ABSTRACT

Porites porites, *P. furcata*, *P. divaricata* and *P. astreoides* were clearly distinguished off Belize using multivariate morphometric techniques. The holotype of *P. clavaria* classified within the range of variation of the Belize *P. porites*. The *P. furcata* holotype classified within the range of variation of the Belize *P. furcata*. The holotypes of *P. branneri* and *P. colonensis* are also morphologically distinct species. Multivariate morphometric evidence does not support the distinctiveness of *P. verrilli*. Traditional corallite characters are not adequate to distinguish the Poritidae off Belize. *Porites porites*, *P. furcata*, and *P. divaricata* off Belize can be distinguished using multivariate discriminant analysis and a minimum of five characters: columellar synapticula ring width, septal denticle synapticula thickness, ventral palus thickness, pali elevation, and septa elevation. *Porites astreoides* is distinguished qualitatively from *Porites porites*, *P. furcata*, and *P. divaricata* off Belize by its lack of pali, or when rarely present, their reduced size and number. User-friendly qualitative and quantitative keys are provided.

INTRODUCTION

In the Caribbean Sea and western Atlantic Ocean, living representatives of the stony coral family Poritidae Gray, 1842 consist of the single genus *Porites* Link, 1807. A clear understanding of the taxonomy and systematics of recent and fossil poritids in the Caribbean and western Atlantic is important 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). Poritids have also been a key part of many geological and ecological studies in the Caribbean and western Atlantic (Ginsburg 1994). In addition, *Porites* species benefit humans esthetically, ecologically and economically, and are also used in medical applications as a substitute for bone. Recently, *Porites* species have been used by researchers for detecting global climate change (Pernetta 1993).

The overlapping morphological variation within and among *Porites* species makes their taxonomy among the most difficult of all Scleractinians. It did not take long after the descriptions of *Porites porites* (Pallas, 1766); *Porites clavaria* Lamarck, 1816; *Porites furcata* Lamarck, 1816; *Porites astreoides* Lamarck, 1816; *Porites divaricata* Lesueur, 1821; *Porites branneri* Rathbun, 1888; and *Porites verrilli* Rehberg, 1892 for the confusion to begin among taxonomists using qualitative techniques on morphological characters. This long festering debate resulted in the emergence of different qualitative classification schemes for *Porites* in the Caribbean and western Atlantic. Smith (1971) recognized six species: the three ramose species *P. porites*, *P. furcata*, *P. divaricata,* the encrusting *P. branneri*;

the massive and encrusting *P. astreoides* and the very similar Brazilian *P. verrilli*. Goreau and Wells (1967) and Wells and Lang (1973) listed all of these species from Jamaica except *P. verrilli*. Vaughan (1901a) thought the Brazilian *P. verrilli* should be placed in synonomy with *P. astreoides* as the specimens in the United States National Museum of Natural History (USNM) had the same general appearance (i.e., twelve septa, no pali, and similar wall structure) as *P. astreoides.* Vaughan (1901a) was also unsure of the specific status of *P. branneri*. Vaughan (1901a), Almy and Carrion-Torres (1963), Roos (1971), and Zlatarski et al. (1982) considered the three ramose species to be forms of *P. porites*, as did Cairns (1982) for the ramose species off Belize.

Brakel (1977) made the first quantitative attempt to study corallite variation in *Porites* at Discovery Bay, Jamaica, but was not able to clarify the taxonomy. He concluded that heterogeneity of the environment, coupled with the diversifying forces of natural selection, produced a complex pattern of genetic variation that could not be resolved into a simple classification scheme. He also suggested that the species problem in corals is not necessarily an artifact of poor methodology or insufficient data, but may reflect intrinsic genetic and ecological properties of coral populations. Brakel (1977) was also the first to suggest that intraspecific skeletal variation in *Porites* is not only caused by phenotypic plasticity but is also caused by high genetic variability. This was later reiterated by Foster (1986) and confirmed via allozyme surveys by Weil (1992). Subsequent studies also recognized that variation within and among coral species is subtle and complex and requires the study of numerous characters in populations from a wide variety of habitats (Foster 1980). No firm conclusions could be drawn from the preliminary analysis of modern Caribbean species of *Porites* by Foster (1986) because of the very small number of specimens (1 to 4) and corallites per specimen (5) measured. Zlatarski (1990) described the new species, *P. colonensis*, and distinguished it from all other non-astreoid *Porites* by its foliacious colony form and the two colors of its living tissue. Electrophoretic results of Potts et al. (1993), working with *Porites* off Miami and St. Croix, 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.* Using electrophoresis on 11 polymorphic loci from 9 enzyme systems, Weil (1992) found fixed allele differences among *P. astreoides*, *P. porites*, *P. furcata*, *P. divaricata*, *P. colonensis*, and *P. branneri* off Panama.

