Siamaná Formation, Arroyo Ekieps, Colombia. Recent occurrences: Brazil (Vieira et al., 2008), central Atlantic Ocean (Harmer, 1957), and in the Caribbean Sea associated to coral reefs (Winston, 1986).

Description.—Colony erect, articulated. Autozooids flask-shaped, more than twice as long as wide (mean L/W 2.35), arranged in whorls of three. Frontal shield evenly perforated by large, circular pseudopores arranged in rows between ridges; circular ascopore placed medially at the base of the peristome. Peristome tubular, ridged and porous as the frontal shield. Fertile zooids with peristomes swollen proximally, upturned, and tapering distally. Secondary orifice circular, primary orifice hidden by the peristome. Basis rami bipartite.

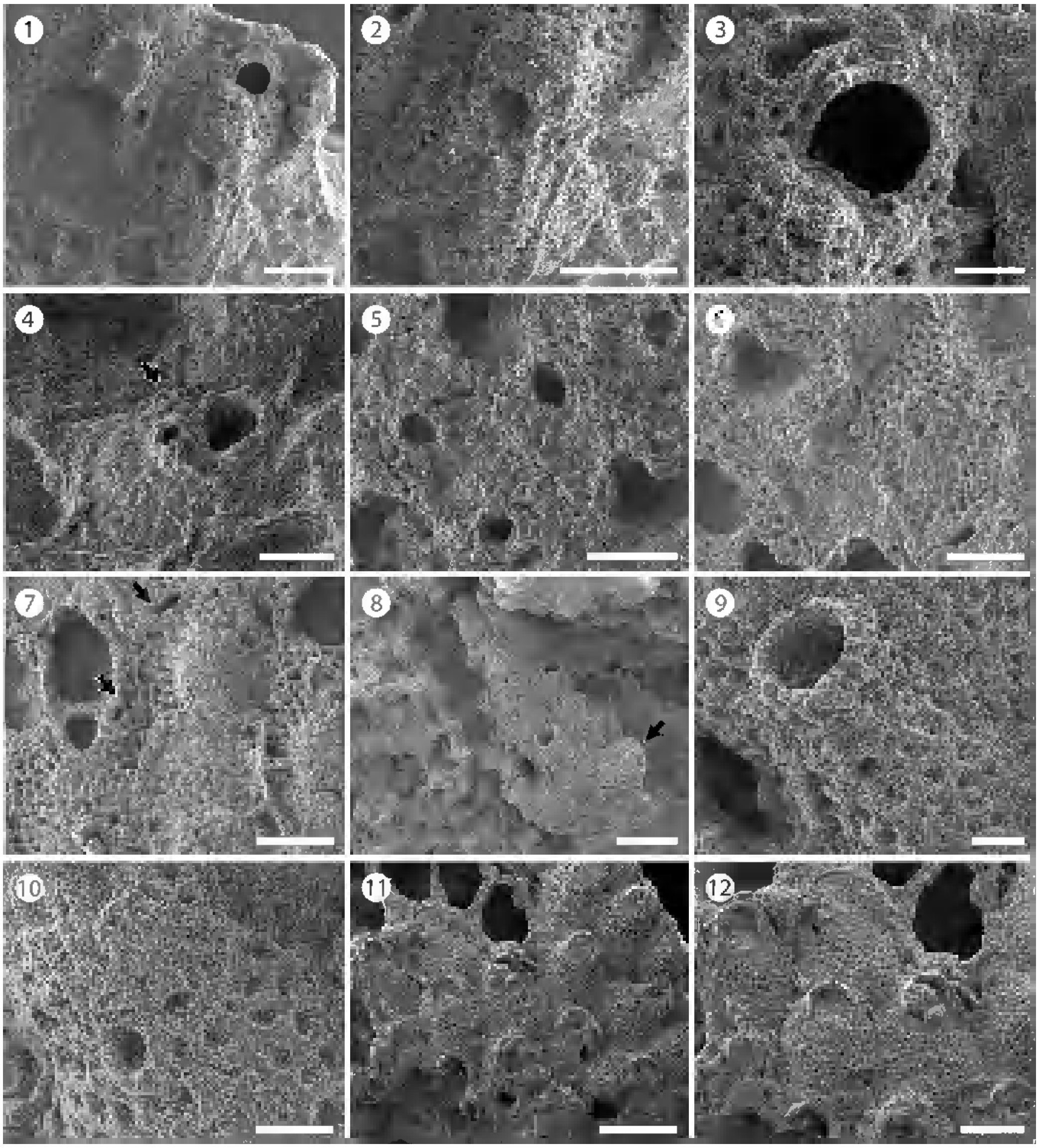

Figure 31. ?*Hippopleurifera* sp. indet. (MUN-STRI-47698): (1) general view; (2) detail of the ooecium, apparently bifenestrate; (3) detail of the orifice, oral spines and avicularia; (MUN-STRI-47697): (4) detail of the suboral avicularia, oral spines and lateral avicularia (arrowed). *Gemelliporidra* aff. *magniporosa* Canu and Bassler, 1923 (MUN-STRI-47701): (5) detail the of zooids shape; (6) detail of the orifice and pattern of pseudopores on the frontal shield; (7) detail of the orifice showing the V-shaped sinus, ovicell, and putative avicularia (arrowed). *Margaretta buski* Harmer, 1957 (MUN-STRI-47705): (8) branch fragment showing the peristome upturned of the fertile zooids (arrowed); (9) detail of the peristome and secondary orifice; (10) detail of the circular ascopore. *Hippopodina* aff. *iririkiensis* Tilbrook, 1999 (MUN-STRI-47707): (11) general view; (12) detail of the zooids bearing oral avicularia. All illustrated specimens are from the Siamaná Formation, Arroyo Ekieps. Scale bars are (1, 2, 5, 6, 7, 8, 12) 0.5 mm; (3) 0.15 mm; (4) 0.25 mm; (9, 10) 0.1 mm; (11) 1mm.

Discussion.—Six additional fossil species of *Margaretta* were recorded in the American continent. Canu and Bassler (1920) introduced the species (as *Tubucellaria*) *M. fallax*, *M. nodifera* and *M. parviporsosa* from the Eocene of Alabama, Florida and North Carolina, respectively, and *M. vicksburgica* from the Oligocene of Alabama. *Margaretta buski* differs from all these species in having smaller zooids, less than 1 mm long; in addition, *M. nodifera* has zooids with tuberosities. The Eocene species *M. congesta* (Cheetham, 1963) and the Miocene species *M. pentaceratops* Di Martino, Taylor and Portell, 2017, both from Florida, differ from *M. buski* in having eight rows of smaller and densely packed zooids and peristome with five spiniform processes, respectively. *Margaretta buski* resembles *M. cereoides* (Ellis and Solander, 1786), known from the Mediterranean and east Atlantic from the Miocene to Recent, in the general appearance including the shape and arrangement of autozooids; however, it differs in having bipartite basis rami instead of undivided, and three zooids per whorl instead of four or five (Harmer, 1957). The small fragments of *Margaretta buski* studied here were found in the sediment cemented to the corals *Goniopora hilli* and *Acropora panamensis*, co-occurring with *Nellia tenella* (Lamarck 1816), *Ditaxiporina* n. sp., *Mecynoecia* sp., *Catenicella* sp., *Reteporellina* sp., and '*Licornia*' sp.

Table 29. Measurements of *Margaretta buski*.

Character	**X**	**R**	**SD**	**N**
Autozooid length	0.91	0.82–1.06	0.104	4
Autozooid width	0.39	0.35–0.42	0.026	5
Orifice diameter	0.17	0.16–0.18	0.008	5
Peristome width	0.19	0.11–0.26	0.106	2
Foramen diameter	0.03	0.03–0.04	0.006	3
Pores diameter	-	0.02	-	10

Family Hippopodinidae Levinsen, 1909

Genus *Hippopodina* Levinsen, 1909

Type species.—*Lepralia feegeensis* Busk, 1884 from Bisayas Sea, Philippines, Recent; by original description.

