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Neotypes for *Porites porites* (Pallas, 1766) and *Porites divaricata* Le Sueur, 1820 and remarks on other western Atlantic species of *Porites* (Anthozoa: Scleractinia)

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Abstract.—To stabilize the taxonomy of the genus *Porites* in the western Atlantic and provide a foundation from which to launch future taxonomic research, neotypes for the coral species *Porites porites* and *P. divaricata* are chosen and *Porites verrillii* is proposed as a junior synonym of *P. astreoides*. Colony photographs and stereo scanning electron micrographs are provided of corallites of: 1) neotypes of *P. porites* (i.e., the *P. clavaria* holotype) and *P. divaricata,* 2) the holotypes of *P. furcata, P. branneri, P. colonensis,* and *P. verrillii,* and 3) a common *P. astreoides*. A brief taxonomic history of the genus is also provided.

Keywords: coral taxonomy, neotypes, *Porites divaricata*, *Porites porites*, *Porites verrillii*, western Atlantic

The purpose of this nomenclatural rectification (i.e., this is not a taxonomic revision of the western Atlantic species of *Porites*) is to stabilize the taxonomy of western Atlantic branching species of *Porites* in an effort to provide a strong foundation for launching future *Porites* taxonomic research. Whether a species is valid or not, their names need to be defined by a type species, in this case neotypes. This stabilization process will accomplish the following: 1) provide a brief taxonomic history of the western Atlantic species of the genus *Porites*; 2) designate neotypes for the coral species *Porites porites* and *P. divaricata*; 3) propose *Porites verrillii* as a junior synonym of *P. astreoides*; and 4) provide stereo scanning electron micrographs of corallites of neotypes for the coral species *Porites porites* (i.e., the *P. clavaria* holotype) and *P. divaricata* and of the holotypes of *P. furcata, P. branneri, P. colonensis,* and *P. verrillii*. Stereo scanning electron micrographs of corallites of a common *P. astreoides* from Belize are also provided to compare against those of *P. verrillii*.

By creating a reliable suite of type specimens for the Poritidae in the western Atlantic, we will enable researchers to be more confident when they are choosing field specimens of *Porites* for taxonomic analysis and be more confident when they are making scientific comparisons among species of *Porites*.

In the western Atlantic Ocean, living representatives of the stony coral family Poritidae Gray, 1842 consist of the single genus *Porites* Link, 1807. For the purpose of stabilizing the taxonomy of *Porites* in the western Atlantic, the species *P. astreoides* Lamarck, 1816 is recognized with the astreoid-type corallite structure of (Figs. 1A, B, 2) (Bernard 1906, Jameson

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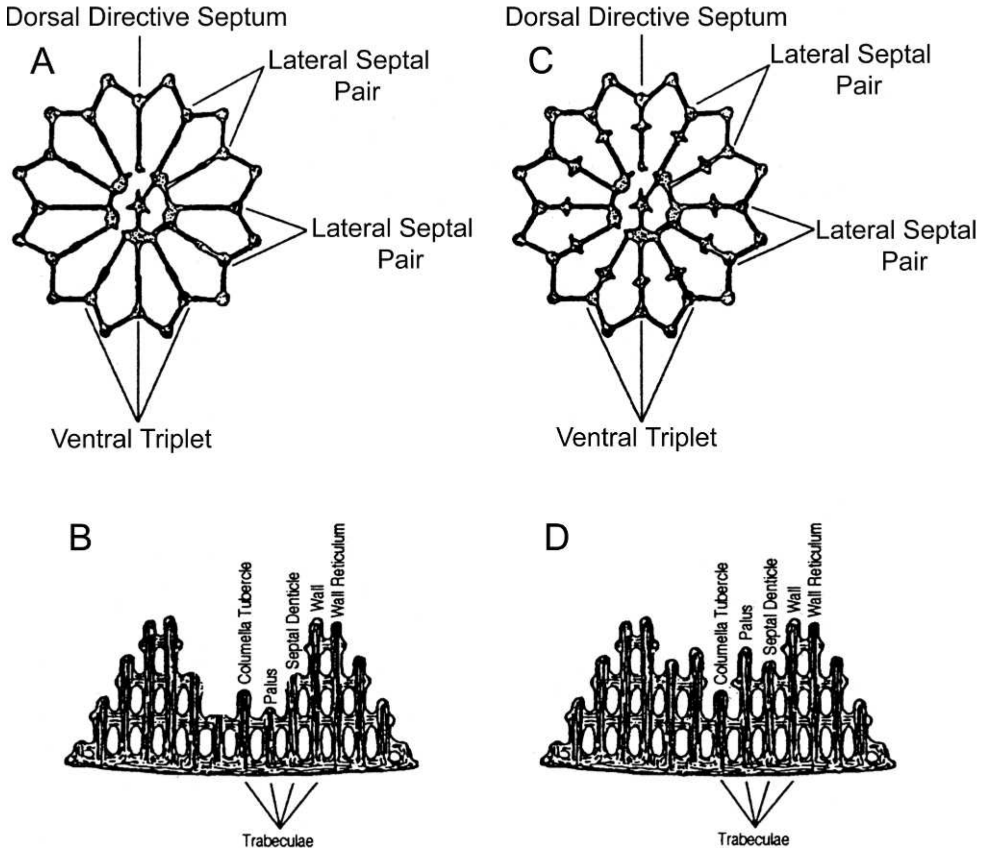

Fig. 1. Stylized diagrams (modified after Bernard 1906) illustrating the two basic forms of the theca of *Porites*. A and B illustrate "ideal" horizontal and vertical sections, respectively, of the astreoid-type corallite form found in *Porites astreoides*. C and D illustrate ideal horizontal and vertical sections, respectively of the non-astreoid corallite form found in *P. porites, P. furcata, P. divaricata, P. colonensis*, and *P. branneri*.

1995, 1997), whereas the species *P. porites* (Pallas, 1766)*, P. furcata* Lamarck, 1816*, P. divaricata* Le Sueur, 1820*, P. branneri* Rathbun, 1887, and *P. colonensis* Zlatarski, 1990 are recognized with the non-astreoid type (Figs. 1C, D, 3) corallite structure (Bernard 1906, Jameson 1995, 1997). Colony photographs are provided in Fig. 4.

It is important to understand the taxonomy and systematics of recent and fossil poritids in the western Atlantic because of the major role they have and continue to play in the structure, ecology, and evolution of coral reef ecosystems (Garthwaite et al. 1994) and because they have been and continue to be an important component of many geological and biological studies in the Caribbean and western Atlantic (Ginsburg 1994). Poritids also play a variety of important roles: 1) esthetically, as a beautiful natural component of coral reefs and as one of four genera that constitute the majority of the dead coral trade for ornaments and jewelry; 2) ecologically, as prime habitat for a wide variety of tropical organisms; 3) economically, in the aquarium industry; 4) medically, for use in bone grafts (Green & Shirley 1999); and 5) scientifically, as indicators of climate change (Pernetta 1993, Omata et al. 2006, Tanzil et al. 2009).

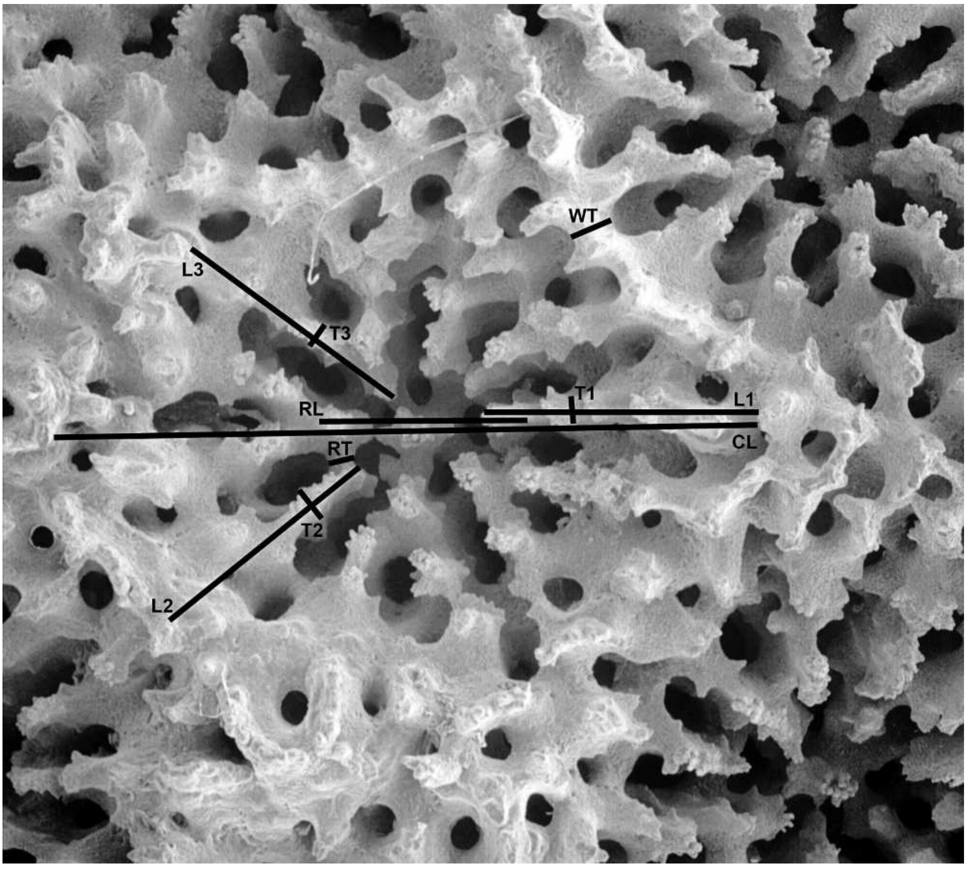

Fig. 2. Illustration showing how astreoid corallite characters were measured in Jameson (1995). Corallite characters: CL = corallite length; L1 = septum length (dorsal); L2 = septum length (ventral); L3 = septum length (lateral); RL = columella synapticular ring length; RT = columella synapticular ring thickness; T1 = septum thickness (dorsal); T2 = septum thickness (ventral); T3 = septum thickness (lateral); WT = wall thickness.