Despite this recent genetic progress in many areas related to Scleractinian taxonomy, a reliable independent morphometric method for identifying *Porites* and other sibling living and fossil coral species remains elusive. The problem centers around finding diagnostic characters that will consistently produce species

groups when an independent grouping procedure, such as cluster analysis, is used. Budd et al. (in press) derived characters by using size and shape coordinates (Bookstein 1991). However, despite these techniques they were not able to independently distinguish Caribbean *Porites* species groups using cluster analysis. This dilemma has left researchers working with fossil species, and those working with living species that need a reliable method for making field identifications, at a distinct disadvantage.

The purpose of this research is to demonstrate that the Poritidae off Belize can be distinguished using linear morphometric characters. In this process I will describe the relationship of Belize species to type specimens, discuss what corallite characters are important in distinguishing Caribbean and western Atlantic poritids, and comment on the usefulness of traditional characters. This research will also advance the understanding of *Porites* corallite variation in the ongoing effort to improve our ability to distinguish these species using morphometric techniques. A multicharacter statistical approach is employed in this study, since focusing on isolated single characters often produces misleading results (Cheetham 1987). Results should be considered valid only for the Poritidae off Belize.

MATERIAL AND METHODS

Sampling and documentation

To obtain a sample of all possible growth forms from a range of environmental conditions, I collected a total of 589 colonies arbitrarily from 7 habitats on the Belize Barrier Reef around Carrie Bow Cay during expeditions in August 1985 and 1986.

Character measuring

Within the Caribbean and western Atlantic Poritidae there are two basic types of corallites, astreoid and non-astreoid (Bernard 1906). Species with the non-astreoid type corallite include *P. porites*, *P. furcata*, *P. divaricata*, *P. branneri*, and *P. colonensis*. Species with the astreoid type corallite include *P. astreoides* and *P. verrilli.* Ten non-astreoid and ten astreoid type colonies from each of the 7 habitats were randomly selected for measuring. Within each of the 140 colonies ten corallites were measured following the approach of Foster (1980) using a stereo-microscope, camera lucida and digitizing tablet. Ten corallites per colony were also measured on the holotypes of *P. clavaria*, *P. furcata*, *P. branneri*, *P. colonensis*, and *P. verrilli* so they could be compared to Belize specimens. The holotype for *P. astreoides* was too large to mail from France and was not measured in the study. The type specimens for *P. porites* do not exist. It is believed they were not retained after the original description, as was often common in those days (Potts pers. comm.). The type specimens for *P. divaricata* were destroyed during the bombings of La Havre, France in World War II (Guillaume pers. comm., Zibrowius pers. comm.) and were therefore not included in this study. Twenty-eight corallite characters were recorded for each of the 1450 corallites measured. These characters represent a modified version of those used by Foster (1986) and encompass the features commonly used to classify modern *Porites* species in the Indo-Pacific and Caribbean. These characters were described in detail by Jameson (1995), Foster (1986), and Bernard (1906).

Morphometric analysis

Discriminant, stepwise discriminant, and canonical discriminant analysis on colony character means using *a priori* designated groups were the multivariate statistical techniques used in the morphometric analysis because, I felt I could more accurately group species based on my knowledge of *Porites* morphology and ecology than a clustering technique that would have to deal with overlapping character values among species. Initial tests using average linkage cluster analyses on Mahalanobis distance matrices failed to independently distinguish Belize *P. porites*, *P. furcata,* and *P. divaricata* species groups and did not distinguish the *P. verrilli* holotype from Belize *P. astreoides*.

