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Early Miocene coral reef-associated bryozoans from Colombia. Part I: Cyclostomata, "Anasca" and Cribrilinoidea Cheilostomata

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Abstract.—This is the first of two comprehensive taxonomic works on the early Miocene (ca. 23–20 Ma) bryozoan fauna associated with coral reefs from the Siamaná Formation, in the remote region of Cocinetas Basin in the La Guajira Peninsula, northern Colombia, southern Caribbean. Fifteen bryozoan species in 11 families are described, comprising two cyclostomes and 13 cheilostomes. Two cheilostome genera and seven species are new: *Antropora guajirensis* n. sp., *Calpensia caribensis* n. sp., *Atoichos magnus* n. gen. n. sp., *Gymnophorella hadra* n. gen. n. sp., *Cribrilaria multicostata* n. sp., *Cribrilaria nixor* n. sp., and *Figularia bragai* n. sp. Eight species are identified only at genus level and remain in open nomenclature. Of the species found, 27% have erect colonies and 73% encrusting colonies. Both types contributed to the reef framework and produced sediment. The observed bryozoan diversity was higher in the barrier reefs than in the lagoonal patch reefs.

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Introduction

Within a generally high marine biodiversity (Jackson and Johnson, 2001; Buzas et al., 2002), bryozoan diversity in Cenozoic tropical latitudes was also very high (Di Martino et al., 2017, 2019). In the Caribbean, a notable increase of bryozoan species richness has been recorded since the Burdigalian (ca. 18 Ma) (Cheetham and Jackson, 1996; Cheetham et al., 1999; O'Dea et al., 2004; Di Martino et al., 2017, 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), and several other factors, have undoubtedly biased against the fossil record of bryozoans in the Cenozoic tropics (Taylor and Di Martino, 2014). In addition to the limited collection effort, small bryozoan colonies tended to be overlooked in the field and inventories are therefore largely incomplete. Consequently, taxonomic studies of bryozoan faunas from the early Miocene are generally limited not only for the Caribbean/Gulf of Mexico region (e.g., Sandberg, 1962; Cheetham et al., 1999, 2007; Herrera-Cubilla and Jackson, 2014; Di Martino et al., 2017), the western Atlantic (e.g., Zágoršek et al., 2014; Ramalho et al., 2015, 2017, 2019), or the Indo-Pacific (e.g., Li, 1990; Guha and Gopikrishna, 2005, 2007; Di Martino and Taylor, 2014, 2015), but also for the more thoroughly investigated Paratethys/Mediterranean Sea (e.g., Duvergier, 1920; Buge, 1973; Nikulina and Taylor, 2010; Vávra, 2012; Di Martino and Taylor, 2017).

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; Ramalho et al., 2018). In addition, a high diversity of macroinvertebrates (e.g., sponges, crabs, and mollusk shells) are susceptible to colonization by bryozoans (e.g., Almeida et al., 2017; Di Martino et al., 2019). Although bryozoans are not the most abundant organisms in these tropical ecosystems in terms of biomass, their species diversity is relatively high (e.g., Santodomingo et al., 2015).

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 and Winston, 1982; Choi, 1984; Winston, 1984, 1986; Winston and Jackson, 1984; Jackson et al., 1985). However, comprehensive taxonomic studies of bryozoan faunas in ancient coral reefs remain scarce.

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 federal states of Maryland, Virginia, North Carolina, and Florida (USA); by McGuirt (1941) in

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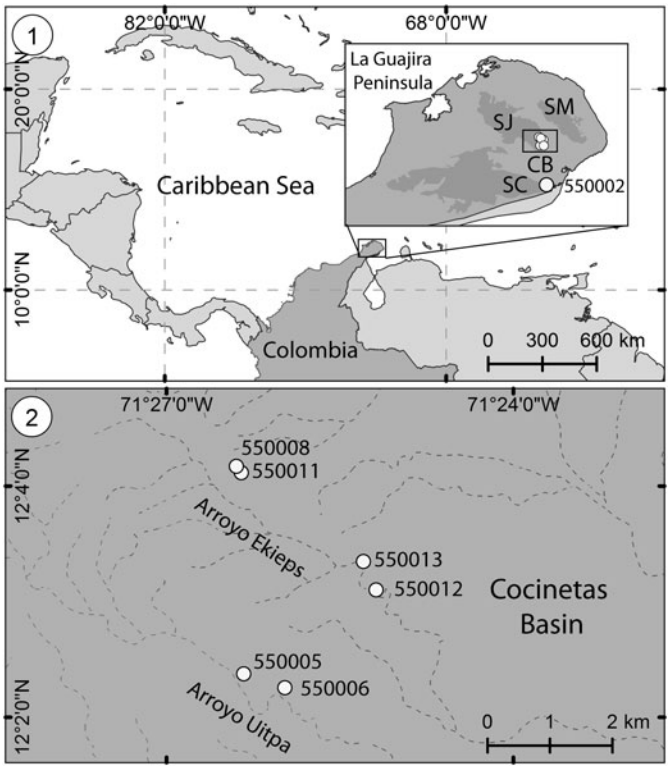


Figure 1. Locality maps. (**1**) Location of the La Guajira Peninsula in the Caribbean region with detail of the sampled zone showing Serranía de Cocinas (SC), Serranía de Jarara (SJ), and Serranía de Macuira (SM) surrounding the Cocinetas Basin (CB) (box), and including the locality La Flor de La Guajira (station 550002). (**2**) Close-up of localities Arroyo Ekieps (stations 550008, 550011, 550012, 550013) and Arroyo Uitpa (stations 550005, 550006) at the foothills of the of Serranía de Jarara in the Cocinetas Basin.

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 work has been done 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).

The purpose of this paper is to: (1) describe the bryozoan species associated with shallow coral reefs in the Siamaná Formation (Aquitanian, ca. 23–20 Ma), thereby contributing to knowledge of bryozoan assemblages in the Caribbean Basin; (2) estimate the role played by bryozoans in reefs from the Siamaná Formation; and (3) identify the biogeographical patterns of the bryozoan fauna during the early Miocene in the southern Caribbean.

Geologic setting

The Siamaná Formation crops out in the La Guajira Peninsula (northeast Colombia), in the northeastern foothills of Serranía de Cocinas, south of Serranía de Jarara and west of Serranía de Macuira (Fig. 1) (Rollins, 1965). The formation consists of conglomerates, sandstones, and fossiliferous limestones (Renz, 1960). This formation is a diachronic sedimentary unit ranging from the late Oligocene to the early Miocene (Duque-Caro, 1974; Silva-Tamayo et al., 2017). Although the age of the upper limit of the Siamaná Formation continues to be a subject of study (Jaramillo et al., 2020), the presence of corals, such as *Siderastrea siderea* (Ellis and Solander, 1786) (Flórez et al., 2019b, p. 427), bivalves, such as *Mimachlamys canalis* (Brown and Pilsbry, 1913) (Hendy et al., 2015, p. 50), and principally the large benthic foraminifera assemblages found in the studied localities (W. Renema, personal communication, 2015) point to an early Miocene age. The early Miocene beds are mainly shallow-water marine carbonates deposited over the basement rocks of the Cocinas, Jarara, and Macuira paleoislands (Rollins, 1965, fig. 19.7; Bloch et al., 2016, fig. 4). Coral reefs grew fringing the paleoislands (Rollins, 1965; Flórez et al., 2019a, b). Deep marine siliciclastic sediments of the Uitpa Formation (Aquitanian–Burdigalian) unconformably overlie the Siamaná Formation (Renz, 1960; Hendy et al., 2015; Moreno et al., 2015). Details about the stratigraphy of the collecting localities are provided in Flórez et al. (2019a, fig. 2).

Materials and methods

The studied material was collected in the coral reef facies of the Siamaná Formation during two expeditions to the Cocinetas Basin carried out in 2011 and 2014. The bryozoan specimens were obtained from the surfaces of coral colonies and in the attached sediment. The coral samples were collected from seven stations along transects of 10 m (Fig. 1; Table 1). These were washed and scrubbed with a soft brush; the residual sediment was wet-sieved over mesh-sizes of 250 and 63 µm. In some cases, the sediment was gently removed from the corals with a needle and a paintbrush to preserve erect bryozoan fragments. To separate the encrusting colonies from the large coral substrates, when possible, small fragments of the corals were cut using a motor tool. Bryozoan specimens were cleaned using an ultrasonic bath for a few seconds to a few minutes, depending on the fragility of the colony. Coated and uncoated

Table 1. Siamaná Formation localities and stations studied in the present paper. Age is from Silva-Tamayo et al. (2017) and based on strontium isotopes in coralline algae.

Locality	Station code	Latitude N	Longitude W	Age
Arroyo Ekieps	550008	12°04'11.02"	71°26'23.09"	Aquitanian–Burdigalian
Arroyo Ekieps	550011	12°04'08.06"	71°26'22.2"	Aquitanian–Burdigalian
Arroyo Ekieps	550012	12°03'5.70"	71°25'10.80"	Aquitanian–Burdigalian
Arroyo Ekieps	550013	12°03'20.5"	71°25'18.4"	Aquitanian–Burdigalian
Arroyo Uitpa	550005	12°01'50.04"	71°25'24.04"	Aquitanian
Arroyo Uitpa	550006	12°01'49.0"	71°25'16.07"	Aquitanian
Flor de La Guajira	550002	11°49'52.08"	71°23'58.07"	Aquitanian?

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specimens were examined with scanning electron microscopy (SEM) at the "Centro de Instrumentación Científica, Universidad de Granada," employing FEI Quanta 400 and FEI Qemscan 650F microscopes operating at low- and high-vacuum modes using backscattered and secondary electron detectors. Measurements of zooidal characters were made from SEM images using the image-processing program ImageJ (https://imagej.nih.gov/ij) and are given in mm, including mean (X), observed range (R), standard deviation (SD), and the number of measurements (N) (see tables for each species). The systematic paleontology section of Cheilostomatida follows the interim classification compiled by D.P. Gordon for the Treatise on Invertebrate Paleontology (2011). A list of collected specimens included in this study with catalog numbers, locality names, station numbers, type of colony, substrate, and number of specimens available is provided in Appendix 1. Descriptions and illustrations of the ascophoran-grade cheilostomes mentioned in the "Remarks" will be part of a separate work currently in preparation.

Repositories and institutional abbreviations.—The samples described and illustrated and the type specimens are 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); Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH); and Muséum national d'Histoire naturelle, Paris, France (MNHN).

Systematic paleontology

Order Cyclostomatida 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 2.1, 2.2; Table 2

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

Description.—Colony erect with branches circular in cross section, ~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 absent. Gonozooids not observed.

Remarks.—Canu and Bassler (1920, p. 734) expanded the genus *Entalophora* Lamouroux, 1821 to include 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 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 the British Isles, Recent; by subsequent designation (Taylor and Zatoń, 2008).

?*Oncousoecia* sp. indet.
Figure 2.3, 2.4; Table 3

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, apparently bifurcating. Zooids tubular (mean L/W = 1.66); zooidal boundaries not clearly demarcated. Zooidal surface densely perforated by rounded pseudopores, sometimes with transverse striations. Peristomes rising almost perpendicularly to the zooidal surface, with presumably circular to oval apertures. Gonozooids not observed.