Brief taxonomic history.—The overlapping morphological variation within and among poritids makes their taxonomy among the most difficult of all scleractinians (Rathbun 1887, Rehberg 1893, Vaughan 1901, Bernard 1906, Brakel 1977, Cairns 1982, Foster 1986, Zlatarski 1990, Weil 1992, Potts et al. 1993, Garthwaite et al. 1994, Jameson 1995, 1997).

Weil (1992) found fixed allele differences among *P. astreoides*, *P. porites*, *P. furcata*, *P. divaricata*, *P. colonensis*, and *P. branneri* off Panama, using electrophoresis on 11 polymorphic loci from 9 enzyme systems. Working with *Porites* off Miami, Florida, and St. Croix, U.S. Virgin Islands, electrophoretic results of Potts et al. (1993) found fixed allele differences that distinguished *P. porites* and *P. furcata* from *P. divaricata* and that distinguished *P. astreoides* from *P. porites*, *P. furcata*, and *P. divaricata* (as would be expected because of the astreoid vs. non-astreoid corallite structural differences). Potts et al. (1993) made no mention of fixed allele differences among all three branching species.

An independent morphometric method for identifying species of *Porites* remained elusive until Jameson (1995, 1997) deter-

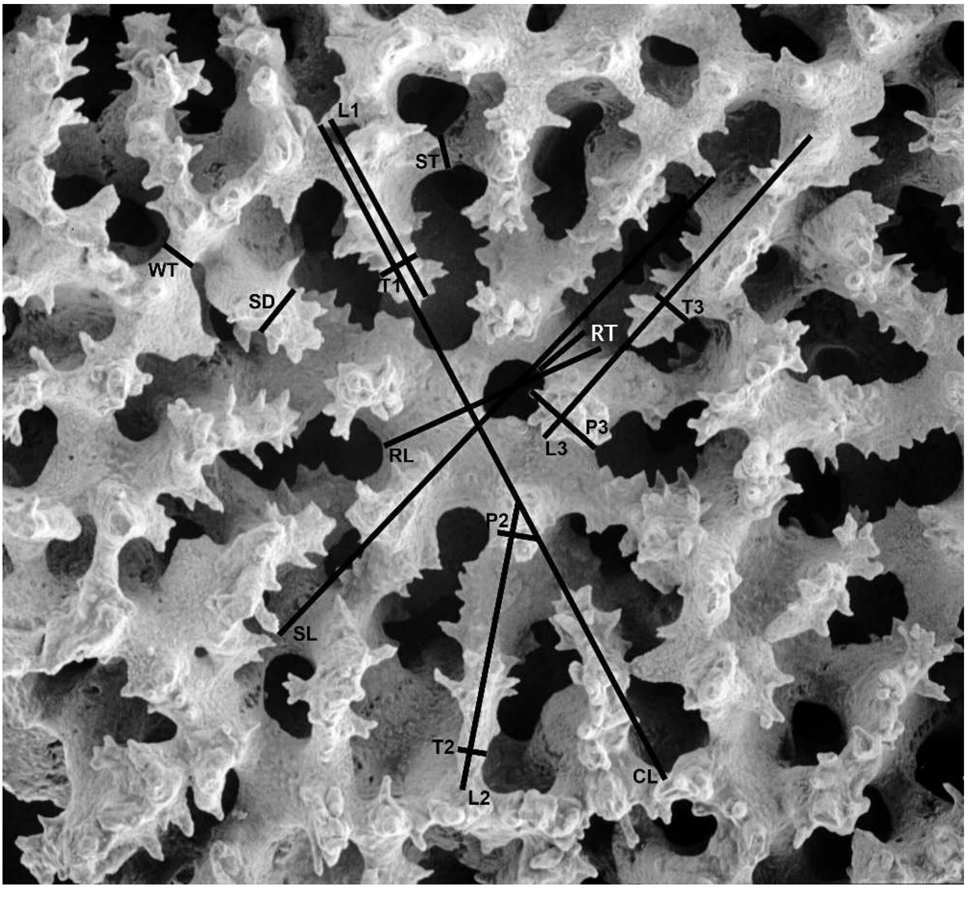

Fig. 3. Illustration showing how non-astreoid corallite characters were measured in Jameson (1995). Corallite characters: CL = corallite length; L1 = septum length (dorsal); L2 = septum length (ventral); L3 = septum length (lateral); P2 = palus thickness (ventral); P3 = palus thickness (lateral); RL = columella synapticular ring length; RT = columella synapticular ring thickness; SD = septal denticle thickness; SL = septal denticle synapticular ring length; ST = septal denticle synapticular ring thickness; T1 = septum thickness (dorsal); T2 = septum thickness (ventral); T3 = septum thickness (lateral); WT = wall thickness.

mined that the Poritidae off Belize can be distinguished in most cases (i.e., there is a certain degree of overlap in the canonical discriminant analysis polygons used in this tool, more so between *P. porites* and *P. furcata* than between *P. furcata* and *P. divaricata* – Fig. 4 in Jameson 1997), using carefully selected linear morphometric characters and multivariate discriminant analysis. Jameson (1995, 1997) also provided qualitative and quantitative keys for distinguishing species of *Porites* in the field off Belize.

Based on the fixed allele differences found among the branching *Porites* by Weil (1992) and Potts et al. (1993), their morphometric differences (Jameson 1995, 1997), and their unique habitat preferences and colony colors (Jameson 1995, 1997), this paper treats the branching *Porites* as three distinct species (*P. porites, P. furcata, P. divaricata*), not *forma* per Vaughan (1901). Veron (2000) also recognizes the western Atlantic branching *Porites* as three distinct species.