A priori groups were created based on the fact that recent genetic work by Potts et al. (1993) and Weil (1992) confirmed that the three ramose species of *Porites* were in fact true species and not forms of *P. porites*, and based on my knowledge of the Poritidae off Belize in the following areas.

- Corallite and colony form characters (Corallite characters used to distinguish groups were the lack of a columella tubercle for *P. branneri* and lack of or reduced size and/or number of pali for *P. astreoides*. These characters were not used in the discriminate analysis.)

- Habitat preferences
- Color
- Colony distributions

Characters were tested for normality using the Shapiro-Wilk test and a log10 transformation was applied to all characters to help correct for non-normality. The homogeneity of within-group covariance matrices was tested using the SAS DISCRIM POOL=TEST option that conducts a likelihood ratio test (Chi-square) of the homogeneity of the within-group covariance matrices.

For the Belize non-astreoid species, discriminant, stepwise discriminant, and canonical discriminant analysis were run on three *a priori* created groups (group 1 = *P. porites* (n = 37), group 2 = *P. furcata* (n = 23), group 3 = *P. divaricata* (n = 10). To show the relationship between Belize specimens and type specimens, a canonical discriminant analysis was performed that included the Belize specimens (groups 1, 2 and 3 above) and the type specimens for *P. clavaria* (included in group 1), *P. furcata* (included in group 2), *P. branneri* (group 4) and *P. colonensis* (group 5). A discriminant analysis was also run with the same groups as described above, with the exception that the *P. colonensis* holotype (group 5) was left unclassified, to see what the probability was of *P. colonensis* belonging to the *P. porites*, *P. furcata, P. divaricata*, or *P. branneri* groups. Because of the clear qualitative (Bernard 1906) and quantitative (Budd et al. in press) differences in the non-astreoid and astreoid species, these tests were run exclusively on non-astreoid species to maximize the number of characters in the analyses and to avoid obscuring subtle patterns of within-group morphological variation that would occur if astreoid species were included and fewer characters were used. Descriptive statistics were calculated for all corallite characters for each colony. The following characters were removed from the analysis because character values for some corallites were often missing (percent of corallites missing values for Belize *P. porites*, *P. furcata,* and *P. divaricata*, respectively in parenthesis); dorsal palus thickness (**P1**) (51.1, 67.8, 51.0) and columella tubercle length, width and elevation (**C1, C2, CE**) (18.7, 49.1, 32.0). This left 24 characters; corallite length (**CL**), corallite width (**CW**), nearest neighboring corallite (**NC**), farthest neighboring corallite (**FC**), wall thickness (**WT**), total calice elevation (**WE**), dorsal septum length (**L1**), dorsal septum thickness (**T1**), ventral septum length (**L2**), ventral septum thickness (**T2**), lateral septum length (**L3**), lateral septum thickness (**T3**), septal denticle thickness (**SD**), septa elevation (**SE**), number of pali (**PL**), ventral palus thickness (**P2**), lateral palus thickness (**P3**), pali elevation (**PE**), columellar synapticular ring length (**RL**), columellar synapticular ring width (**RW**), and columellar synapticular ring thickness (**RT**), septal denticle synapticular ring length (**SL**), septal denticle synapticular ring width, and septal denticle synapticular ring thickness (**ST**) for use in the analysis. The following of the above characters had missing corallite values but were used in the analysis because the number

of missing values were considered acceptable (< 5% missing): *P. porites* group (**P2** = 11/370, 2.9 %, **P3** = 1/370, 0.27 %), *P. furcata* group (**P2** = 4/230, 1.7 %), *P. divaricata* group (**SD** = 1/100, 1%). No other characters used in the analysis had any missing corallite values, for non-astreoid Belize or type specimens.

