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New records of azooxanthellate stony corals (Cnidaria: Scleractinia and Stylasteridae) from the Neogene of Panama and Costa Rica

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Abstract.—Five new species of azooxanthellate Scleractinia are described from the Panamanian-Costa Rican Neogene: *Septastraea altispina, Antillocyathus gracilis, Paracyathus adetos, Oxysmilia pliocenica,* and *Asterosmilia irregularis.* Three additional species of azooxanthellate stony corals are also reported for the first time in the fossil record: *Gardineria minor, Schizocyathus fissilis,* and *Stylaster roseus.* The records of *S. roseus* are the first fossil occurrence of a stylasterid in the western Atlantic.

The specimens that form the basis for this paper were collected in the first seven years (1986–1992) of the Panama Paleontology Project, a multiphyletic survey of the marine invertebrate Neogene fauna of the Neotropics, especially southern Central America. The purpose of the first phase of the project was to determine the biotic response to the Neogene closure of the Caribbean-eastern Pacific seaway through a detailed analysis of the stratigraphic and geographic distributions of various invertebrate groups. An early review of this project was published (Coates et al. 1992, Collins 1993), which included a general description of the Panama and Costa Rica localities, their lithostratigraphy, and their biostratigraphic correlations. A much more detailed analysis of the stratigraphy of various groups, including Scleractinia, is now in preparation (Collins & Coates in lett) as an edited volume. In that volume I (Cairns 1996) list and document the 18 species of azooxanthellate stony corals that are known to occur in the Panamanian and Costa Rican Neogene, eight of which are discussed herein, i.e., the five new species and the three previously described species that are new to the fossil record.

Species synonymies are considered to be complete or give a reference to a complete synonymy. In the Material Examined sections, each record begins with a PPP locality number, followed by the number of specimens in that lot, followed by its catalog number. The PPP collection sites, with their original "CJ" field numbers, are listed in the Appendix. Absolute ages were derived from biostratigraphic dating using planktic foraminifera, calcareous nannoplankton, and the geological time scale of Berggren, et al (1985).

The following abbreviations are used in the text: GCD, Greater Calicular Diameter; GCD:LCD, Ratio of greater calicular diameter to lesser calicular diameter; H:W, Ratio of height to width of a corallum; PD:GCD, Ratio of pedicel diameter to greater calicular diameter; PPP, Panama Paleontology Project; Sx, Cx, Px, Cycle of septa, costae, or pali (respectively) designated by numerical subscript; USGS, United States Geological Survey; USNM, United States National Museum (part of the National Mu-

seum of Natural History, Smithsonian Institution, Washington, D.C.).

Systematic Account

Class Anthozoa
Order Scleractinia
Suborder Faviina
Family Rhizangiidae d'Orbigny, 1849
Septastraea d'Orbigny, 1849

Diagnosis.—Encrusting or ramose colonies having closely spaced cerioid corallites. Intercorallite coenosteum sparse. Corallites with two, rarely three, cycles of septa. Inner edges of septa finely dentate. Pali absent; fossa shallow; columella a solid fusion of inner septal edges. Miocene to Pleistocene: eastern and southern U.S., Central America, Colombia, Europe.

Type species.—Hinde (1888) argued that d'Orbigny's (1849) originally designated type species (and only species listed by him in 1849) of *Septastraea subramosa* could not be considered the type species of the genus because it was not described by d'Orbigny in 1849. Because Milne Edwards & Haime (1849) described four species of *Septastraea* later in the same year, including *S. forbesi,* and because d'Orbigny (1852) later synonymized *S. forbesi* with his *S. subramosa,* Hinde logically reasoned that *S. forbesi* must be the type species, being the only apparent valid species of the pair. However, the ICZN (1985), written long after Hinde's intellectual exercise, clearly states in Article 12b6 that a description of a new genus before 1931 that includes reference to a new species without further description of that species does constitute availability of the species name through indication, i.e., the generic description also serves as the species description. The type species of *Septastraea* must therefore be *S. subramosa* d'Orbigny, 1849 (=*S. forbesi* Milne Edwards & Haime, 1849; =*S. marylandica* (Conrad, 1841)).

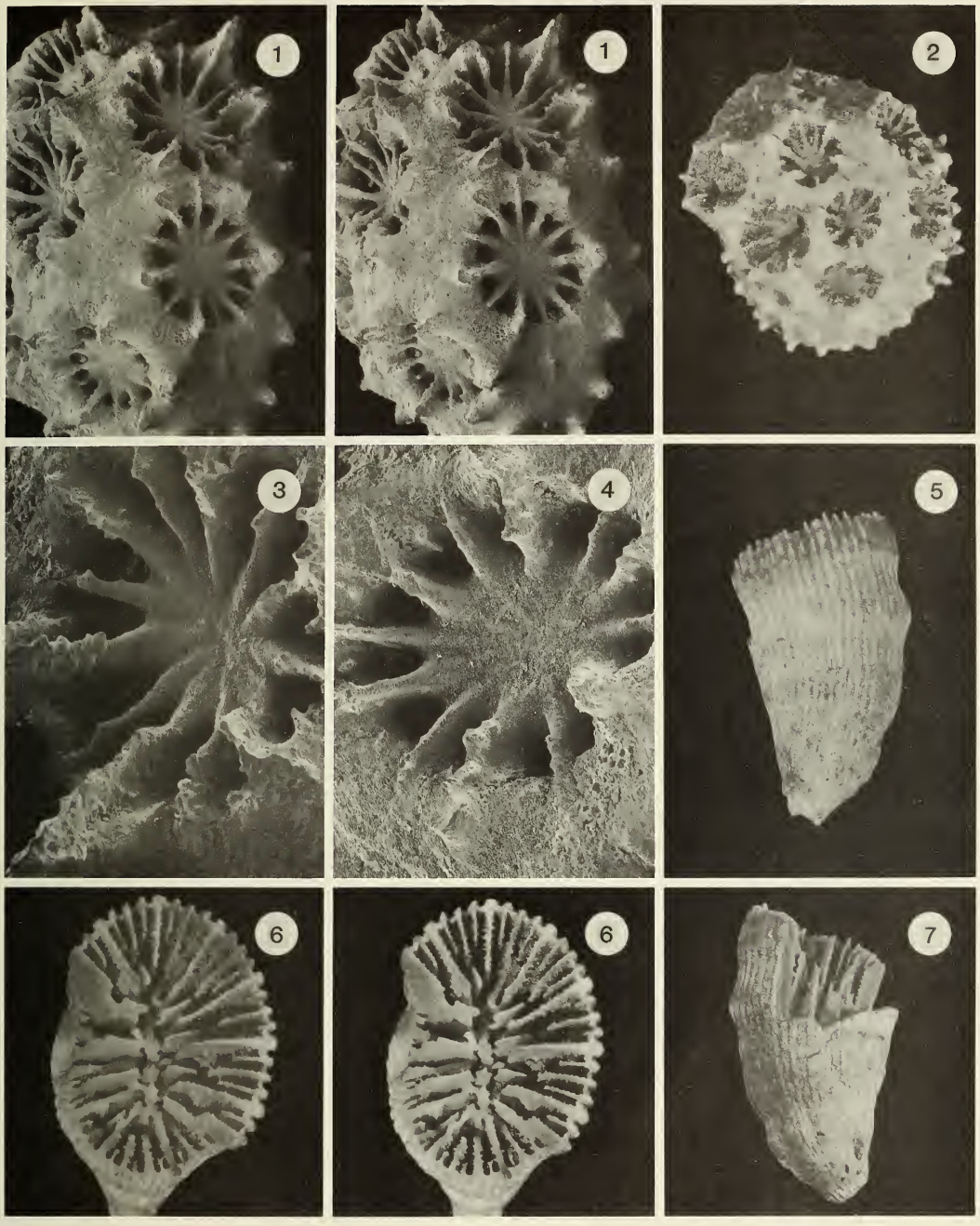
Septastraea altispina, new species
Figs. 1–4

Diagnosis.—Corallum small and cerioid, encrusting gastropod shells. Intercalicular coenosteum well developed. Septa hexamerally arranged in two cycles (12 septa). CS1 highly exsert, each rising to a massive, reddish-brown coensteal spine that is triangular in cross section. Columella massive and flat.