Hippopodina aff. *iririkiensis* Tilbrook, 1999

Figures 31.11, 31.12, 32.1, 32.2; Table 30

Occurrence.—Early Miocene in Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids distinct by deep furrows and a narrow thread, rounded polygonal, longer than wide (mean L/W 1.38). Frontal shield convex, finely granular, evenly perforated by numerous (around 130), circular pores, about 0.20 mm in diameter. Larger, fusiform pores at the distal corners of the zooids sometimes visible. Orifice terminal, hoof-shaped, two robust condyles separating a semicircular anter from a shallow, broad sinus with proximal border flat to slightly concave. Adventitious avicularium single, sometimes absent, lateral to the orifice, originating at the same level as the orificial proximal margin and extending for the total length of the orifice; rostrum raised, narrow and acutely triangular, oriented distolateral and medially; crossbar complete. Ovicells and ancestrula not observed.

Discussion.—In the fossil record of North America two species of *Hippopodina* are known from the Eocene of Georgia and Florida (USA): *H. stephensi* Cheetham, 1962 and *H. vibraculifera* Canu and Bassler, 1917, respectively. The former species differs from *Hippopodina* aff. *iririkiensis* in having adventitious avicularia often paired, placed and directed proximolaterally to the orifice, while the latter species has avicularia placed distally and oriented proximally. In addition, five Recent species are known from off North America: *H. pulcherrima* (Canu and Bassler, 1928) from Western Atlantic; *H. bernardi* Lagaaij, 1963 from the Gulf of Mexico; *H. irregularis* Osburn, 1940 from the Caribbean Sea; *H. tahitiensis* Leca and d'Hondt, 1993 from the Caribbean Sea, India and Africa; and *H. californica* Osburn, 1952 from the Pacific coast of USA. However, *Hippopodina californica* and *H. irregularis* lack avicularia; *H. bernardi* has centrally imperforate frontal shield; *H. tahitiensis* bears single or paired, small, drop-shaped avicularia placed distolaterally and oriented distally; and *H. pulcherrima*, the most common in the Caribbean region (Tilbrook, 1999), has a narrower sinus and avicularia single or paired, located beside the orifice, oriented proximomedially. *Hippopodina indicata* Di Martino and Taylor, 2015 found in Miocene (late Burdigalian) coral reefs from East Kalimantan shows similar adventitious avicularia which, however, originate more proximally and point to the orificial condyles. Our specimens closely resemble the Recent *H. iririkiensis* Tilbrook, 1999 recorded in the Indo-West Pacific, Australia and the Mediterranean Sea in the shape, location and direction of the avicularia, and the shape of the orifice; however, *H.* aff. *iririkiensis* has larger zooids (1.12 x 0.82 mm vs. 0.9 x 0.62 mm). In the Siamaná Formation, *Hippopodina* aff. *iririkiensis* was found encrusting the coral species *Porites anguillensis* and *Millepora* sp., co-occurring with *Poricella* n. sp.

Table 30. Measurements of *Hippodina* aff. *iririkiensis*.

Character	X	R	SD	N
Autozooid length	1.12	0.97–1.24	0.091	14
Autozooid width	0.82	0.71–1	0.082	11
Orifice length	0.32	0.29–0.35	0.023	8
Orifice width	0.31	0.29–0.34	0.016	9
Avicularium length	0.40	0.36–0.45	0.045	3
Avicularium width	0.13	0.12–0.15	0.015	3

Family Marcusadoreidae Winston, Vieira and Woollacott, 2014

Genus *Marcusadorea* Vieira, Migotto and Winston, 2010

Type species.—*Marcusadorea jamaicensis* Vieira, Migotto and Winston, 2010 from Jamaica, Caribbean Sea, Recent, by original description.

Marcusadorea n. sp.

Figure 32.3–32.6; Table 31

Holotype.—MUN-STRI-47709, from the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting. Orifice surrounded by a well-developed, imperforate peristome, taller distolaterally, forming a U-shaped sinus proximally. Frontal shield granular, evenly pseudoporous except for the peristome. Two small adventitious avicularia placed at the distolateral corners of the zooid. Ovicell globular, granular and porous as the frontal shield, placed on the peristome.

Description.—Colony encrusting, multiserial, uni- to multilaminar. Autozooids large, distinct by narrow grooves, recumbent to semi-erect, rhomboidal to irregularly polygonal, slightly longer than wide (mean L/W 1.15). Frontal shield slightly convex, granular, evenly perforated, except for the peristome, by 20 to 100 (depending on the length of the zooid) circular pseudopores about 0.03 mm in diameter; occasionally two to three rows of marginal pores distally, and slightly larger pores along the zooidal edges. Orifice terminal to subterminal; primary orifice hidden by a distolaterally well-developed peristome forming a secondary orifice with U-shaped sinus; secondary orifice slightly larger in ovicellate zooids. Adventitious avicularia small, circular, placed on the distolateral corners of the zooids; crossbar or pivotal condyles not preserved. Ovicell hyperstomial, globular, opening into the peristome; ooecium surface granular and pseudoporous as the frontal shield. Ancestrula unknown.

Discussion.—Based on the presence of a well-developed peristome and peristomial ovicells, we assign this specimen to the genus *Marcusadorea*. *Marcusadorea* n. sp. closely resembles *M. pinheroi* Almeida, Souza, Menegola and Vieira, 2017 in the general aspect and size of the zooids and ovicells, as well as in the density and distribution of the pores. However, it differs from this species and other congeners in having two small avicularia in the distolateral corners of the zooids. In addition, it differs from *M. pinheroi* in having recumbent zooids and secondary orifice with a narrower sinus and, and from other congeners in having the frontal shield highly pseudoporous and in the lack of suboral avicularia. Species of the genus *Saevitella* Bobies, 1956 also have granular and pseudoporous frontal shield and ovicells (Berning, 2012, p. 43, Fig. 13–18) but lack avicularia. *Marcusadorea* n. sp. also resembles *Cosciniopsis lonchaea* (Busk, 1884) in having a developed peristome, frontal shield tuberculate and pseudoporous, and adventitious avicularia, but the latter species has one or two triangular avicularia close to the orifice, conspicuous condyles, and lateral walls with uniporous septula (Tilbrook, 2006, p. 236, 237, pl. 52, figs. a–c). In the Siamaná Formation, *Marcusadorea* n. sp. was found encrusting cavities of the coral *Porites anguillensis*.

Table 31. Measurements of *Marcusadorea* n. sp.

Character	**X**	**R**	**SD**	**N**
Autozooid length	0.77	0.54–0.94	0.120	8
Autozooid width	0.67	0.6–0.84	0.089	8
Orifice primary length	0.18	0.17–0.19	0.014	2
Orifice primary width	0.18	0.17–0.18	0.007	2
Orifice secondary length	0.22	0.21–0.25	0.014	12
Orifice secondary width	0.18	0.16–0.21	0.014	11
Avicularium diameter	0.12	0.1–0.14	0.012	10
Avicularian opesia diameter	0.06	0.06–0.06	0	7
Ooecium length	-	0.24	-	1
Ooecium width	-	0.4	-	1

Superfamily Celleporoidea Johnston, 1838
Family Phidoloporidae Gabb and Horn, 1862

Pleuromucrum sp. indet.
Figure 32.7–32.9; Table 32

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Uitpa, Colombia.

Description.—Colony encrusting, multiserial, unilaminar. Autozooids almost indistinct, subrhomboidal to oval, slightly longer than wide (mean L/W 1.19). Frontal shield smooth, generally slightly depressed but raised suborally, imperforate except for two to four, small marginal pores. Orifice bell-shaped, almost as long as wide, bearing two robust, triangular condyles; four distolateral oral spine bases; proximal border with a poorly developed or poorly preserved umbo. Adventitious avicularium single, placed on one side of the frontal shield slightly below the orifice; rostrum rounded triangular, directed proximolaterally, seemingly with pivotal condyles. Ooecium broken, apparently small and circular in outline.

Discussion.—We place this specimen in *Pleuromucrum* Vigneaux, 1949 based on the shape of the orifice, the imperforate frontal shield with few, sparse marginal pores, the presence of frontal triangular avicularia, oral spines and suboral umbo, and the proportionally small ovicell (Di Martino and Taylor, 2017). The smooth appearance of the frontal shield (in *Pleuromucrum* is usually nodular) is likely due to preservation, which also prevents species-level assignment. In the Siamaná Formation, *Pleuromucrum* sp. indet. was found encrusting coralline algae.

