



Use of X-radiographs to distinguish members of the *Montastraea annularis* reef-coral species complex

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Abstract

Recent work suggests the *Montastraea annularis* species complex consists of at least three species, which can be distinguished qualitatively in the field using features related to colony growth (e.g. overall growth form, bumpiness, growth along the colony edge). However, when whole colonies are not available and surfaces are eroded, identification becomes problematic when relying on such characteristics. Characters based on internal skeletal structures are less prone to loss due to taphonomic processes. Previous work has shown that internal corallite architectural features measured in transverse thin sections can be used to distinguish species. To determine whether internal colony-level features measured on X-radiographs can be used, eight characters related to corallite budding and accretionary growth were measured on specimens representing three modern members of the *M. annularis* species complex (*M. annularis*, *M. faveolata* and *M. franksi*), as well as two fossil forms (columnar and organ-pipe). All eight characters showed significant differences among species. Discriminant function analysis using seven of these characters resulted in distinct species groupings in canonical scores plots and a 100% classification success for specimens from Panamá. These results suggest that measurements made on X-radiographs provide a useful tool for quantitatively distinguishing members of the *M. annularis* complex as well as between other massive reef corals.

Introduction

Montastraea annularis sensu lato is one of the dominant reef-building corals in the Caribbean and is found essentially on all Caribbean reefs over a wide range of depths (Goreau & Wells, 1967; Logan, 1988; Van Veghel & Bak, 1993). For the past several decades, *M. annularis* was considered to be a single species that exhibited considerable morphological variation, with much, though not all, of that variation being associated with differences in light availability (Dustan, 1975; Graus & Macintyre, 1976, 1982). Recently, work by Knowlton et al. (1992) led to the conclusion that

Montastraea annularis is actually three distinct species and the consequent re-recognition of two previously described species, *M. franksi* and *M. faveolata* (Weil & Knowlton, 1994).

With the breakup of *M. annularis* into at least three species comes the need to distinguish these species in both modern and fossil materials. Means of separating the different species include molecular techniques, growth rates, aggression, ecology, corallite structure, whole colony morphology, transverse thin-sections, and surface-skeletal characteristics (Graus & Macintyre, 1982; Budd, 1993; Budd et al., 1994; Weil & Knowlton, 1994; Van Veghel & Bosscher, 1995; Budd & Johnson,

1996; Van Veghel et al., 1996; Budd & Klaus, 2001; Knowlton & Budd, 2001; Pandolfi et al., 2001, 2002). Unfortunately, many of the conventional techniques used to distinguish members of the *Montastraea annularis* species complex are ineffective in distinguishing fossilized specimens. Species determination in fossilized material is especially difficult when relying on 3-dimensional morphometric characteristics because corallite surfaces are easily eroded, (Budd & Klaus, 2001; Knowlton & Budd, 2001; Pandolfi et al., 2002). Likewise, full, intact colonies are not readily available for many fossil specimens or for core samples, so growth form is not always known. Further complications with fossilized materials arise from the presence of additional species, or morphotypes, during the Pleistocene co-occurring with modern day members of the complex (Budd & Klaus, 2001; Pandolfi et al., 2001, 2002).

As the internal structure of coral colonies is much less prone to weathering than surficial features, identification based on internal-skeletal characteristics may be more diagnostic for fossilized specimens. Internal corallite structures, examined in transverse thin-sections, have been found useful in differentiating the species (Budd & Klaus, 2001); however, internal structures reflecting whole colony morphology have not been examined. X-ray analysis allows for the examination of density differences within skeletal slabs (Macintyre & Smith, 1974). X-rays are commonly used for growth rate measurements by examining annual density bands; however, the use of X-rays to examine other skeletal details related to colony growth has not been investigated extensively (Macintyre & Smith, 1974; Graus & Macintyre, 1976, 1982; Knowlton et al., 1992; Darke & Barnes, 1993). By examining additional skeletal details, measurements made on X-radiographs may be able to serve as proxies for whole colony morphology, and thus serve as useful indicators of species.

Methods

Sampling

Collections of both modern and fossil coral specimens were analyzed. Forty-eight living coral specimens from the San Blas Islands, Panamá, were

Table 1. Number of each species (living colonies) or growth form (Pleistocene colonies) collected from each location and total numbers

| Species or growth form | Panamá | Belize | Barbados | Total |
|------------------------|--------|--------|----------|-------|
| <i>M. annularis</i> | 14 | 15 | – | 29 |
| <i>M. faveolata</i> | 9 | 5 | – | 14 |
| <i>M. franksi</i> | 25 | 6 | – | 31 |
| Columnar | – | – | 27 | 27 |
| Organ pipe | – | – | 30 | 30 |
| Total | 48 | 26 | 57 | 131 |