Description.—Corallum cerioid, known only to encrust gastropod shells, the largest colony examined (the holotype) a spherical mass about 11 mm in diameter consisting of approximately 25 corallites. Calices circular to elliptical, larger calices up to 3.3 mm in GCD. Coenosteum well developed: corallites not directly adjacent but separated by 0.50-0.75 mm of coenosteum. In one specimen (USNM 95738), a shallow sulcus surrounds several corallites. Otherwise, coenosteum finely granular (nonspinose) and white, the exsert portions of the 6 CS1 being reddish-brown.

Septa hexamerally arranged in two cycles (12 septa), with no indication of additional S3. S1 highly exsert (up to 1.1 mm), the distal portion of each S1 forming a massive spine that is triangular in basal cross-section (up to 0.3 mm thick), resulting in a crown of 6 CS1 guarding each calice. Inner edges of S1 finely dentate and inclined obliquely toward columella. S2 nonexsert and sometimes rudimentary, their inner edges also finely dentate and oriented obliquely to horizontally, fusing with the columella lower in fossa. Septa relatively thin (0.05–0.11 mm) and well separated from one another by a distance of about four times a septal width (0.3–0.4 mm). Fossa shallow. Columella a solid, massive central structure up to 1.2 mm in diameter, which is flat to slightly concave and granular like the coenosteum.

Discussion.—It may seem inadvisable to describe a new species of *Septastraea* when most, if not all, of the five or six nominal species in this genus have been previously



Figs. 1–7. (1–4, *Septastraea altispina*: 1, 3–4, paratype from PPP326, USNM 95738; 2, holotype, USNM 95735): 1, Stereo view of corallum showing highly exsert costoseptal spines, ×8.1; 2, Holotype, ×4; 3–4, Two corallites illustrating the massive columella, both ×22. (5–7, holotype of *Antillocyathus gracilis,* USNM 95469): 5, 7 Lateral views of holotype, both × 2.6; 6, Stereo view of calice, ×3.8.

synonymized (see Vaughan 1904, Weisbord 1971, Meeder 1987) as the morphologically variable and stratigraphically widespread (New Jersey to Louisiana, ?Colombia; Miocene to Pleistocene) *Septastraea marylandica* (Conrad, 1841). Nonetheless, although both species are similar in habit (encrusting shells), have the same number of septa, and have a massive columella, *S. altispina* differs in having highly exsert, massive, pigmented S1, which are easily seen on all specimens examined and are not present on *S. marylandica.*

Etymology.—The species name *altispina* (from the Latin *altus,* high + *spina,* thorn) refers to the six prominent CS1 that crown each calice.

Material examined.—Holotype: PPP326, 1 colony, USNM 95735.—Paratypes: PPP195, 1 corallite, USNM 95736; PPP196, 1 colony and 2 corallites, USNM 95737; PPP326, 10 colonies, USNM 95738; PPP379, 2 colonies, USNM 95739; PPP422, 2 corallites, USNM 95740.

Type locality.—PPP326: Caribbean Panama, Cayo Agua, north side Pta de Nispero (9°10′4.8″N, 82°02′0.6″W); Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

Distribution and Age.—Cayo Agua, Isla Popa, and Valiente Peninsula, all Bocas del Toro, Caribbean Panama. Cayo Agua Formation (early Late Pliocene), Shark Hole Point Formation (early Late Pliocene).

Suborder Caryophylliina
Family Caryophylliidae Dana, 1846
Antillocyathus Wells, 1937

Diagnosis.—Corallum solitary and usually highly compressed. Septotheca costate and granular. One crown of pali before S3 or before penultimate septal cycle when hexameral symmetry lost. Columella lamellar or formed of aligned, fused papillae. Dissepiments rare or absent. Miocene to Pliocene: West Indies, Central America.

Type species.—*Placotrochus maoensis* Vaughan *in* Vaughan & Hoffmeister (1925), by original designation.

Antillocyathus gracilis, new species
Figs. 5–7

Diagnosis.—Corallum ceratoid and usually curved about 45° in plane of GCD. GCD:LCD = 1.1–1.3. Small edge crests present on both concave and convex thecal edges near base. Septa hexamerally arranged in four cycles (S1–2>S3>S4). One crown on 12 P3.

Description.—Corallum ceratoid (edge angle 14°–19°), compressed, and usually slightly curved about 45° in plane of GCD. Largest specimen examined (USNM 95539) 13.5 × 10.3 mm in calicular diameter and 27.0 mm in height; holotype slightly smaller and somewhat damaged, but otherwise in excellent preservation, measuring 10.3 × 7.7 mm in calicular diameter and 18.6 mm in height. Calice elliptical, GCD:LCD = 1.12–1.33. Pedicel quite small, only 0.4–0.9 mm in diameter, and invariably detached from substrate. Costae equal, convex, and highly granular. Costae 0.40–0.45 mm wide, separated by shallow intercostal furrows about 0.15 mm wide. Thecal edge crests present on lower 2–3 mm of corallum, best preserved in juvenile coralla before they become broken or worn. Edge crests quite thin, semi-circular in shape, and up to 2.6 mm in height, occurring on both concave and convex thecal edges, but usually more prominent on convex edge. On upper convex thecal edge of many coralla a second, lower crest may be present or the principal costa on that edge may be slightly more produced. Corallum white to reddish-brown.

Septa hexamerally arranged in four cycles (some large coralla have some pairs of S4, up to 60 septa) according to the formula S1–2>S3>S4. S1–2 slightly exsert (about 1 mm) and have straight, vertical inner edges that reach about three-quarters distance to columella. S3 less exsert and about half width of S1–2. Each S3 bordered by a wide (up to 1.6 mm), lamellar palus, the 12 P3 forming a distinct elliptical crown encircling the columella. S4 about half width of an S3. Fossa moderate in depth, containing an elongate,

Table 1.—Diagnostic characters of the four species of *Antillocyathus*.

Character	*A. maoensis*	*A. alatus*	*A. cristatus*	*A. gracilis*
Typical size (GCD)	13–18 mm	9–11 mm	22–26 mm	10–13 mm
Shape; lateral edge angle	Straight, compressed; 45°–80°	Straight, full; parallel in upper corallum	Curved, full; 36°–44°	Curved, compressed; 14°–19° (ceratoid)
GCD:LCD	1.75–2.50	1.3–1.75	1.6–1.7	1.1–1.3
Edge crests	Basally only	Basally only	Basally and convex edge	Basally and convex edge
Septal arrangement	19–24:19–24:38–48: 0–8 (78-*80*-104)	14–16:14–16:24–32: 0–8 (48-*64*-72)	>S5 (106 septa)	S1–2 > S3 > S4 (*48*-60)
Pali	19–24 secondary pali (P2)	14–16 P2	24 P4	12 P3
Columella	Solid, lamellar	Solid, lamellar	Lamellar to spongy	Fused papillose to sublamellar
Age and Distribution	Late Miocene to early Pliocene of Dominican Republic	Late Miocene to early Pliocene of Dominican Republic	Late Miocene to early Pliocene of Dominican Republic; Pliocene of Panama and Costa Rica	Early to middle Pliocene of Panama

papillose to lamellar columella consisting of three or four fused papillae or a thin, dissected lamella.

Discussion.—*Antillocyathus gracilis* is compared to the three other species in the genus in Table 1. To summarize, it is distinguished by having a curved, slender corallum; a low GCD:LCD; hexamerally arranged septa in four cycles; and 12 P3.