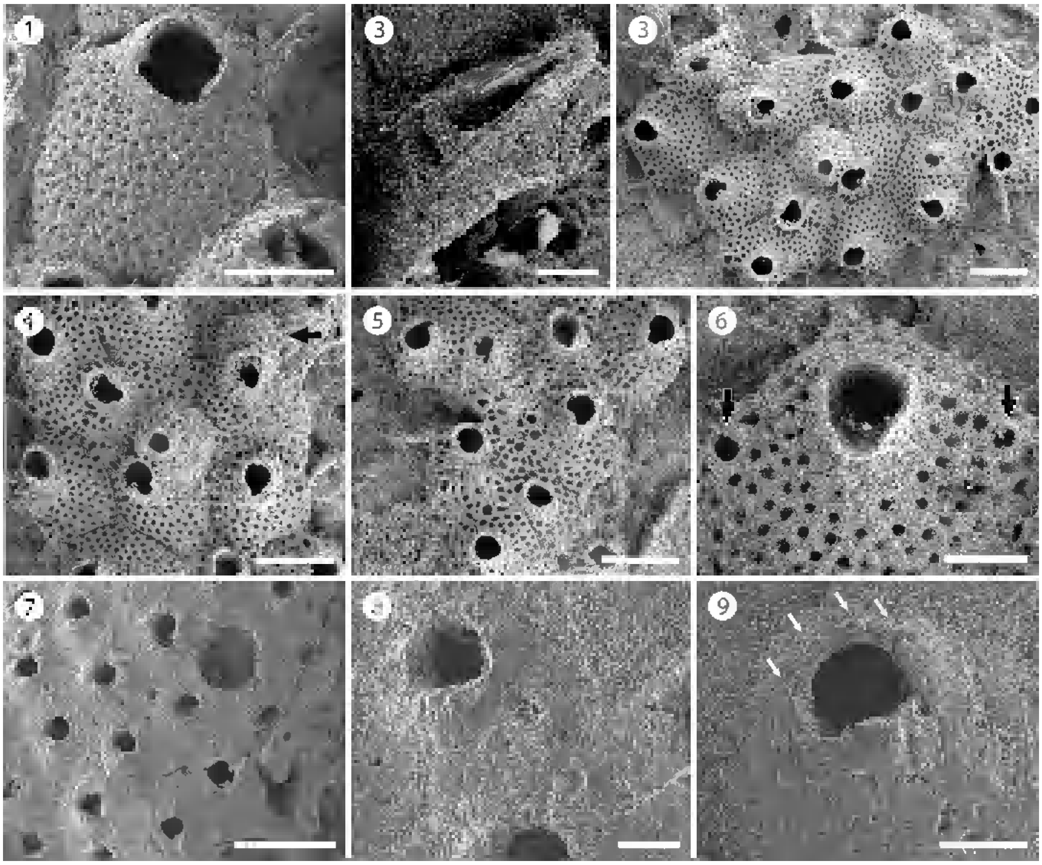

Figure 32. *Hippopodina* aff. *iririkiensis* Tilbrook, 1999 (MUN-STRI-47708) from the Siamaná Formation, Arroyo Ekieps: **(1)** detail of a zooid, orifice showing a condyle; **(2)** detail of an avicularium with crossbar complete. *Marcusadorea* n. sp. (Holotype MUN-STRI-47709) from the Siamaná Formation, Arroyo Ekieps: **(3)** general view; **(4)** detail of a group of zooids recumbent and a fertile zooid (arrowed); **(5)** detail of the peristomes and sinus of the secondary orifice; **(6)** detail of the avicularia rounded (arrowed). *Pleuromucrum* sp. indet. (MUN-STRI-47710) from the Siamaná Formation, Arroyo Uitpa: **(7)** general view; **(8)** detail of a zooid bearing an avicularium; **(9)** detail of the orifice showing oral spines (arrowed), condyles and suboral umbo. Scale bars are **(1, 3, 4, 5, 7)** 0.5 mm; **(2, 8, 9)** 0.1 mm; **(6)** 0.2 mm.

Table 32. Measurements of *Pleuromucrum* sp. indet.

Character	**X**	**R**	**SD**	**N**
Autozooid length	0.44	0.43–0.45	0.008	4
Autozooid width	0.37	0.31–0.42	0.047	4
Orifice length	0.10	0.09–0.11	0.006	9
Orifice width	0.11	0.1–0.12	0.010	8
Avicularium length	0.12	0.11–0.13	0.010	3
Avicularium width	0.08	0.08–0.08	0.000	2
Ooecium length	-	0.12	-	1
Ooecium width	-	0.15	-	1

Genus *Reteporellina* Harmer, 1933

Type species.—*Retepora denticulata* Busk, 1884 from Honolulu, Hawaii, North Pacific, Recent; by original description.

Reteporellina sp. indet.

Figure 33.1–33.5; Table 33

Occurrence.—Early Miocene, Siamaná Formation, Arroyo Ekieps, Colombia.

Description.—Colony erect, rigid. Branches cylindrical to slightly flattened, 0.32–0.50 mm wide. Autozooids distinct by raised ridges, subrhomboidal, arranged alternately in three longitudinal rows on one side of the branch, more than twice as long as wide (mean L/W 2.10). Primary orifice hidden by a rpoximally well-developed peristome with a U-shaped sinus medially. Frontal shield slightly convex, perforated by a pair of marginal areolar pores placed proximally at about one-third of the total length of the zooid. Adventitious avicularia large, placed on a suboral, raised cystid; rostrum bifid, oriented laterofrontally. Ovicell hyperstomial, globular, longer than wide, seemingly with a medial suture. Abfrontal surface smooth with irregular vibices; no avicularia or pores observed.

Table 33. Measurements of *Reteporellina* sp. indet.

Character	X	R	SD	N
Autozooid length	0.36	0.3–0.41	0.057	3
Autozooid width	0.17	0.17–0.18	0.006	3
Orifice length	-	0.08	-	1
Orifice width	0.10	0.09–0.1	0.006	4
Avicularium length	-	0.13	-	1
Ooecium width	0.16	0.15–0.17	0.010	4

Discussion.—Seven Recent species of *Reteporellina* are known in America: *R. marsupiata* (Smitt, 1873) from West Atlantic; *R. prominens* (Canu and Bassler, 1928) from the Gulf of Mexico; *R. directa* Winston and Woollacott, 2009 from Barbados; *R. evelinae* Marcus, 1955 from Brazil; *R. moyanoi* d'Hondt, 1981 from Uruguay and the Pacific coast; *R. bilabiata* Osburn, 1952 from the Gulf of California; and *R. denticulata gracilis* Osburn, 1952 from Ecuador and Costa Rica. Among them, *R. directa* and *R. moyanoi* differs from *Reteporellina* sp. indet. in having the frontal avicularia oriented proximally not laterofrontally. *Reteporellina prominens* and *R. denticulata gracilis* have small frontal avicularia, rounded and drop-shaped, respectively; *R. bilabiata* has frontal avicularia with triangular rostrum, placed proximolateral to the orifice, and avicularia also on the abfrontal surface. *Reteporellina* sp. indet. closely resembles *R. evelinae* and *R. marsupiata* in the arrangement of the zooids and in having frontal avicularia with bifid rostra. However, the poor preservation of the specimen prevents any further comparison. In the Siamaná Formation, *Reteporellina* sp. indet. was found in the sediment adhering to the corals *Acropora panamensis* and Caryophyllidae sp., co-occurring with *Margaretta buski, Catenicella* sp., *Licornia* sp. and *Ditaxiporina* n. sp.

Genus *Rhynchozoon* Hincks, 1895

Type species.—*Lepralia bispinosa* Johnston, 1847 from Berwick Bay, United Kingdom, North Sea, Recent; by original description.

Rhynchozoon sp. indet.