Remarks.—Based on the encrusting and apparently bifurcating colony form, as well as relatively widely spaced and oligoserially arranged autozooids with circular apertures (Taylor and Zatoń, 2008), we tentatively attribute this specimen to *Oncousoecia*. The specimen from the Siamaná Formation is an incomplete, poorly preserved colony. The broken peristomes and the absence of gonozooids prevent further identification. *Oncousoecia* has a long 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 the 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. resembles the early astogenetic stages of both *O. contortilis* and *O. abrupta*, but differs from the former species in having slightly curved instead of contorted branches, and from the latter Pliocene species in having wider

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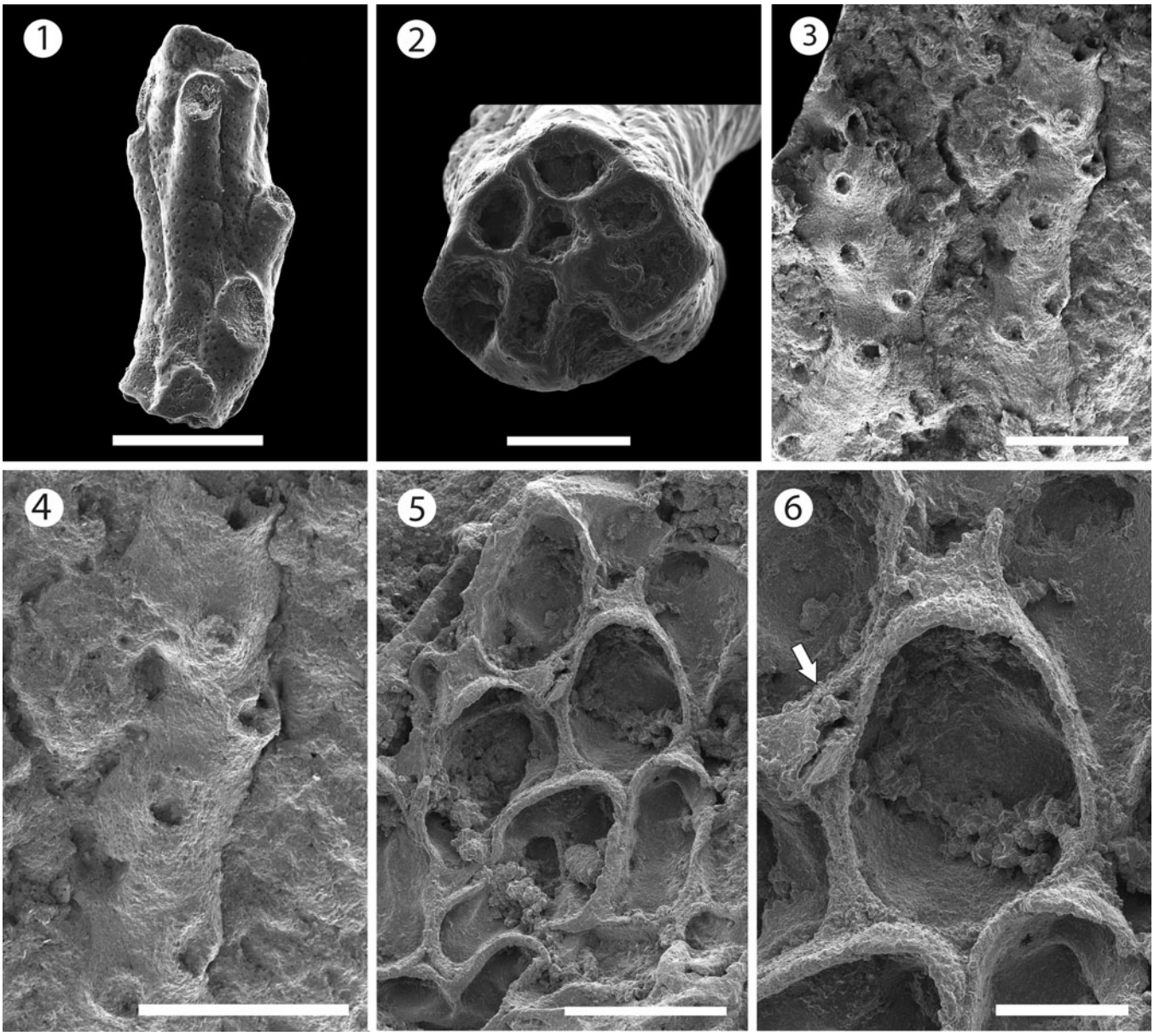


Figure 2. *Mecynoecia* sp. indet. (MUN-STRI-47623): (**1**) branch fragment; (**2**) view of the base of the branch fragment showing the absence of an axial lumen in cross-section. ?*Oncousoecia* sp. indet. (MUN-STRI-47625): (**3**) general view, (**4**) detail of the bifurcate branch. *Copidozoum* sp. indet. (MUN-STRI-47627): (**5**) general view of the colony, (**6**) detail of the zooid and avicularium (arrowed). 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.

branches (0.66 vs. 0.45 mm). Furthermore, it resembles *O. arcuata* in the shape of the branch and autozooidal arrangement, but differs in having a larger peristome diameter. ?*Oncousoecia* sp. indet. differs also from the European Miocene *Oncousoecia biloba* (Reuss, 1848) and *Oncousoecia repens* (Wood, 1844). The former species has multiserial and unilamellar erect colonies (Zágoršek, 2003, 2010), while *O. repens* differs in having bi-, tri-, or multiserial branches (Busk, 1859). ?*Oncousoecia* sp. indet. was found, along with the ascophoran-grade cheilostome bryozoan *Poricella* sp., encrusting a fragment of the scleractinian coral *Alveopora tampae* Weisbord, 1973.

Table 2. Measurements of *Mecynoecia* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

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

Order Cheilostomatida 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.

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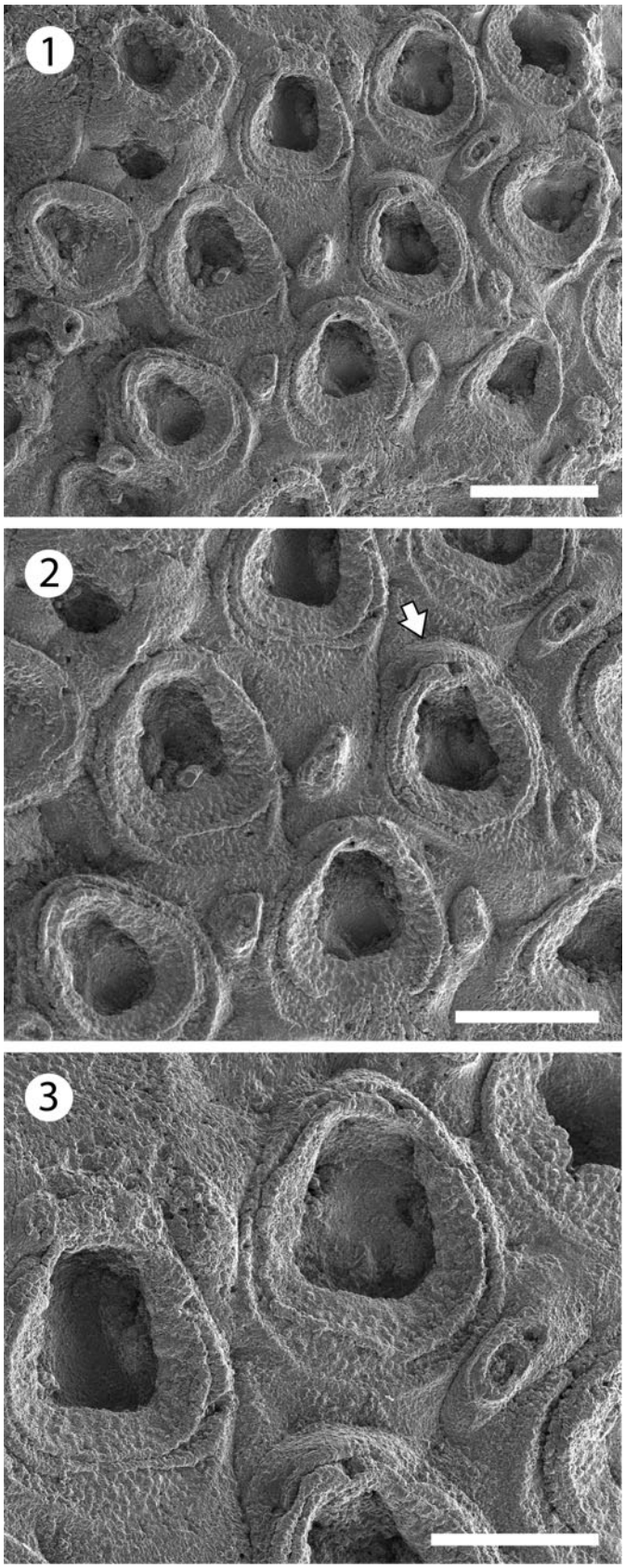


Figure 3. *Antropora guajirensis* n. sp. from the Siamaná Formation, Arroyo Uitpa (holotype MUN-STRI-47628): (**1**) general view; (**2**) detail of the autozooids with intramural reparative budding, drop shaped interzooidal avicularia, and cap-like ooecium (arrowed); (**3**) close-up of two autozooids and interzooidal avicularia. Scale bars are (**1**) 0.25 mm; (**2**) 0.2 mm; (**3**) 0.15 mm.

Table 3. Measurements of ?*Oncousoecia* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

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	10

Copidozoum sp. indet.
Figure 2.5, 2.6; Table 4

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

Description.—Colony encrusting, unilaminar and multiserial. Zooids oval to irregular, distinctly separated 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.

Remarks.—Based on the characters of the interzooidal avicularium and autozooids, we place this specimen in *Copidozoum*. Other species of *Copidozoum* recorded in American Miocene 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 and 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* (Vaughan, 1919), along with the microporid *Calpensia caribensis* n. sp. and the phidoloporid *Rhynchozoon* sp.

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

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

Table 4. Measurements of *Copidozoum* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

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	3

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Table 5. Measurements of *Antropora guajirensis* n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

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	10
Ooecium length	0.04	0.03–0.04	0.01	2
Ooecium width	0.16	0.15–0.17	0.01	2

Antropora guajirensis new species
Figure 3; Table 5

Holotype.—MUN-STRI-47628, from the early Miocene Siamaná Formation, Arroyo Uitpa, La Guajira, Colombia.

Diagnosis.—Colony encrusting. Zooids oval to elliptical with oval to pear-shaped opesia. Gymnocyst smooth, developed proximally. Cryptocyst granular, surrounding the opesia, tapering distally. Interzooidal avicularia elliptical to drop-shaped, randomly placed, oriented distolaterally. Ooecium cap-like, imperforate.

Description.—Colony encrusting, multiserial, and unilaminar. Zooids distinctly separated by deep grooves, oval to elliptical in shape (mean L/W = 1.37), sometimes polygonal where the proximal gymnocystal area is more extensive. Opesia oval to pear-shaped, 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. Ovicells endozooidal; ooecium small, cap-like, smooth, and imperforate. Intramural reparative budding common. Large vicarious avicularia not observed.

Etymology.—Named after the La Guajira Peninsula, in reference to the region where it was collected for the first time, plus the Latin suffix *-ensis*, meaning originating in.

Remarks.—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 the American fossil species of *Antropora*, the late Pliocene *Antropora parvicapitata* (Canu and Bassler, 1923) differs from *A. guajirensis* n. sp. 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). The Recent *A. typica* Canu and Bassler (1928) differs in having a pair of small interzooidal avicularia placed at the distal end of most autozooids and oriented distally (Tilbrook, 1998), while the new species has interzooidal avicularia oriented distolaterally, placed randomly. In the Siamaná Formation, it was found encrusting the rubble of *Porites* sp., and co-existing with the bryozoans *Gymnophorella hadra* n. gen. n. sp. and ?*Hippopleurifera* sp. 1.

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

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

Nellia cf. *N. tenella* (Lamarck, 1816)
Figure 4.1–4.3; Table 6

cf. 1816 *Cellaria tenella* Lamarck, p. 135.
cf. 1920 *Nellia oculata*; Canu and Bassler, p. 196, pl. 82, figs. 6–10.
cf. 1984 *Nellia tenella*; Winston and Cheetham, p. 257, figs. 1, 2.
cf. 2017 *Nellia tenella*; Di Martino et al., p. 109, fig. 9.
cf. 2019 *Nellia tenella*; Ramalho et al., p. 111, figs. 2a–c.

Syntypes.—MNHN-IB-2008-4546, MNHN-IB-2008-5255, Southern seas (?), Recent.

Occurrence.—?Late Cretaceous to Recent. The oldest record is from the Maastrichtian of Jamaica (Cheetham, 1968). Eocene Crystal River Formation, Florida, USA (Winston and Cheetham, 1984). Eocene Upper Bracklesham Beds, England; France, Spain, and Senegal (Cheetham, 1966). 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). Miocene from Egypt and Australia (Cheetham, 1966). 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 positions with their lateral neighbors. Zooids distinct, delimited by a slender groove, all similar in size, elongate and sub-rectangular in shape. Opesia oval, occupying most of the frontal surface. Gymnocyst smooth, extended proximally and reduced laterally and distally. Cryptocyst smooth, forming a rim around the opesia. 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 not observed.