Etymology.—The species name *gracilis* (from the Latin *gracilis,* slender) refers to the slender ceratoid growth form of the species.

Material examined.—Holotype: PPP63, 1 corallum, USNM 95469. Paratypes: PPP56, 15, USNM 95524; PPP57, 3, USNM 95522; PPP63, 18, USNM 95470; PPP196, 27, USNM 95523; PPP345, 17, USNM 95521. Nontypes: PPP55, 2, USNM 95525; PPP193, 27, USNM 95527; PPP194, 2, USNM 95526; PPP197, 8, USNM 95528; PPP198, 25, USNM 95529; PPP208, 1, USNM 95530; PPP294, 7, USNM 95532; PPP295, 2, USNM 95533; PPP298, 1, USNM 95534; PPP306, 1, USNM 95535; PPP307, 8, USNM 95536; PPP308, 2, USNM 95537; PPP311, 3, USNM 95538; PPP335, 1, USNM 95539; PPP346, 6, USNM 95540; PPP348, 1, USNM 95541; PPP350, 3, USNM 95542; PPP355, 3, USNM 95543; PPP357, 1, USNM 95544; PPP423, 1, USNM 95545.

Type locality.—PPP63: Caribbean Panama, Cayo Agua, small island offshore (9°10′44.0″N, 82°03′11.0″W); Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

Distribution and Age.—Most records from Cayo Agua, Bocas del Toro, Caribbean Panama; also known from Isla Colon and Isla Popa, both also Caribbean Panama. Cayo Agua Formation (early Late Pliocene).

Paracyathus Milne Edwards & Haime, 1848a

Diagnosis.—Corallum solitary; trochoid to turbinate; fixed or free. Base often polycyclic. Paliform lobes usually multilobate, occurring before all but last cycle of septa. Columella papillose, elements often indistinguishable from lower paliform lobes. Eocene to Recent: cosmopolitan.

Type species.—*Paracyathus procumbens* Milne Edwards & Haime, 1848a, by subsequent designation (Milne Edwards & Haime 1850: xv).

Paracyathus adetos, new species
Figs. 8–14

Diagnosis.—Corallum tympanoid, cylindrical, or trochoid, often overgrowing its substrate of attachment to become free. Base polycyclic. Septa hexamerallay arranged in four cycles: S1>S2>S4≥S3. Each S1–3 bears several narrow paliform lobes. Columella papillose or solid.

Description.—Corallum solitary, attached when young but often incorporating the substrate into its base (Fig. 13) and thus becoming free in adult stage. Young coralla cylindrical and squat (tympanoid); older coralla persist as short cylinders if the substrate is too large to overgrow, but become bowl-shaped to trochoid or turbinate if the substrate is overgrown. Largest specimen examined (holotype) 6.7 mm in circular calicular diameter and 3.9 mm in height, the height usually being about half the calicular diameter. Base polycyclic (Figs. 10, 12, 14), larger coralla having up to five concentric thecal rings occurring at the following approximate diameters and septal complements: first ring, 0.5–0.7 mm (6 septa); second, 1.05–1.20 mm (12 septa); third, 1.4–1.9 mm (about 18 septa); fourth, 2.2–3.6 mm (24 septa); and fifth, 2.6–6.7 mm (48 septa). Coralla usually attach to a small bivalve shell or piece of a bivalve shell or to a small gastropod shell, and less frequently to another coral, a brachiopod shell, or a bryozoan colony. Costae highly ridged and dentate, the C1–2 up to 0.4 mm in height, the C3–4 less prominent.

Septa hexamerally arranged in 4 complete cycles above a GCD of about 4.3 mm according to the formula: S1>S2>S4≥S3. S1 highly exsert (up to 0.7 mm) and have straight inner edges that extend about 0.8 distance to columella. Inner edges of each S1 bears one small, blunt paliform lobe adjacent to the columella. S2 less exsert and extend only 0.6 distance to columella, each S2 internally bordered by two or three small, blunt paliform lobes. S3-4 equally exsert, the S3 extending about half the distance to columella, the S4 equal to or slightly wider than the S3. Each S3 internally bordered by three or four tall, blunt paliform lobes; inner edges of S4 finely serrate. Inner edges of each pair of S4 within a half-system fuse to their common S3, each pair of S3 within a system, in turn, fuses to its common S2 through its innermost teeth, directly adjacent to the columella. All septa covered with tall granules. Fossa quite shallow. Columella papillose in small coralla, the papillae fusing in larger coralla to form a massive, slightly concave solid structure.

Discussion.—*Paracyathus adetos* is similar to *P. vaughani* Gane, 1895, a species known from the Late Miocene of the southeastern United States from Virginia to Florida (see Vaughan 1904, Weisbord 1971). Both species have low, tympanoid coralla, polycyclic bases that are often attached to bivalve shells, and similarly shaped paliform lobes. *Paracyathus vaughani,* however, differs in attaining a larger size (e.g., up to 11 mm GCD with 88 septa and eight thecal rings), always remaining attached, having a papillose (never solid) columella, and having a deeper fossa (Figs. 15, 18). *Paracyathus adetos* differs from *P. henekeni* Duncan, 1863 in having a larger corallum and more septa; a lower H:W; and a more solid columella.

Etymology.—The species name *adetos* (from the Greek *adetos,* loose, free, unbound) refers to the tendency of mature coralla of this species to become free attachment by incorporating the substrate into its base.

Material examined.—Holotype: PPP196, 1, USNM 95575. Paratypes: PPP56, 6, USNM 95576; PPP57, 3, USNM 95577; PPP63, 13, USNM 95578; PPP65, 14, USNM 95579; PPP66, 1, USNM 95580;

PPP194, 13, USNM 95581; PPP195, 16, USNM 95582; PPP196, 42, USNM 95583; PPP197, 7, USNM 95584; PPP198, >100, USNM 95585; PPP205, 2, USNM 95586; PPP306, 32, USNM 95588; PPP307, 53, USNM 95589; PPP311, 11, USNM 95590; PPP352, 22, USNM 95591; PPP475, 28, USNM 95587.

Type locality.—PPP196: Caribbean Panama, Cayo Agua, SW Pt. Norte (9°10′42.5″N, 82°03′9.0″W); Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

Distribution and Age.—All records from Cayo Agua, Bocas del Toro, Caribbean Panama (early Late Pliocene).

Oxysmilia Duchassaing, 1870

Diagnosis (emended).—Corallum solitary; ceratoid to trochoid; attached or free. Base composed of concentric, partitioned thecal rings achieved by formation of exothecal dissepiments over ridged costa, or the base may be narrow and unattached. Septotheca costate. Rudimentary paliform lobes occasionally present before S3. Fossa deep. Columella variable, ranging from massive granular papillae to lamellar or aligned fused papillae. Dissepiments absent. Late Pliocene to Recent: Central America, western Atlantic (46–640 m).

Type species.—*Lophosmilia rotundifolia* Milne Edwards & Haime, 1848c, by monotypy.