Figure 33.6–33.10; Table 34

Description.—Colony encrusting, multiserial, uni- to multilaminar. Autozooids distinct at the colony growing edge, oval to claviform, longer than wide (mean L/W 1.82) but indistinct, erect to semi-erect, and irregularly arranged in central, older areas. Frontal shield convex, smooth to slightly ribbed, imperforate except for 14–16 circular to drop-shape marginal areolar pores (0.03 mm in diameter) separated by ridges. Orifice subcircular. Suboral mucro bearing apically a small, rounded avicularium with complete crossbar, and rostrum oriented laterally. Often, two additional, raised hooked processes flanking the medial mucro. Dimorphic interzooidal avicularia placed between the erect zooids: large, triangular, placed proximolateral to the orifice, oriented proximally or elliptical oriented proximolaterally; both types with complete crossbar. Ovicells not observed.

Discussion.—Based on its general appearance including the arrangement of the zooids, the well developed suboral processes, and monomorphic suboral avicularia, we assign these specimens to *Rhynchozoon*. However, the poor preservation prevents the comparison with congeners and nomenclature remains open. In the Siamaná Formation, *Rhynchozoon* sp. indet. was found encrusting the hydrocoral *Millepora alcicornis* Linnaeus, 1758 and the scleractinian *Colpophyllia willoughbiensis*, co-occurring with *Calpensia nobilis* and *Copidozoum* sp. indet.

Table 34. Measurements of *Rhynchozoon* sp. indet.

Character	X	R	SD	N
Autozooid length	0.65	0.54–0.72	0.066	5
Autozooid width	0.36	0.33–0.41	0.031	6
Orifice length	0.14	0.13–0.14	0.006	3
Orifice width	0.15	0.14–0.17	0.015	3
Avicularium suboral rounded length	0.12	0.11–0.13	0.012	3
Avicularium suboral rounded width	0.09	0.08–0.09	0.006	3
Avicularium suboral tiangular length	-	0.43	-	1
Avicularium suboral tiangular length	-	0.28	-	1
Avicularium frontal length	0.14	0.13–0.15	0.014	2
Avicularium frontal length	0.11	0.11–0.11	0	2

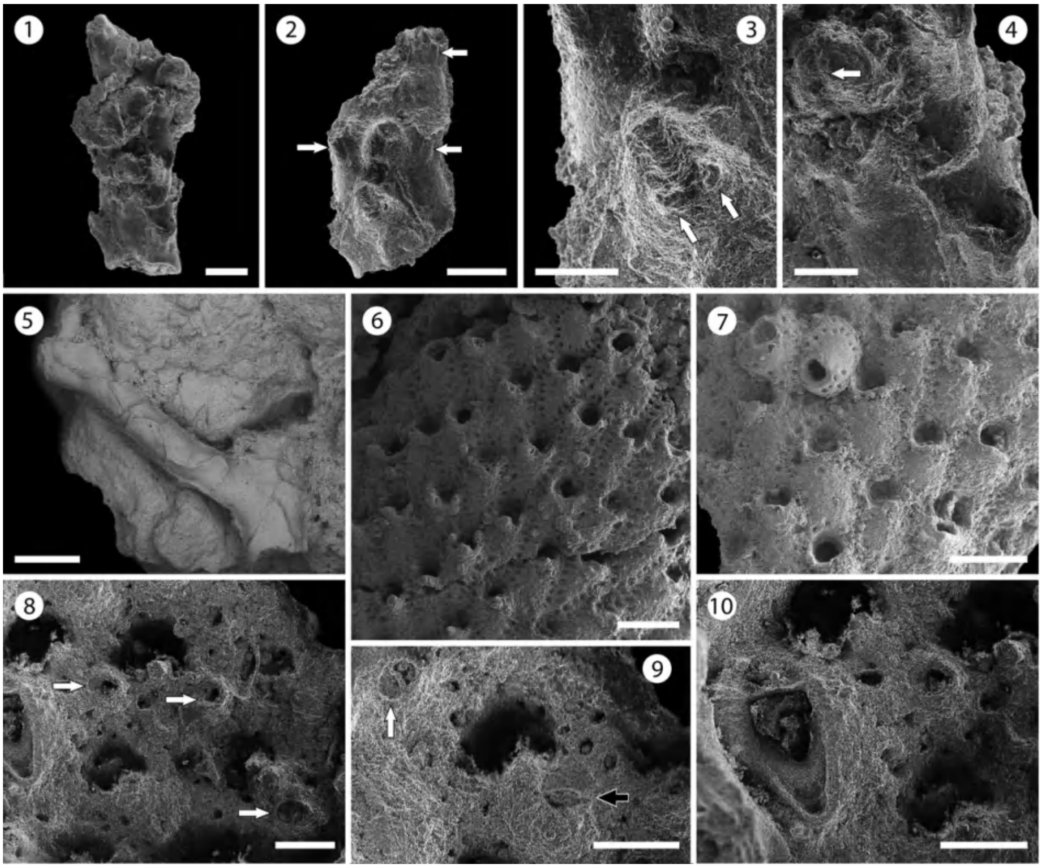

Figure 33. *Reteporellina* sp. indet. (MUN-STRI- 47712): **(1)** general view of the branch fragment showing three rows of zooids; **(2)** detail of the sinus in the peristomes (arrowed); **(3)** detail of the suboral avicularia bifid (arrowed); **(4)** detail of the medial suture of the ovicell (arrowed); **(5)** detail of the vibices of the abfrontal surface. *Rhynchozoon* sp. indet. (MUN-STRI-47713): **(6)** general view of the zooids; **(7)** group of zooids showing the primary subcircular orifice; **(8)** detail of erect zooids and rounded avicularium (arrowed); **(9)** detail of the secondary orifice showing suboral avicularia (black arrow) and oval avicularia (white arrow); **(10)** detail of the interzooidal triangular avicularia. All illustrated specimens are from the Siamaná Formation, Arroyo Ekieps. Scale bars are **(1, 2, 8, 9, 10)** 0.2 mm; **(3, 4)** 0.1 mm; **(5, 6, 7)** 0.5 mm.

5.2 Paleocologic and paleobiogeographic significance of bryozoan assemblages

The early Miocene (ca. 23–20 Ma) coral reefs of the Siamaná Formation in Colombia yielded 32 bryozoan morphospecies. Among them, 19% are species previously described and recorded in the Caribbean region. Except for *Nellia tenella* and *Calpensia nobilis*, the Colombian early Miocene represents the oldest occurrence of these species (Fig. 34, indicated with stars) and consequently their age range is extended. In addition, *Hippopleurifera mucronata*, *Smittipora elongata* and *Calpensia nobilis* were for the first time found associated with coral reef environments.

New species account for the 25% of the whole assemblage. Three new species belong to the family Cribrilinidae, and one each to Onychocellidae, Steginoporellidae, Catenicellidae, Arachnopusiidae and Marcusadoreidae. Two new genera, one in Onychocellidae and other in Steginoporellidae, were also introduced to accommodate two new species.

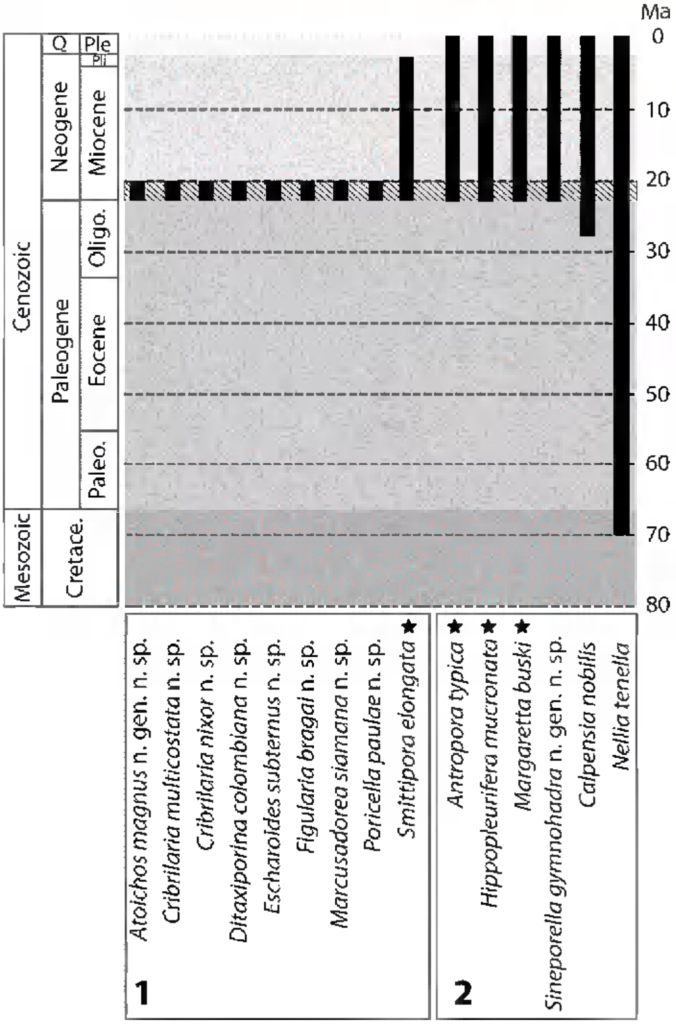

Figure 34. Range chart of first and last occurrence in the Great Caribbean Region and Gulf of Mexico of the species reported here, indicating the species whose range has been extended to the early Miocene (stars). Striped interval indicates the estimated stratigraphic range of reefs in the Siamaná Formation (ca. 23–20 Ma).