Recent DNA-based taxonomic research reported in conference presentations [e.g.,

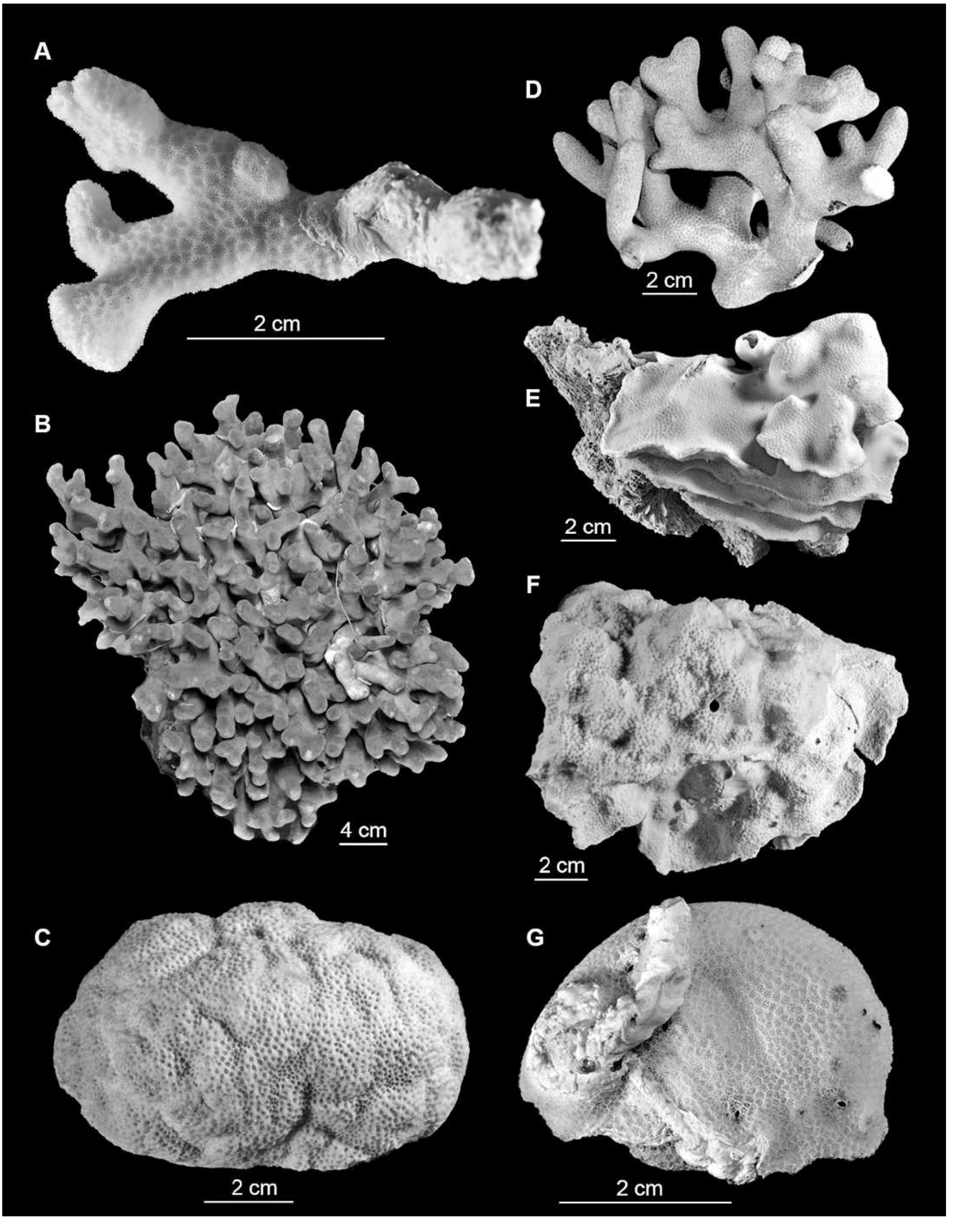

Fig. 4. Colony photographs of neotype and holotype specimens of *Porites*. Note: the holotype of *Porites astreoides* was unavailable to photograph, so common specimen from Carrie Bow Cay, Belize was used as a representative specimen. A, *Porites divaricata* Le Sueur, 1820, neotype, USNM 78996, Blue Ground Range, Belize; B, *Porites furcata* Lamarck, 1816, holotype, MNHNP 154, western Atlantic; C, *Porites verrillii* Rehberg, 1893, holotype, YPM 4539, Abrolhos reefs, Brazil; D, *Porites porites* (Pallas, 1766), neotype, MNHNP 150, Antilles. (*Porites clavaria* holotype); E, *Porites colonensis* Zlatarski, 1990, holotype, USNM 82020, off southeast coast of island of Largo Remo, east of Colon, Bahia Las Minas, Panama; F, *Porites astreoides* Lamarck, 1816, USNM 78935, common specimen from Carrie Bow Cay, Belize; G, *Porites branneri* Rathbun 1887, holotype, USNM 10961, Parahyba do Norte, Brazil.

Lucas & Romano (2007), Romano et al. (2007), and Stake & Neigel (2007, 2008)] questions whether the three western Atlantic branching *Porites* (*P. porites, P. furcata,* and *P. divaricata*) are distinct species. However, they have not produced any peer-reviewed publications to date. Molecular research by Forsman et al. (2006, 2009) advanced our understanding of skeletal homoplasy in *Porites*. In support of the taxonomic key provided by Jameson (1995, 1997), which is based on the observation that the branching species of *Porites* dwell in different reef zones, Bongaerts et al. (2010) found striking differences between shallow environments (e.g., 2 and 6 m) favors the ecological speciation of corals. Bongaerts et al. (2010) found that corals become so adapted to a specific environmental niche, that strong associations to distinct reef environments present a compelling case for ecological speciation in reef corals (i.e., evolutionary processes are occurring in the absence of physical barriers). Bongaerts et al. (2010) demonstrate that corals become so adapted to a specific environmental niche, that selection drives them to become genetically distinct from neighboring populations. Ecological speciation is a critical mechanism for diversification on reefs; however, it was previously assumed that physical geographical barriers isolating populations (i.e., allopatric speciation) were the primary driving diversification force on reef corals (Bongaerts et al. 2010).

Materials and Methods

Neotype designations.—Article 75 of the International Code of Zoological Nomenclature (1999) and Recommendation 75B (Consultation with specialists) are invoked to designate neotypes for *P. porites* (Pallas, 1766) and *P. divaricata* Le Sueur, 1820.

Jameson (1995, 1997) provides a quantitative method for distinguishing the branching *Porites*. Using step-wise discriminant analysis, Jameson (1995, 1997) also demonstrates that the branching species of *Porites* can be distinguished using five corallite characters: 1) columellar synapticular ring width (RW), 2) septal denticle synapticular ring thickness (ST), 3) ventral palus thickness (P2), 4) pali elevation (PE), and 5) septa elevation (SE).

Therefore, neotype descriptions in this paper highlight the corallite measurements for these five critical characters. It is hoped taxonomists will use the detailed habitat information in the "Results" section of this paper, and in Jameson (1995, 1997), as an aid in collecting branching specimens of *Porites*, ensuring consistency of comparisons among species of *Porites*.

Porites porites (Pallas, 1766) neotype

Jameson (1995) provides a complete synonymy of the genus *Porites* in the western Atlantic and found that there is no holotype designated for *P. porites* (Pallas, 1766) by Vaughan (1901), only a topotype. Below is an annotated history of events in the evolution of the name *Porites porites* (Pallas, 1766).

1756 – Seba describes and figures *Corallium poris stellatis* from Curaçao. Note: the original Seba specimen is lost.

1766 – Pallas describes *Madrepora porites* from the western Atlantic to apply to any *Porites* of that genus (no original figure published or holotype designated, Pallas references Seba). The name *Madrepora porites* did not apply to a specific species.

1807 – Link describes *Porites polymorphus*.

1816 – Lamarck describes *Porites clavaria* from the western Atlantic.

1860 – Milne Edwards describes *Porites clavaria* and places *Madrepora porites* (pars) Pallas and *Corallium poris stellatis* in the synonymy of *P. clavaria* Lamarck.

1887 – Rathbun describes and figures specimens of *P. clavaria* Lamarck from Florida and Bermuda and *P. furcata*

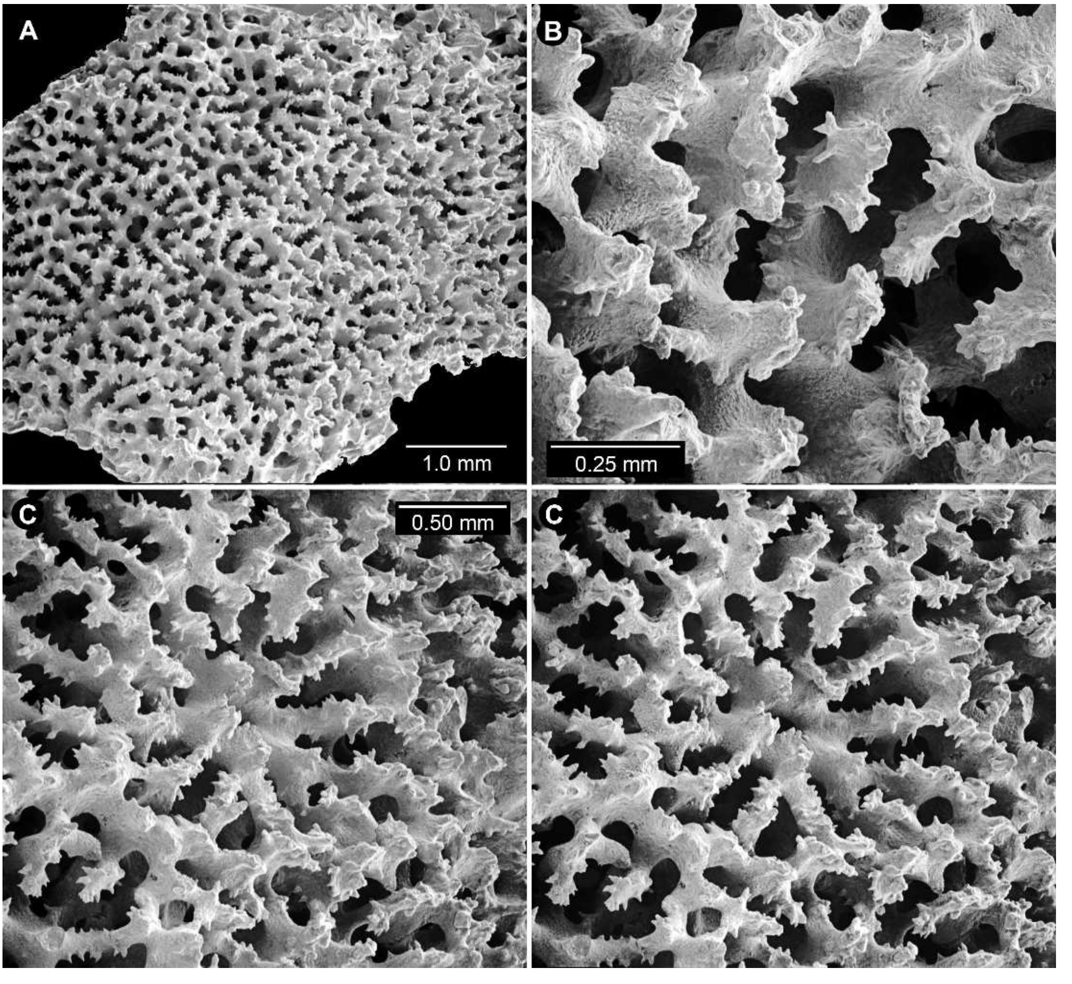

Fig. 5. *Porites clavaria*, holotype, MNHNP Lamarck collection 150 (also designated as neotype of *Porites porites*). A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

Lamarck from Florida, Barbados, and Curaçao.