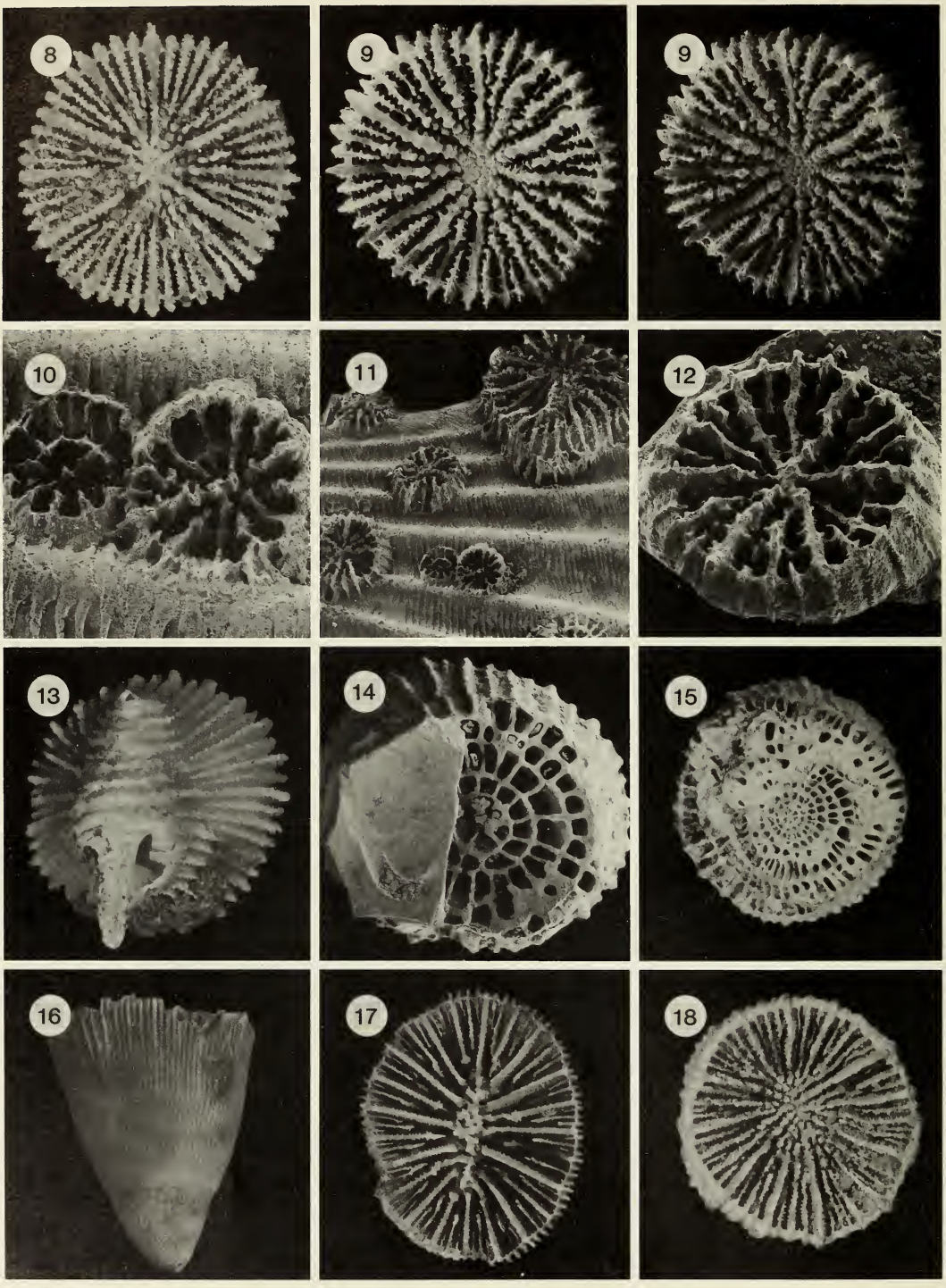
Oxysmilia pliocenica, new species
Figs. 16–17

Diagnosis.—Corallum ceratoid and free, with a narrow pedicel. Septa hexamerally arranged in five cycles, the last cycle incomplete: S1–2>S3>S4>S5. Rudimentary paliform lobes (P3) sometimes present. Columella papillose or lamellar.

Description.—Corallum ceratoid and free, the largest specimen examined (holotype) 14.2 × 11.8 mm in calicular diameter and 18.4 mm in height. Pedicel very narrow, only 1.0–1.2 mm in diameter, in most cases partially incorporating a small gastropod shell into its base. Calice elliptical: GCD: LCD = 1.20–1.25. Costae poorly defined on lower third of corallum; broad, slightly convex, and granular on middle third; and ridged and rather thin in upper third adjacent to calice, where intercostal furrows are correspondingly broader. Upper half to third of corallum reddish-brown. Theca quite thin, only about 0.05 mm in thickness.

Septa hexamerally arranged in five cycles, the last cycle incomplete. The holotype has 92 septa and the largest paratype of GCD 13.9 mm has 82 septa, consisting of seven half-systems with both pairs of S5, three with one pair of S5, and two half-systems with no S5. Septal formula: S1–2>S3>S4>S5. Relative exsertness of septal cycles unknown due to poor preservation of calicular edges. S1–2 broad, extending 0.8–0.9 distance to columella, and have straight, vertical, slightly thickened inner edges. S3 about three-quarters width of an S1–2 and have finely sinuous inner edges, some of which extend to the columella low in fossa as irregular trabecular ribbons. S4 half width of S3 and have finely dentate inner edges. S5 rudimentary, about one-third width of an S4. Faces of S1–4 homogeneously covered with low, pointed granules. Fossa moderate in depth. Columella variable in shape: in the holotype and three paratypes it consists of an alignment of slender, fused papillae, but in one paratype (USNM 95594) the columella is a thin, dissected lamella.

Discussion.—*Oxysmilia pliocenica* is quite similar to the only other species in the genus, *O. rotundifolia* (Milne Edwards & Haime, 1848c), a species known only from the Recent western Atlantic from North Carolina to Surinam and the western Gulf of Mexico at 46–640 m (Cairns 1979). Points of similarity include septal number, arrangement, and size; costal shape; and variation in columella shape, the columella of *O. rotundifolia* also ranging from elongate



Figs. 8–18. (8–14, *Paracyathus adetos*: 8, holotype, USNM 95575; 9, paratype, PPP196, USNM 95583; 10–12, paratype, PPP198, USNM 95585; 13, paratype, PPP63, USNM 95578; 14, paratype, PPP475, USNM 95587): 8, Calice of holotype, ×6.4; 9, Stereo view of a paratype, ×7.8; 10–12, Young stages attached to bivale shells (calices of fig. 10 illustrating 2 thecal rings, calices of fig. 12, 3 rings), ×28, ×6.3, ×26, respectively; 13,

papillose to solid lamellar. Also, in both species some specimens bear trabecular processes on the inner edges of their S3 that resemble small paliform lobes. *Oxysmilia pliocenica* differs in having a simple base (not partitioned concentric rings similar to polycyclic development), being smaller in size, and having a reddish-brown corallum.

Lophosmilia Milne Edwards & Haime, 1848b is a closely related genus of three or four species known from the Cretaceous to Eocene of Europe, Texas, and Peru, differing from *Oxysmilia* in having a deep-seated lamellar columella (Wells 1956). But, given the range of columellar variation found in the two known species of *Oxysmilia,* this difference hardly seems significant. In fact, *O. rotundifolia* was originally described in the genus *Lophosmilia.*

Etymology.—Named for the geological epoch in which it occurs.

Material examined.—Holotype: PPP311, USNM 95593. Paratypes: PPP196, 1, USNM 95595; PPP311, 3, USNM 95594.

Type locality.—PPP311: Caribbean Panama, Cayo Agua, S of Pt. de Nispero (9°09′57.4″N, 82°01′48.6″W); Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

Distribution and age.—Known only from Cayo Agua, Bocas del Toro, Caribbean Panama (early Late Pliocene).

Asterosmilia Duncan, 1867

Diagnosis.—Corallum solitary; ceratoid, trochoid, or flabellate; free or attached. Septotheca costate. Paliform lobes present before penultimate septal cycle. Columella lamellar or fascicular. Vesicular endotheca abundant. Oligocene to Recent: West Indies, Central America.

Type species.—*Trochocyathus abnormalis* Duncan, 1864, by subsequent designation (Vaughan 1919:354).

Asterosmilia irregularis, new species
Figs. 19–20

Asterosmilia abnormalis.—Cairns & Wells, 1987: 37 (in part: USGS 8321).

