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THE ORIGIN AND EARLY EVOLUTION OF THE *MONTASTRAEA* ''*ANNULARIS*'' SPECIES COMPLEX (ANTHOZOA: SCLERACTINIA)

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ABSTRACT—This study represents the first in a series tracing the early evolution of a dominant Caribbean reef coral, the *Montastraea* ''*annularis*'' species complex, using a combination of morphometric and phylogenetic approaches. It focuses on Costa Rica and Panama; additional geographic locations and reef environments will be treated in subsequent work. To distinguish species, new landmark methods are developed by comparisons with genetically characterized modern colonies from Panama. The fossil material consists of transverse thin-sections of 94 well-preserved specimens of *M. annularis*-like corals collected in Plio-Pleistocene reef sequences in the Limón basin of Costa Rica and the Bocas del Toro basin of Panama. The landmarks comprise 27 spatially homologous points, which define the thickness and structure of the corallite wall and associated costosepta. Bookstein size and shape coordinates are analyzed using cluster analysis and canonical discriminant analysis, and a total of 10 morphotypes are distinguished. Cladistic analyses are performed using characters derived partially from morphometric data. A matrix consisting of 16 taxa and eight characters is analyzed using global parsimony and a sister group of two species as the outgroup. The results reveal two distinct evolutionary groups, which are distinguished by the new corallite wall characters. One group contains one modern species, and the other contains a second; the relationships of the third are poorly resolved.

Despite the low number of equally parsimonious trees, high numbers of plesiomorphic taxa, long range extensions, and lack of agreement with genetic data indicate that the new characters alone are inadequate for completely interpreting evolutionary relationships, and more samples and characters are needed. Nevertheless, these preliminary results do show that three modern species of the *M.* ''*annularis*'' complex arose prior to accelerated extinction at the end of late Pliocene to early Pleistocene faunal turnover of Caribbean reef corals, and two may have originated younger than 4 Ma. Six or more new species may be represented in upper Pliocene to lower Pleistocene sequences in Costa Rica and Panama. Coexistence of predominantly pre- and post-turnover clades may have been responsible for the high diversity observed within the species complex in these two sequences.

INTRODUCTION

RECOGNITION OF origination and extinction events in the fossil record and long-term patterns of biotic change depends on the rigor and consistency with which taxa are distinguished and traced through geologic time. Interpreting the causes for these events requires a more refined understanding of the morphologic characters that distinguish species and their patterns of evolutionary change. Understanding speciation and extinction events is especially important in coral reef communities, which are currently among the most diverse but most threatened marine ecosystems, and is essential for designing conservation measures to protect them (Paulay, 1997). In the present study, we explore character change associated with origination and extinction events within a species complex of reef corals during a period of regional turnover. Specifically, we analyze the *Montastraea annularis* (Ellis and Solander, 1786) complex during late Pliocene to early Pleistocene turnover of the Caribbean reef coral fauna. We attempt not only to distinguish species and trace their stratigraphic distributions, but also to provide a starting point for interpreting evolutionary relationships and identifying patterns of character change. Because of the complexity of the data, it is impossible to accomplish these objectives in one article. Instead, a series of articles is planned, each of which treats a separate geographic region and each of which builds upon the results of the previous paper. The present paper is the first in the series.

We have selected *Montastraea annularis* sensu lato for study, because it ecologically dominates many modern reefs within the Caribbean region, and has done so since the end of late Pliocene to early Pleistocene faunal turnover, approximately 2–1.5 Ma (Knowlton and Budd, in press). Members of the genus have dominated portions of Caribbean reefs for at least the past 22 m.y. (Budd, 1991). The complex and other closely related ''*M. annularis*-like'' species, therefore, offer relatively large and continuous samples through geologic time, and provide an excellent model system for examining species-level character evolution in scleractinian reef corals. The complex was first recognized by Knowlton et al. (1992) and Weil and Knowlton (1994), who proposed that the widely known generalist *M.* ''*annularis*'' was actually a complex of at least three species in shallow to mid depths of southern Central America: 1) *M. annularis* sensu stricto, which forms smooth columns; 2) *M. faveolata* (Ellis and Solander, 1786), which forms bumpy or keeled heads and sheets; and 3) *M. franksi* (Gregory, 1895), which forms bumpy mounds and plates. The original evidence for the complex was based on the discovery of covariation between colony morphology and a number of traits including allozymes, aggressive behavior, ecology, growth rate, life history, corallite morphometrics, and stable isotopes (Tomascik, 1990; Knowlton et al., 1992; Van Veghel and Bak, 1993). In addition to the *M.* ''*annularis*'' complex, a number of other widely-known reef coral ''species'' are also suspected to be complexes, including *M. cavernosa, Diploria labyrinthiformis, Colpophyllia natans, Porites astreoides, Siderastrea siderea,* and *Meandrina meandrites* among others (Knowlton and Budd, in press). The possible existence of complexes such as these complicates our ability to recognize and interpret speciation and extinction events.