Three morphospecies are identified as *affinis* to preexisting species. The remaining species (47%) were left in open nomenclature, one identified at family level and 15 at genus level. This high percentage of undetermined morphospecies depends on the poor preservation caused by weathering, dissolution and recrystallization, and/or mechanical abrasion, which resulted in the loss or deformation of key skeletal features. It is well known that tropical Cenozoic carbonates, especially coral reefs, experience rapid cementation (Macintyre, 2011) and severe diagenetic alterations greatly affecting aragonitic organisms, even to the complete loss of the aragonitic component. According to a survey conducted by Taylor and Di Martino (2014) on tropical cheilostome bryozoans encrusting the underside of platy corals, 27% of species are aragonitic and 30% bimineralic, suggesting a loss of species richness by default. Furthermore, the preservation of bryozoan skeletons may be impacted by the diagenetic processes affecting their aragonitic substrates, such as scleractinian corals (as in this case) or mollusks (Taylor and Di Martino, 2014).

Six out of the seven previously known species are still living today (Fig 34, box 2), the exception being *Smittipora elongata* recorded in the Caribbean only until the end of the Pliocene. At the present day, two of these species, *Sineporella gymnohadra* and *Calpensia nobilis*, are absent from the Caribbean but thrives in the American Pacific waters (Schäfer et al., 2012), and in the Mediterranean Sea (Rosso and Di Martino, 2016) and eastern central Atlantic (Buge, 1957; Hayward and Ryland, 1998), respectively. All the remaining species continue to inhabit the Caribbean Sea, in particular *Nellia tenella* and *Margaretta buski* are present in the Colombian Caribbean (Flórez et al., 2007; Montoya-Cadavid et al., 2007).

Some species found in the Siamaná Formation were previously recorded in other Oligocene and Miocene formations in North America, the Caribbean region and Brazil: *Nellia tenella* (Pirabas Fm., early Miocene, Brazil; Chickasawhay Fm., Oligocene, Alabama USA; Cercado Formation, late Miocene, Dominican Republic); *Calpensia nobilis* (Antigua Fm., Oligocene, Antigua); *Smittipora elongata* (Duplin Marl, late Miocene, North Carolina, USA); and *Hippopleurifera mucronata* (Chipola Fm., early Miocene, Burdigalian, Florida, USA). *Antropora typica* was also found in Pleistocene continental shelf sediments in Venezuela. Nevertheless, the Siamaná bryozoan assemblage as a whole is different from the bryozoan faunas of those formations.

The finding of *C. nobilis* in the Siamaná Formation confirms the isolated record of Canu and Bassler (1923) in Antigua Island. The distribution of *C. nobilis* may suggest a faunal connection in the Miocene between the southern Caribbean and the Mediterranean Sea across Macaronesia, favored by the high capacity of this species to grow on several kind of substrates and to live in several environments at different depths from 10 to 100 m (Canu and Bassler, 1930). However, the existence of a species complex cannot be completely ruled out.

Except '*Lepralina*', which was described from the Miocene of Austria, all genera found in the Siamaná Formation were previously recorded, both fossil and live, in the Great Caribbean Region and Gulf of Mexico (Cheetham et al., 1999, 2007; Taylor, 2001; Winston, 1984, 1986, 2005; Montoya-Cadavid et al., 2007; Di Martino et al., 2017, 2019). The age range of six genera was extended to the early Miocene (Fig. 35).

The relative proportions of cyclostomes (6%) and cheilostomes (94%) follow the general pattern observed from the Miocene to the Pleistocene in the Caribbean region (Cheetham et al., 1999; Taylor, 2001; Di Martino and Taylor, 2014, 2015), and in Recent coral-associated bryozoan faunas (Winston, 1986).

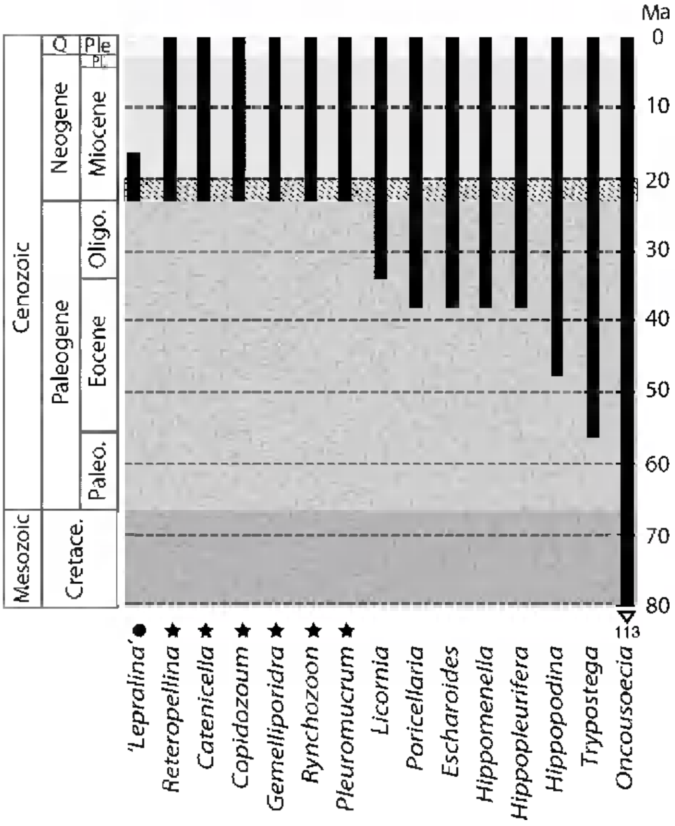

Figure 35. Range chart of first and last occurrence in the Great Caribbean Region and Gulf of Mexico of the genera reported here, indicating the genera whose range has been extended to the early Miocene (stars), and the genus recorded for the first time in the Caribbean Region (black circle). Striped interval indicates the estimated stratigraphic range of reefs in the Siamaná Formation (ca. 23–20 Ma). Sources information: Canu and Bassler (1920, 1923); Kühn (1925); Bobies (1956); Cheetham (1962, 1963); Cheetham et al. (1999); Di Martino et al. (2017, 2019); Martha et al. (2019).

In the Siamaná Formation, 75% of species are encrusting, 24% erect including 18% articulated and 6% rigid. These proportions are similar in Recent communities and in some fossil assemblages in tropical coral reef environments (Winston, 1986; Cheetham and Jackson, 2000; Hamdane and Moissette, 2002; Cuffey, 2011; Di Martino et al., 2015). By contrast, taxa with free-living colonies, which are diverse and abundant from the middle Miocene (from ca. 15 Ma) to Recent environments in the Caribbean region (Cheetham and Jackson, 2000; O'Dea, 2009; Flórez et al., 2007) are absent in this study. This is probably a sampling bias due to collection focused on reef framework, whereas free-living bryozoans live on soft bottoms surrounding the reefs, as well as at greater depths in muddy environments (O'Dea, 2009).