Only living colonies were collected in Panamá and Belize, and only fossil colonies were collected in Barbados.

collected from patch reefs at depths between 3 and 12 m from 1995 to 1997 (Table 1). The specimens were identified in the field as belonging to the three recently described species of the *M. annularis* complex based on the following characteristics: (1) *M. annularis* sensu stricto (Ellis & Solander, 1786), which forms multiple smooth columns with diameters usually 100–350 mm and senescent colony edges, (2) *M. faveolata* (Ellis & Solander, 1786), which forms smooth to keeled mounds (single mound-shaped skeletal mass with a diameter >350 mm) with non-senescent edges, and (3) *M. franksi* (Gregory, 1895), which forms bumpy mounds and plates (single and multiple) with non-senescent edges. The field-based identifications were subsequently confirmed by molecular analyses (Fukami et al., in press), and corroborated by transverse thin section morphometrics (Knowlton & Budd 2001; Pandolfi et al., 2002).

Twenty-six living coral specimens from various reef settings at Carrie Bow Cay, Belize, were collected from depths between 0.5 and 30 m from 1970 to 1975 (Table 1); most were previously analyzed by Graus & Macintyre (1982). The specimens were identified as belonging to the three recently described species of the *M. annularis* complex based on the gross appearance (shape) of colonies in X-radiographs.

In Barbados, 57 fossil coral specimens were collected from an 82 000 year old reef terrace (Table 1) (specimens from Pandolfi et al., 2002). In Barbados, only the organ-pipe and columnar growth forms described by Pandolfi et al. (2001, 2002) were analyzed and these were collected from a shallow water (<5 m) back-reef setting. Organ-

pipe colonies were defined qualitatively as composed of numerous elongate skeletal pipes whose diameters were usually less than 100 mm thick; in contrast, columnar colonies are composed of multiple skeletal columns (higher than wide) with diameters usually 100–350 mm thick. Both of these forms differ morphologically from modern *M. annularis*; however, only the organ-pipe growth form has thus far been considered a distinct, extinct species (Pandolfi et al., 2002). Both modern *M. annularis* and fossil-columnar forms have columns lacking living corallites along their sides, while the organ-pipe form had living corallites along the column sides (Pandolfi et al., 2002).

Morphological characters

Specimens were cut through the top of the colony, parallel to the growth axis, into ~5 mm thick slabs. Slabs were X-rayed and the negatives digitized using a Umax Power Look II scanner with

transmitted light. Image-Pro Plus v. 3.1 was used to record the morphological measurements. Eight characters were measured from the digitized X-ray images (Figs 1, 2; Table 2).

Wherever possible, measurements were made on five replicate corallites or sections of each colony for all characters, except growth angle and maximum angle for which only one determination was made. For specimens on which five replicate measures could not be made of a given character, as many measurements as possible were made. For some specimens certain characters could not be measured.

Data analysis

For each coral colony, replicate measurements of each characteristic were averaged before being used in statistical analysis. Pearson correlation coefficients were calculated for each pair of characters. Significant differences between species and

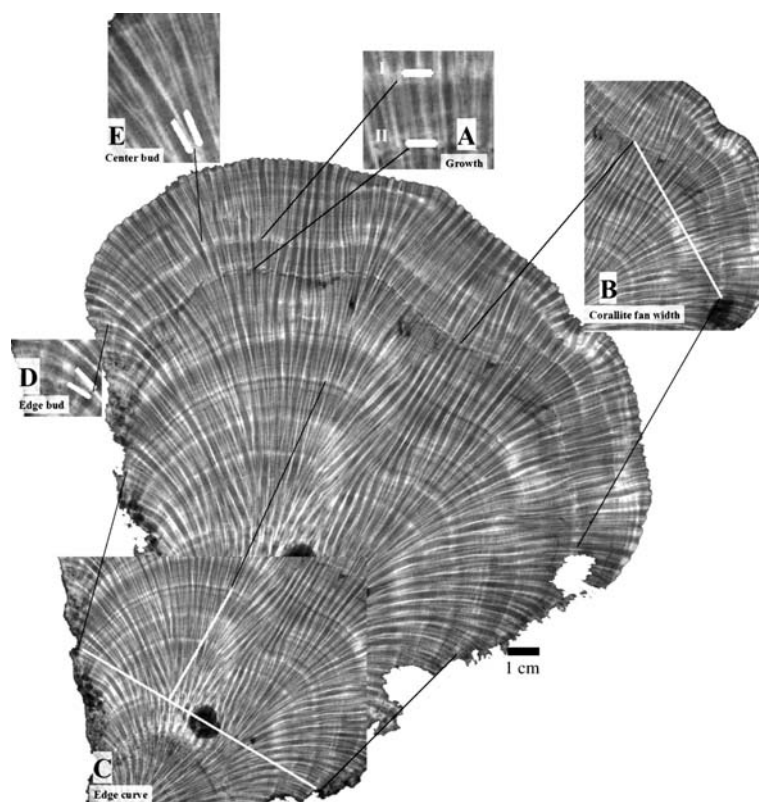


Figure 1. Longitudinal X-radiograph of a specimen of *M. annularis* from Panamá with characters described in Table 2 depicted. Characters are: (A) growth (I and II indicate high density bands), (B) corallite fan width, (C) edge curve, (D) edge bud, (E) center bud.