1901 – Vaughan restricts the broad use of the Pallas (1766) species name *porites* and creates the name *P. porites* (Pallas) to apply to the three branching forms of *Porites*. Vaughan uses the following three formae names of *P. porites* (Pallas): *P. porites* forma *clavaria* Lamarck; *P. porites* forma *furcata* Lamarck; and *P. porites* forma *divaricata* Le Sueur. Vaughan "seizes upon" *Corallium poris stellatis* Seba, 1756 from Curaçao as the type of *P. porites* (Pallas), because in his synonymy, Pallas references Seba (1756) and because Milne Edwards (1860) place *Corallium poris stellatis* and *Madrepora porites* (pars) Pallas in the synonymy of *Porites clavaria* Lamarck. Not finding a *P. porites* specimen from Curaçao to duplicate the holotype specimen figured by Seba (1756), Vaughan describes a *P. furcata* "looking" specimen (based on calicular structure) from Curaçao that closely resembles Seba's figures, except the branches are more crowded, and calls it a topotype for *P. porites* (Pallas, 1766).

Table 1.—Description of corallite characters measured (adapted from Jameson 1995). See Figs. 2 and 3 for illustration of these measurements. Abbreviations in parentheses following character.

Corallite character (abbreviation)	Description
Corallite length (CL)	Linear measure across corallite center, parallel to dorsal/ventral axis, between corallite cavity margins
Corallite width (CW)	Linear measure across corallite center, perpendicular to dorsal/ventral axis, between corallite cavity margins
Nearest neighboring corallite (NC)	Linear measure between center of measured corallite and center of nearest neighbor
Farthest neighboring corallite FC)	Linear measure between center of measured corallite and center of farthest neighbor
Wall thickness (WT)	Linear measure between thecal margins of nearest neighboring corallite
Total calice elevation (WE)	Distance estimate using focus knob: from calice base to uppermost mural trabeculae
Septum length, dorsal (L1)	Linear measure from septum tip to inner thecal margin
Septum thickness, dorsal (T1)	Linear measure across septum at its midpoint
Septum length, ventral (L2)	Linear measure; see above
Septum thickness, ventral (T2)	Linear measure; see above
Septum length, lateral (L3)	Linear measure; see above
Septum thickness, lateral (T3)	Linear measure; see above
Septal denticle thickness (SD)	Linear measurement across denticle (primary septum) nearest wall
Septa elevation (SE)	Distance estimate using focus knob; from calice base to lateral septa denticle tip
Number of pali (PL)	Count
Palus thickness, dorsal (P1)	Linear measure across palus
Palus thickness, ventral (P2)	Linear measure across palus
Palus thickness, lateral (P3)	Linear measure across palus
Pali elevation (PE)	Distance estimate using focus knob; from calice base to lateral pali tip
Columella tubercle length (C1)	Linear measure along long axis
Columella tubercle width (C2)	Linear measure along short axis
Columella elevation (CE)	Distance estimate using focus knob; from calice base to columella tip
Columella synapticular ring length (RL)	Linear measure; longest distance across outside ring
Columella synapticular ring width (RW)	Linear measure; shortest distance across outside of ring
Columella synapticular ring thickness (RT)	Linear measure; distance across ring band
Septal denticle synapticular ring length (SL)	Linear measure; longest distance across outside of ring
Septal denticle synapticular ring width (SW)	Linear measure; shortest distance across outside of ring
Septal denticle synapticular ring thickness (ST)	Linear measure; distance across ring band

The topotype designated by Vaughan (1901) is not considered valid as a neotype by the International Code of Zoological Nomenclature (1999) because topotypes are simply specimens collected in the same general region as the holotype, i.e., there could be many of them, and they have no nomenclatural significance. Because Vaughan (1901) considered the three branching forms of *Porites* as *P. porites*, it is possible that this topotype corresponds to either *P. furcata* or *P. divaricata*. This topotype is also more recent than the holotype of *P. clavaria*.

In summary, according to the ICZN: article 72.5.6, even if a type is based on an illustration [in this case, Vaughan's designation of *Corallium poris stellatis* Seba, 1756 as the holotype of *P. porites* (Pallas), based only on Seba's figure], the type is the specimen, not the illustration. Therefore, because the holotype of *Corallium poris stellatis* Seba, 1756 is lost, we are designating a neotype for *P. porites* (Pallas,

Table 2.—Corallite character means and standard deviations (mm) for ramose *Porites* type specimens with non-astreoid type corallite. *P. clavaria* Lamarck 1816, holotype (designated as *P. porites* neotype[1]), Muséum National d'Histoire Naturelle, Paris (MHNP) Lamarck Collection No. 150, from the western Atlantic *P. furcata* Lamarck, 1816, holotype, MHNP, Lamarck Collection No. 154, from the western Atlantic *P. divaricata* Le Sueur, 1820, neotype[2], National Museum of Natural History, Smithsonian Institution (USNM), USNM No. 78996, from North Blue Ground Range, Belize. See Jameson (1997) for qualitative and quantitative keys for distinguishing these species. Ten corallites were measured in the colony. n = number of corallites with character present. Character abbreviations are explained in Table 1. Characters with asterisks (*) are distinguishing characters for the neotype of *P. divaricata* and *P. clavaria* (neotype of *P. porites*) from step-wise discriminant analysis of Jameson (1995, 1997). Abbreviation: –, no data.

Corallite character	*P. clavaria*[1]		*P. furcata*		*P. divaricata*[2]	
	n	$\bar{X}$ (*SD*)	*n*	$\bar{X}$ (*SD*)	*n*	$\bar{X}$ (*SD*)
CL	10	1.485 (0.135)	10	1.220 (0.198)	10	1.326 (0.059)
CW	10	1.472 (0.117)	10	1.082 (0.198)	10	1.288 (0.075)
NC	10	1.464 (0.166)	10	1.020 (0.131)	10	1.224 (0.054)
FC	10	1.904 (0.194)	10	1.310 (0.221)	10	1.624 (0.068)
WT	10	0.121 (0.031)	10	0.075 (0.023)	10	0.100 (0.013)
WE	10	0.994 (0.191)	10	1.190 (0.283)	10	0.861 (0.107)
L1	10	0.436 (0.073)	10	0.332 (0.116)	10	0.451 (0.046)
T1	10	0.128 (0.029)	10	0.086 (0.016)	10	0.118 (0.010)
L2	10	0.651 (0.106)	10	0.490 (0.082)	10	0.514 (0.055)
T2	10	0.140 (0.035)	10	0.082 (0.012)	10	0.118 (0.022)
L3	10	0.641 (0.102)	10	0.450 (0.067)	10	0.575 (0.060)
T3	10	0.117 (0.032)	10	0.083 (0.022)	10	0.100 (0.014)
SD	10	0.229 (0.021)	10	0.162 (0.021)	10	0.208 (0.017)
SE*	10	0.722 (0.181)	10	0.955 (0.281)	10	0.546 (0.088)
PL	10	5.200 (0.422)	10	5.000 (0.000)	10	5.600 (0.500)
P1	1	0.125 (0.000)	0	–	4	0.115 (0.012)
P2*	10	0.245 (0.063)	10	0.171 (0.043)	10	0.172 (0.064)
P3	10	0.242 (0.049)	10	0.163 (0.041)	10	0.156 (0.011)
PE*	10	0.758 (0.189)	10	1.024 (0.243)	10	0.437 (0.042)
C1	10	0.170 (0.050)	0	–	10	0.144 (0.037)
C2	10	0.109 (0.037)	0	–	10	0.073 (0.013)
CE	10	0.630 (0.158)	0	–	10	0.319 (0.084)
RL	10	0.758 (0.096)	10	0.487 (0.041)	10	0.624 (0.078)
RW*	10	0.632 (0.075)	10	0.418 (0.042)	10	0.582 (0.036)
RT	10	0.124 (0.024)	10	0.080 (0.010)	10	0.105 (0.011)
SL	10	1.234 (0.128)	10	0.937 (0.146)	10	1.072 (0.058)
SW	10	1.308 (0.129)	10	0.887 (0.086)	10	1.026 (0.042)
ST*	10	0.121 (0.015)	10	0.093 (0.023)	10	0.100 (0.017)

1766) and considering *P. porites* (Pallas, 1766) a distinct species.