Species richness varies greatly among the three sampling localities: 75% of species were found in Arroyo Ekieps, 25% in Uitpa and 3% in Flor de La Guajira (Appendix 2). The highest species richness in Arroyo Ekieps is associated with a higher structural complexity compared to Arroyo Uitpa and Flor de La Guajira. The paleoenvironments of Arroyo Uitpa locality was characterized as patch reefs developed in a shallow lagoon close to the shore-line, while Arroyo Ekieps was a discontinuous barrier reef system, which offered a wide variety of microhabitats enhanced by the structural complexity of the reef framework. This suggests an increase of bryozoan diversity with higher reef complexity, as has been observed in modern reefs off Andros and Eleuthera in the Bahamas (Cuffey and Fonda, 1977). A single species, ?*Hippomenella* sp. indet. 1, was found in Flor de La Guajira, and was also present in Arroyo Uitpa. The remaining species are exclusive of each locality.

Compared to other bryozoan faunas associated with Miocene coral reefs, the species diversity in the Siamaná Fm. is significantly lower, e.g., 123 species were reported from Indonesia (Di Martino and Taylor, 2014, 2015), and 56 species from the Mediterranean (Hamdane and Moissette, 2002). In addition to sampling intensity in fresh exposures, the difference in species diversity of the Indonesian reefs can be explained by the high input of siliciclastic sediment that facilitate preservation of the material (Di Martino et al., 2015).

In the Siamaná Formation, the principal substrates encrusted by bryozoans were the bases and undersurfaces of scleractinian corals *Alveopora tampae*, *Acropora panamensis*, *Colpophyllia willoughbiensis*, *Goniopora hilli*, *Porites anguillensis*, *Porites baracoaensis*, *Acropora* sp. and *Porites* sp., the hydrocoral *Millepora* sp., as well as coralline algae and mollusk shells. While the erect articulated species were found in the sediment attached to the bases and inter-branch spaces of corals such as *Goniopora hilli, Alveopora tampae, Acropora panamensis* and Caryophyllidae gen. sp. indet.

Despite to the reduced size of the colonies, the cryptic encrusting bryozoan colonies contribute to the fill of cavities reinforcing the reef framework, and articulated colonies contribute to production of sediment, in accordance to roles of bryozoans in fossil and modern coral reef building in tropical shallow waters (Insalaco, 1998; Cuffey 1977, 2011; Taylor and James, 2013; Ramalho et al., 2018).

Future studies including other reef zones will increase the information about the bryozoan fauna in the Siamaná Formation.

6. Sinopsis

During the late Oligocene–early Miocene (ca. 23 Ma), the present-day Serranías of Macuira, Jarara and Cosinas, in the La Guajira Peninsula, were a cluster of paleoislands, relatively isolated from the continent (Bloch et al., 2016). These ancient islands were surrounded by shallow waters with coral reefs. These reef ecosystems are recorded in coral reef deposits of the Siamaná and Jimol Formations in the Cocinetas Basin.

The Siamaná Formation is a diachronic unit ranging from the late Oligocene to the early Miocene (Silva-Tamayo et al., 2017). Our biostratigraphic findings, point to an early Miocene age for coral reefs in the localities of Arroyo Uitpa, SW Ekieps and Arroyo Ekieps in the Siamaná Formation, while the age of the locality Flor de La Guajira remains unclear. On the other hand, the Jimol Formation is dated as Burdigalian (late early Miocene) (Moreno et al., 2015).

In the Arroyo Uitpa locality, the sedimentological analysis revealed lens-shaped lithofacies of pillarstones and mixstones, separated by rudstones, with some clastic inputs from the Jarara paleoisland. These patch reefs were overlain by prograding beach deposits (grainstone–packstone with low-angle parallel cross-bedding). These features suggest that small coral patch reefs grew close to the shoreline in the Arroyo Uitpa locality.

The SW Ekieps section also reveals small patch reefs, with lens-shaped mixstones and pillarstones surrounded by rudstones, and absence of siliciclastic material, suggesting a higher distance from the paleoshoreline, far from sediment influx from the Jarara paleoisland.

In the Arroyo Ekieps laterally continuous (hundreds of meters) mixstones are interbedded with minor rudstones. Exposures perpendicular to the strike reveal that mixstones and rudstones occur as laterally prograding and offlapping clinobeds. This locality has the highest species richness of corals. The reef-framework geometry, stratigraphic patterns and species richness indicate that reefs in Arroyo Ekieps formed a discontinuous barrier, parallel to the paleoshoreline, which probably enclosed the lagoon where the patch reefs of Arroyo de Uitpa and SW Ekieps sections developed. In general, the maintenance of shallow coral assemblages throughout the sections, the low-relief morphology of the reef bodies, as well as the lateral progradation in Arroyo Ekieps suggest they were keep-up reefs (Newmann and Macintyre, 1985), growing in a stable relative sea level.

The coral taxonomy results show that of the total of 116 species of scleractinian corals from the Oligocene and Miocene known in the Caribbean region, only 22.4%

were observed in the Cocinetas Basin. The morphospecies found were common from the late Oligocene to the early Miocene in the Caribbean region; however, most of them became extinct either at the end of the Burdigalian or in the Pliocene-Pleistocene transition, one of the most critical turnovers for scleractinian corals in the Caribbean (Budd et al., 1996; Budd, 2000; Klaus and Budd, 2003). Except by a member of the family Caryophylliidae and the species *Stylophora minor*, the species studied were considered important building components of shallow coral reefs during the late Oligocene and early Miocene in the Caribbean Sea (Johnson et al., 2009; Budd, 2000). Most corals displayed massive and branching morphologies, and were the main components of the mixstones and pillarstones found in the Siamaná Formation. The species assemblages, both from the Siamaná and Jimol formations, suggest shallow and clear water environments, with moderate physical disturbance.

Regarding the bryozoan fauna, of the total 32 morphospecies found, 25% are new species, probably indicating a low sampling of lower Miocene coral reefs in the southern Caribbean. On the other hand, 56% of morphospecies remain in open nomenclature, due to poor preservation and loss of aragonitic structures during the diagenetic processes. Only 2.6% of the 151 species of Cheilostomes known in the middle-late Miocene from the Caribbean region (Di Martino et al., 2018) were reported in the Siamaná Formation.

The principal substrates of the bryozoans in the Siamaná Formation were the scleractinian corals *Alveopora tampae*, *Acropora panamensis*, *Colpophyllia willoughbiensis*, *Goniopora hilli*, *Porites anguillensis*, *Porites baracoaensis*, *Acropora* sp., *Porites* sp., and Caryophylliidae gen. sp. indet., the hydrocoral *Millepora* sp., as well as coralline algae and mollusk shells. Coral samples from the Jimol Formation lack preserved associated bryozoan fauna, probably due to the high recrystallization of coral samples. Despite of the reduced size of the encrusting and erect bryozoan colonies, they played a role in the cementation and accretion of coral frameworks.

In the Siamaná Formation, both corals as bryozoans showed the highest species richness in coral reefs at the Arroyo Ekieps locality, what is probably the result of increased habitat complexity in barrier reefs compared to coral patches in lagoons, as can be observed in modern analogs.

Our findings contribute to fill information gaps about the early Miocene history of the Caribbean Basin and provide new data about corals and bryozoan fauna in the ancient southern Caribbean. Future studies extending the spatial and temporal sampling will help to understand the local factors that determine the persistence and demise of coral reefs in the Southern Caribbean, as well as to discover new paleoenvironments and species in the region.

7. Conclusions

Coral reefs were widespread in the shallow-water marine ecosystems surrounding the paleoisland of Jarara, in the present-day Colombian Guajira, during the early Miocene (ca. 23-20 Ma).

These reefs developed both as patch reefs in a lagoon, and as a discontinuous coral barrier that surrounded the Jarara paleoisland.

The reefs were mainly built by scleractinian corals. The lithofacies consist of mixstones and pillarstones, dominated by the genera *Porites*, *Montastraea*, *Orbicella* and *Antiguastrea*, surrounded by rudstones dominated by coralline algae, mollusks, echinoderms, bryozoans and larger benthic foraminifera. Grainstones to packstones with low-angle parallel cross-bedding made up of fragments of echinoderms, small and larger benthic foraminifers, bivalves, calcareous algae and corals represent beach deposits that locally prograded on patch reefs.