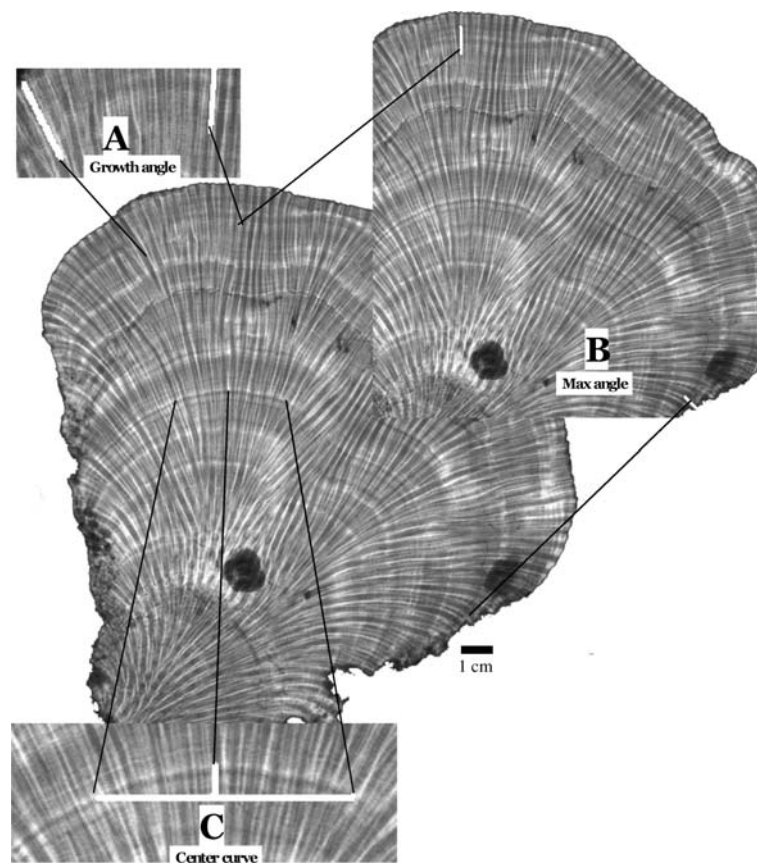


Figure 2. Depictions of characters described in Table 2 continued: (A) growth angle, (B) maximum angle, (C) center curve.

locations were evaluated using the Kruskal–Wallis test, and each species/location combination was specified as the treatment variable. Nonparametric pairwise comparisons followed procedures described by Zar (1999). Canonical discriminant function analysis (DFA) was carried out using the quadratic mode to classify specimens and identify characters important in distinguishing among species. When it was not possible to measure any given character for a specimen, the overall mean value for the character was substituted prior to running DFA.

Results

There was considerable variability in most traits both between species and locations and within a given location for a single species (Fig. 3). Despite such variability, significant differences were ob-

served between species for all characters (Table 3). Significant differences were not observed within a species between localities. The overall means for each character are given in Table 4. Correlations between characters are shown in Table 5. For DFA, elimination of individual characters from the model revealed edge curve had little effect on canonical-scores plots and thus was eliminated from the model.

Panamá specimens were classified correctly (DFA assigned all specimens to the same species as had been determined genetically) using seven of the eight morphological characters, and the canonical-scores plots show three distinct groups, with no overlap between *M. franksi* and *M. annularis* (Fig. 5). When Belize specimens were run unclassified in the Panamá DFA, canonical-scores plots showed general agreement between visual assignments of specimens and their clustering with Panamá species (Fig. 5A).