To show the morphometric relationship between *P. astreoides* off Belize and the *P. verrilli* holotype, canonical discriminant analysis was run on four *a priori* created groups (group 1 = *P. porites* (n = 37), group 2 = *P. furcata* (n = 23), group 3 = *P. divaricata* (n = 10), group 4 = *P. astreoides* and the *P. verrilli* holotype (n = 71). Non-astreoid species groups were included in this analysis because canonical discriminant analysis must have a minimum of three groups to plot polygons. Descriptive statistics were calculated for all corallite characters for each colony. The following characters were excluded from the analysis because character values for some *P. astreoides* colonies were not present (percent of total corallites missing values in parentheses **SD** (99.4%), **PL** (35.3%), **P1** (98.4%), **P2** (93.3), **P3** (86.4), **PE** (84%), **C1** (8.6%), **C2** (8.6%), **CE** (8.6), **SL** (99.9%), **SW** (99.9%), and **ST** (99.9%). The missing columella tubercles were not isolated occurrences. They were absent in 60 out of 700 corallites, in a total of 30 colonies, distrib-uted among the seven habitats (habitat followed by number of corallites missing columella tubercle: Carrie Bow Cay outer fore reef at 20 m depth - 10; Carrie Bow Cay inner fore reef at 10 m depth - 5; Carrie Bow Cay inner fore reef at 01 m depth - 25; Carrie Bow Cay reef flat - 12; Carrie Bow Cay lagoon patch reef - 6; Blue Ground Range windward *Thalassia* bed - 2; Wee Wee Cay south - 2). Since I did not know if this character was absent because it did not grow, or was missing because of natural damage, I conducted the morphometric analyses without these three charact-ers. In the *P. astreoides* group **RL**, **RW**, and **RT** char-acters each had one missing value out of the 700 (0.1%) corallites measured due to a recording error so these characters were used in the analysis. Therefore, this left the following 16 characters for the analysis: **CL**, **CW**, **NC**, **FC**, **WT**, **WE**, **L1**, **T1**, **L2**, **T2**, **L3**, **T3**, **SE**, **RL**, **RW**, and **RT**.

To test the effect of using the columella tubercle characters in the *P. verrilli* analyses above, I performed cluster, stepwise, and canonical discriminant analysis using the sixteen original characters plus the three columella tubercle characters, and compared results to similar tests without the columella tubercle characters.

All data analyses were performed on the University of Maryland IBMD mainframe computer using SAS version 6.08 and SASTAXAN (Jacobs 1990) software. All data are available from the author.

RESULTS

Morphometric Analysis

Since all characters in all groups were not normally distributed the power of the probability tests may be slightly reduced. The within covariance matrices were homogenous ($P < 0.1$) for all tests except the test using the three Belize non-astreoid groups and the holotypes. The within covariance matrices were not homogenous in this test therefore a pooled covariance matrix was used.

In the discriminant analysis of the three Belize non-astreoid groups 92.9%, or 65/70 of all colonies were correctly classified. The percent of correctly classified colonies per group was: 94.6 for group 1 (*P. porites*), 87.0 for group 2 (*P. furcata*), and 100 for group 3 (*P. divaricata*). The 5 misclassified colonies were reexamined and maintained in their original groups for the stepwise and canonical discriminant analyses. The stepwise discriminant analysis showed that the three species could be distinguished using just five characters **RW**, **ST**, **P2**, **PE**, and **SE**. In the canonical discriminant analysis two canonical variables (CV1 and CV2) were calculated, with CV1 accounting for 86.2 percent of the variation and CV2 accounting for 13.8 percent. The two canonical variables had significant discriminant power ($P<.0001$). CV1 distinguished groups 1, 2 and 3. CV2 also distinguished between groups 1, 2 and 3. Canonical discriminant analysis results are plotted in Figure 1.

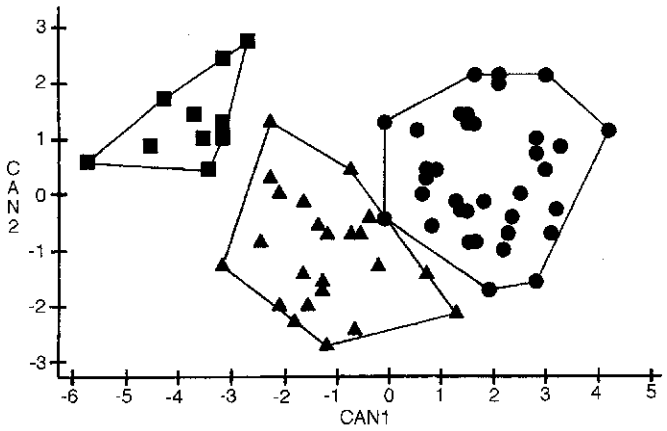

Fig. 1: Canonical discriminant analysis of non-astreoid *Porites* off Belize using corallite characters. Plots of the first two canonical variables. Symbols represent individual colonies. = *P. porites*, = *P. furcata*, = *P. divaricata*.