Diagnosis.—Corallum ceratoid, elongate, and gently curved. Septa arranged in 15–18 sectors, with the following septal complements: 15–18:15–18:30–36:0–10 (up to 76 septa). Paliform lobes present on secondary septa and tertiary septa that are flanked by quaternary septa. Columella lamellar.

Description.—Corallum ceratoid, elongate, and usually gently curved about 90° in basal region. Largest specimen examined (USGS 20468) 19.4 × 16.8 mm in calicular diameter and 72.9 mm in length; holotype 16.3 × 14.6 mm in calicular diameter and 52.1 mm in length. Corallum always free, narrowing to a slender, invariably broken pedicel 1.0–1.5 mm in diameter (PD:GCD = 0.06–0.12), which usually reveals the 6 protosepta. Original object of attachment never seen and apparently not incorporated into base. Calice consistently elliptical: GCD:LCD = 1.15–1.27. Costae slightly convex and equal in width, none more prominent than others. Each costa about 0.5 mm wide near calice and separated by narrow (0.08 mm), shallow intercostal striae. Each costa covered with low, rounded granules about 0.15 mm in diameter, arranged two or three across a costa at any level. Theca not very thick (only about 0.4 mm wide near calice), a deep reddish-brown color.

Septa of adult coralla arranged in 15–18 sectors, each sector flanked by two primary

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Corallum base overgrowing a small gastropod shell, ×5.9; 14, Broken base revealing 5 thecal rings. (15, 18, syntype of *Paracyathus vaughani* from Miocene of Virginia, USNM 68311): 15, 18, Basal view showing thecal rings, and calice, both ×2.8. (16–17, holotype of *Oxysmilia pliocenica,* USNM 95593): 16, 17, Side and calicular views, both ×2.

Table 2.—Diagnostic characters of the three Panamanian Neogene species of *Asterosmilia*.

Character	*A. profunda*	*A. irregularis*	*A. exarata*
Corallum size; shape	GCD max. = 35.7 mm; trochoid to ceratoid, occasionally attached	GCD max. = 19.4 mm; ceratoid, free	GCD max. = 10.4 mm; ceratoid, free
PD:GCD	0.11–0.29	0.06–0.12	0.06–0.11
Costae	C1–2 usually more pronounced than others	All costae equal	C1–2 usually broader than others
Septal arrangement	S1–2 > S3 > S4 > S5 (96–108 septa), S1–2 highly exsert	15–18:15–18:30–36:0–10 (68–76 septa), not exsert	S1–2 > S3 > S4 (48 septa), not very exsert
Paliform lobes	24 P4	16–18 lobes before secondaries and some tertiaries	12 P3
Vesicular dissepiments	Abundant, inclined, 1–5 "rings"	Less common, inclined, 1–2 "rings"	Sparse, horizontal, one ring
Columella	Coarse papillose or crispate	Plate-like (lamellar or labyrinthiform)	Lamellar to crispate

septa and containing a medial secondary septum, two tertiary septa and 0–2 quaternary septa, resulting in a calicular total of 68–76 septa. Septal formula of holotype: 15:15:30:10 (70 septa, 17 well-developed pali and three rudimentary ones); other specimens having: 17:17:34:4 (72 septa, 17 well-developed pali), USNM 95611; 17:17:34:6 (74 septa, 17 well-developed pali and three rudimentary), USNM 95615; and 18:18:36:4 (76 septa, 18 well-developed pali and two rudimentary), USNM 95615. Preservation of most coralla does not allow analysis of septal or palar number. Primary septa only slightly exsert (1.0–1.2 mm), of moderate thickness (about 0.4 mm), and have straight, vertical inner edges that extend about three-quarters distance to columella. Secondary septa less exsert and less thick, and only about half width of a primary. Each secondary septum bordered internally by a broad, lamellar paliform lobe of equal width to the secondary septum. Inner edges of paliform lobes fuse to columella. In sectors lacking quaternaries, tertiary septa are about one-third width of a secondary, but if a pair of S4 flank a tertiary, the tertiary is doubled in width and sometimes bears a broad paliform lobe (P3) of variable size, sometimes as large as a P2 but occasionally rudimentary. S4 rudimentary. Thin vesicular dissepiments occur in upper corallum, inclined and structured as in *A. profunda*, but occurring less abundantly, i.e., only one or two dissepiments present at a level in any interseptal space. Fossa of moderate depth, containing a plate-like columella of variable construction. Often the plate is a single, thin, medial lamella; occasionally it is expressed as several parallel, slightly overlapping plates; and in one case (USNM 95615) the plates were labyrinthiform in arrangement.

Discussion.—*Asterosmilia irregularis* differs from its congeners in having nonhexameral septal symmetry. It is intermediate in size between the two other Neogene species known from Panama and differs from them in other characters as well (Table 2).

Etymology.—The species name *irregularis* (from the Latin *in regularis*, not according to rule) refers to the variable number of septal sectors contained by specimens of this species.

Material examined.—Holotype: PPP1119, USNM 95609. Paratypes: PPP627, 38, USNM 95618; PPP757, 4, USNM 95617; PPP1101, 12, USNM 95610; PPP1102, 2, USNM 95611; PPP1103, 1, USNM 95612;

PPP1104, 1, USNM 95613; PPP1105, 10, USNM 95614; PPP1107, 13, USNM 95615; PPP1118, 1, USNM 95616; USGS 8321, 1, USNM 65323; USGS 20468, 69, USNM 64024; Limon Centro, Costa Rica, 3, USNM 81310; Moin Formation, Costa Rica, 4, USNM 72351.

Type locality.—PPP1119: Lomas del Mar, Limon, Costa Rica, (construction site): 9°59′31.0″N, 83°02′12.2′W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

Distribution and Age.—All specimens from Lomas del Mar, Limon, Caribbean Costa Rica (Late Pliocene).

Family Flabellidae Bourne, 1905
Gardineria Vaughan, 1907

Diagnosis.—Corallum solitary, ceratoid to turbinate; transverse division lacking. Corallum attached through a pedicel as well as having a massive lateral secondary rootlet. Epitheca transversely wrinkled. Upper, outer septal edges separated from smooth calicular edge by a deep notch. P2 usually present; columella papillose. Late Pliocene (Costa Rica) to Recent (tropical western Atlantic, Hawaiian Islands, Philippines, Antarctica, South Africa).

Type species.—*Gardineria hawaiiensis* Vaughan, 1907, by original designation.

Gardineria minor Wells, 1973
Figs. 21–26

Gardineria minor Wells, 1973: 49–53, figs. 36a–g; Cairns, 1979: 162–163, pl. 31, figs. 7–9 (complete synonymy).

Description.—Corallum small, subcylindrical to ceratoid, and firmly attached to substrate by a small pedicel 0.9–1.3 mm in diameter and a larger, irregularly-shaped lateral rootlet, which issues from the lower side of the theca and appears as a broad thecal adhesion to the substrate. Base polycyclic, usually with only two rings—the protothecal and the outer epithecal—the latter being smooth but circumferentially finely wrinkled. The seven fossil specimens examined range in calicular diameter from 2.6–4.9 mm. Corallum white.

Septa hexamerally arranged in two or three cycles, depending on calicular diameter. Coralla 2.6–3.0 mm in diameter have only 12 septa (Figs. 23, 26), whereas those over 3.3 mm usually have 24 septa arranged: S1>S2>S3 (Figs. 21–22, 24–25). S1 exsert, thick (about 0.25 mm), and have entire inner edges that attain the columella. S2 nonexsert, much thinner than S1, and have sloping, dentate to laciniate inner edges that also merge with the columella. S3 rudimentary, each represented only as a series of spines. Tall, slender P2 sometimes present. Fossa shallow. Columella small and papillose.