Table 2. Characters examined, how they were measured, and the number of replicate measurements made per colony

| Character | Description | Replicates |
|--------------------------|---|------------|
| Growth (mm/year) | Growth rates were estimated based upon the distances between successive annual high density bands along the growth axis (line with maximal linear extension) (Fig. 1A). | 5 |
| Corallite-fan width (mm) | A corallite-fan system was considered to be the collection of corallites spreading from a growth axis, giving rise to a fan shaped pattern with largely convex density bands. The widths of individual corallite-fan systems were measured in each specimen by determining the distance between the two most distant points that could be identified as lying on the same high density band in a given fan (Fig. 1B). | 5 |
| Edge curve | Colony curvature was expressed as the ratio of the length of a line between the two most distant points on a single high density band and the distance (perpendicular) between that line and the highest point on the same high density band (Fig. 1C). | 5 |
| Edge bud (°) | Corallite budding angles were measured by placing lines parallel to the corallite wall of the mother and daughter polyps and calculating the angle of intersection for polyps near the edge of each corallite-fan system (Fig. 1D). | 5 |
| Center bud (°) | Same as edge bud, except polyps were near the center of the corallite fan system (Fig. 1E). | 5 |
| Growth angle (°) | The angle between the growth axis and the corallite with the greatest angle that was part of the same corallite-fan system, with the bulk of its recent growth (within two density bands) parallel to the growth axis, was measured (Fig. 2A). | 1 |
| Max angle (°) | The maximum corallite angle was determined by measuring the angle between the growth axis and a line parallel to the corallite wall of the corallite angled the furthest from the growth axis (Fig. 2B) (from Graus & Macintyre, 1982). | 1 |
| Center curve | Same as edge curve, except measurements were along the growth axis (Fig. 2C). | 5 |

In the DFA of Panamá specimens with Barbados specimens unclassified, canonical-scores plots show the two Pleistocene forms to be distinct from each other, and neither form appears to overlap well with any single extant species (Fig. 5B).

Discussion

Characters

Many of the quantitative differences between species are consistent with both the apparent differences observed in X-radiographs and the reported morphological differences between species observed in the field. Patterns of average growth-rate variation between the members of the *M. annularis* species complex (Table 4) are consistent with those reported in other studies (Knowlton et al., 1992; Szmant et al., 1997; Pandolfi et al., 2002). The larger and more variable budding angles observed in *M. franksi* (Table 4)

would seem consistent with the uneven calice distribution and greater spacing reported for *M. franksi* (Budd, 1993; Van Veghel & Bak, 1993; Szmant et al., 1997). Specimens of *M. annularis* tended to consist of single corallite fan systems, or multiple, poorly separated, corallite-fan systems arising from a single corallite fan. Such single fans were associated with smooth hemispherical and columnar growths; corallites grew at larger angles relative to the growth axis, thus resulting in higher values for maximum angle and edge curve for *M. annularis* relative to other species (Table 4; Fig. 4). In *M. faveolata*, specimens consisted of large relatively smooth regions interspersed with well-defined corallite-fan systems, likely responsible for the 'keeled' appearance of colonies. Corallite-fan systems in *M. faveolata* tended to be highly curved near their centers and gradually merged with the surrounding flatter skeleton, thus yielding relatively narrow fan systems with a high degree of center curvature (Table 4). *M. franksi*, like *M. faveolata*, tended to have relatively smooth regions, but these were frequently interrupted with