Remarks.—The internode fragments available in our material are poorly preserved and lack ooecia, preventing species-level identification. However, they resemble *Nellia tenella* in the characteristic arrangement and shape of the autozooids and avicularia. The specimens from the Siamaná Formation are similar to those from the Miocene of the Dominican Republic

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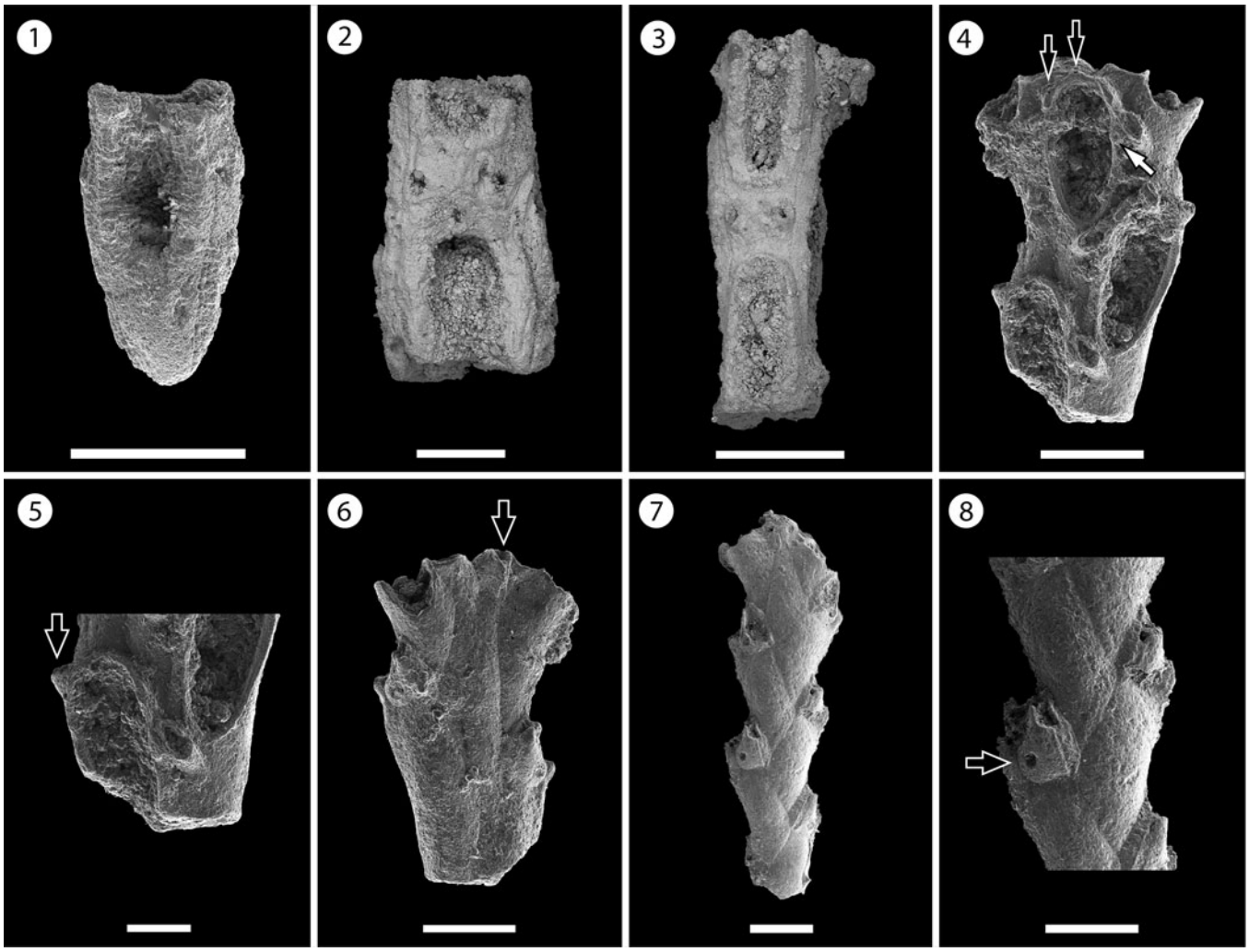


Figure 4. *Nellia* cf. *N. tenella* (Lamarck, 1816) (MUN-STRI-47630): (**1**) part of a tapering zooid at the tip of the branch, (**2**) paired elliptical avicularia, (**3**) branch fragment with incomplete zooids. *Licornia* sp. indet. (MUN-STRI-47632): (**4**) frontal view of the branch at bifurcation showing the breaking point of the nodal joint crossing through the proximal part of the zooid, 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.

figured by Winston and Cheetham (1984, fig. 2D). However, the size of the opesia in these fragments is smaller than those of the Dominican specimens, as well as the syntype (MNHN-IB-2008-4546), and other specimens from different regions and ages (Cheetham, 1963, 1966; Winston et al., 2014; Di Martino et al., 2017). Although Winston and Cheetham (1984) suggested that the variation in size is not significant, and proposed to consider *N. tenella* as a living fossil, based on the results of the statistical analyses performed on specimens ranging from the Late Cretaceous to the Recent, certain characters, which could reveal differences between localities and periods, such as ooecium morphology, have seldom been recorded. New fossil collections and phylogenetic studies using Recent material are needed to confirm its living-fossil status or to reveal that it is a species complex.

"*Nellia tenella*" was very common in the Miocene (Winston and Cheetham, 1984). Its Recent distribution is circumtropical to subtropical and it has been recorded on coral reefs (Winston, 1986). In the Siamaná Formation, *N.* cf. *N. tenella* was found in the sediment cemented to the scleractinian coral *Goniopora hilli*, co-occurring with the bryozoan *Poricellaria* sp. (as also observed in other fossil and recent localities and environments, e.g., intertidal rocks; Winston and Cheetham, 1984), *Margaretta* sp., *Ditaxiporina* sp., and *Mecynoecia* sp.

Table 6. Measurements of *Nellia* cf. *N. tenella*. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid width	0.14	0.12–0.16	0.02	4
Opesia width	0.07	0.06–0.08	0.01	5
Avicularium length	0.05	0.04–0.06	0.01	4
Avicularium width	0.04	0.03–0.04	0.01	4

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

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

Licornia sp. indet.
Figure 4.4–4.8; Table 7

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 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 avicularium of the adjacent zooid. Gymnocyst smooth, well 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. Nodal joints crossing the proximal opesia of the outer zooids and below the opesia of the inner zooids at the bifurcation. Single axial vibraculum in the bifurcation, with straight setal groove and lacking a rhizoidal pore. Ooecium not observed. Scutum and spines not preserved.

Remarks.—We place these specimens 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 a 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* sp., *Catenicella* sp., and *Margaretta* sp.

Table 7. Measurements of *Licornia* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.50	0.47–0.52	0.03	3
Autozooid width	0.17	0.16–0.2	0.02	6
Opesia length	0.27	0.26–0.28	0.01	3
Opesia width	0.11	0.10–0.11	0.01	4
Avicularium frontal length	0.07	0.07	0	3
Avicularium frontal width	0.04	0.03–0.05	0.01	4
Avicularium lateral length	0.05	0.04–0.05	0.01	2
Avicularium lateral width	0.02	0.02–0.03	0.01	3
Vibracular chamber length	0.17	0.14–0.2	0.02	10
Rhizoidal pore diameter	0.03	0.03	0	6

Superfamily Microporoidea Gray, 1848
Family Microporidae Gray, 1848
Genus *Calpensia* Jullien, 1888

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

Calpensia caribensis new species
Figure 5.1–5.3; Table 8

Holotype.—MUN-STRI-47635. Paratypes: MUN-STRI-47634, MUN-STRI-47636. From the early Miocene Siamaná Formation, Arroyo Ekieps, La Guajira, Colombia.

Diagnosis.—Colony encrusting, multiserial. Zooids sub-rectangular with semicircular orifice, placed over the raised opercular region. Cryptocyst granular, densely perforated (>100 pseudopores). Two symmetrical, elliptical opesiules, placed proximolaterally to the orifice.

Description.—Colony encrusting, multiserial, unilaminar. Zooids separated by a suture on 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; opercular region slightly developed. Cryptocyst flat proximally, depressed towards the opesiular area at about two-thirds of zooidal length, and raised distally; granular surface, densely and evenly perforated with up to ~110–120 circular pseudopores, absent in the area surrounding the opesia and between the opesia and the opesiules; pseudopores ~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, ~0.14 mm below the opesia.

Etymology.—From the Caribbean Sea, in reference to the biogeographic region that the new species inhabited, plus the Latin suffix *-ensis* meaning originating in.

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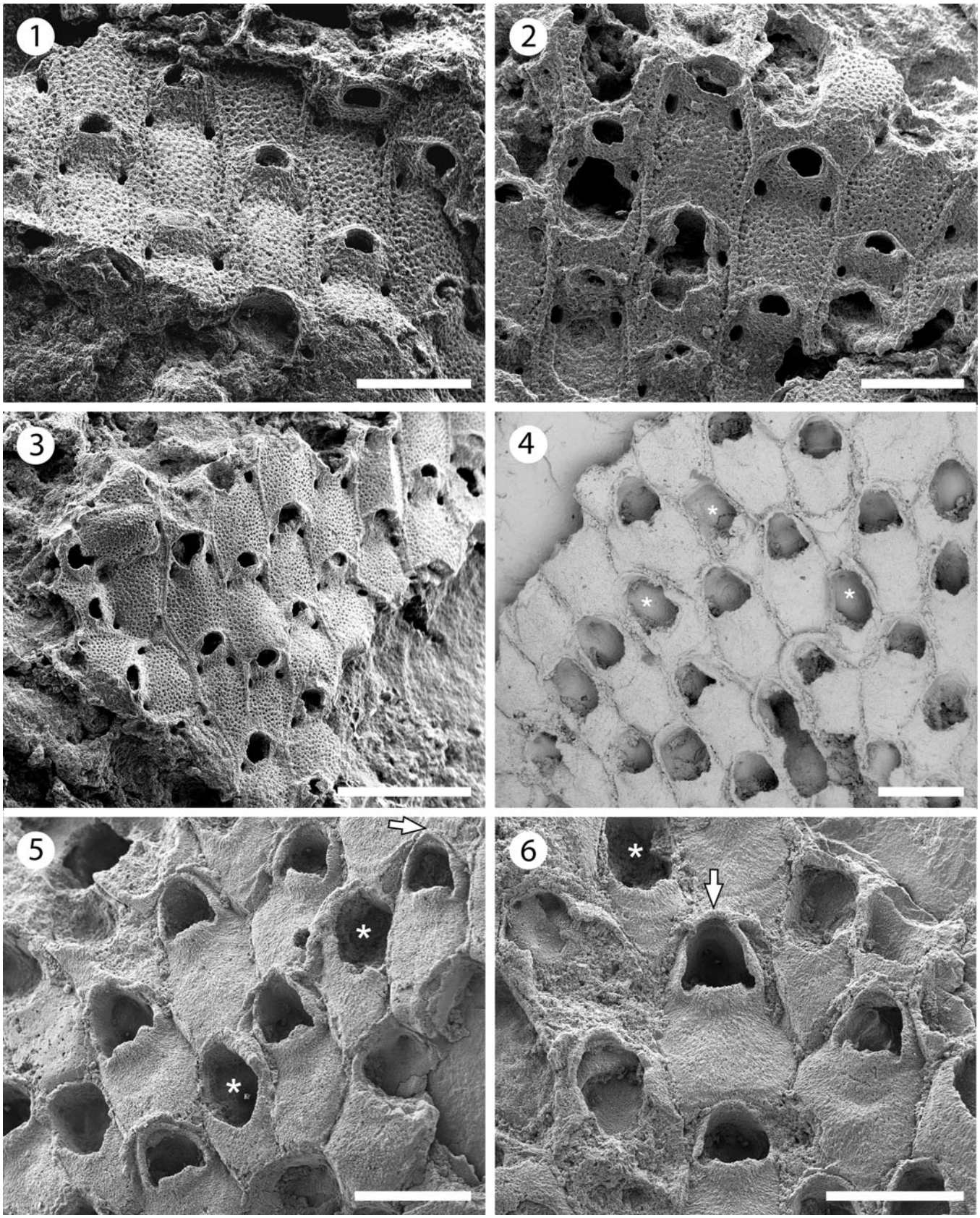


Figure 5. *Calpensia caribensis* n. sp. from the Siamaná Formation, Arroyo Ekieps (holotype MUN-STRI-47635): (**1**) autozooids showing the semicircular opesia and the proximally raised opercular region, (**2**) close-up of autozooids showing paired opesiules, (**3**) general view of the colony. *Atoichos magnus* n. gen. n. sp. from the Siamaná Formation, Arroyo Ekieps (holotype MUN-STRI-47637); asterisks indicate putative avicularia: (**4**) group of autozooids, (**5**) oblique view showing the development and shape of the cryptocyst and the distal raised opesial margin (arrowed), (**6**) zooids showing well-preserved opesia with opesiular indentations and the distal opesial margin (arrowed). Scale bars are (**1, 2, 4–6**) 0.5 mm; (**3**) 1 mm.