The holotype of *P. clavaria* from the western Atlantic, was chosen as the neotype for *P. porites* because it was from the same region as the original holotype. In addition, Milne Edwards (1860) placed *Corallium poris stellatis* and *Madrepora porites* (pars) Pallas in the synonymy of *Porites clavaria* Lamarck. The holotype of *P. clavaria* also plots in the middle of Belize specimens of *P. porites* in the multivariate discriminant analysis shown in Fig. 2 of Jameson (1997), demonstrating it is morphologically an excellent representative of the species. The holotype of *P. clavaria* is the oldest extant specimen described for *P. porites*.

Porites divaricata Le Sueur, 1820 neotype

Jameson (1995) found that the type specimens for *Porites divaricata* Le Sueur,

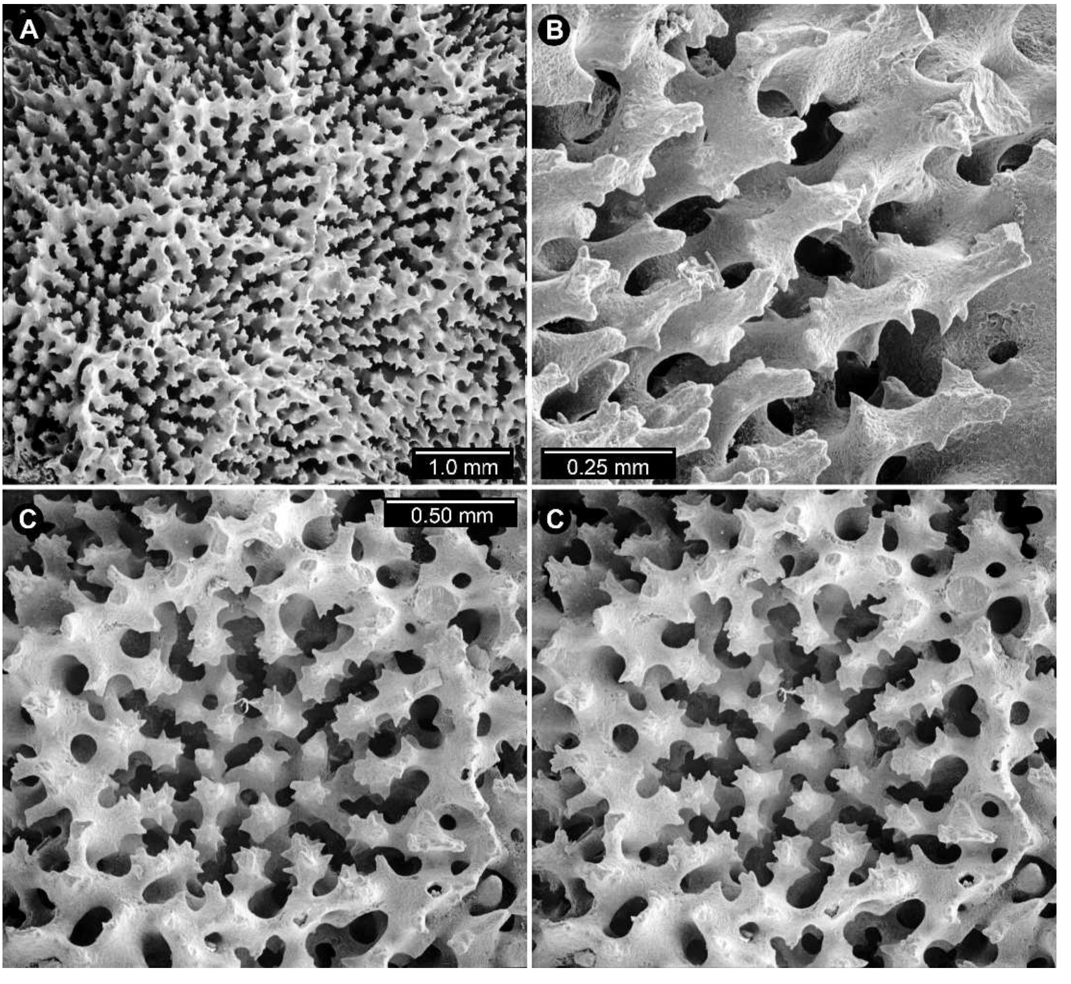

Fig. 6. *Porites divaricata*, neotype, USNM 78996. A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

1820 could not be located by Guillaume (pers. com.), cnidarian curator of the Muséum National d'Histoire Naturelle, Paris who contacted the curator of the Natural History Museum in Le Havre, France. Zibrowius (pers. com.) was also unable to locate the type specimens in these locations. The literature does not specify where the type specimens were deposited; however, Le Sueur became curator of the Natural History Museum in Le Havre, France, in 1845 and donated part of his collections to this museum. All of the Le Sueur collections in the Le Havre Natural History Museum were destroyed during the bombings of Le Havre in 1944. Therefore, the loss of the type specimen, lack of an original illustration, and adequate diagnostic characters in the Le Sueur description necessitate the designation of a neotype for *P. divaricata*.

The location of collection of the type specimen stated in Le Sueur (1820) is "*Habite la Guadeloupe*." A specimen collected by Jameson (1995, 1997) from Belize was selected for the neotype because it is from the same general region as the original holotype and the branching spe-

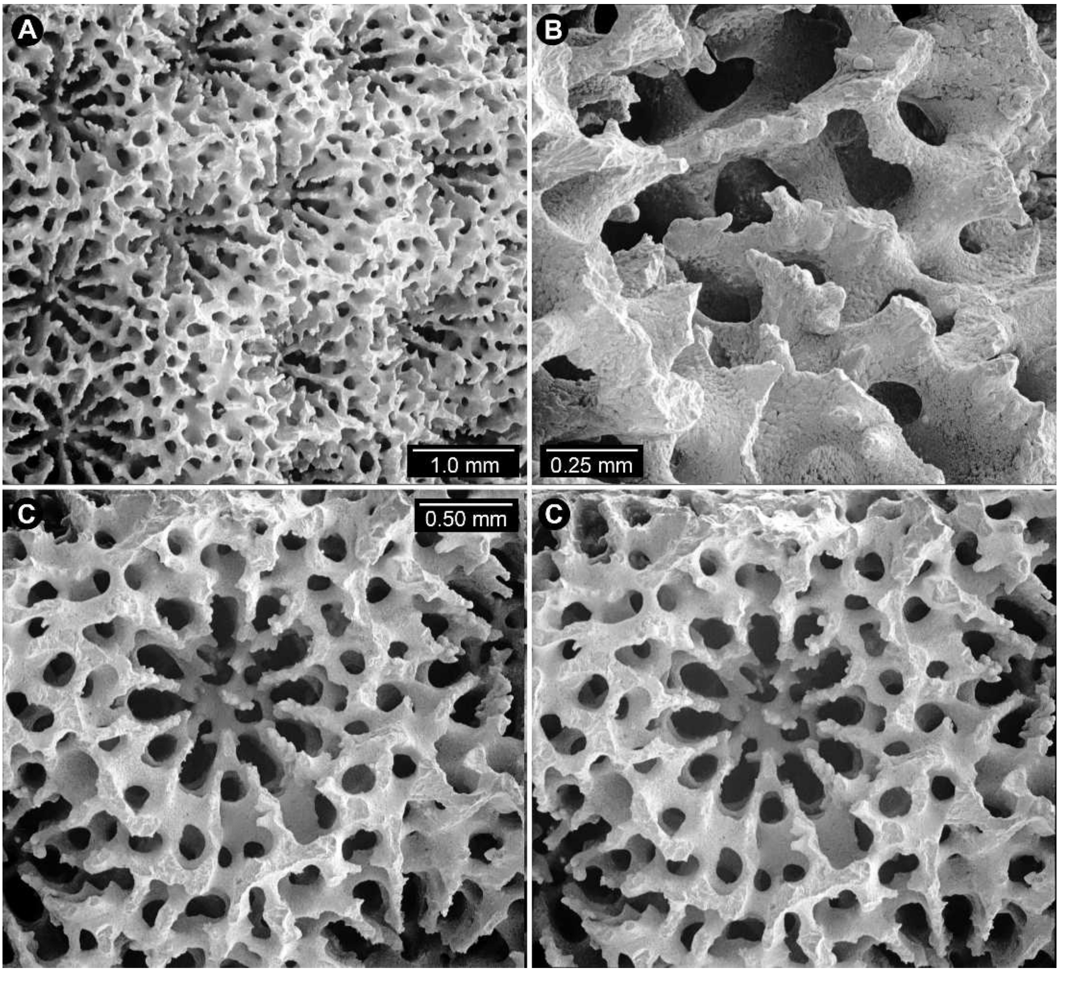

Fig. 7. *Porites verrillii*, holotype, YPM 4539. A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

cies of *Porites* (*P. porites*, *P. furcata*, and *P. divaricata*) are clearly segregated by habitat preference off Belize (Jameson 1997) and easily distinguished by knowledgeable experts. In addition, detailed corallite measurements and the scanning electron microscopic (SEM) photos were available for the selected neotype specimen.