Discussion.—The fossil specimens reported herein are indistinguishable from Recent *G. minor* (Figs. 24–25), a species that is common throughout the Caribbean. Large living specimens (e.g., over 5 mm GCD) are known to have a fourth cycle of septa.

Material examined.—PPP466, 1, USNM 95689; PPP710, 6, USNM 95690; type series, USNM; specimens reported by Cairns (1979).

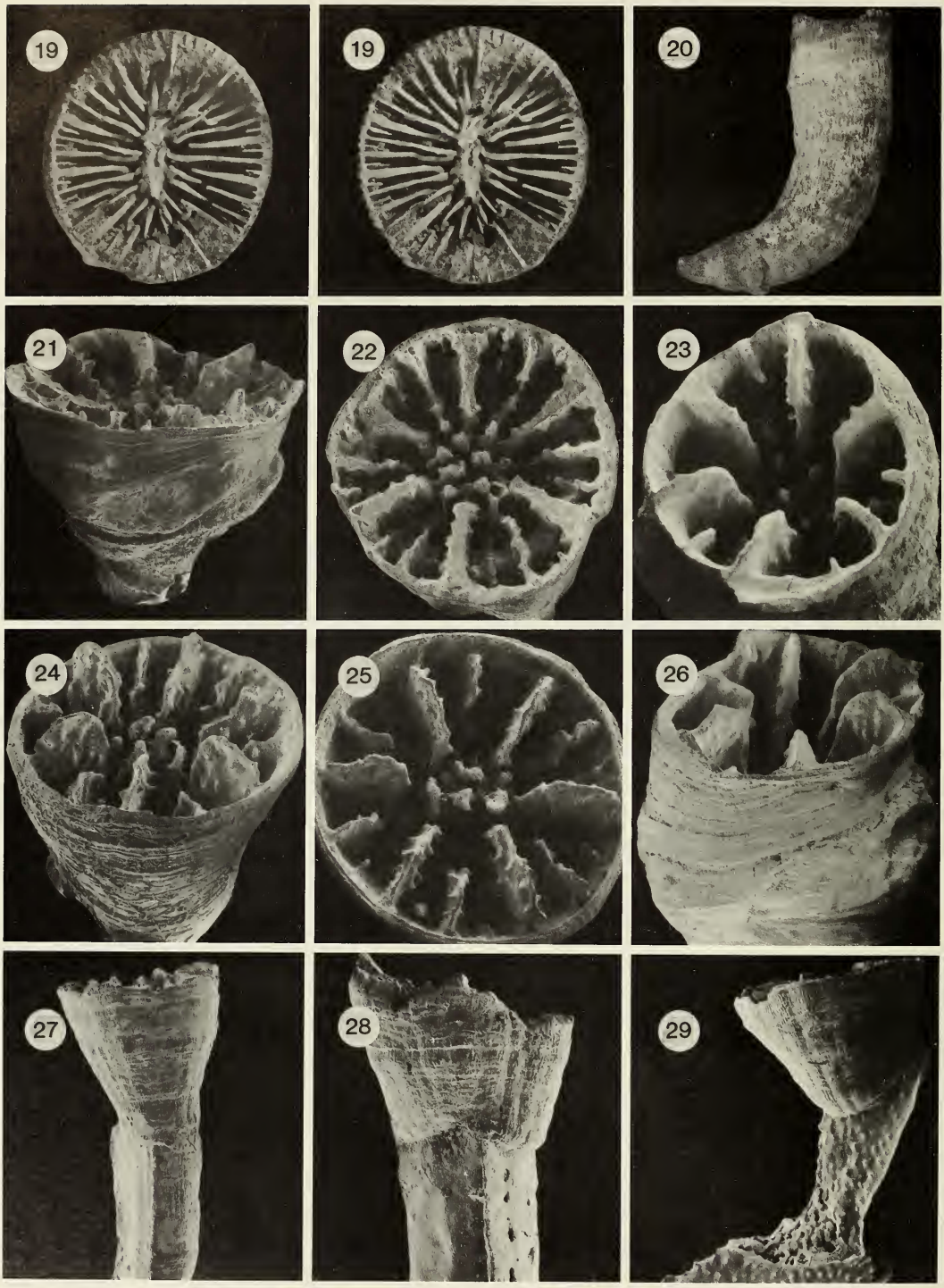
Types.—The holotype and 11 paratypes of *G. minor* are deposited at the USNM (53503-53506) (Cairns 1991).

Type locality.—off Yallahs, Jamaica, 15 m.

Distribution and age.—Santa Rita and Limon, Caribbean Costa Rica; Moin Formation (Late Pliocene). Previously known only from the Recent throughout the Caribbean and Bahamas, including off Panama, at 2–241 m (Cairns 1979).

Family Guyniidae Hickson, 1910
Schizocyathus Pourtalès, 1874

Diagnosis.—Corallum solitary, ceratoid, and invariably attached to a fragment of its parent corallum through longitudinal parricidal budding. Smooth epitheca bears 12



Figs. 19–29. (19–20, holotype of *Asterosmilia irregularis,* USNM 95609): 19–20, Stereo calicular and lateral views of holotype, ×2.5, ×0.9, respectively. (21–26, *Gardineria minor*: 21–23, 26, PPP710, USNM 95690; 24–25, Recent, Jamaica, 31 m, USNM 80892): 21–22, Side and calicular views of a specimen with 3 cycles of septa,

rows of mural pores (spots), a pair of rows flanking each S2. P1 often present; P3 always present, each pair within a system uniting in a V-shaped structure. Columella absent. ?Paleocene, ?Eocene, Late Pliocene to Recent: ?Russia, ? South Australia, Costa Rica, Atlantic (88–1300 m).

Type species.—*Schizocyathus fissilis* Pourtalès, 1874, by monotypy.

Discussion.—The illustrations of the species described from the Danian of Russia, *S. daschsalachlyensis* Kuzmicheva, 1987, are not typical for the genus. Likewise, the description and figures of *Cyathosmilia velata* Dennant, 1902 (Eocene, South Australia), doubtfully placed in *Schizocyathus* by Vaughan & Wells (1943), are also inconsistent with the type species of the genus. Therefore the early Tertiary records of this genus are strongly doubted.

Schizocyathus fissilis Pourtalès, 1874
Figs. 27–29

Schizocyathus fissilis Pourtalès, 1874: 36–37, pl. 6, figs. 12–13; Cairns, 1979: 166–167, pl. 32, figs. 4–7 (complete synonymy); Zibrowius, 1980: 166, pl. 85, figs. A–O.

Discussion.—The single specimen reported herein measures only 1.9 mm in calicular diameter and 1.5 mm in height, but is attached to a one-sixth sector of its parent corallum, which is 1.6 mm long. Both parent fragment and budded corallum display external mural pores about 0.11 mm in diameter. The septal pattern is obscured by sediment within the calice, but the specimen appears to have three cycles of septa, the S1 being quite exsert.

Even though the Panamanian specimen is small and poorly preserved, there is little doubt it is *S. fissilis*. Asexual fragmentation from a wedge of a parent corallum, usually a longitudinal one-sixth of the corallum, is the most common mode of reproduction in this species (Figs. 27–29). The Panamanian specimen is the first fossil occurrence of this species.

Material examined.—PPP362, 1, USNM 95675; syntype series.

Types.—Forty-one syntypes are deposited at the MCZ (5470 and 2791).

Type locality.—off Barbados, 183 m.

Distribution and age.—Escudo de Veraguas, Bocas del Toro, Caribbean Panama; Escudo de Veraguas Formation, 1.8–1.9 Ma (Late Pliocene). Previously known only from the Recent of Caribbean and Gulf of Mexico, including off Honduras, and northeastern Atlantic, at 88–1300 m (Cairns 1979, Zibrowius 1980).