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Table 8. Measurements of *Calpensia caribensis* n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.67	0.62–0.75	0.05	11
Autozooid width	0.43	0.38–0.49	0.03	16
Opesia length	0.09	0.08–0.1	0.01	10
Opesia width	0.15	0.14–0.18	0.01	13
Opesiule length	0.08	0.05–0.11	0.02	11
Opesiule width	0.05	0.04–0.06	0.01	11
Pores number	116	98–144	16.85	6

Remarks.—The specimens of *Calpensia caribensis* n. sp. found in the Siamaná Formation resemble specimens of the Recent Mediterranean *Calpensia nobilis* (Esper, 1797). *Calpensia nobilis* is commonly found in the late Miocene to the Recent of the Mediterranean (Hayward and McKinney, 2002; Moissette et al., 2007). Canu and Bassler (1923) identified specimens of *Calpensia* as *C. impressa* (Moll, 1803) in the Oligocene of the southern Caribbean, which were subsequently attributed to *C. nobilis* by Buge (1957). The new species is similar to Mediterranean specimens of *C. nobilis* in the size of the opesia and opesiules (Hayward and McKinney, 2002, p. 31, fig. 13 a–c), as well as in the mean ratios of opesia length/zooid length (0.13 vs. 0.12), and opesia width/zooid width (0.36 vs. 0.39). However, *C. caribensis* n. sp. has squatter autozooids (zooid length 0.67 mm vs. 0.82 mm; zooid width 0.43 mm vs. 0.38 mm). Although Canu and Bassler (1930) and Buge (1957) reported wide variations of the size of the zooids in this species, the mean ratio of zooid length/zooid width between our specimens and Recent material differs greatly (1.58 vs. 2.15), indicating a different zooidal shape. In addition, the Siamaná Formation specimens have a greater number of pseudopores in the cryptocyst (almost twice as many; mean of pores number 116 vs. 61). Based on these differences, as well as the spatial and temporal distance between the two populations, we introduce this new species. In the Siamaná Formation, *Calpensia caribensis* n. sp. was found encrusting coralline algae covering the coral *Alveopora tampae* and on the basal surface of the coral *Colpophyllia willoughbiensis*, while small detached fragments were scattered in the sediment associated with *Goniopora hilli*. In our material, *Calpensia caribensis* n. sp. co-occurs with *Copidozoum* sp., *Gemelliporidra* sp., and *Rhynchozoon* sp.

Family Onychocellidae Jullien, 1882
Genus *Atoichos* new genus

Type species.—*Atoichos magnus* n. gen. n. sp., from Arroyo Ekieps, Colombia, early Miocene, Siamaná Formation; by monotypy.

Diagnosis.—As the type species by monotypy.

Etymology.—From the Greek privative prefix *a-* and *toichos* (masculine), meaning wall, alluding to the absence of a raised mural rim surrounding the autozooids.

Remarks.—We place *Atoichos* n. gen. in the family Onychocellidae because of its extensive cryptocyst, the bell-shaped opesia with opesiular identations, the probable presence of vicarious avicularia, and the absence of a gymnocyst and spines (Taylor et al., 2018). *Atoichos* 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, as in remaining genera of this family, in lacking a raised margin around the proximal two-thirds of the zooid. 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, as observed in some calloporids in the studies carried out by Cook (1968) on the Recent genus *Crassimarginatella* Canu, 1900 and by Cheetham et al. (2006) on the fossil genus *Wilbertopora* Cheetham, 1954, 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).

Atoichos magnus new species
Figure 5.4–5.6; Table 9

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 raised opesial margin distally and a deep groove proximolaterally. Opesia terminal, triangular to bell-shaped, as long as wide, occupying the distal third of the frontal surface; opesiular indentations shallow; proximal edge projected, straight to slightly curved. Cryptocyst extensive, granular, flat to slightly convex. Gymnocyst absent. 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 raised opesial margin, and a fine and deep groove proximo-laterally. Opesia terminal, wide,

Table 9. Measurements of *Atoichos magnus* n. gen. n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.74	0.57–0.93	0.09	19
Autozooid width	0.43	0.31–0.83	0.12	17
Opesia length	0.22	0.16–0.28	0.03	15
Opesia width	0.20	0.17–0.23	0.02	11
Interzooidal avicularium length	0.63	0.49–0.72	0.08	11
Interzooidal avicularium width	0.32	0.26–0.4	0.04	10
Avicularian opesia length	0.37	0.35–0.38	0.02	3
Avicularian opesia width	0.23	0.22–0.24	0.01	3

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triangular to bell-shaped, as long as wide; borders raised forming a lateral furrow between the opesia margin and the adjacent zooids; opesiular indentations located at the proximolateral corners, slightly constricted laterally, proximal edge projecting distally with straight to slightly concave 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 only twice, probably rounded (Fig. 5.4). Ovicells not observed.

Etymology.—From the Latin *magnus*, large, in reference to the large size of the autozooids.

Remarks.—The single colony found in the Siamaná Formation exhibits signs of dissolution. However, its morphological features are well preserved enough to allow comparisons with other genera and species in the family Onychocellidae. *Atoichos magnus* 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 an acutely triangular rostrum, while *Aechmellina* differs in having frequent, small interzooidal avicularia with a pointed rostrum. *Atoichos magnus* n. gen. n. sp. also resembles *Floridinella vicksburgica* Canu and Bassler, 1917 in having a wide opesia, but differs in having kenozooids and avicularia with a triangular rostrum oriented laterally (Cook and Bock, 2001, p. 547). In the Siamaná Formation, *Atoichos magnus* n. gen. n. sp. was found encrusting a mollusk shell, sharing the substrate with *Glabrilaria* sp. indet. and a poorly preserved cyclostome.

Genus *Smittipora* Jullien, 1882

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

Smittipora sp. indet.
Figure 6; Table 10

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

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. Ovicellate zooids with the distal edge formed by the 'cryptocyst' of the distal zooid; fertile zooids slightly longer than non-fertile autozooids.

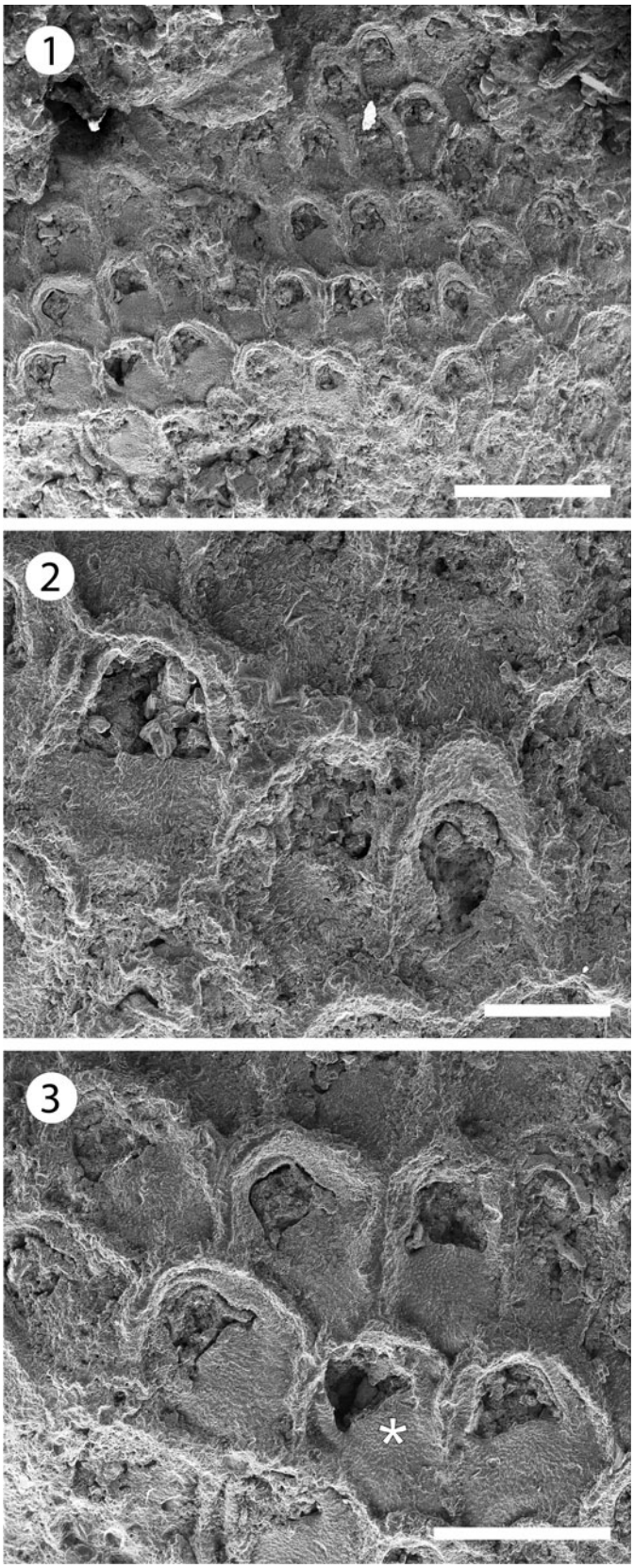


Figure 6. *Smittipora* sp. indet. from the Siamaná Formation, Arroyo Uitpa (MUN-STRI-47638): (**1**) general view of the colony, (**2**) two zooids and a vicarious avicularium with round rostrum, (**3**) close-up of autozooids and a fertile zooid (asterisk). Scale bars are (**1**) 1 mm; (**2**) 0.25 mm; (**3**) 0.5 mm.

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Table 10. Measurements of *Smittipora* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.57	0.5–0.65	0.03	17
Autozooid width	0.43	0.36–0.51	0.05	18
Opesia length	0.21	0.18–0.25	0.02	7
Opesia width	0.23	0.2–0.26	0.02	13
Interzooidal avicularium length	0.53	0.51–0.55	0.03	2
Interzooidal avicularia width	0.28	0.25–0.31	0.03	3
Avicularian opesia length	–	0.3	–	1
Avicularian opesia width	–	0.16	–	1

Remarks.—Among genera of the family Onychocellidae, our specimen fits better in the genus *Smittipora* because of the symmetrical and rounded rostrum of its avicularia (Taylor et al., 2018, p. 1702). Although some similarities in the general morphology of the zooid can be found also with species of the genus *Floridina* Jullien, 1882, this latter genus differs in having acutely triangular rostra, as well as deep opesiular indentations, resulting in a more trifoliate opesia with lateral constrictions (Taylor et al., 2018, p. 1678). Three species of *Smittipora* have been described from the North American Oligocene and two from the Miocene: *S. fusiformis* (Canu and Bassler, 1917), *S. lineata* (Canu and Bassler, 1920), *S. tenuis* (Canu and Bassler, 1920), *S. levinseni* (Canu and Bassler, 1917), and *S. elongata* (Canu and Bassler, 1923), respectively. The Oligocene species differ from *Smittipora* sp. indet. in having exclusively fusiform avicularia; *S. levinseni*, from the early Miocene to Recent, has smaller zooids and avicularia (Di Martino et al., 2017). *Smittipora elongata* from the late Miocene lacks proximolateral indentations and a tongue-like medial process on the opesia proximal border. Our specimen 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 a higher ratio between the length of the opesia and the length of the zooid. In the Siamaná Formation, *Smittipora* sp. indet. was found encrusting coralline algae covering the coral *Porites* sp., co-occurring with the ascophoran-grade cheilostome *Hippopleurifera* sp. and an undetermined cheilostome.

Family Steginoporellidae Hincks, 1884
Genus *Gymnophorella* new genus

Type species.—*Gymnophorella hadra* n. gen. n. sp., from Arroyo Uitpa, Siamaná Formation, Colombia, early Miocene; by monotypy.

Diagnosis.—As the type species by monotypy.

Etymology.—From the Greek *gymno-*, referring to the gymnocystal calcification that can form in anascan-grade bryozoans in the frontal wall between the frontal membrane and the free edges of the vertical walls, and *-phor* meaning carrier, alluding to the presence of a gymnocyst in this *Steginoporella*-like genus, plus the suffix *-ella* commonly used in bryozoan names.