The present study focuses on the period of time marked by late Pliocene to early Pleistocene faunal turnover, a regional episode of accelerated evolution that set the stage for the development of modern Caribbean reef ecosystems. The event involved a more than five million year period of high speciation in reef corals (see Johnson, 2001) followed by a less than one million year pulse of regional extinction (Budd and Johnson, 1999). During turnover, 80 percent of the more than 100 Mio-Pliocene reef coral species (32 percent of 38 genera) living in the Caribbean became extinct, and more than 60 percent of the species now living in the region originated (Budd et al., 1996; Budd and Johnson, 1997). Because of the unusual pattern of speciation preceding extinction, the region contained a mix of extinct and living species through the period of change. In fact, this mix is observed not only among but also within local assemblages, which vary in composition from 12 to 100 percent living species between 3.5–2.5 Ma and from 20 to 100 percent living species between 2.5–1.5 Ma (Budd and Johnson, 1999).

Preliminary data suggest that eight or more species of *Montastraea* with calice diameters and numbers of septal cycles similar to the modern *M. ''annularis''* complex (i.e., *''M. annularis*-like corals'') may have lived in the Caribbean during late Pliocene to early Pleistocene faunal turnover. Qualitative examination of colony shape and of calice diameter and spacing across colony surfaces suggests that the three species of the *M. ''annularis''* complex were among the species that originated during turnover. Moreover, cursory observations suggest that, throughout faunal turnover, the complex coexisted with an older morphologically similar ''complex'' containing *M. limbata* (Duncan, 1863), which is characterized by widely spaced calices, prominent primary septa, and paliform lobes (Vaughan, 1919; Budd, 1991; Budd et al., 1994a). This older ''complex'' dominated Caribbean reefs during the late Miocene to early Pliocene (Budd, 1991), and as many as three members of the ''complex'' may have become extinct during late Pliocene to early Pleistocene time (Budd et al., 1998). Other possible members of the *M. ''annularis''* complex have been recognized in late Pliocene of Costa Rica (e.g., a morphotype with corallites <2 mm in diameter and 22 septa per corallite; Budd et al., 1999) and the late Pleistocene of Barbados and Curaçao (e.g., a morphotype forming large organ-pipe-shaped colonies; Pandolfi, 1999; Pandolfi et al., in press).

The analyses in the present study use new morphologic characters that covary with molecular and reproductive data to begin to address the following evolutionary questions: 1) When did the modern species within the *M. ''annularis''* complex arise? 2) Were there additional species within the complex during the early stages of its evolution? 3) What was the pattern of speciation within the complex at the time when it arose? Was increased speciation restricted to a few clades? 4) Did species within the *M. ''annularis''* complex coexist with species in the *M. limbata* ''complex'', or did the latter become extinct before the *M. ''annularis''* complex arose?

As a first step in answering these questions, we examine colonies of *M. annularis*-like corals collected from two mixed carbonate and siliciclastic upper Pliocene to lower Pleistocene sequences on the Caribbean coast of southern Central America (Coates et al., 1992; Coates, 1999; McNeill et al., 2000): 1) the Quebrada Chocolate and Moín Formations (Limón Group) of Costa Rica; and 2) an unnamed formation in the Bocas del Toro Group of Panama. These two sequences range in age from 3.5–1 Ma, and are among the best-preserved reefal sequences in the Caribbean, which extend through the highest extinction peak at 2–1.5 Ma (Budd et al., 1999). They are the subject of intensive ongoing investigation by the Panama Paleontology Project (Jackson et al., 1996; Collins and Coates, 1999), because they provide a rich marine faunal history that spanned the closure of the Central American Isthmus and the cessation of marine circulation between the Pacific Ocean and the Caribbean Sea. Our present analyses focus on recognizing species and characterizing their morphology. We also consider the implications of these analyses for tree construction and character coding, which will be treated in more detail after additional characters have been analyzed in subsequent work. We recognize species using morphometrics and a statistical population approach. We use the results of morphometric analyses to aid in the recognition of morphologic ''characters,'' which can be used in interpreting evolutionary relationships among taxa and long-term patterns of morphologic change.