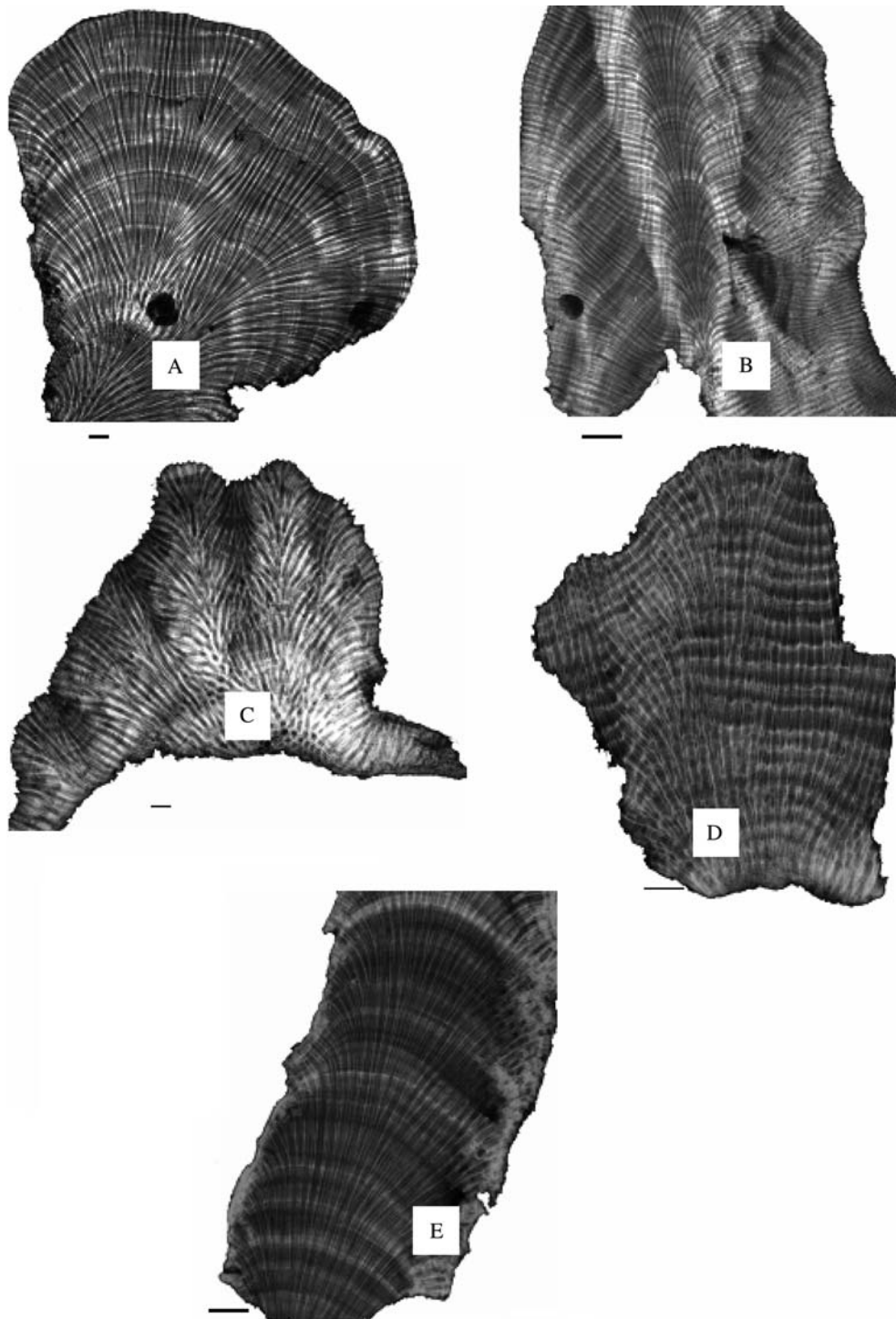


Figure 3. Longitudinal X-radiographs of modern and Pleistocene lineages of the *Montastraea annularis* species complex: (A) *M. annularis*, (B) *M. faveolata*, (C) *M. franksi*, (D) columnar, (E) organ pipe. Bars represent approximately 1 cm.

Table 3. Significant differences in each character between species at a given location as indicated by pairwise comparisons

| Character | Location | | |
|---------------------|------------------|--------|----------|
| | Panamá | Belize | Barbados |
| Growth | A >>> K; F >>> K | A >> K | OP >>> C |
| Corallite-fan width | A >> F; A >> K | n.s. | n.s. |
| Edge curve | n.s. | A > K | n.s. |
| Edge bud | K >>> A | n.s. | C >> OP |
| Center bud | K >>> A | n.s. | n.s. |
| Growth angle | n.s. | n.s. | OP >>> C |
| Maximum angle | n.s. | n.s. | OP > C |
| Center curve | n.s. | n.s. | OP >> C |

Overall Kruskal–Wallis tests were all significant at the $p < 0.001$ level. Significance values are as follows: n.s. = not significant = $p > 0.05$; > = $p < 0.05$; >> = $p < 0.01$; >>> = $p < 0.001$. A, *M. annularis*; F, *M. faveolata*; K, *M. franksi*; C, columnar; OP, organ pipe.

small fan systems (giving rise to ‘bumps’). Regions with well defined growth banding or a single extensive growth axis were rare in *M. franksi*, budding angles tended to be larger, and growth slower than in other species (Table 3). The columnar growth form consisted of very flat, linear growth bands, occasionally interrupted by small corallite-fan systems (Table 4). The organ-pipe form consisted of single corallite-fan systems with well-defined growth banding, relatively narrow widths, and more curvature than columnar forms (Table 4).

The negative correlation of corallite-budding angles with both growth and fan width (Table 5) seems consistent with the expectation that colonies exhibiting more vertical growth would tend to have corallites more or less parallel to each other; similarly, more corallites growing parallel to each other should give a wider corallite-fan system. However, corallite-budding angles showed no correlation with any of the measures of colony curvature (edge curve, growth angle, maximum angle, and center curve) (Table 5), suggesting that the angle at which polyps divide does not necessarily reflect the overall curvature of the colony. Most measures of colony curvature (edge curve, growth angle, maximum angle, and center curve) were correlated with each other as might be expected (Table 5). Edge bud and center bud were highly correlated with each other, suggesting that budding angles remain similar across the colony (Table 5).