Remarks.—Specimens of *Gymnophorella* n. gen. from the Siamaná Formation are similar to the fossil morphospecies "*Steginoporella*" *cornuta* (Osburn, 1950) recorded by Cheetham et al. (1999) from the Dominican Republic (ca. 7.1 Ma) and Panamanian Caribbean (ca. 3.5 and 1.8 Ma), as well as from the Recent Panamanian Pacific (figured in Cheetham and Jackson, 2000, fig. 2; NMiTA Database, 1996–2016 as aff. "*Steginoporella*" *cornuta* and "*S.*" *cornuta*; STRI Database, 2017 as *S. cornuta*), and to the Brazilian species *Steginoporella evelinae* Marcus, 1949 (see Winston et al., 2014, p. 147, fig. 5). They all have a narrow band of gymnocyst, more developed proximally, surrounding the cryptocyst and the opesia, a pair of conspicuous tubercles placed at the distal corners of the opesia, and similar shape of the opesia and opesiular indentations. 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 holotype (SBMNH 635758, Fig. 7.1, 7.2), but present in a paratype (SBMNH 636427, Fig. 7.3, 7.4). In addition, Osburn (1950) described B-zooids, also present in "*Steginoporella*" *cornuta* from the Pliocene of Panama (Cheetham and Jackson, 2000), but these were not observed or preserved in the material from the Siamaná Formation. On the other hand, the Siamaná specimens differ from *S. evelinae* in having an extended gymnocyst and an evenly granular cryptocyst. The family Steginoporellidae includes to date six genera, of which only *Siphonoporella* Hincks, 1880 develops a narrow gymnocyst, and has no avicularia or B-zooids (e.g., *S. nodosa* Hincks, 1880 and *S. delicatissima* [Busk, 1861]). However, this genus differs from *Gymnophorella* n. gen. in having a lightly calcified skeleton and a 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 those (morpho-) species of *Steginoporella* and *Siphonoporella* discussed above. However, *Gymnophorella* n. gen. is also similar to some members of Cymuloporidae Winston and Vieira, 2013, Electridae d'Orbigny, 1852 (e.g., *Pyripora magna* Larwood, 1973), and Calloporidae Norman, 1903 (e.g., *Tylopora* Lang, 1917) in having oligoserial colonies, and in the morphology of the autozooids showing a well-developed gymnocyst. It differs in having deep opesiular indentations outlining a tongue-like process medially. In addition, Cymuloporidae have colonies exclusively uniserial, and opesia occupying the distal half of the zooid total length; *P. magna* has a reduced cryptocyst and larger opesiae; and *Tylopora* spp. has ovicells, avicularia, and sometimes spines on the cryptocyst.

Although the paratype of the Recent Pacific species "*Steginoporella cornuta*" (SBMNH 636427) exhibits some morphological differences compared to the holotype, and it is likely a new species, its description is not within the objectives of this paper.

Gymnophorella hadra new species
Figures 7.5, 8; Table 11

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

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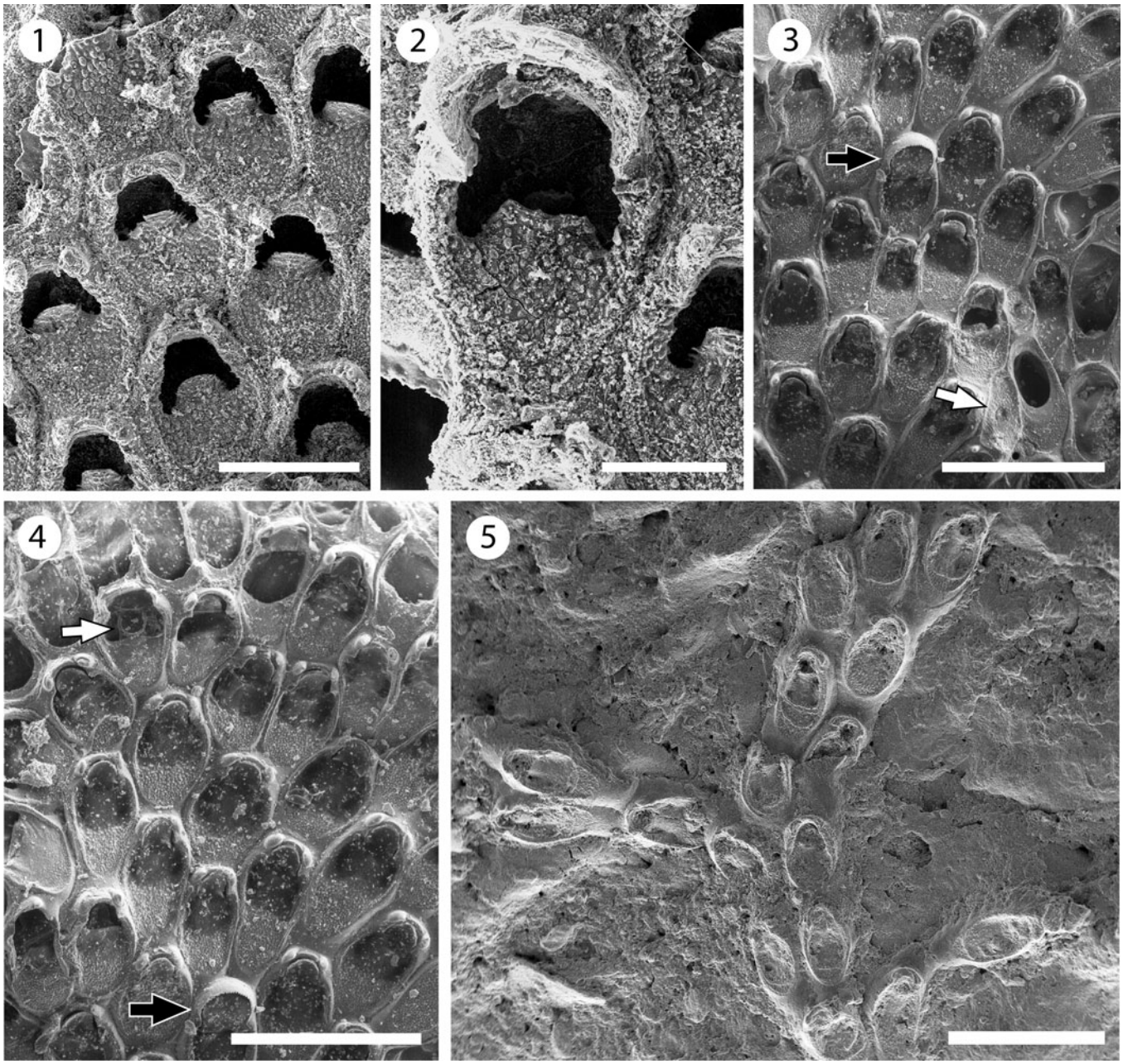


Figure 7. *Steginoporella cornuta* (Osburn, 1950), Recent, Acapulco, Mexico, Pacific Ocean (holotype SBMNH 635758) (photos courtesy of V. Delnavaz): (**1**) detail of the autozooids, note the absence of gymnocyst, (**2**) detail of a B-zooid; Recent, Isla Rancheria, Panama, Pacific Ocean (paratype SBMNH 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 (white arrow) and B-zooid (black arrow). *Gymnophorella hadra* 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. Scale bars are (**1**) 0.5 mm; (**2**) 0.25 mm; (**3–5**) 1 mm.

Diagnosis.—Colony encrusting, uni- to multiserial. Zooids oval, distinctly separated laterally by a narrow groove. Opesia terminal, trifoliate with deep opesiular indentations outlining a tongue-like process medially; distal opesial margin distinctly raised, lateral margin with two conspicuous tubercles. Cryptocyst granular, unperforated, slightly concave, occupying three-quarters of the zooidal length, surrounded by a raised oval rim that is constricted in the distal opercular region. Gymnocyst relatively extensive, smooth, slightly convex, surrounding the cryptocyst and the opesia, without edges between distal and proximal zooids, more extended proximally in early astogeny. B-zooids seemingly absent. 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 ~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, ovate to

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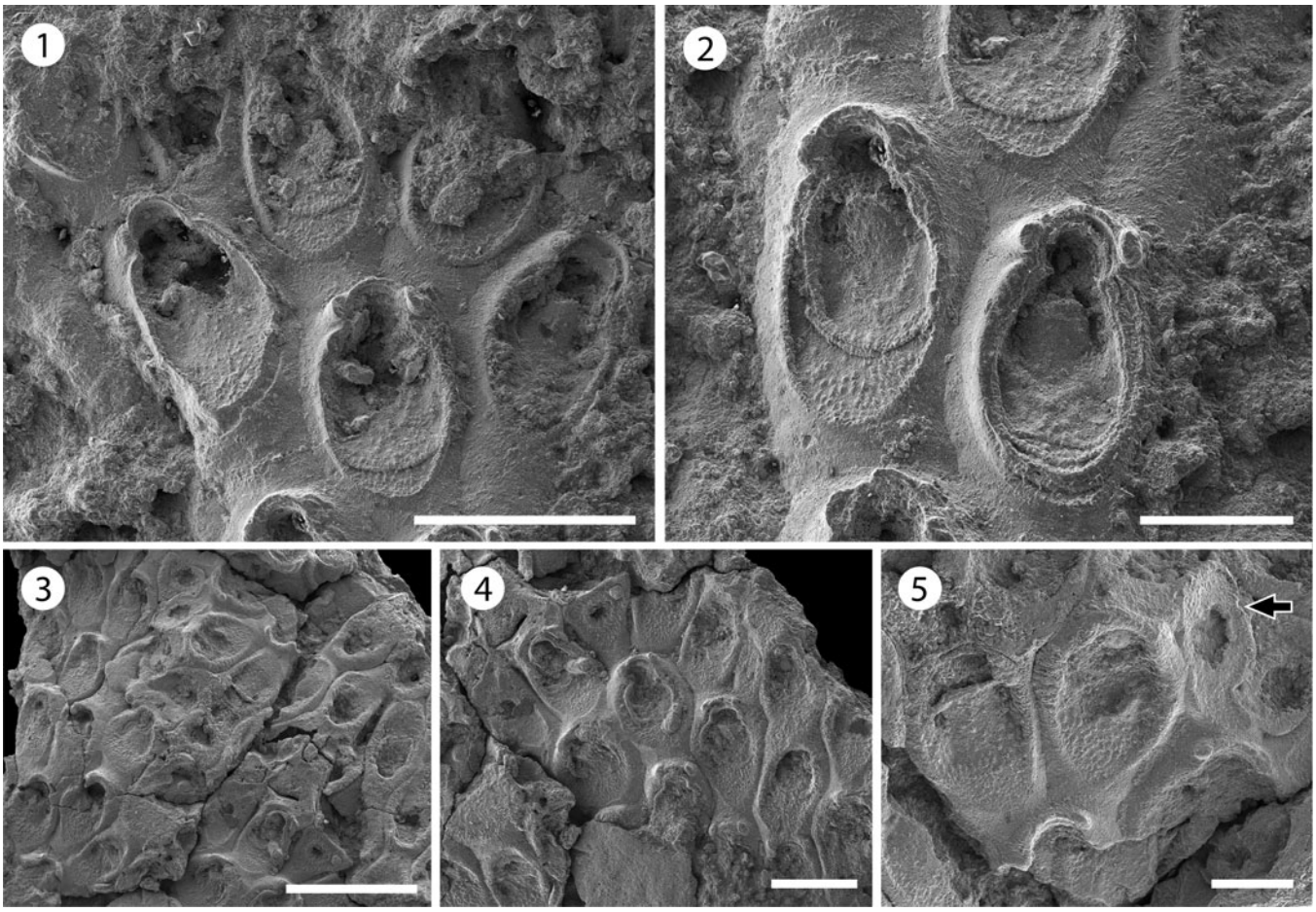


Figure 8. *Gymnophorella hadra* n. gen. n. sp. from the Siamaná Formation, Arroyo Uitpa (holotype MUN-STRI-47640): (**1**) detail of the regular autozooids, (**2**) detail of two autozooids with intramural buds and opesia showing opesiular indentations; (paratype MUN-STRI-47641): (**3, 4**) general view of the multiserial stage, (**5**) close-up of autozooids and a kenozooid (arrowed). Scale bars are (**1, 4**) 0.5 mm; (**2, 5**) 0.25 mm; (**3**) 1 mm.

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 and being distinctly constricted in the distal opercular region. 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 early astogeny and the proximal part of the zooid. Kenozooids frequent in the multiserial stages: triangular, elliptical, or similar in shape to the zooids. Polypide tube and rosette-plates not observed.

Etymology.—From the Greek *hadros*, meaning well developed, declined in accordance to the gender of the genus, which is feminine, in reference to the well-developed gymnocyst differentiating this genus from other Steginoporellidae.

Remarks.—The absence of B-zooids in the material found in the Siamaná Formation may be a bias related to the limited number of colonies available. For instance, in *Steginoporella evelinae*, the B-zooids are infrequent and similar in size and shape to the A-zooids (Winston et al., 2014). In the Siamaná Formation, *Gymnophorella hadra* n. gen. n. sp. was found growing over coral rubble of *Porites* sp., covered by coralline algae, and sharing the substrate with *Antropora guajirensis* n. sp., *Cribrilaria* sp., ?*Hippopleurifera* sp. 1, and *Escharoides* sp.