Figure 2 shows the relation of Belize specimens to the type specimens after the canonical discriminant analysis of Belize non-astreoid species and holotypes. The holotypes of *P. branneri* and *P. colonensis* are clearly morphologically distinct species and the *P. clavaria* and *P. furcata* holotypes lie inside the perimeter of the polygons for the Belize *P. porites* and *P. furcata* species. In the canonical discriminant anal-

ysis four canonical variables (CV1, CV2, CV3 and CV4) were calculated, with CV1 accounting for 58.3% of the variation, CV2 accounting for 24.4%, CV3 for 10.7%, and CV4 for 6.6%. The four canonical variables had significant discriminant power (P<.0001). In the stepwise discriminant analysis groups could be distinguished using a minimum of 9 characters; **RW**, **PE**, **L1**, **ST**, **T1**, **P2**, **NC**, width **SW**, and **WT**. CV2 distinguished the type specimens of *P. branneri* and *P. colonensis* from the Belize species. Discriminant analysis showed the probability of *P. colonensis* belonging to any of the other species groups was unlikely (*P. porites* group 0.3406, *P. furcata* group 0.6594, *P. divaricata* and *P. branneri* groups zero). *Porites branneri* was not checked in this manner because it is clearly distinguished qualitatively by columella tubercle free corallites.

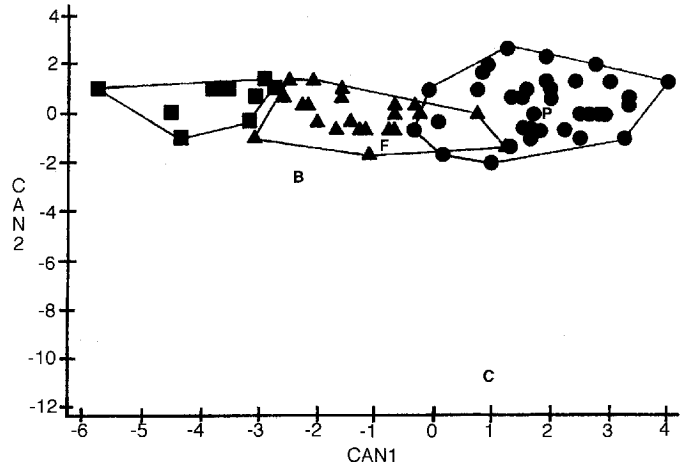

Fig. 2: Canonical discriminant analysis using corallite characters showing relation of Belize specimens to type specimens. Plots of the first two canonical variables. Symbols represent individual colonies. = *P. porites*, = *P. furcata*, = *P. divaricata*, B = *P. branneri* holotype, C = *P. colonensis* holotype, P = *P. clavaria* holotype, and F = *P. furcata* holotype.

Canonical discriminant analysis (CV1) clearly separated the astreoid species from the non-astreoid species and plotted the *P. verrilli* holotype near the *P. astreoides* from Belize. In the canonical discriminant analysis three canonical variables (CV1, CV2, and CV3) were calculated. The three canonical variables had significant discriminant power (P<.0001). CV1 accounted for 88.7% of the variation, CV2 accounted for 9.9%, and CV3 for 1.4%.

Test results using the three columella tubercle characters plus the 16 original characters showed that cluster analysis did not distinguish *P. verrilli* from the Belize *P. astreoides*. The stepwise discriminant analysis results showed that one of the three columella tubercle characters (**CE**) was used in the stepwise model to distinguish the species but it was not heavily weighted. Canonical discriminant results using the

three columella tubercle characters did not help distinguish *P. verrilli* from the Belize *P. astreoides*, but to the contrary, classified *P. verrilli* closer to the *P. astreoides* colonies than the canonical discriminant analysis where the columella tubercle characters were not used (Figure 3). In the canonical discriminant analysis, three canonical variables (CV1, CV2, and CV3) were calculated. The three canonical variables had significant discriminant power (P<.0001). CV1 accounted for 88.3% of the variation, CV2 accounted for 10.3%, and CV3 for 1.4%.