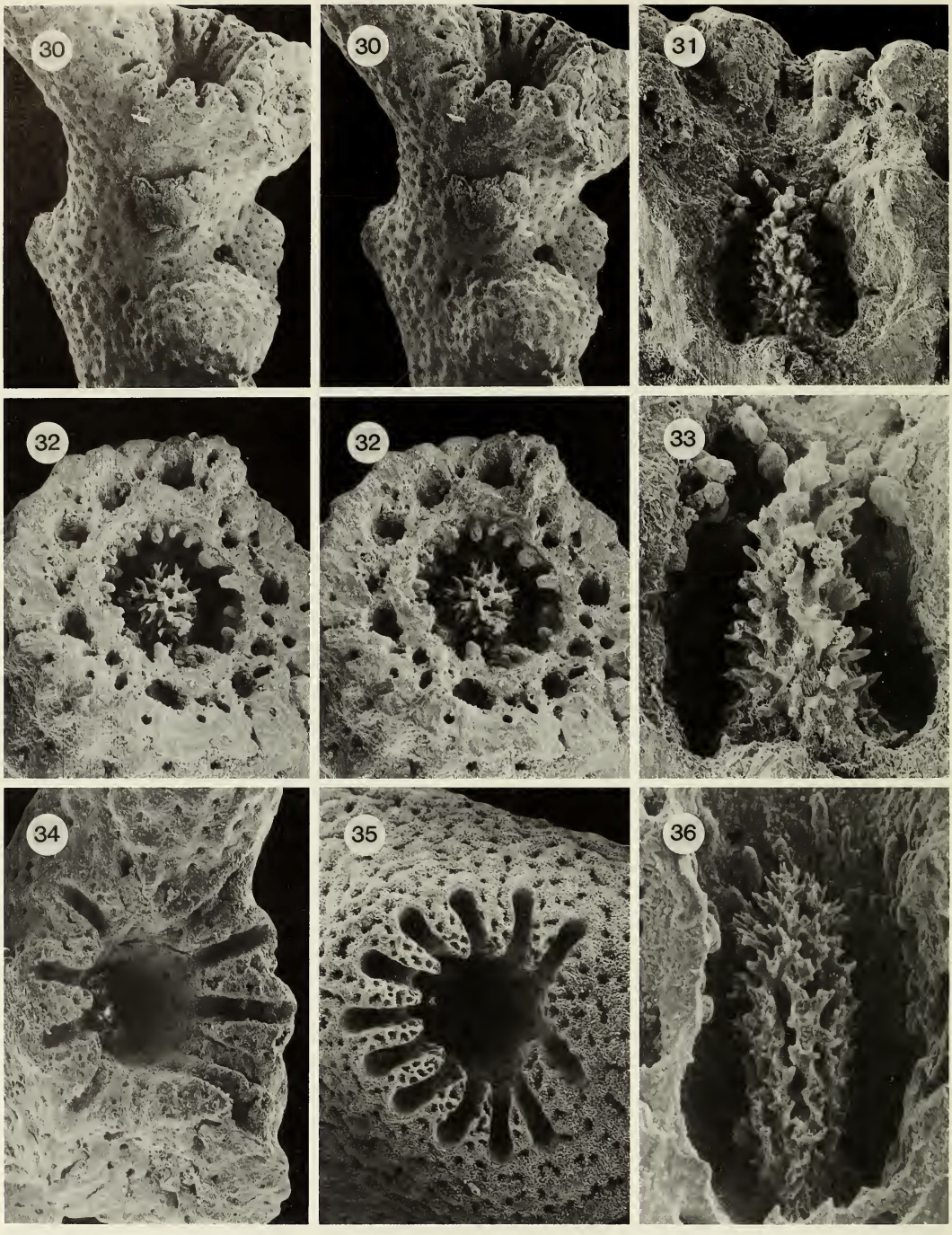
Class Hydrozoa
Family Stylasteridae Gray, 1847
Stylaster Gray, 1831

Diagnosis.—Gastro- and dactylopores arranged in cyclosystems. Cyclosystems variable in location, ranging from a uniform coverage of all branch surfaces to a strictly sympodial arrangement. Coenosteal texture also variable, but usually linear-imbricate or reticulate-granular. Gastro- and dactylostyles present; gastrostyles usually ridged; ring palisade often present. Ampullae superficial. Oligocene to Recent: cosmopolitan.

Type species.—*Madrepora rosea* Pallas, 1766, by subsequent designation (Milne Edwards & Haime 1850: xxii).

←

×13.8, 12.2, respectively; 23, 26, A smaller specimen with only 2 cycles of septa, both ×16.2; 24–25, Oblique calicular and calicular views of a Recent specimen included for comparison to fossil specimens, ×14, ×15, respectively. (27–29, *Schizocyathus fissilis*: 27, Recent, off Barbados, 200 m, USNM 61747; 28, PPP362; 29, Recent, Gulf of Mexico off Florida, 221 m, USNM 61744): 27–28, Small coralla budded asexually from a parent fragment, ×11, ×18, respectively; 29, A three-generation budded corallum, ×10.4.



Figs. 30–36. (*Stylaster roseus*: 30–34, PPP710, USNM 95724; 35–36, Recent, Carrie Bow Cay, Belize, 3 m, USNM 47807): 30, Stereo view of a branch illustrating a cyclosystem and a female ampulla, ×32; 31, 33, Longitudinal fracture through cyclosystems revealing gastrostyles and elements of ring palisade, ×92, ×190, respectively; 32, Stereo view of cross section of a cyclosystem just above gastrostyle tip, illustrating ring palisade and circle of dactylopores, ×80; 34, A cyclosystem, ×50; 35–36, Cyclosystem and gastrostyle of a Recent specimen, ×50, ×155, respectively.

Stylaster roseus (Pallas, 1766)
Figs. 30–36

Madrepora rosea Pallas, 1766: 312-313.
Stylaster roseus.—Cairns, 1986: 61–65, pl. 27, figs. A–H, pl. 28, figs. A–C, pl. 53, fig. D (complete synonymy and distribution map).

Description.—Only relatively small branch fragments are reported herein, the longest (USNM 95724) 9 mm long consisting of nine cyclosystems. Coenosteum composed of slightly convex, worn strips 80–90 μm wide arranged in a reticulate fashion.

Cyclosystems circular to slightly elliptical, 0.8–1.0 mm in greater diameter, and arranged in a strictly sympodial manner. Based on 14 cyclosystems, the range of dactylopores per cyclosystem is 10–13, average = 11.1 (σ = 0.86), and mode = 11. Gastropores circular (about 0.25 mm in diameter) and contain a well-developed, diffuse ring palisade consisting of robust, cylindrical elements up to 35 μm in height and 14–21 μm in diameter. Gastrostyles lanceolate, highly ridged, and very spinose. Illustrated gastrostyle (Figs. 31, 33) 0.24 mm in height and 0.11 mm in diameter, bearing slender spines up to 35 μm long and only 3–4 μm in basal diameter. Dactylotomes 60–65 μm wide; pseudosepta wedge-shaped and about two times width of a dactylotome. An adcauline diastema three times dactylotome width is often present. Dactylostyles rudimentary, composed of widely-spaced, linearly arranged cylindrical elements up to 25 μm in height and only about 7 μm in diameter.

Female ampullae 0.55–0.65 mm in diameter, sometimes clustered. Lateral efferent pore 0.15–0.18 mm in diameter. Male ampullae not observed.

Discussion.—Direct comparison of the Neogene stylasterids to Recent *S. roseus* shows no significant differences, *S. roseus* being the only shallow-water stylasterid known from the western Atlantic (Cairns 1986). Although the genus *Stylaster* is known from the fossil record, these records are believed to be the first fossil stylasterids of any kind reported from the western Atlantic.