Species differences

The clear separation of species observed in the Panamanian specimens (Fig. 5) combined with their 100% classification success demonstrates that characters based on X-radiographs effectively distinguish members of the *Montastraea annularis* species complex. As all of the characters are based on internal skeletal structures, they should be diagnostic regardless of surface weathering. Three of the most heavily weighted characters in the DFA (growth, center bud, and center curve) are readily measurable on even small skeletal sections such as might be obtained in core samples. Thus, since members of the *M. annularis* species complex differ in their stable isotope ratios (Knowlton et al., 1992), and stable isotope ratios are routinely used in paleoclimatic reconstructions (Knowlton et al., 1992; Druffel, 1997), such characters as growth, center bud, and center curve may prove valuable in differentiating among species for paleoclimatic studies.

The canonical-score plot of the Belize specimens based upon Panamanian specimens was in good agreement with visual identifications based on X-radiographs (Fig. 5A). Thus, at least over a few degrees change in latitude, X-radiographic characteristics appear to be useful in assigning identities to corals from different localities.

Barbados and Panamá specimens run together show clear groupings of the organ-pipe and columnar growth forms (Fig. 5B) described by

Table 4. Mean values for each character (sites pooled) with standard deviations in parentheses and the number of colonies measured in brackets

| Species/growth form | Character | Growth (mm/year) | Corallite fan width (mm) | Edge curve | Edge bud (°) | Center bud (°) | Growth angle (°) | Maximum angle (°) | Center curve |
|---------------------|-----------|------------------|--------------------------|------------------|--------------|----------------|------------------|-------------------|-------------------|
| <i>M. annularis</i> | | 10.1 (2.6) [29] | 109 (50) [29] | 0.27 (0.10) [28] | 10 (2) [29] | 8 (2) [29] | 36 (19) [29] | 120 (27) [29] | 0.11 (0.05) [29] |
| <i>M. faveolata</i> | | 8.6 (2.5) [14] | 44 (11) [14] | 0.25 (0.14) [12] | 13 (2) [13] | 11 (2) [14] | 47 (19) [14] | 95 (14) [14] | 0.19 (0.09) [14] |
| <i>M. franksi</i> | | 4.1 (2.1) [31] | 62 (41) [30] | 0.16 (0.06) [8] | 19 (5) [18] | 17 (5) [31] | 29 (17) [31] | 84 (27) [31] | 0.09 (0.07) [31] |
| Columnar | | 5.4 (1.3) [27] | 35 (15) [6] | 0.16 (0.06) [12] | 13 (3) [14] | 9 (3) [27] | 22 (17) [22] | 35 (24) [27] | 0.08 (0.07) [27] |
| Organ pipe | | 12.6 (2.1) [30] | 66 (27) [16] | 0.21 (0.08) [30] | 9 (2) [30] | 8 (1) [30] | 50 (10) [30] | 75 (12) [30] | 0.11 (0.04) [30] |
| Overall | | 8.1 (3.9) [131] | 73 (46) [95] | 0.22 (0.10) [90] | 12 (4) [104] | 11 (5) [131] | 36 (19) [126] | 81 (36) [131] | 0.11 (0.07) [131] |

Table 5. Correlations between characters

| | Growth (mm/year) | Corallite fan width (mm) | Edge curve | Edge bud (°) | Center bud (°) | Growth angle (°) | Max angle (°) |
|--------------------------|----------------------|--------------------------|--------------------|---------------------|---------------------|---------------------|---------------------|
| Corallite fan width (mm) | n.s. (0.194) [95] | | | | | | |
| Edge curve | n.s. (0.090) [90] | n.s. (0.196) [70] | | | | | |
| Edge bud (°) | 0.000 (-0.568) [104] | 0.000 (-0.402) [82] | n.s. (-0.008) [83] | | | | |
| Center bud (°) | 0.000 (-0.560) [131] | 0.001 (-0.332) [95] | n.s. (-0.090) [90] | 0.000 (0.718) [104] | | | |
| Growth angle (°) | 0.000 (0.567) [126] | n.s. (0.010) [95] | n.s. (-0.007) [89] | n.s. (-0.105) [104] | 0.01 (-0.229) [126] | | |
| Maximum angle (°) | 0.002 (0.272) [131] | 0.024 (0.232) [95] | 0.000 (0.556) [90] | n.s. (-0.027) [104] | n.s. (0.024) [131] | 0.003 (0.261) [126] | |
| Center curve | 0.005 (0.244) [131] | 0.003 (-0.301) [95] | 0.000 (0.484) [90] | n.s. (0.066) [104] | n.s. (0.005) [131] | 0.000 (0.361) [126] | 0.001 (0.288) [131] |

The significance of each correlation is shown, in parenthesis is the correlation coefficient (r), and in brackets is the number of specimens on which the correlation is based. n.s. = not significant = $p > 0.05$.