Porites verrillii Rehberg, 1893 as a junior synonym of *Porites astreoides*

Vaughan (1901) thought the Brazilian *P. verrillii* Rehberg, 1893 should be placed in synonomy with *P. astreoides,* as specimens in the United States National Museum from Brazil had the same general appearance , i.e., 12 septa, no pali, and similar wall structure, as *P. astreoides.* Goreau & Wells (1967), and Wells & Lang (1973) did not list *P. verrillii* in Jamaica.

Jameson's (1995, 1997) test results using three columella tubercle characters, plus 16 original characters, showed that cluster analysis did not distinguish *P. verrillii* from the Belize *P. astreoides.* Stepwise discriminant analysis results showed that one of the three columella

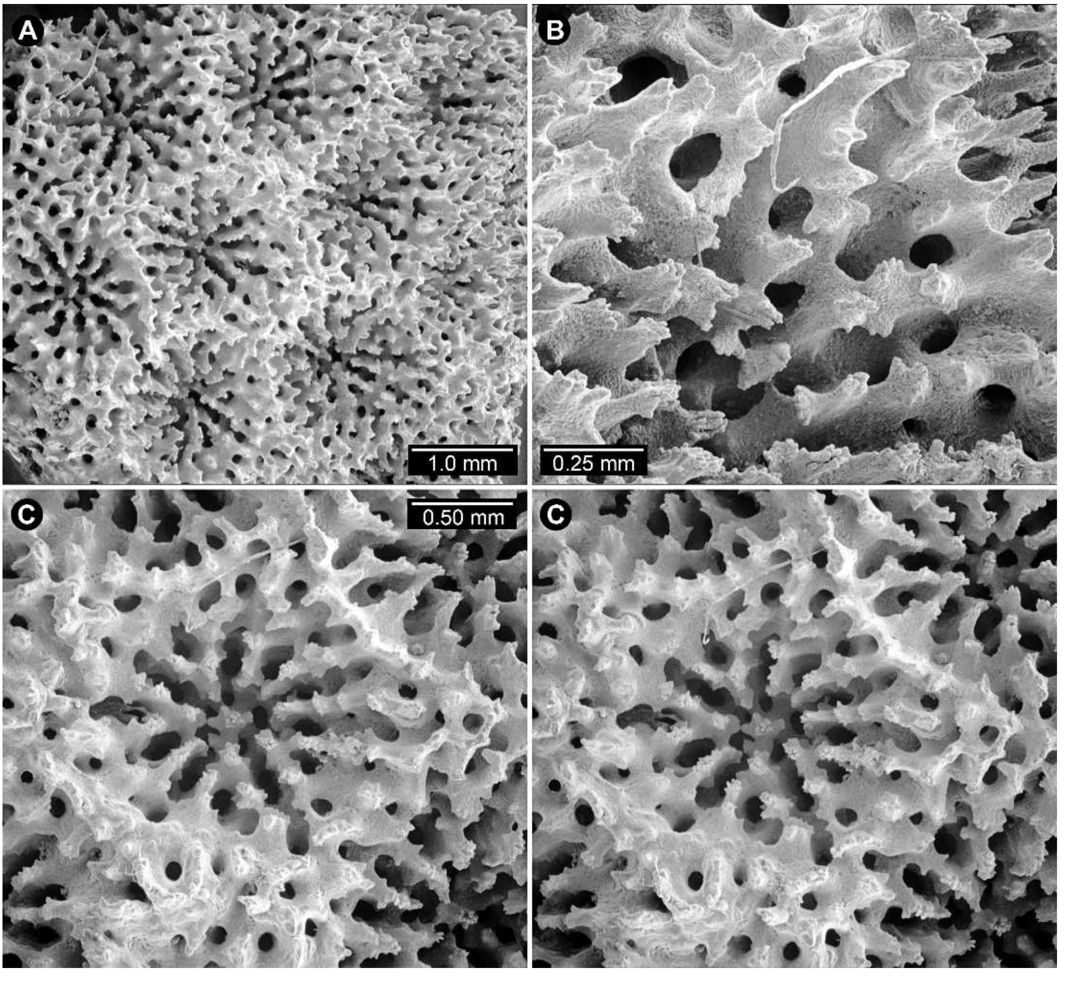

Fig. 8. *Porites astreoides*, USNM 78935. A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

tubercle characters (CE: columella elevation) was used in the stepwise model, but it was not heavily weighted. Canonical discriminant results using the three columella tubercle characters did not help distinguish *P. verrillii* from the Belize *P. astreoides*, but to the contrary, classified *P. verrillii* closer to the *P. astreoides* colonies than the canonical discriminant analysis where the columella tubercle characters were not used (Jameson 1997:Fig. 3). In the canonical discriminant analysis, three canonical variables (CV1, CV2, and CV3) were calculated. The three canonical variables had significant discriminant power ($p < 0.0001$). CV1 accounted for 88.3% of the variation, CV2 accounted for 10.3%, and CV3 for 1.4%. Based on this, it is proposed that *P. verrillii* is a junior synonym of *P. astreoides*.

Stereo photomicrographs for the holotypes of the western Atlantic non-astreoid species in the genus *Porites*

The Amray 1810 scanning electron microscope (SEM) at the National Museum

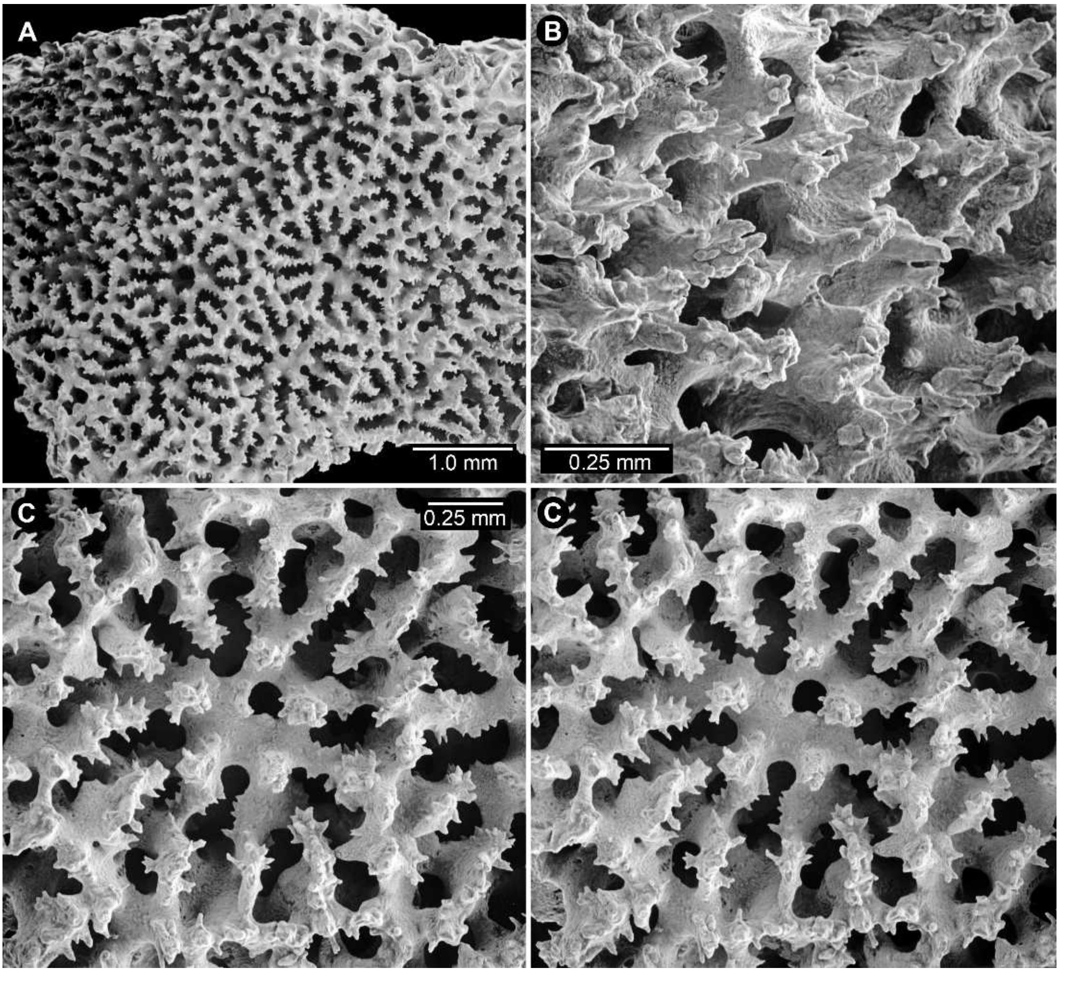

Fig. 9. *Porites furcata*, holotype, MNHNP 154. A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of a typical corallite.

of Natural History, Smithsonian Institution was used to provide SEM photomicrographs of corallites of the *P. porites* (*P. clavaria* holotype used for neotype) and *P. divaricata* neotypes. Stereo SEM was also used to document corallite characteristics of the holotypes of *P. furcata, P. branneri, P. colonensis,* and *P. verrillii*. Stereo scanning electron micrographs of corallites of a common *P. astreoides* from Belize are also provided to compare against those of *P. verrillii*.