Material examined.—PPP55, 1, USNM 95720; PPP634, 3, USNM 95721; PPP639, 2, USNM 95722; PPP708, 3, USNM 95723; PPP710, 12, USNM 95724; PPP720, 30, USNM 95725; PPP738, 10, USNM 95726.

Types.—Not traced.

Type locality.—off Santo Domingo, depth unknown.

Distribution and age.—Isla Colon, Bocas del Toro, Caribbean Panama; Pueblo Nuevo, Limon, and Santa Rita, Caribbean Costa Rica; Moin Formation (early Late to Late Pliocene). Previously known from Recent throughout Caribbean and Bahamas, including off Caribbean Panama, Costa Rica, Honduras, and Belize, at 0.5–73 m (Cairns 1986).

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Appendix: PPP Collection Sites, Including Original CJ Field Numbers

PPP55 (CJ86-31-1) Isla Colon, Bocas del Toro: 9°25′23.2″N, 82°15′36.8″W; age and formation unknown.

PPP56 (CJ86-32-1) Cayo Agua, Bocas del Toro, SW of Pt. Norte: 9°10′39.1″N, 82°03′8.8″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP57 (CJ86-33-1) Ibid.: 9°10′48″N, 82°03′6.7″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP63 (CJ8639-1) Cayo Agua, Bocas del Toro, small island offshore: 9°10′44.0″N, 82°03′11.0″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP65 (CJ86-40-2) Cayo Agua, Bocas del Toro, S of Pt. de Nispero: 9°09′57.4″N, 82°01′48.6″W; Cayo Agua Formation, 3.4–10.8 Ma (age uncertain).

PPP66 (CJ86-40-3) Ibid.

PPP193 (CJ87-27-1) Cayo Agua, Bocas del Toro, SW of Pt. Norte: 9°10′35.1″N, 82°03′8.7″W; Cayo Agua Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP194 (CJ87-28-1) Ibid.

PPP195 (CJ87-29-1) Ibid.: 9°10′37.0″N, 82°03′9.0″W.

PPP196 (CJ87-29-2) Ibid.: 9°10′42.5″N, 82°03′9.0″W.

PPP197 CJ87-29-3) Ibid.: 9°10′45.8″N, 82°03′8.3″W.

PPP198 (CJ87-29-4) Ibid.: 9°10′48.0″N, 82°03′6.7″W.

PPP205 (CJ87-33-4) Cayo Agua, Bocas del Toro, SW of Pt. Piedra Roja: 9°08′29.3″N, 82°00′43.8″W; age and formation unknown.

PPP208 (CJ87-33-7) Ibid.: 9°08′33.3″N, 82°00′38.4″W; ?Cayo Agua Formation (age uncertain).

PPP294 (CJ88-18-2) Cayo Agua, Bocas del Toro, W side of Pt. de Tiburon: 9°09′18.0″N, 82°01′34.1″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP295 (CJ88-18-3) Ibid.

PPP298 (CJ88-18-6) Ibid.

PPP306 (CJ88-20-4) Cayo Agua, Bocas del Toro, E side Pt. de Nispero: 9°10′3.1″N, 82°01′48.2″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP307 (CJ88-20-5) Ibid.

PPP308 (CJ88-20-6) Ibid.

PPP311 (CJ88-21-1) Cayo Agua, Bocas del Toro, S side Pt. de Nispero: 9°09′57.4″N, 82°01′48.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP326 (CJ88-25-12) Cayo Agua, Bocas del Toro, N side Pt. de Nispero: 9°10′4.8″N, 82°02′0.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP335 (CJ88-26-2) Cayo Agua, Bocas del Toro, E tip Pt. de Tiburon: 9°09′11.4″N, 82°01′21.6″W; Cayo Agua Formation, 2.9–3.6 Ma (early Late Pliocene).

PPP345 (CJ88-27-1) Cayo Agua, Bocas del Toro, between Tiburon and Piedra Roja: 9°08′50.2″N, 82°00′54.4″W; ?Cayo Agua Formation (age uncertain).

PPP346 (CJ88-27-2) Ibid.: 9°08′48.5″N, 82°00′56.6″W.

PPP348 (CJ88-27-4) Ibid.: 9°08′45.3″N, 82°01′2.0″W.

PPP350 (CJ88-28-1) Ibid.: 9°08′48.6″N, 82°00′53.1″W.

PPP352 (CJ88-28-3) Ibid.: 9°08′48.4″N, 82°00′50.3″W.

PPP355 (CJ88-28-6) Ibid.: 9°08′47.1″N, 82°00′46.9″W.

PPP357 (CJ88-29-2) Cayo Agua, Bocas del Toro, E end Pt. Piedra Roja: 9°08′35.3″N, 82°00′30.1″W; ?Cayo Agua Formation (age uncertain).

PPP362 (CJ88-30-5) Escudo de Veraguas, Bocas del Toro, NW coast: 9°06′4.5″N, 81°34′18.3″W; Escudo de Veraguas Formation, 1.8–1.9 Ma (Late Pliocene).

PPP379 (CJ88-32-4) Valiente Peninsula, Bocas del Toro, NW side Bruno Bluff: 9°02′32.2″N,

81°44′42.0″W; Shark Hole Point Formation, 3.5–3.6 Ma (early Late Pliocene).

PPP442 (CJ88-59-1) Isla Popa, Bocas del Toro, NE coast: 9°12′57.7″N, 82°06′24.7″W; ?Cayo Agua Formation (age uncertain).

PPP423 (CJ888-59-2) Ibid.

PPP466 (CJ88-00-35) Limon, Costa Rica, near Progressive Baptist Church: 9°59′28.2″N, 83°02′29.9″W; age and formation unknown.

PPP475 (CJ88-00-44) Cayo Agua, Bocas del Toro, SE of Pt. Norte: 9°10′26.3″N, 82°02′26.9″W; Cayo Agua Formation, 4.6–5.0 Ma (Early Pliocene).

PPP627 (CJ89-14-1) Pueblo Nuevo, Limon, Costa Rica (Cerro Mocho subdivison): 9°59′51.0″N, 83°02′36.0″W; Moin Formation, 1.5–3.5 Ma (early Late to Late Pliocene).

PPP634 (CJ89-16-1) Ibid. (cemetery): 9°59′28.2″N, 83°02′29.2″W; Moin Formation, 1.9–2.4 Ma (Late Pliocene).

PPP639 (CJ89-17-2) Lomas del Mar, Limon, Costa Rica (construction site): 9°59′46.3″N, 83°02′26.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

PPP708 (CJ89-33-1) Santa Rita, Limon, Costa Rica (near stream): 9°58′24.5″N, 83°07′22.4″W; formation unknown, 2.4–3.4 Ma (early Late Pliocene).

PPP710 (CJ89-35-1) Limon, Costa Rica, Santa Eduviges subdivision: 10°00′14.9″N, 83°02′30.9″W; Moin Formation, less than 1.8 Ma (Late Pliocene).

PPP720 (CJ89-39-1) Santa Rita, Limon, Costa Rica (near stream): 9°58′10.3″N, 83°07′48.9″W; formation unknown, 2.2–3.4 Ma (Late Pliocene).

PPP738 (CJ89-47-1) Limon, Costa Rica, Hotel Olas: 10°00′41.1″N, 83°02′49.3″W; formation unknown, 0.01–1.7 Ma (Pleistocene).

PPP757 (CJ89-00-19) Limon, Costa Rica (Lomas del Mar construction site): 9°59′46.3″N, 83°02′26.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

PPP1101-1119 (CJ92-00-21 to 40) Ibid.: 9°59′31.0″N, 83°02′12.2″W; Moin Formation, 1.7–1.9 Ma (Late Pliocene).

USGS 8321 Costa Rica, north shore of Provision Island, Gatun Formation; Late Miocene.

USGS 20468 Puerto Limon, Costa Rica; ?Late Pliocene.