The bryozoans played a secondary role in the consolidation of reefs. Their cryptic, erect and encrusting colonies contributed in a certain degree to the cementation and accretion of the structure.

These coral ecosystems developed at depths of 2-30 m, in low turbidity and low energy environments, with limited siliciclastic inputs and in relatively stable conditions.

A total of 32 coral morphospecies were identified, described and illustrated. They were classified in two orders (Scleractinia and Anthoathecata), 12 families and 15 genera. Most of them are common from the late Oligocene–early Miocene geologic formations in the Caribbean region.

In the bryozoan assemblages, 32 morphospecies were identified, described and illustrated. They were classified in two orders (Cyclostomata and Cheilostomata), 20 families and 28 genera. Among them, two genera and eight species new to science were discovered. The temporal range of four species and six genera has been extended to the early Miocene, and the paleobiogeographic distribution of a genus has been expanded to the Caribbean region.

The species richness, both of corals and bryozoans, was higher in the discontinuous barrier reefs than in the patch reefs.

Conclusiones

Durante el Mioceno temprano (ca. 23–20 Ma) los ecosistemas marinos de aguas poco profundas que circundaron las paleoisla de Jarara, actual Guajira colombiana, estuvieron dominados por arrecifes de coral.

Estos se desarrollaron coetáneamente en parches arrecifales en una zona de laguna, y en una barrera coralina discontinua que bordeó la paleoisla de Jarara.

Los arrecifes fueron construidos principalmente por corales escleractinios. Las litofacies están constituidas por "mixstones" and "pillarstones", dominadas por los géneros *Porites*, *Montastraea*, *Orbicella* y *Antiguastrea*, rodeadas por "rudstones" con algas, moluscos, equinodermos, briozoos y grandes foraminíferos bentónicos. "Grainstones" a "packstones" con estratificación cruzada paralela de bajo ángulo, compuestos por fragmentos de equinodermos, foraminíferos bentónicos pequeños y grandes, bivalvos, algas calcáreas y coral representan depósitos de playa que localmente progradaron sobre los parches arrecifales.

Los briozoos cumplieron un rol secundario en la consolidación de las construcciones arrecifales. Sus colonias incrustantes y erectas de carácter críptico contribuyeron en algún grado a la cementación y acreción de la estructura.

Estos ecosistemas coralinos se desarrollaron a profundidades de 2–30 m, en ambientes de baja turbidez, baja energía, con aportes limitados de terrígenos y en condiciones relativamente estables.

En total fueron identificadas, descritas e ilustradas 32 morfo-especies de corales, las cuales fueron clasificadas en dos órdenes (Scleractinia y Anthoathecata), 12 familias y 15 géneros. La mayoría de ellas son comunes en las formaciones del Oligoceno terminal–Mioceno temprano en la región del Caribe.

En cuanto a la fauna de briozoos, fueron identificadas, descritas e ilustradas 32 morfo-especies, las cuales fueron clasificadas en dos órdenes (Cyclostomata y Cheilostomata), 20 familias y 28 géneros. Entre los briozoos se han descubierto dos géneros y ocho especies nuevas para la ciencia. Se ha ampliado el registro temporal al Mioceno temprano de cuatro especies y seis géneros, y la distribución paleobiogeográfica de un género se ha extendido a la región Caribe.

En comparación con los parches arrecifales, los arrecifes de barrera discontinua fueron más ricos en especies, tanto de corales como de briozoos.

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List of abbreviations and repositories

MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil.
MUN-STRI	Mapuka Museum of the Universidad del Norte, Barranquilla, Colombia.
NHMUK	Natural History Museum, London, United Kingdom.
NHMUK	The Natural History Museum, London, United Kingdom.
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, USA.
USNM	U.S. National Museum of Natural History, Washington, USA.

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Annex

Annex 1.

Summary of the ages and location of the Caribbean region stratigraphic units, and references used to create the range chart (Fig. 19) and species occurrences (Annex 2). Sources with (*) are stratigraphic works without coral records.

Geologic age	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.,

Geologic age	Age	(Ma)	Formation	Country	Source
					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*.

Geologic age	Age	(Ma)	Formation	Country	Source
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.

Annex 2.

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 Annex 1.

	RB	T	A	LQ	An	L	Nw	BT	Ar	S	P	AC	SL	Cu	Ag	C	SA	PI	Ch	J	Bt	Ta	Sn	V	SD
Formations	**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)**
Species **Age**	**Oligocene**						**O–M**			**Miocene**															
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						

	RB	T	A	LQ	An	L	Nw	BT	Ar	S	P	AC	SL	Cu	Ag	C	SA	PI	Ch	J	Bt	Ta	Sn	V	SD
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											

	RB	**T**	**A**	**LQ**	**An**	**L**	**Nw**	**BT**	**Ar**	**S**	**P**	**AC**	**SL**	**Cu**	**Ag**	**C**	**SA**	**PI**	**Ch**	**J**	**Bt**	**Ta**	**Sn**	**V**	**SD**
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			

	RB	T	A	LQ	An	L	Nw	BT	Ar	S	P	AC	SL	Cu	Ag	C	SA	PI	Ch	J	Bt	Ta	Sn	V	SD
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		
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

	RB	**T**	**A**	**LQ**	**An**	**L**	**Nw**	**BT**	**Ar**	**S**	**P**	**AC**	**SL**	**Cu**	**Ag**	**C**	**SA**	**PI**	**Ch**	**J**	**Bt**	**Ta**	**Sn**	**V**	**SD**
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															

Annex 3.

Coral specimens collected in 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
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

Species	Formation	Locality	Station code	Catalog number MUN-STRI
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

Species	Formation	Locality	Station code	Catalog number MUN-STRI
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
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

Species	Formation	Locality	Station code	Catalog number MUN-STRI
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
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

Species	Formation	Locality	Station code	Catalog number MUN-STRI
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

Species	**Formation**	**Locality**	**Station code**	**Catalog number MUN-STRI**
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
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

Annex 4.

List of bryozoans found in the Siamaná Formation (Cocinetas Basin in La Guajira Peninsula, Colombia). The collection will be hosted at the Mapuka Museum of the Universidad del Norte, Barranquilla-Colombia. Specimens studied but not included in the descriptions because poorly preserved are indicated with an asterisk (*).

Family	Species	Cataloge number MUN-STRI	Locality	Station number	Type of colony	Substrate
Antroporidae	*Antropora* sp.*	47629	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Antroporidae	*Antropora typica*	47628	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Arachnopusiidae	*Poricella* n. sp.	47676	Arroyo Ekieps	550013	Encrusting	*Millepora* sp.
Arachnopusiidae	*Poricella* n. sp.	47677	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Arachnopusiidae	*Poricella* n. sp.	47678	Arroyo Ekieps	550013	Encrusting	*Alveopora tampae*
Arachnopusiidae	*Poricella* n. sp.	47679	Arroyo Ekieps	550013	Encrusting	Caryophylliidae - *Alveopora* sp.
Arachnopusiidae	*Poricella* n. sp.	47680	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Arachnopusiidae	*Poricella* n. sp.	47681	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Arachnopusiidae	gen. sp. indet.	47682	Arroyo Ekieps	550013	Encrusting	*Porites baracoaensis*
Calloporidae	*Copidozoum* sp. indet.	47627	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*
Candidae	*Licornia* sp. indet.	47632	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Candidae	*Licornia* sp. indet.	47633	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Catenicellidae	*Catenicella* sp. indet.	47666	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Catenicellidae	*Ditaxiporina* n. sp.	47668	Arroyo Ekieps	550012	Erect articulated	*Porites* sp.
Catenicellidae	*Ditaxiporina* n. sp.	47667	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*
Catenicellidae	*Ditaxiporina* n. sp.	47669	Arroyo Ekieps	550012	Erect articulated	*Alveopora tampae*
Catenicellidae	*Ditaxiporina* n. sp.	47670	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Catenicellidae	*Ditaxiporina* n. sp.	47671	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Catenicellidae	*Ditaxiporina* n. sp.	47672	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*
Cribrilinidae	'Lepralina' sp. indet.	47646	Arroyo Ekieps	550013	Encrusting	Mollusk shell
Cribrilinidae	*Cribrilaria* n. sp. 1	47653	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 1	47654	Arroyo Ekieps	550013	Encrusting	Mollusk shell
Cribrilinidae	*Cribrilaria* n. sp. 1	47652	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 1	47655	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 1	47656	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*