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 9.1, 9.2; Table 12

Table 11. Measurements of *Gymnophorella hadra* n. gen. n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.68	0.56–0.86	0.08	33
Autozooid width	0.40	0.35–0.46	0.03	25
Cryptocyst length	0.38	0.32–0.46	0.05	7
Cryptocyst width	0.29	0.24–0.33	0.03	14
Opesia length	0.11	0.09–0.12	0.02	4
Opesia width	0.12	0.09–0.17	0.03	8
Kenozoo length	0.51	0.37–0.66	0.12	4
Kenozoo width	0.34	0.21–0.47	0.11	4
Opesiule length	0.08	0.07–0.08	0.01	3
Opesiule width	0.04	0.03–0.04	0.01	2

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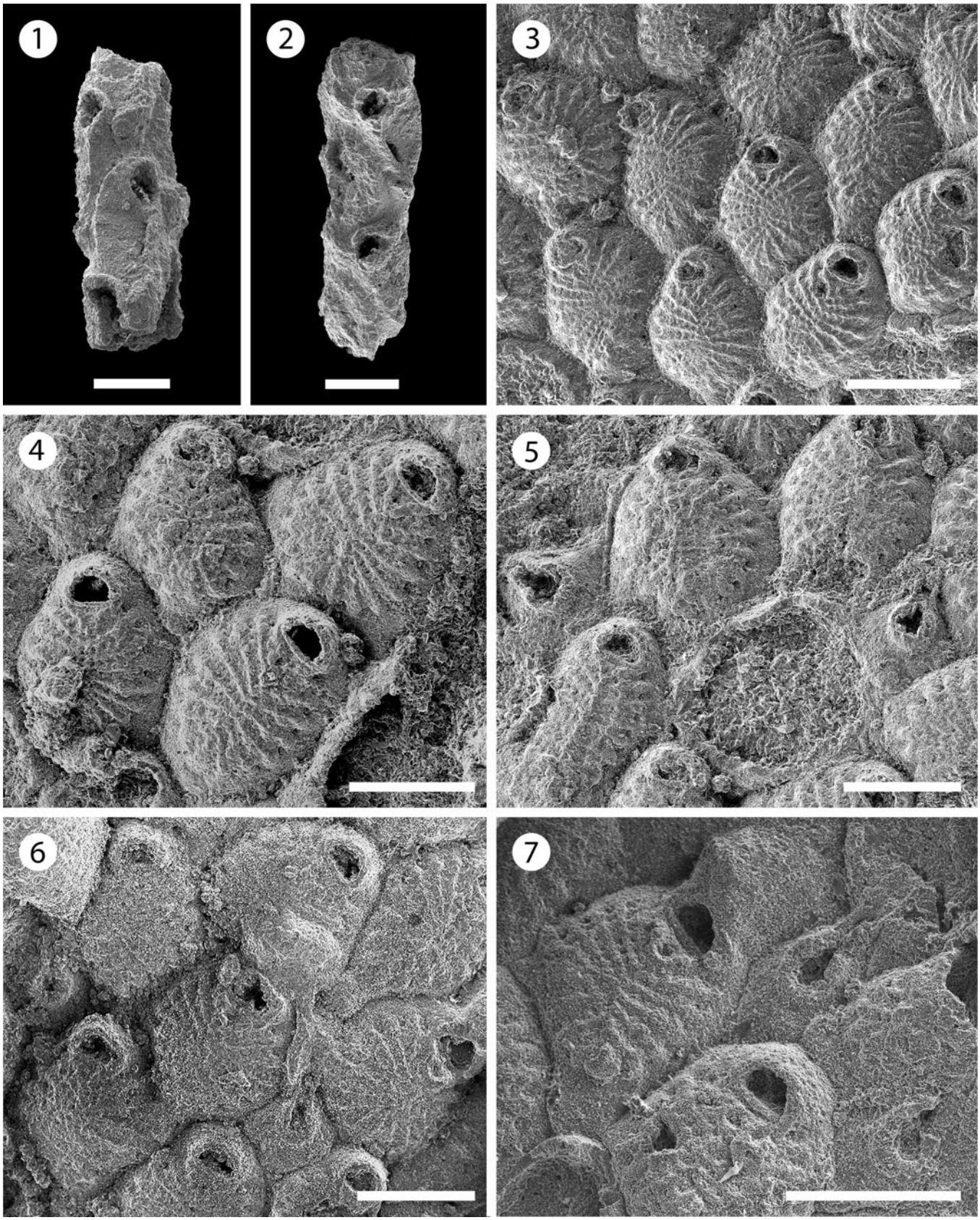


Figure 9. *Poricellaria* sp. indet. (MUN-STRI-47645): (**1, 2**) branch fragments showing the oblique orifice and the slit-like opesiule on the cryptocyst. *Cribrilaria multicostata* n. sp. (holotype MUN-STRI-47650): (**3**) general view of the autozooids, (**4**) autozooids showing the orifice shape, spine bases, and suboral lacuna, (**5**) detail of the avicularium with flared rostrum; (paratype MUN-STRI-47651): (**6**) fertile zooid with type A ovicell; (paratype MUN-STRI-47652): (**7**) detail of the avicularium and ovicell. Scale bars are (**1**) 0.15 mm; (**2, 4–6**) 0.2 mm; (**3, 7**) 0.25 mm.

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Table 12. Measurements of *Poricellaria* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.25	0.24–0.25	0.01	3
Autozooid width	0.14	0.13–0.14	0.01	3
Orifice length	0.06	0.05–0.06	0.01	2
Orifice width	0.08	0.07–0.08	0.01	3
Avicularium length	–	0.07	–	1
Avicularium width	–	0.04	–	1
Opesiule length	0.07	0.06–0.07	0.01	2
Branch width	0.21	0.2–0.21	0.01	2

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

Description.—Colony erect. Branches slender and sub-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° relative to the branch axis, facing frontally and laterally, 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.

Remarks.—Only two broken and recrystallized fragments were found in the samples. However, the inclined zooids with the oblique opesia and slit-like opesiule, as well as the avicularia placed on the gymnocyst of each autozooid, are features diagnostic of the genus *Poricellaria* (Harmer, 1926, p. 313). 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* cf. *N. tenella*, as is common in other fossil localities and environments (Winston and Cheetham, 1984), as well as *Margaretta* sp., *Ditaxiporina* sp., and *Mecynoecia* sp.

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 multicostata new species
Figure 9.3–9.7; Table 13

Holotype.—MUN-STRI-47650. Paratypes: MUN-STRI-47651–47656. 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, produced by the distal zooid (type A of Bishop and Househam, 1987), smooth, imperforate, and with a median umbo.

Description.—Colony unilaminar, forming extensive and irregular encrustations. Zooids oval to rhomboidal, distinctly separated 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 on a rhombic cystid with a well-developed gymnocyst; 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 and with a median umbo or keel, not punctate.

Etymology.—From the Latin *multus*, meaning many, and *costa*, meaning rib in reference to the greater number of costae that distinguish this species from other *Cribrilaria* spp. with flared avicularia, plus the suffix *-ata*, pertaining to.

Remarks.—Two fossil species of *Cribrilaria* from North America, both from the early Oligocene, are known: *Cribrilaria anaticula* Canu and Bassler, 1920 and *Cribrilaria carolinensis* Gabb and Horn, 1862. They resemble *Cribrilaria multicostata* n. sp. in having five oral spines and large interzooidal avicularia. However, *C. multicostata* differs from both in having avicularia with a flared rostrum. Nine Recent *Cribrilaria* morphospecies are described in the literature having avicularia

Table 13. Measurements of *Cribrilaria multicostata* n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.34	0.28–0.44	0.03	29
Autozooid width	0.29	0.25–0.4	0.04	29
Orifice length	0.04	0.03–0.06	0.01	17
Orifice width	0.07	0.06–0.1	0.01	12
Avicularium length	0.29	0.25–0.36	0.06	3
Avicularium width	0.15	0.11–0.17	0.02	9
Ooecium length	0.14	0.12–0.17	0.02	5
Ooecium width	0.16	0.15–0.19	0.02	6

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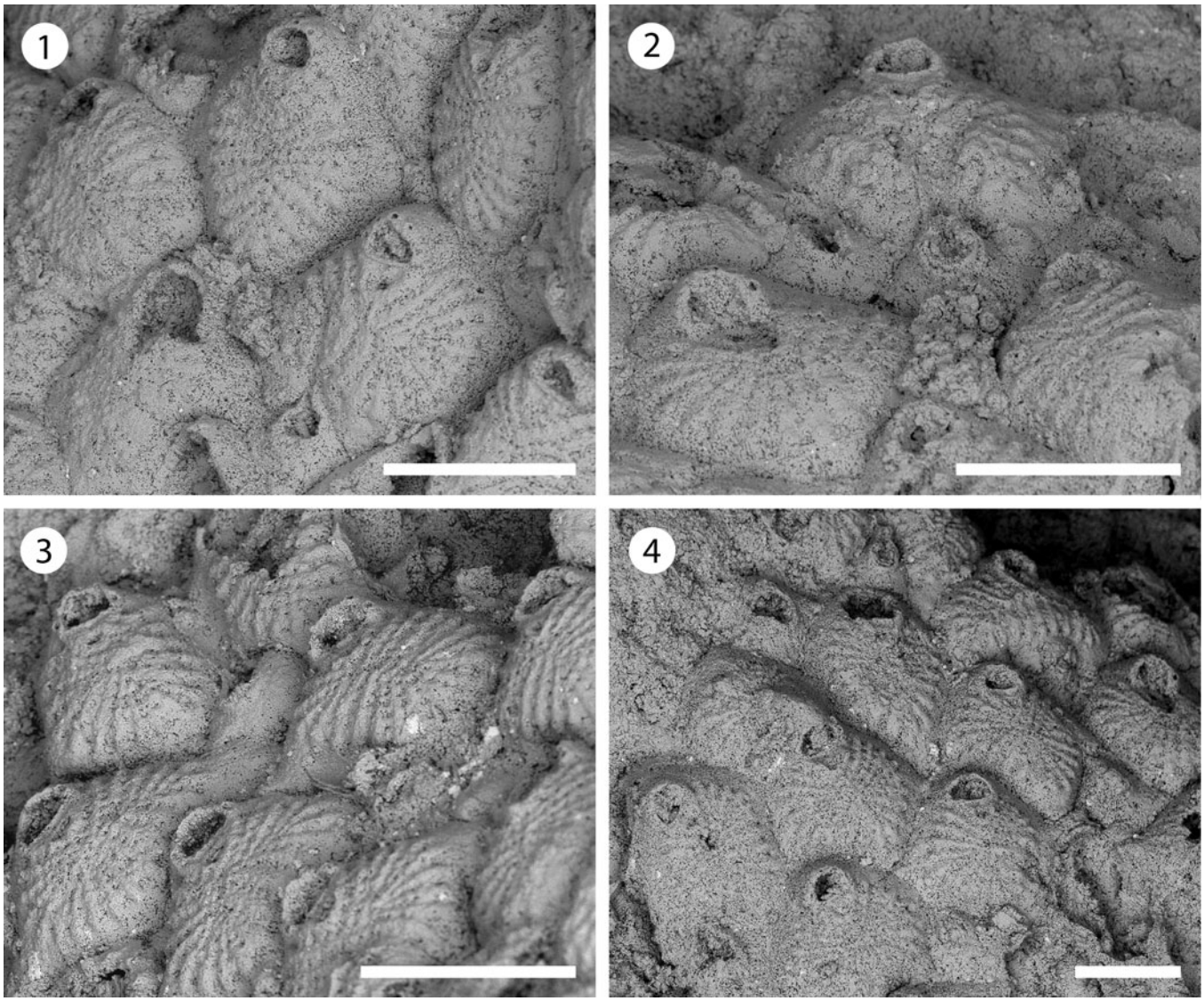


Figure 10. *Cribrilaria nixor* n. sp. (holotype MUN-STRI-47657): (**1–3**) autozooids (showing the orifice shape, spine bases, and suboral lacuna) and interzooidal avicularia, (**4**) fertile zooid with type B ovicell. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are (**1–3**) 0.3 mm; (**4**) 0.25 mm.

with flared mandibles (Harmelin, 2006), seven of them at species level: *C. flabellifera* (Kirkpatrick, 1888) and *C. vaceleti* (Harmelin, 2006) from the Indo-Pacific; *C. arrecta* Bishop and Household, 1987, *C. atlantis* (Harmelin, 2006), *C. macaronensis* (Harmelin, 2006), and *C. mikelae* (Harmelin, 2006) from the central Atlantic and Mediterranean Sea; and *C. smitti* (Winston, 2005) from Florida and the Caribbean. *Cribrilaria multicostata* n. sp. is distinguishable from all of these by having a greater number of costae, up to 17 instead of 5–12, and five oral spines instead of six or seven (except in *C. mikelae*, which also bears five). *Cribrilaria smitti*, the geographically closest congener, differs also in having the first pair of costae more pronounced, leaving a wider space between it and the orifice, where it develops a bifid median umbo. In the Siamaná Formation, *Cribrilaria multicostata* n. sp. was found encrusting the surface of the coral *Acropora panamensis*, co-occurring with the bryozoans *Cribrilaria nixor* n. sp., *Poricella* sp., *Hippoporina* sp., and ? *Hippopleurifera* sp. 2.