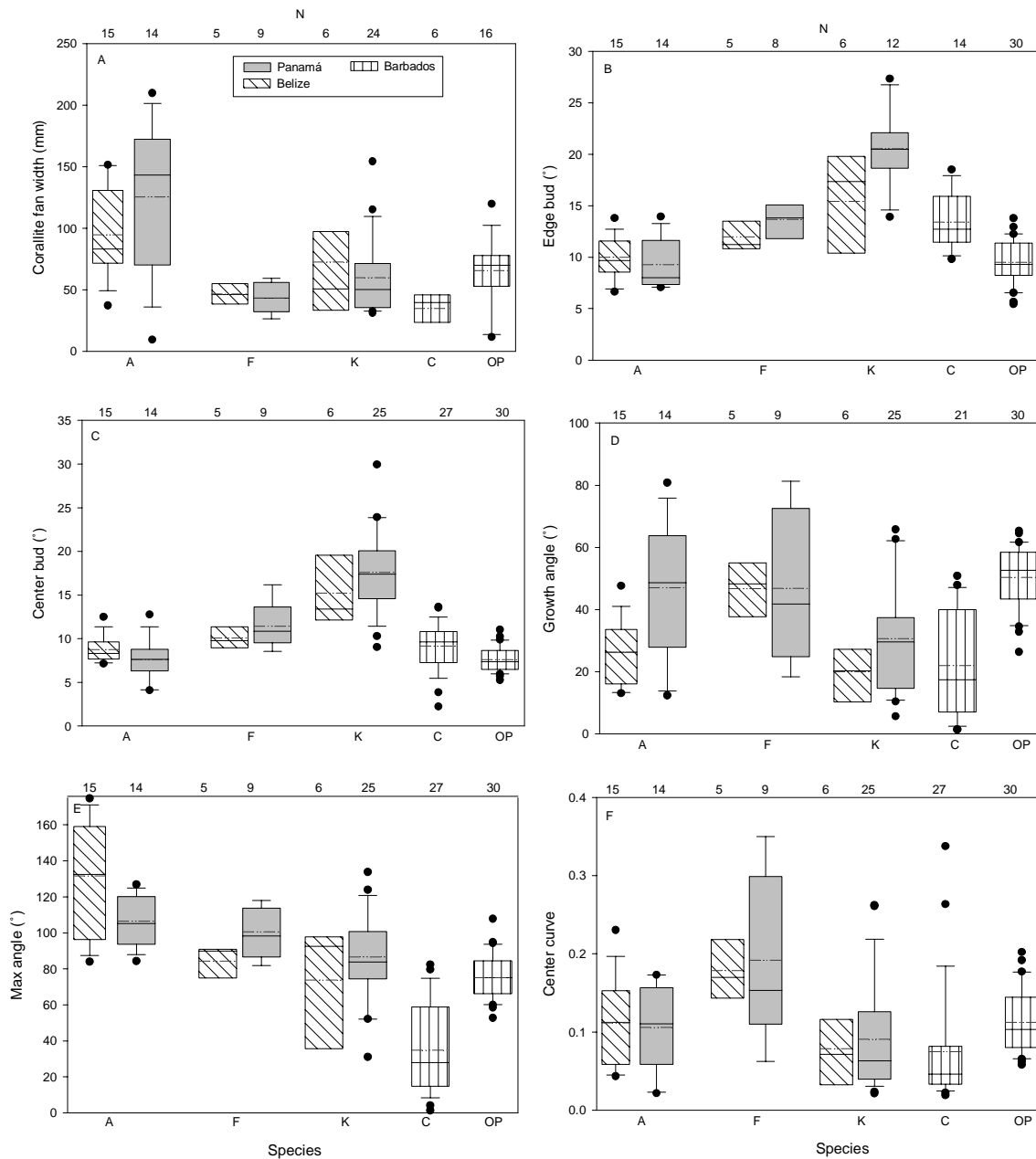


Figure 4. Box plots for selected characters. Plots show the median as a solid line, mean as a dashed gray line, quartiles as ends of boxes, extremes as whiskers, and outliers as dots. The upper horizontal axis (N) gives the number of specimens represented by each plot, the lower horizontal axis (Species) gives the species or growth form designation (A. *M. annularis*; F. *M. faveolata*; K. *M. franksi*; C. columnar; OP. organ pipe). The Y axis is the character represented in the plots: (A) corallite-fan width, (B) edge bud, (C) center bud, (D) growth angle, (E) max angle, (F) center curve.