Results

Porites porites (Pallas, 1766) neotype description Figs. 4D, 5

The holotype of *Porites clavaria* Lamarck, 1816 from the western Atlantic (Muséum National d'Histoire Naturelle, Paris (MHNP) Lamarck Collection No. 150) is designated as the neotype for *Porites porites* (Pallas, 1766).

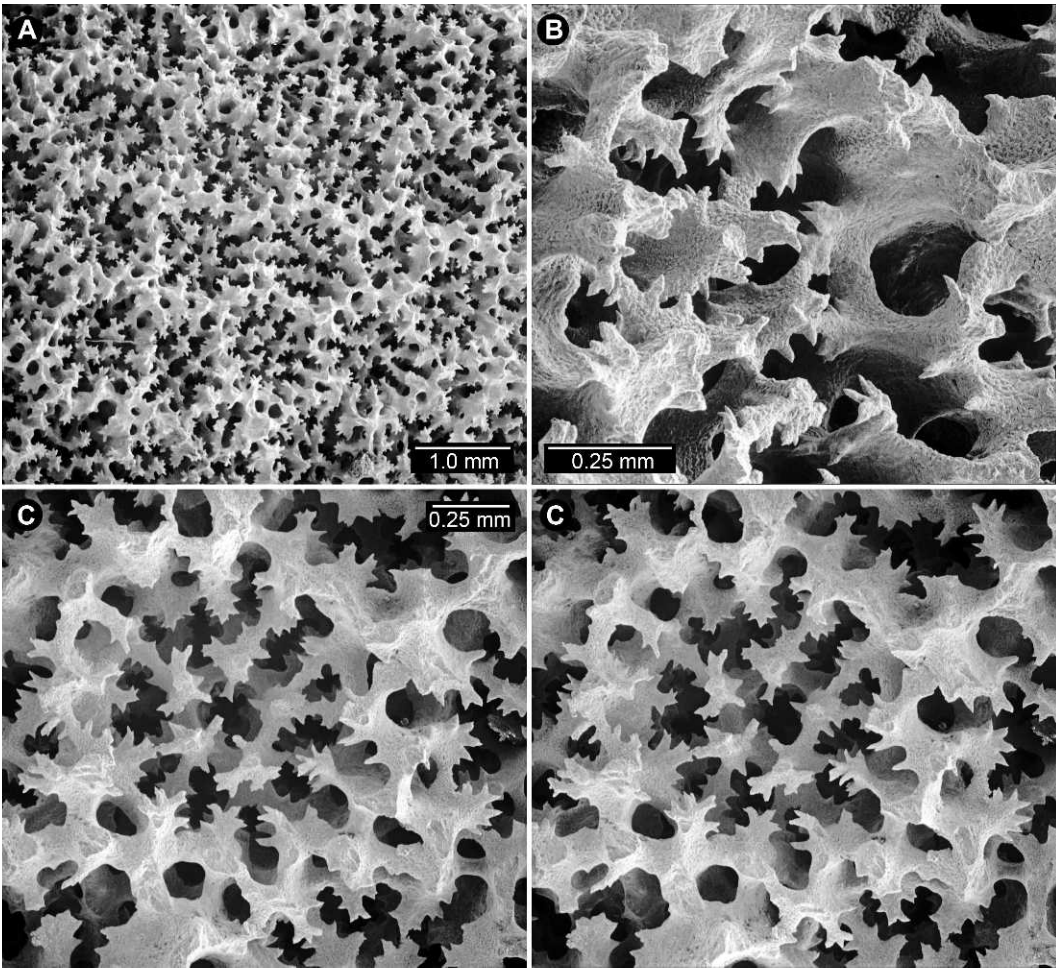

Fig. 10. *Porites branneri*, holotype, USNM 10961. A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

Characters.—Colonies are ramose with sturdy fused branches with rounded tips. The smallest branch diameter (measured at a point half-way down the living part of a branch) is 7.6 mm. The largest branch diameter is 15.8 mm. Tentacles are usually extended during day.

Corallites are deeply excavated and have a coarse coenosteum that form a rough surface. Septa are arranged in three cycles. The first two cycles dominate and form twelve septa with a paliform lobe at the axial end (the dorsal septum is isolated, whereas the ventral and lateral septa merge). The third cycle merges with the former at close proximity of the corallite wall. The tall columella is usually submerged (mean CE is 0.630 mm). Tubercles are present on the corallite wall. Radii fuse all pali to the columella. There are five to six pali, one on the ventral septum, none on dorsal septum, and the triplet is fused. There is one denticle per septum. The wall has three denticles. Calices are deeply excavated. Wall elevation (WE) mean is 0.994 mm. Mean corallite length (CL) is 1.485 mm and mean corallite width (CW) is 1.472 mm.

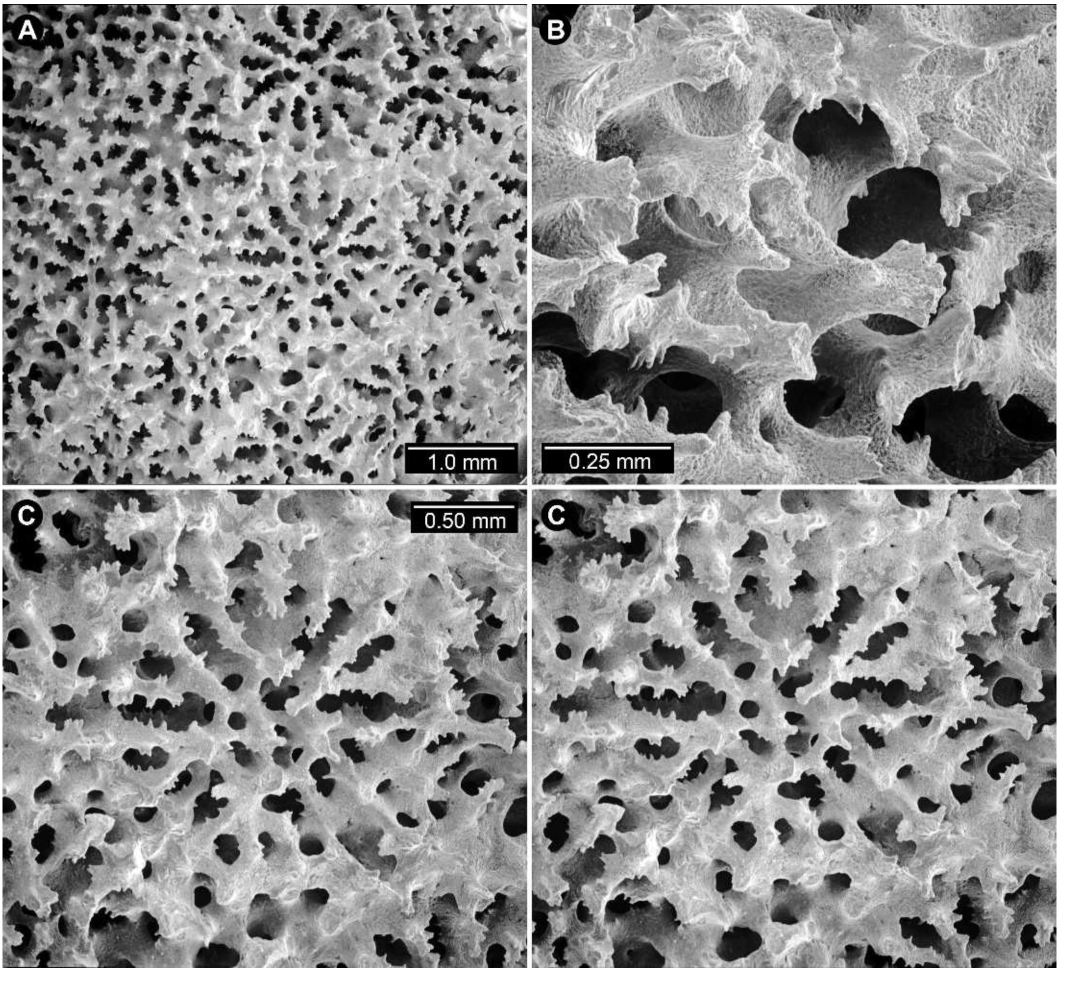

Fig. 11. *Porites colonensis*, holotype, USNM 82020: A, several adjacent corallites; B, close-up of palar and columellar region; C, stereo view of typical corallite.