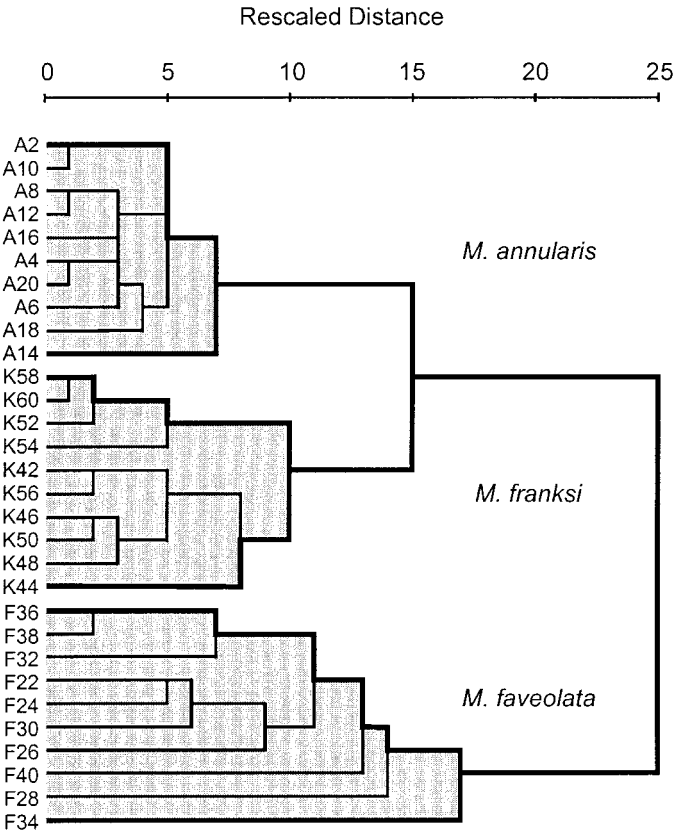
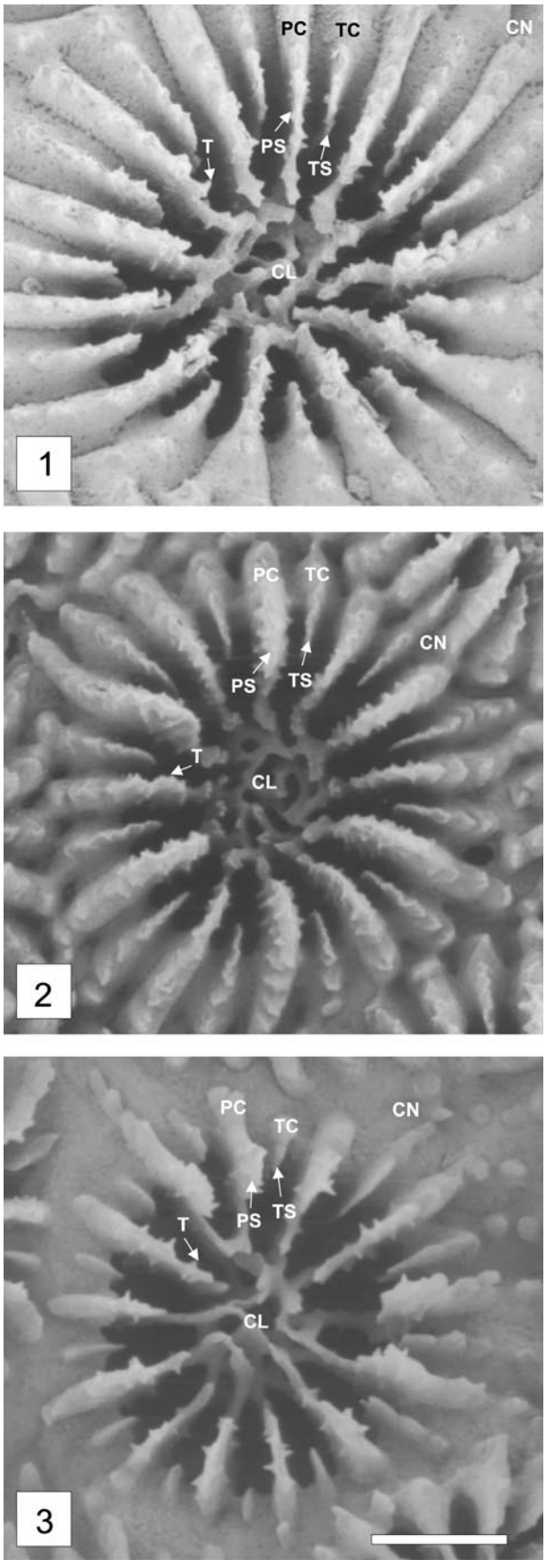