Family	**Species**	**Cataloge number MUN-STRI**	**Locality**	**Station number**	**Type of colony**	**Substrate**
Cribrilinidae	*Cribrilaria* n. sp. 1	47650	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 1	47651	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 2	47657	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	*Cribrilaria* n. sp. 2	47658	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	Cribrilinidae*	47659	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	Cribrilinidae*	47660	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Cribrilinidae	Cribrilinidae*	47661	Arroyo Ekieps	550013	Encrusting	Undetermined
Cribrilinidae	Cribrilinidae*	47662	Arroyo Ekieps	550013	Encrusting	Mollusk shell
Cribrilinidae	Cribrilinidae*	47663	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	Cribrilinidae*	47664	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Cribrilinidae	Cribrilinidae*	47665	Arroyo Uitpa	550006	Encrusting	Algae over Porites sp.
Cribrilinidae	*Figularia* n. sp.	47647	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*
Cribrilinidae	*Figularia* n. sp.	47648	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Cribrilinidae	*Figularia* n. sp.	47649	Arroyo Ekieps	550013	Encrusting	*Porites baracoaensis*
Entalophoridae	*Mecynoecia* sp. indet.	47624	Arroyo Ekieps	550013	Erect rigid	*Goniopora hilli*
Entalophoridae	*Mecynoecia* sp. indet.	47623	Arroyo Ekieps	550013	Erect rigid	*Goniopora hilli*
Hippopodinidae	*Hippopodina* aff. *iririkiensis*	47708	Arroyo Ekieps	550013	Encrusting	*Millepora* sp.
Hippopodinidae	*Hippopodina* aff. *iririkiensis*	47707	Arroyo Ekieps	550012	Encrusting	*Porites anguillensis*
Marcusadoreidae	*Marcusadorea* n. sp.	47709	Arroyo Ekieps	550011	Encrusting	*Porites anguillensis*
Margarettidae	*Margaretta buski*	47703	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*
Margarettidae	*Margaretta buski*	47704	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*
Margarettidae	*Margaretta buski*	47705	Arroyo Ekieps	550013	Erect articulated	*Acropora panamensis*
Margarettidae	*Margaretta buski*	47706	Arroyo Ekieps	550013	Erect articulated	*Acropora panamensis*
Microporidae	*Calpensia nobilis*	47634	Arroyo Ekieps	550013	Encrusting	*Alveopora tampae*
Microporidae	*Calpensia nobilis*	47635	Arroyo Ekieps	550013	Encrusting	*Colpophyllia willoughbiensis*
Microporidae	*Calpensia nobilis*	47636	Arroyo Ekieps	550013	Encrusting	*Goniopora hilli*
Oncousoeciidae	*Proboscina* sp. indet.	47626	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Oncousoeciidae	*Proboscina* sp. indet.	47625	Arroyo Ekieps	550013	Encrusting	*Alveopora tampae*
Onychocellidae	n. gen. n. sp.	47637	Arroyo Ekieps	550013	Encrusting	Mollusk shell
Onychocellidae	*Smittipora elongata*	47638	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Onychocellidae	*Smittipora elongata*	47639	Arroyo Uitpa	550005	Encrusting	*Porites* sp.

Family	**Species**	**Cataloge number MUN-STRI**	**Locality**	**Station number**	**Type of colony**	**Substrate**
Phidoloporidae	*Rhynchozoon* sp. indet.	47713	Arroyo Ekieps	550008	Encrusting	*Millepora alcicornis*
Phidoloporidae	*Rhynchozoon* sp. indet.	47714	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*
Phidoloporidae	*Rhynchozoon* sp. indet.	47715	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*
Phidoloporidae	*Rhynchozoon* sp. indet.	47716	Arroyo Ekieps	550012	Encrusting	*Goniopora hilli*
Phidoloporidae	*Rhynchozoon* sp. indet.	47717	Arroyo Ekieps	550012	Encrusting	*Goniopora hilli*
Phidoloporidae	*Rhynchozoon* sp. indet.	47718	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*
Phidoloporidae	*Reteporellina* sp. indet.	47711	Arroyo Ekieps	550013	Erect rigid	Caryophylliidae - *Acropora panamensis*
Phidoloporidae	*Reteporellina* sp. indet.	47712	Arroyo Ekieps	550013	Erect rigid	*Acropora panamensis*
Phidoloporidae	*Pleuromucrum* sp. indet.	47710	Arroyo Uitpa	550006	Encrusting	Coraline algae
Poricellariidae	*Poricellaria* sp. indet.	47645	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*
Quadricellariidae	*Nellia tenella*	47630	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*
Romancheinidae	?*Hippomenella* sp. indet. 1	47686	Flor de La Guajira	550002	Encrusting	Caryophylliidae
Romancheinidae	?*Hippomenella* sp. indet. 1	47687	Arroyo Uitpa	550005	Encrusting	*Porites* sp. - Algae
Romancheinidae	?*Hippomenella* sp. indet. 1	47688	Arroyo Uitpa	550005	Encrusting	*Porites* sp. - Algae
Romancheinidae	?*Hippopleurifera* sp. indet.	47696	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Romancheinidae	?*Hippopleurifera* sp. indet.	47697	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Romancheinidae	?*Hippopleurifera* sp. indet.	47698	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Romancheinidae	?*Hippomenella* sp. indet. 2	47691	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Romancheinidae	?*Hippopleurifera* sp. indet.	47699	Arroyo Ekieps	550013	Encrusting	Caryophylliidae - *Acropora* sp.
Romancheinidae	?*Hippomenella* sp. indet. 2	47692	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*
Romancheinidae	?*Hippomenella* sp. indet. 1	47689	Arroyo Uitpa	550006	Encrusting	?*Millepora* sp.
Romancheinidae	?*Hippomenella* sp. indet. 1	47690	Arroyo Uitpa	550006	Encrusting	?*Millepora* sp.
Romancheinidae	*Escharoides* aff. *martae*	47683	Arroyo Uitpa	550006	Encrusting	*Porites* sp.
Romancheinidae	*Escharoides* aff. *martae*	47685	Arroyo Uitpa	550006	Encrusting	*Porites* sp.
Romancheinidae	*Hippopleurifera mucronata*	47693	Arroyo Uitpa	550005	Encrusting	*Porites* sp. - Algae
Romancheinidae	*Hippopleurifera mucronata*	47694	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Romancheinidae	*Hippopleurifera mucronata*	47695	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Schizoporellidae	*Gemelliporidra* aff. *magniporosa*	47700	Arroyo Ekieps	550012	Encrusting	*Porites baracoaensis*
Schizoporellidae	*Gemelliporidra* aff. *magniporosa*	47701	Arroyo Ekieps	550012	Encrusting	*Alveopora tampae*
Schizoporellidae	*Gemelliporidra* aff. *magniporosa*	47702	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.
Steginoporellidae	n. gen. n. sp.	47641	Arroyo Uitpa	550006	Encrusting	*Porites* sp.

Family	**Species**	**Cataloge number MUN-STRI**	**Locality**	**Station number**	**Type of colony**	**Substrate**
Steginoporellidae	n. gen. n. sp.	47642	Arroyo Uitpa	550005	Encrusting	Undetermined
Steginoporellidae	n. gen. n. sp.	47643	Arroyo Uitpa	550005	Encrusting	Algae over *Porites* sp.
Steginoporellidae	n. gen. n. sp.	47640	Arroyo Uitpa	550005	Encrusting	Algae over *Porites* sp.
Steginoporellidae	n. gen. n. sp.	47644	Arroyo Uitpa	550005	Encrusting	*Porites* sp.
Trypostegidae	*Trypostega* sp. indet.	47675	Arroyo Uitpa	550005	Encrusting	*Porites* sp.

Appendix

Appendix 1.

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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).

Appendix 2.

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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

Appendix 3.

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Early Miocene coral reef-associated bryozoans from Colombia. Part I: Cyclostomata, 'Anascan', Cribrilinoidea and Catenicelloidea Cheilostomata

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