The five distinguishing corallite characters of *Porites clavaria* (designated *P. porites* neotype) and *P. divaricata* neotype from the Jameson (1995, 1997) step-wise discriminant analysis of the branching species of *Porites* are shown in Table 2. Table 1 provides a description of all corallite characters measured. All corallite measurements are in Table 2.

Color.—Uniform white, brown, grey-brown, or brown with white tips.

Habitat.—Prefers fore-reef and patch reef environments.

Porites divaricata Le Sueur, 1820
neotype description
Figs. 4A, 6

USNM specimen number 78996 from north Blue Ground Range near Carrie Bow Cay, Belize (depth 1.22 m, color brown, collected 12 Aug 1986 as Jameson specimen #422) is designated as the neotype.

Characters.—Colonies are ramose and composed of thin fused branches with flattened tips. The smallest branch diame-

Table 3.—Corallite character means and standard deviations (mm) for non-ramose type specimens of *Porites* with non-astreoid type corallite. *Porites branneri* Rathbun, 1887, holotype, USNM 10961, from Parahyba do Norte, Brazil. *P. branneri* is distinguished from *P. colonensis* by its thin encrusting plates with nodular upgrowths, blue color (which may photograph purple), and corallites without columella tubercle (Venera-Pontón et al. 2008). *Porites colonensis* Zlatarski, 1990, holotype, USNM 82020, from Largo Remo Island, Panama. *P. colonensis* is distinguished from *P. branneri* by its thin foliacious undulated colony form that can form tiers, corallites with or without columella tubercle, and dark brown tissue color with polyps containing white centers (most common), although polyps may be dark red with green centers (Zlatarski 1990, Venera-Pontón et al. 2008). Ten corallites were measured in the colony. n = number of corallites with character present. Character abbreviations explained in Table 1.

Corallite character	*P. branneri*		*P. colonensis*	
	n	$\bar{X}$ (*SD*)	n	$\bar{X}$ (*SD*)
CL	10	1.106 (0.123)	10	1.617 (0.246)
CW	10	1.037 (0.107)	10	1.677 (0.170)
NC	10	1.041 (0.075)	10	1.549 (0.270)
FC	10	1.333 (0.170)	10	1.867 (0.311)
WT	10	0.128 (0.037)	10	0.131 (0.041)
WE	10	1.256 (0.157)	10	1.180 (0.252)
L1	10	0.380 (0.129)	10	0.614 (0.197)
T1	10	0.101 (0.023)	10	0.142 (0.038)
L2	10	0.482 (0.089)	10	0.724 (0.152)
T2	10	0.089 (0.024)	10	0.113 (0.020)
L3	10	0.516 (0.098)	10	0.697 (0.071)
T3	10	0.078 (0.020)	10	0.123 (0.030)
SD	10	0.153 (0.040)	10	0.240 (0.068)
SE	10	1.093 (0.221)	10	0.909 (0.204)
PL	10	4.900 (0.316)	10	5.900 (0.316)
P1	0	–	9	0.126 (0.041)
P2	10	0.193 (0.054)	10	0.245 (0.061)
P3	10	0.176 (0.048)	10	0.220 (0.050)
PE	10	1.017 (0.241)	10	0.887 (0.253)
C1	0	–	6	0.133 (0.029)
C2	0	–	6	0.085 (0.029)
CE	0	–	6	0.809 (0.235)
RL	10	0.433 (0.080)	10	0.517 (0.085)
RW	10	0.399 (0.065)	10	0.504 (0.051)
RT	10	0.083 (0.011)	10	0.078 (0.013)
SL	10	0.906 (0.144)	10	0.931 (0.109)
SW	10	0.822 (0.168)	10	0.891 (0.102)
ST	10	0.086 (0.014)	10	0.077 (0.018)

ter (measured at a point half-way down the living part of a branch) is 5.6 mm. The largest branch diameter is 9.1 mm. Tentacles are usually extended during the day.

Table 4.—Corallite character means and standard deviations (mm) for non-ramose type specimens *Porites* with astreoid type corallite. *Porites verrillii* Rehberg, 1893, holotype, Yale Peabody Museum of Natural History No. 4539 from Abrolhos Reefs, Brazil. A common *P. astreoides* specimen (USNM 78935) from 10 m depth off Carrie Bow Cay, Belize. *Porites astreoides* is distinguished by its missing, or greatly reduced in size, pali. Ten corallites were measure in each of seventy *P. astreoides* colonies. Ten corallites were measured in the holotype colony of *P. verrillii*. n = number of corallites with character present. Character abbreviations explained in Table 1.

Corallite character	*P. astreoides*		*P. verrillii*	
	n	$\bar{X}$ (*SD*)	n	$\bar{X}$ (*SD*)
CL	700	1.539 (0.286)	10	1.499 (0.187)
CW	700	1.445 (0.267)	10	1.363 (0.102)
NC	700	1.483 (0.266)	10	1.471 (0.202)
FC	700	2.016 (0.339)	10	1.999 (0.227)
WT	700	0.148 (0.091)	10	0.249 (0.100)
WE	700	1.229 (0.239)	10	1.301 (0.305)
L1	700	0.482 (0.172)	10	0.516 (0.136)
T1	700	0.090 (0.026)	10	0.076 (0.020)
L2	700	0.502 (0.172)	10	0.504 (0.129)
T2	700	0.091 (0.025)	10	0.069 (0.011)
L3	700	0.518 (0.166)	10	0.477 (0.097)
T3	700	0.095 (0.032)	10	0.070 (0.008)
SD	4	0.858 (0.145)	0	–
SE	700	0.850 (0.216)	10	1.014 (0.239)
PL	453	0.505 (1.102)	0	–
P1	11	0.093 (0.045)	0	–
P2	47	0.117 (0.048)	0	–
P3	95	0.110 (0.048)	0	–
PE	112	0.332 (0.127)	0	–
C1	640	0.174 (0.076)	10	0.184 (0.051)
C2	640	0.085 (0.045)	10	0.103 (0.036)
CE	640	0.365 (0.128)	10	0.479 (0.093)
RL	699	0.699 (0.143)	10	0.593 (0.070)
RW	699	0.699 (0.155)	10	0.515 (0.045)
RT	699	0.108 (0.032)	10	0.077 (0.012)
SL	1	0.762 (0.000)	0	–
SW	1	0.916 (0.000)	0	–
ST	1	0.120 (0.000)	0	–

Corallites are deeply excavated and, with a coarse coenosteum, form a rough surface. Septa are arranged in three cycles. The first two cycles dominant and form twelve septa with a paliform lobe at the axial end (dorsal septum is isolated, while ventral and lateral septa merge), while the third cycle merges with the former at close proximity of the corallite wall. Tubercles are present on the corallite walls. There are four to seven irregular pali. Submerged columella is small (mean CE is 0.32 mm). There are irregular septa. Calices are deeply excavated. Wall elevation (WE) mean is 0.86 mm. Mean corallite length (CL) is 1.33 mm and mean corallite width (CW) is 1.29 mm. Table 1 provides a description of corallite characters measured. All corallite measurements and distinguishing corallite characters from step-wise discriminant analysis (Jameson 1997) are shown in Table 2.

Color.—Uniform brown, grey-brown or greenish-yellow.

Habitat.—Found only in *Thalassia* (sea grass) beds in leeside shallow protected environments around islands or in low wave energy *Thalassia* environments.

Porites verrillii Rehberg, 1893 as a junior synonym of *Porites astreoides* Lamarck, 1816

The multivariate discriminant analysis results of Jameson (1995, 1997) did not provide convincing evidence that *P. verrillii* was morphologically distinct from *P. astreoides* and, therefore, we recommend that *P. verrillii* be considered a junior synonym of *P. astreoides*.

Corallite character measurements and stereo photomicrographs for holotypes of *Porites* Figs. 5–11

Corallite character means and standard deviations for the ramose holotype specimens with non-astreoid type corallite structure (*P. clavaria, P. furcata,* and *P. divaricata*) are in Table 2. Corallite character means and standard deviations for the non-ramose holotype specimens with non-astreoid type corallite structure (*P. branneri* and *P. colonensis*) are in Table 3. Corallite character means and standard deviations for non-ramose *Porites* type specimens with the astreoid type corallite (*P. astreoides* and *P. verrillii*) are in Table 4. The holotype of *P. astreoides* located in the Muséum National d'Histoire Naturelle in Paris, France was not provided to measure or photograph due to the difficulty of mailing a large specimen, so measurements and scanning electron micrographs of corallites from a common *P. astreoides* from Belize are in Table 4 to compare against those of *P. verrillii*.

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