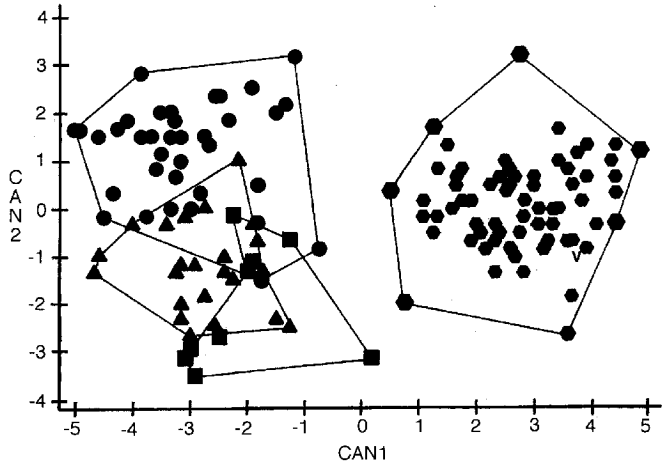

Fig 3: Canonical discriminant analysis *of P. astreoides*, *P. porites*, *P. furcata*, *P. divaricata*, with *P. verrilli* classified with *P. astreoides*. Plots of the first two canonical variables. Symbols represent individual colonies (4 colonies hidden). = *P. porites*, = *P. furcata*, = *P. divaricata*, = *P. astreoides*, V = *P. verrilli* holotype.

DISCUSSION AND CONCLUSION

Character selection

The failure of cluster analysis to independently distinguish Belize *P. porites*, *P. furcata*, and *P. divaricata* species groups is due to intercorrelations among *Porites* linear character dimensions that adversely affect the resolution of cluster analysis (Budd et al. in press). Cluster analysis also did not independently distinguish *Porites* species using landmark-based methods (Budd et al. in press) thus leaving the problem of discovering high resolution characters for the Poritidae open for further research.

Selecting the characters to be used in a morphometric study is the first instance where bias is introduced. Results will change with every different character combination used. Selecting truly diagnostic characters is important in any taxonomic study but particularly so with *Porites* where many characters values overlap among species. In the search for truly diagnostic characters I eliminated all characters that had an unusual percent of partially missing values. The

decision to use or not use a character with partially missing values is a judgment call based on an understanding of the total amount of corallites with the missing value, the number of colonies affected, and the cause of the missing character (i.e., natural damage or because it did not grow). This important protocol should be performed in all morphometric studies and documented so the use of inconsistent and unreliable characters do not skew results.

It is interesting to note that the most important distinguishing character in the corallite discriminant analysis of ramose Panamanian poritids conducted by Weil (1992) was the number of corallites per area. This character in my view is not reliable because it is affected by budding corallites. He also used columella diameter as a character to distinguish ramose species, which is commonly absent (missing in up to 49% of the corallites) in the Belize species (totally missing in 5 out of 70 colonies).

Use of the inconsistent columella tubercle character as an anchor for landmark method measurements on *Porites* (Potts et al. 1993, Budd et al. in press) should not be tied to the structure of the columella tubercle, but should be redefined as the center of the corallite.

Importance of Traditional Characters

Stepwise discriminant analysis showed that the best model for distinguishing *P. porites*, *P. furcata,* and *P. divaricata* off Belize used a minimum of five characters: **RW**, **ST**, **P2**, **PE**, and **SE**. The traditional corallite characters of corallite diameter, number of pali, aspects of the columella tubercle, and wall elevation (Smith 1971, Foster 1986) were not components of this model.

Porites astreoides is distinguished from the other *Porites* in the Caribbean and western Atlantic by its lack of pali, or when rarely present, their reduced size and number. Therefore, the traditional astreoid characters of calice depth, corallite length and width, and size of the columella tubercle (Smith 1971, Foster 1986) are not relevant in distinguishing *P. astreoides* from the non-astreoid species.