Pandolfi et al. (2002). Such distinct groupings appear consistent with the separation of the organ-pipe growth form as a separate species; however, the columnar form appears to be distinct from

M. annularis as well (also observed by Pandolfi et al., 2002).

Despite the apparent utility of morphological characters derived from X-radiographs in differ-

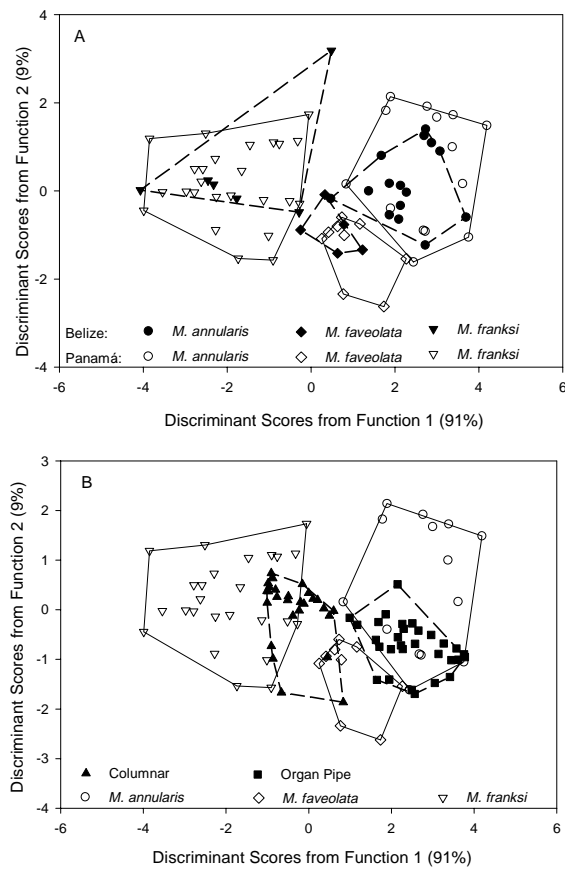


Figure 5. Plot of discriminant scores for Panamá species, based on all factors excluding edge curve. Heavily weighted characters were edge bud (-0.600), center bud (-0.572), and growth (0.547) in function 1, and fan width (0.686) and center curve (-0.454) in function 2. Variance explained by each function is given in parentheses. Symbols represent individual specimens. (A) Belize specimens were run with no identity assigned. (B) Barbados specimens were run with no identity assigned. Indicated species/form designations are based on visual assignments, not DFA assignments.

entiating species in the *M. annularis* species complex, a number of potential concerns remain to be addressed. Many morphological characters, including growth and maximum angle, have been shown to vary with light (or depth) and other environmental factors such as water energy and sedimentation (Dustan, 1975; Graus & Macintyre, 1982; Foster, 1985; Hubbard & Scaturro, 1985; Huston, 1985; Budd, 1993; Darke & Barnes, 1993). Work by Graus & Macintyre (1982) demonstrated that intercorallite spacings (likely similar to budding angles in the current study), maximum angle

(determined via a different technique from that used in the current study), and growth (equivalent to the current study) are all significantly correlated with depth. Colony form changes with depth, progressing from hemispheres at shallow depths to flared columns at intermediate depths and, finally, plates at the greatest depths (Graus & Macintyre, 1982). Species composition also changes with depth, with *M. annularis* being most common at shallow depths, and *M. franksi* more abundant at greater depths (Van Veghel & Bak, 1993; Weil & Knowlton, 1994; Szmant et al., 1997). Increases in intercorallite spacings, decreasing growth, and decreasing maximum angle were all consistent with models of responses to decreasing light intensity with increasing depth (Graus & Macintyre, 1982). Changing species composition with depth would also yield a similar pattern of changes in these characters, thus the differing skeletal morphologies may represent specific adaptations by members of the *M. annularis* complex to different light regimes. The relative importance of species identity versus light availability in determining these characters, or the additional characters measured in the current study, is not known; it remains to be established whether species or environmental differences are of primary importance in determining values for a given character.

Further, caution must be taken in interpreting characters from X-radiographs since work by Darke & Barnes (1993) on *Porites* spp. demonstrates that X-radiographs present an average image and do not necessarily reflect the true positions of corallites. In *M. annularis*, the direction of corallite growth may depart from that of the apparent growth axis. This is particularly common in *M. franksi* where corallites, which are only a short distance below the surface, may have orientations approaching perpendicular to that of the apparent growth axis. Difficulties such as these may limit both the resolution of separations based on X-radiographs and the utility of radiographs for understanding internal skeletal structure. Finer resolution might be obtained through 3-dimensional imaging such as that obtained in CAT scans (Dodge, 1980).

In summary, morphological characters derived from X-radiographs appear to provide a useful means of differentiating the members of the *M. annularis* species complex. These data demon-

strate that characters from X-radiographs show similar diagnostic power to that achieved with other methods of identifying members of the *M. annularis* species complex. With further work and additional characters, especially those defining and quantifying corallite-fan systems, characteristics from X-radiographs may prove to be a valuable tool for determining species identities in both extant and extinct corals. This tool would aid identification of species when the growth form was unknown, for example from cores. Future work should address whether or not characters measured from X-radiographs are diagnostic across broad geographic areas, large intervals of time, and wide ranging environmental conditions.

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