Cribrilaria nixor new species
Figure 10; Table 14

Table 14. Measurements of *Cribrilaria nixor* n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.45	0.36–0.6	0.06	12
Autozooid width	0.37	0.32–0.52	0.07	7
Orifice length	0.06	0.05–0.07	0.01	9
Orifice width	0.08	0.06–0.08	0.01	12
Avicularium length	–	0.34	–	1
Avicularium width	0.23	0.17–0.31	0.06	4
Ooecium length	–	0.16	–	1
Ooecium width	–	0.17	–	1

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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 slender rostrum, cystid rhombic with extensive gymnocyst. Ovicell hyperstomial, ooecium produced by the distal zooid or kenozooid (type A and B, Bishop and Household, 1987), smooth, imperforate, and with a median keel.

Description.—Colony encrusting, multiserial, unilaminar. Zooids ovate to elliptical, distinctly separated 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 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 long and slender, cystid rhombic with a well-developed gymnocyst, oriented distally, sometimes lying on the frontal shield of the distal zooid, opesia oval. Ooecium type A and B (Bishop and Household, 1987), longer than wide, surface smooth, not punctate, and with a median keel. Kenozooids present.

Etymology.—From the Latin *nixor*, meaning leaning against, and used as a name in apposition, in reference to the interzooidal avicularia that lean against the frontal shield of the distal autozooids.

Remarks.—Although a single colony is available for this species, several features (e.g., the number of costae, length of the zooids, type of ovicell budding from a kenozooid [type B], wider avicularian opesia, and long and slender rostrum) allow *Cribrilaria nixor* n. sp. to be distinguished from *Cribrilaria multicostata* n. sp. occurring in the same deposits. *Cribrilaria nixor* n. sp. differs from *Cribrilaria anaticula* and *Cribrilaria carolinensis*, both recorded in the early Oligocene of North America (Canu and Bassler, 1920, p. 297), in having a greater number of costae (17–22 vs. 10–12) and in the shape of the avicularian rostrum, which is duck beak-shaped in *C. anaticula*, or thin and channeled in *C. carolinensis*. In the Siamaná Formation, *Cribrilaria nixor* n. sp. was found encrusting the surface of the coral *Acropora panamensis*, co-occurring with the bryozoans *C. multicostata* n. sp., *Poricella* sp., *Hippoporina* sp., and ?*Hippopleurifera* sp. 2.

Genus *Figularia* Jullien, 1886

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

Figularia bragai new species
Figure 11.1–11.5; Table 15

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 pelma located near the tip close to the median, fusion line of the costate shield. Orifice semi-circular with a centered, suboral pore. Putative, vicarious avicularia infrequent. 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, distinctly separated 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 pelma placed close to the fusion line of the costae. Orifice terminal, wide, semi-circular, straight proximally, with a suboral, small, centered pore. Putative interzooidal avicularia infrequent, narrow, almost half of the zooid width, but similar in length. 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 absent.

Etymology.—Named after Professor Juan Carlos Braga, paleontologist (Departamento de Estratigrafía y Paleontología, Universidad de Granada, Spain), in recognition of his support in the study of recent and fossil bryozoans from Colombia.

Remarks.—*Figularia bragai* n. sp. resembles the Miocene species from Indonesia ?*Filaguria kalimantanensis* Di Martino and Taylor, 2015 in the size of zooids, number of costae, position of the pelma, and the morphology of the ooecium. However, the latter species 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. However, in *Figularia bragai* n. sp. we observed a single polymorph, which can be interpreted either as a putative vicarious avicularium with spoon-shaped rostrum and complete cross-bar, or as a malformed autozooid with broken costate shield, constricted between two neighboring zooids with reversed polarity.

Vicarious avicularia with a spoon-shaped rostrum have been described for several species of *Figularia*: the Recent species *F. fissa* (Hincks, 1880) and *F. fissurata* Canu and Bassler, 1929, and Miocene species *F. rhodanica* Li, 1990 (see Li, 1990, pl. 2, fig. 11), but they all differ from the new species in the number of costae, number and size of pelmata, and/or characters of the ooecium (Rosso et al., 2020). *Figularia bragai* n. sp. also differs from the Recent species recorded from the Gulf

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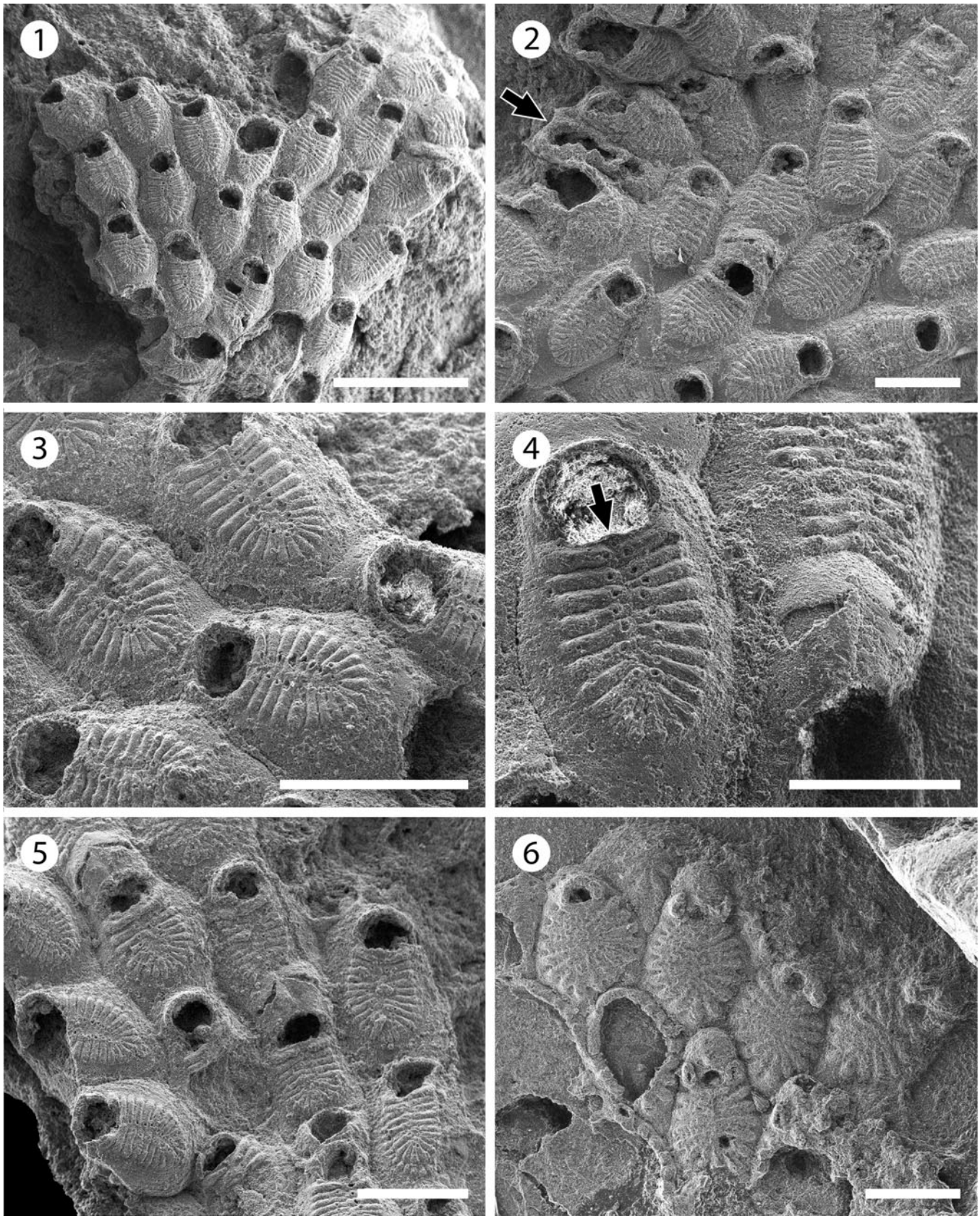


Figure 11. *Figularia bragai* n. sp. (MUN-STRI-47647): (**1**) general view of the colony, (**2**) autozooids and interzooidal avicularia (arrowed), (**3**) close-up of autozooids showing the frontal shield (costae and pelma) and the smooth gymnocyst, (**4**) close-up of a zooid showing the shape of the orifice, the suboral pore (arrowed), and an ovicell, (**5**) group of ovicellate and non-ovicellate zooids. *Glabrilaria* sp. indet. (MUN-STRI-47646): (**6**) general view of the colony. Scale bars are (**1**) 1 mm; (**2, 3, 5**) 0.5 mm; (**4**) 0.3 mm; (**6**) 0.25 mm.

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Table 15. Measurements of *Figularia bragai* n. sp. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.72	0.59–0.88	0.10	10
Autozooid width	0.43	0.34–0.52	0.05	10
Orifice length	0.14	0.11–0.17	0.02	9
Orifice width	0.20	0.17–0.23	0.02	9
Cryptocyst length	0.39	0.29–0.46	0.06	10
Cryptocyst width	0.30	0.25–0.35	0.03	11
Pelma diameter	0.01	0.01	0	2
Avicularium length	–	0.72	–	1
Avicularium width	–	0.2	–	1
Ooecium length	0.21	0.2–0.22	0.01	3
Ooecium width	0.35	0.34–0.35	0.01	3
Fenestra length	0.16	0.12–0.18	0.03	3
Fenestra width	0.03	0.02–0.04	0.01	2

of Mexico and listed as doubtful in Rosso et al. (2020, table 4), ?*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, 1.0 mm wide); while the latter species has 8–11, more commonly nine, costae and a distinctly smaller opesia in ovicellate zooids. The absence of a pelma and proximal and lateral gymnocyst in the species described and figured by Canu and Bassler (1920, p. 316, pl. 43, fig. 9) as ?*Figularia crassicostulata* (Canu and Bassler, 1920) from the late Eocene of North America suggests that this specimen does not belong to the genus *Figularia* (Rosso et al., 2020). In the Siamaná Formation, *F. bragai* n. sp. was found encrusting the underside of the coral *Colpophyllia willoughbiensis* as well as the lateral surface of *Porites baracoaensis* Vaughan, 1919 and *Acropora* sp., sharing the substrate with an undetermined Cribrilinidae, ?*Hippopleurifera* sp. 2, *Gemelliporidra* sp., and ?*Hippomenella* sp.

Genus *Glabrilaria* Bishop and Household, 1987

Type species.—*Puellina pedunculata* Gautier, 1956 from Le Grand Congloué Island, Archipelago of Riou, France, Recent; by original designation.

Glabrilaria sp. indet.
Figure 11.6, 12; Table 15

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 adventitious avicularia with a triangular rostrum located on each side of the orifice of ovicellate zooids, oriented distally; rostrum small, raised at its distal end. Ooecium globular, produced by the distal kenozooid, apparently with a proximo-median umbo or keel. Kenozooids present. Ancestrula not preserved.

Remarks.—Ten species of *Glabrilaria* have been recognized to date. Among them, the Mediterranean *Glabrilaria pedunculata* (Gautier, 1956) has the oldest record, ranging from the late Miocene (Pouyet, 2000) to the Recent. In the American continent, two Recent species, *Glabrilaria hirsuta* Rosso in Rosso et al., 2018 and *Glabrilaria polita* Rosso in Rosso et al., 2018, have been recorded in the deep waters of the central West Atlantic, associated with coral fragments (Rosso et al., 2018). The Siamaná species differs from *G. pedunculata* and *G. polita* in having 6–7 (and not five) oral spine bases in non-ovicellate zooids. Although *G. hirsuta* also has seven oral spines, it differs from the present material in having on average a greater number of costae (13–15 vs. 14–18) and a larger ooecium. However, the Siamaná colony is too small and poorly preserved to observe the characteristic spiny ornamentation, the transversal processes of the ooecia, and/or the clustering of kenozooids typical of *G. hirsuta* (Rosso et al., 2018). Owing to these reasons, we prefer to keep this species in open nomenclature. In the Siamaná Formation *Glabrilaria* sp. indet. was found encrusting a mollusk shell, sharing the substrate with *Atoichos magnus* n. gen. n. sp. and a poorly preserved cyclostome.

Discussion

The majority of the bryozoan species described here are cheilostomes (87%), among which the family Cribrilinidae, with four species, is the most diverse, as already observed in shallow- and deep-water ecosystems with carbonate substrates, both fossil and Recent (Winston, 2016). The family Onychocellidae is represented by two species, while the remaining nine families are represented by only one species each. Only two species, both left in open nomenclature, are cyclostomes (13%).

Seven of the species (47%) found in the Siamaná Formation are new, including three cribrilinids (*Cribrilaria multicostata* n. sp., *Cribrilaria nixor* n. sp., and *Figularia bragai* n. sp.), an antroporid (*Antropora guajirensis* n. sp.), a microporid (*Calpensia caribensis* n. sp.), an onychocellid (*Atoichos magnus* n. gen. n. sp.), and a steginoporellid (*Gymnophorella hadra* n. gen. n. sp.).