Distinguishing the Poritidae off Belize

Porites porites, *P. furcata, P. divaricata* and *P. astreoides* were clearly distinguished off Belize using linear characters and multivariate techniques. As the final step in this research, genetically identified specimens will be measured and incorporated into this analysis to further confirm the validity of the *a priori* designated groups.

Below are two user-friendly methods for distinguishing *Porites* species off Belize, as well as *P. branneri* and *P. colonensis* which to date have not been found off Belize. The first method is qualitative and can be used to distinguish *P. astreoides*, *P. branneri* and *P. colonensis* with excellent reliability and will

distinguish the ramose species of *P. porites*, *P. furcata* and *P. divaricata* in most cases. The second method is quantitative and is designed to help distinguish questionable ramose species.

Qualitative Key

To use this key start at 1. Choose a description from 1a or 1b that most closely fits the specimen. Next to the selected description is the name of the specimen or a number that refers to another set of descriptions further on in the key. By making the appropriate choice and continuing this process one will eventually identify the specimen to the species level. Note that smallest branch diameter ranges overlap for *P. porites*, *P. furcata*, and *P. divaricata.* These values are included in the key to illustrate that usually *P. porites* has larger branch diameters than *P. furcata* and that *P. divaricata* has the smallest branch diameters of the three ramose species. Any specimen with a smallest branch diameter greater than 10.5 mm is *P. porites* and any specimen with a smallest branch diameter less than 4.5 mm is *P. divaricata.*

1a. Pali missing or greatly reduced in size and number. Flattened form in depths >10 m otherwise predominately mound shaped. Mounds may have finger-like protrusions in turbid habitats. Encrusting colonies less common. Found in all habitats. Colors include yellow, brown, tan, mustard, olive drab and various shades in between.

Porites astreoides Lamarck, 1816

1b. Pali present..... 2
2a. Ramose form.....3
2b. Non-ramose form.....4
3a. Prefers fore-reef and patch reef environments. Colors include white, brown, and brown with white tips. Smallest branch diameter (measured at a point half-way down the living part of a branch) mean 11.85 (± 3.22) mm, range 5.66 - 21.48 mm.

Porites porites (Pallas, 1766)

3b. Prefers reef crest and other high wave energy *Thalassia* environments. Yellow or brown with yellow tips in color. Smallest branch diameter (measured at a point half-way down the living part of a branch) mean 7.494 (± 1.076) mm, range 4.5 - 9.96 mm.

Porites furcata Lamarck, 1816

3c. Found only in *Thalassia* beds in leeside habitats around islands or in other low wave energy *Thalassia* environments. Brown in color. Smallest branch diameter (measured at a point half-way down the living part of a branch) mean 5.408 (± 1.874) mm, range 3.7 - 10.5 mm.

Porites divaricata Lesueur, 1821

4a. Encrusting form, corallites without columella tubercle. Not found in Belize.

Porites branneri Rathbun, 1887

4b. Foliacious form, corallites with columella tubercle, green and red polyps. Not found in Belize.
Porites colonensis Zlatarski, 1990

Quantitative Key

Step 1: Obtain a compound microscope with ocular micro-meter for measuring linear distances. Calibrate the focus knob for measuring elevations.

Step 2: Level the corallite to be measured under the microscope by positioning the specimen under the microscope so all sides are in focus.

Step 3: Measure the corallite characters **RW**, **ST**, **P2**, **PE** and **SE** on 10 corallites in your specimen.

Step 4: Take the $\log_{10}$ of each measurement to transform the data. Then calculate a transformed mean (TM) for each character.

Step 5: Calculate CAN 1 and CAN 2 values for plotting on Figure 4 as follows. In the example below, I used values I measured for a colony from Belize. For each of the five characters above:

• Subtract the provided transformed raw total sample mean (TSM) for the Belize data from the TM you obtained. This provides a centered mean (CM).

Character	TM		TSM		CM
RW	-0.550	-	-0.483	=	-0.067
ST	-2.328	-	-2.240	=	-0.088
P2	-1.871	-	-1.591	=	-0.280
PE	-0.845	-	-0.641	=	-0.204
SE	-0.640	-	-0.577	=	-0.063

• Multiply centered mean (CM) times the provided CAN 1 raw canonical coefficient (RCC). Then sum all values. This is your CAN 1 value to plot on Figure 4.

Character	CM		RCC		
RW	-0.067	x	3.467	=	-0.232
ST	-0.088	x	3.692	=	-0.325
P2	-0.280	x	0.934	=	-0.262
PE	-0.204	x	4.078	=	-0.832
SE	-0.063	x	-2.091	=	+0.132
				CAN 1 VALUE	-1.519

• Repeat the above process for CAN 2.

Character	CM		RCC		
RW	-0.067	x	1.531	=	-0.103
ST	-0.088	x	1.954	=	-0.172
P2	-0.280	x	3.324	=	+0.931
PE	-0.204	x	-3.714	=	+0.758
SE	-0.063	x	4.176	=	-0.263
				CAN 2 VALUE	+1.151

• Plot the CAN 1 and CAN 2 values on Figure 4 to correctly identify your specimen. In the above

example, the specimen plots close to the center of the *P. divaricata* polygon.

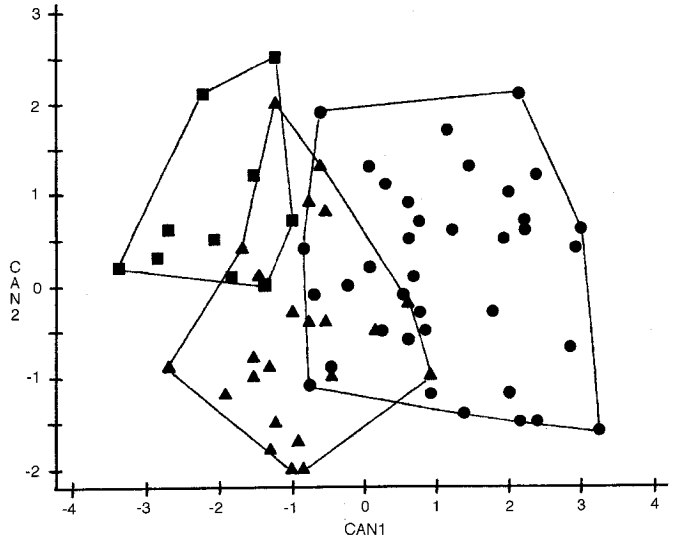

Fig. 4: Canonical discriminant analysis of non-astreoid ramose Porites off Belize using the five corallite characters derived from the stepwise discriminant analysis. Plots of the first two canonical variables. Symbols represent individual colonies. = *P. porites*, = *P. furcata*, = *P. divaricata*.

Relation of Belize specimens to type specimens

The Belize specimens of *P. porites* and *P. furcata* classified around the holotypes for *P. clavaria* and *P. furcata* indicating these holotypes are good average representatives of the Belize species. The results also support the assumption that *P. porites* off Belize is the same species as *P. clavaria* Lamarck, 1816.

While canonical discriminant analysis clearly separated *P. branneri* and *P. colonensis* from other non-astreoid species, these species can be qualitatively distinguished from astreoid *Porites* by the presence of pali. The lack of any columella tubercle, and the foliaceous colony form and dark polyp color with white or green centers are the most important qualitative characteristics that distinguishes *P. branneri* and *P. colonensis,* respectively from all other non-astreoid *Porites* in the Caribbean and western Atlantic. Smith (1971) in his description of *P. branneri* does not mention the lack of a columella tubercle. The total lack of any columella tubercles in the questionable *"P. branneri"* specimens used by Weil (1992) confirms that these specimens were in fact *P. branneri*.

A neotype should be designated for *P. divaricata*. A neotype should also be designated for *P. porites* as the topotype designated by Vaughan (1901a) is not considered valid by the International Code of Zoological Nomenclature (1985). In addition, this topotype was designated to represent all ramose *Porites* as a single

species when in fact they are three distinct species (*P. porites*, *P. furcata,* and *P. divaricata*).

Since multivariate morphometric results do not provide convincing evidence that *P. verrilli* is a distinct species, it is recommended that *P. verrilli* be considered a junior synonym of *P. astreoides*.

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