The remaining species (53%) are left in open nomenclature owing to their poor preservation, the absence of diagnostic features as gonozooids or ovicells, or the scarcity of available material. Species with erect colonies were commonly found only as small branch fragments, while for those with encrusting colonies only a few autozooids were recorded.

In the assemblage, 73% of the species have encrusting colonies, 20% have erect articulated colonies, and the remaining 7% have erected rigid colonies. The dominance of encrusting forms is a typical pattern in coral reef environments, favored by the availability of hard substrates (Winston, 1986; Hamdane and Moissette, 2002; Cuffey, 2011). By contrast, taxa with free-living colonies, which in the Caribbean region are diverse and abundant from the middle Miocene (from ca. 15 Ma) to the Recent (Cheetham and Jackson, 2000; Flórez et al., 2007; O'Dea, 2009) are absent in the material studied here. This is probably a sampling/environmental bias with the collection focused on the reef framework, whereas free-living bryozoans

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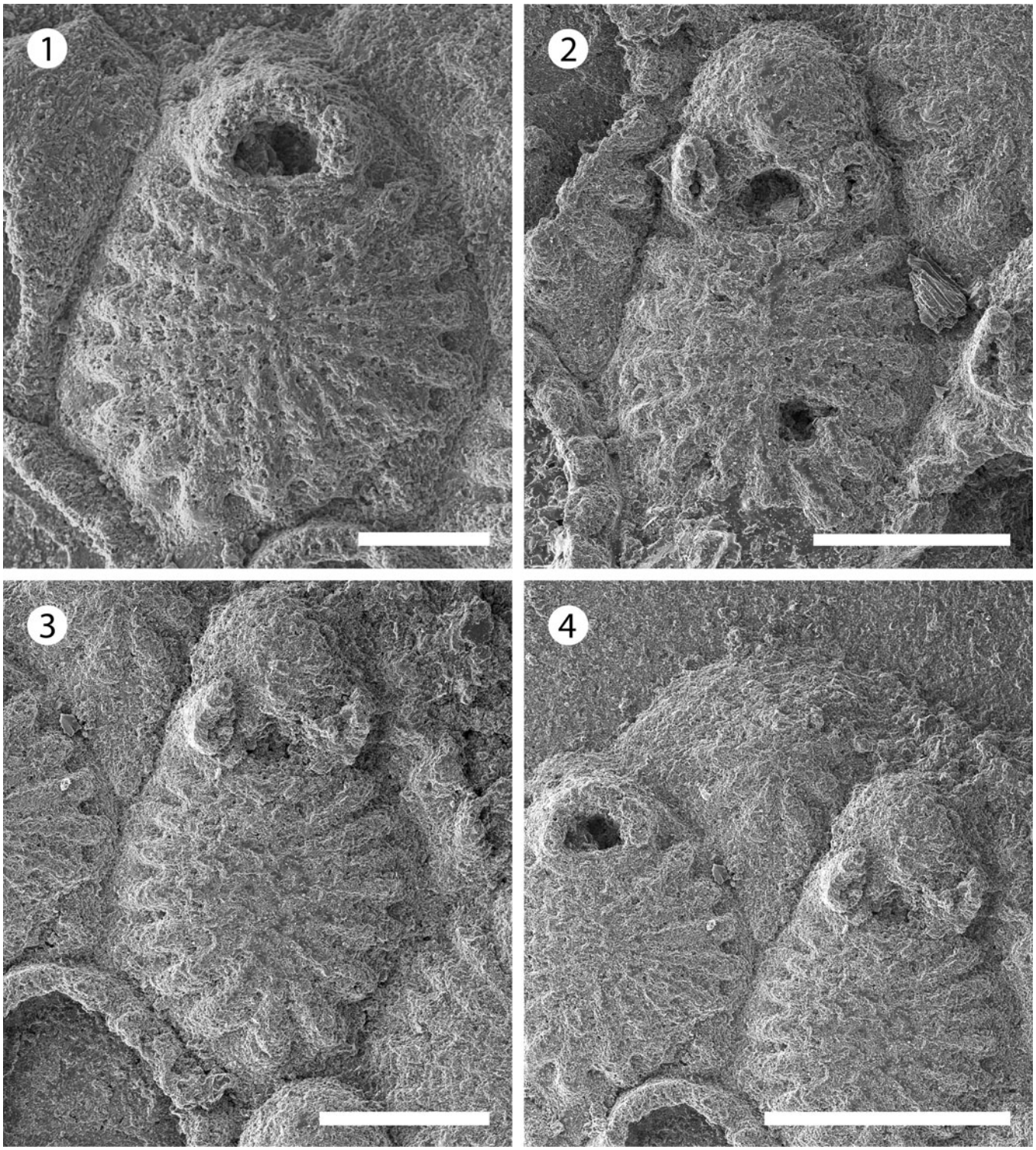


Figure 12. *Glabrilaria* sp. indet. (MUN-STRI-47646): (**1**) close-up of a non-ovicellate autozooid, showing the orifice shape, oral spine bases, and pore chamber windows, (**2, 3**) close-up of ovicellate zooids with paired latero-oral avicularia, (**4**) detail of a kenozooid. All specimens are from the Siamaná Formation, Arroyo Ekieps locality. Scale bars are (**1**) 0.1 mm; (**2, 3**) 0.15 mm; (**4**) 0.25 mm.

are adapted to live on the soft bottoms surrounding the reefs, as well as at greater depths in muddy environments (O'Dea, 2009).

In the Siamaná Formation, encrusting bryozoans were found on the bases and undersurfaces of scleractinian corals (e.g., *Alveopora tampae*, *Acropora panamensis*, *Colpophyllia willoughbiensis*, *Porites baracoaensis*, *Acropora* sp., and *Porites* sp.), as well as on coralline algae that covered the coral rubble, and on mollusk shells. On the other hand, the erect articulated species were found in the sediment attached to the bases and inter-branch spaces of corals such as *Goniopora*

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Table 16. Measurements of *Glabrilaria* sp. indet. X = mean; R = observed range; SD = standard deviation; N = number of measurements.

Character	X	R	SD	N
Autozooid length	0.38	0.34–0.41	0.03	4
Autozooid width	0.28	0.25–0.33	0.04	4
Orifice length	0.04	0.04–0.05	0.01	3
Orifice width	0.06	0.05–0.07	0.01	3
Avicularium rostrum length	0.07	0.06–0.07	0.01	4
Avicularium rostrum width	0.04	0.04–0.05	0.01	4
Ooecium length	0.11	0.11	0	2
Ooecium width	0.15	0.14–0.15	0	2

hilli, *A. tampae*, and *A. panamensis*. Erect articulated bryozoans are also common in coral reefs (Winston, 1986; Cuffey, 2011), both modern and fossil, commonly deeper inside the protected cavities (Hamdane and Moissette, 2002).

Most species were found at the locality Arroyo Ekieps (80%), whereas at Arroyo Uitpa only *Antropora guajirensis* n. sp., *Smittipora* sp. indet., and *Gymnophorella hadra* n. gen. n. sp. were recorded (20%). In both cases, the species were exclusive of the locality. The Arroyo Uitpa paleoenvironment was characterized by patch reefs developed in a shallow lagoon close to the shore-line, while Arroyo Ekieps was a barrier reef system (Flórez et al., 2019a, b; and unpublished data), 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).

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

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Appendix

Appendix 1. List of bryozoans found in the Siamaná Formation (Cocinetas Basin in La Guajira Peninsula, Colombia). The collection is 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 (*).

Familiy	Species	Cataloge number MUN-STRI	Locality	Station number	Type of colony	Substrate	Number of specimens	Coating
Antroporidae	*Antropora* sp.*	47629	Arroyo Uitpa	550005	Encrusting	*Porites* sp.	1	Uncoated
Antroporidae	*Antropora guajirensis* n. sp.	47628	Arroyo Uitpa	550005	Encrusting	*Porites* sp.	1	Coated
Calloporidae	*Copidozoum* sp. indet.	47627	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*	1	Coated
Candidae	*Licornia* sp. indet.	47632	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*	5	Coated
Candidae	*Licornia* sp. indet.	47633	Arroyo Ekieps	550012	Erect articulated	*Acropora panamensis*	2	Coated
Cribrilinidae	*Glabrilaria* sp. indet.	47646	Arroyo Ekieps	550013	Encrusting	Mollusk shell	1	Coated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47653	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	2	Coated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47654	Arroyo Ekieps	550013	Encrusting	Mollusk shell	1	Uncoated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47652	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Coated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47655	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Coated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47656	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47650	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Coated
Cribrilinidae	*Cribrilaria multicostata* n. sp.	47651	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Coated
Cribrilinidae	*Cribrilaria nixor* n. sp.	47657	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Coated
Cribrilinidae	*Cribrilaria nixor* n. sp.	47658	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Cribrilinidae	Cribrilinidae*	47659	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Cribrilinidae	Cribrilinidae*	47660	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.	1	Uncoated
Cribrilinidae	Cribrilinidae*	47661	Arroyo Ekieps	550013	Encrusting	Undetermined	1	Uncoated
Cribrilinidae	Cribrilinidae*	47662	Arroyo Ekieps	550013	Encrusting	Mollusk shell	1	Uncoated
Cribrilinidae	Cribrilinidae*	47663	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Cribrilinidae	Cribrilinidae*	47664	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Cribrilinidae	Cribrilinidae*	47665	Arroyo Uitpa	550006	Encrusting	Coraline algae over *Porites* sp.	1	Uncoated
Cribrilinidae	*Figularia bragai* n. sp.	47647	Arroyo Ekieps	550012	Encrusting	*Colpophyllia willoughbiensis*	1	Coated
Cribrilinidae	*Figularia bragai* n. sp.	47648	Arroyo Ekieps	550013	Encrusting	*Acropora* sp.	1	Uncoated
Cribrilinidae	*Figularia bragai* n. sp.	47649	Arroyo Ekieps	550013	Encrusting	*Porites baracoaensis*	1	Uncoated
Entalophoridae	*Mecynoecia* sp. indet.	47624	Arroyo Ekieps	550013	Erect rigid	*Goniopora hilli*	3	Uncoated
Entalophoridae	*Mecynoecia* sp. indet.	47623	Arroyo Ekieps	550013	Erect rigid	*Goniopora hilli*	1	Coated
Microporidae	*Calpensia caribensis* n. sp.	47634	Arroyo Ekieps	550013	Encrusting	*Alveopora tampae*	1	Uncoated
Microporidae	*Calpensia caribensis* n. sp.	47635	Arroyo Ekieps	550013	Encrusting	*Colpophyllia willoughbiensis*	1	Coated
Microporidae	*Calpensia caribensis* n. sp.	47636	Arroyo Ekieps	550013	Encrusting	*Goniopora hilli*	1	Uncoated
Oncousoeciidae	*Proboscina* sp. indet.	47626	Arroyo Ekieps	550013	Encrusting	*Acropora panamensis*	1	Uncoated
Oncousoeciidae	*Proboscina* sp. indet.	47625	Arroyo Ekieps	550013	Encrusting	*Alveopora tampae*	1	Coated
Onychocellidae	*Atoichos magnus* n. gen. n. sp.	47637	Arroyo Ekieps	550013	Encrusting	Mollusk shell	1	Coated
Onychocellidae	*Smittipora* sp. indet.	47638	Arroyo Uitpa	550005	Encrusting	*Porites* sp.	1	Coated
Onychocellidae	*Smittipora* sp. indet.	47639	Arroyo Uitpa	550005	Encrusting	*Porites* sp.	1	Uncoated
Poricellariidae	*Poricellaria* sp. indet.	47645	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*	2	Coated
Quadricellariidae	*Nellia* cf. *N. tenella*	47630	Arroyo Ekieps	550012	Erect articulated	*Goniopora hilli*	3	Coated
Steginoporellidae	*Gymnophorella hadra* n. gen. n. sp.	47641	Arroyo Uitpa	550006	Encrusting	*Porites* sp.	1	Coated
Steginoporellidae	*Gymnophorella hadra* n. gen. n. sp.	47642	Arroyo Uitpa	550005	Encrusting	Undetermined	1	Coated
Steginoporellidae	*Gymnophorella hadra* n. gen. n. sp.	47643	Arroyo Uitpa	550005	Encrusting	Coraline algae over *Porites* sp.	1	Coated
Steginoporellidae	*Gymnophorella hadra* n. gen. n. sp.	47640	Arroyo Uitpa	550005	Encrusting	Coraline algae over *Porites* sp.	1	Coated
Steginoporellidae	*Gymnophorella hadra* n. gen. n. sp.	47644	Arroyo Uitpa	550005	Encrusting	*Porites* sp.	1	Coated

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