FIGURE *1*—Cluster analysis of 3-D landmark data on calices of living species of the *Montastraea ''annularis''* complex. Each branch of the dendrogram represents one colony. Colony numbers are indicated for each colony; corresponding museum catalog numbers are given in the Appendix I. A's indicate colonies of *M. annularis* s.s., K's indicate colonies of *M. franksi*; and F's indicate colonies of *M. faveolata.* The dendrogram clearly shows the three species in the complex to be distinct, with *M. annularis* s.s. and *M. franksi* being most similar. The most important variables in discriminating species consist of non-traditional morphologic characters related to the elevation and development of the costae, the shape of the septal margin, and the length of the tertiary septa.

MORPHOMETRIC RECOGNITION OF MODERN SPECIES WITHIN THE *MONTASTRAEA ''ANNULARIS''* COMPLEX

Previous work.—One of the main reasons why the *Montastraea ''annularis''* complex was not discovered earlier is because traditional morphologic characters do not provide enough resolution to make fine-scale distinctions among species. Like most members of the family Faviidae Gregory, 1900, the genus *Montastraea* Blainville, 1830, is characterized by regularly dentate septa, which are composed of a single fan system of simple trabeculae. Corallite walls are mostly septothecal (sometimes partially parathecal), and the columella is trabecular. Among faviids, the genus is distinguished by a plocoid colony form, extramural budding, and a costate coenosteum. Species of *Montastraea* have traditionally been distinguished on the basis of corallite diameter and number of septa cycles (Vaughan, 1919). Also important are the relative development of the different septal cycles, and the distance between corallites.

Although species within the *M. ''annularis''* complex can be visually distinguished in the field using colony morphology, initial analyses of traditional characters used in distinguishing species (i.e., number of septa per corallite, calice diameter, and calice spacing) revealed no single diagnostic difference among the three species within the complex (Knowlton et al., 1992; Weil and Knowlton, 1994). Univariate analyses of variance and canonical discriminant analysis of these characters did show statistically significant differences among the three species in both Panama (Weil and Knowlton, 1994) and Curaçao (Van Veghel and Bak, 1993).



However, the data distributions of these characters overlap considerably among species.

Because of these ambiguities, we have been searching for additional, more refined morphologic characters that can be used to distinguish species and interpret their evolutionary relationships. In this search, we are comparing genetic and morphologic data on living colonies collected in the San Blas Islands of Panama, including 10 *M. annularis* s.s., 10 *M. faveolata*, and 10 *M. franksi* (Appendix I). The skeletons are currently deposited at the University of Iowa Paleontology Repository (''SUI''). Analyses of allozymes sampled from these populations show that *M. faveolata* is distinguished by a nearly fixed difference at one locus as well as frequency differences at others (Knowlton et al., 1992; Van Veghel and Bak, 1993; Weil and Knowlton, 1994). Similarly, study of amplified fragment length polymorphisms (AFLP's) reveal two markers that distinguish *M. faveolata* from *M. annularis* s.s. and *M. franksi* (Lopez and Knowlton, 1997; Lopez et al., 1999). Although no fixed or nearly fixed differences have yet been detected between *M. annularis* s.s. and *M. franksi*, analyses of alloyzme data have revealed quantitative differences. Moreover, spawning times in *M. annularis* s.s. and *M. franksi* characteristically differ by 1–2 hours (Knowlton et al., 1997).

Three-dimensional morphometric analyses.—Our search focuses on delimiting skeletal characters with states that are manifestations of the two major components of accretionary growth (Graus and Macintyre, 1982): upward linear extension (often termed ''skeletal growth'') and skeletal thickening (often termed ''skeletal density''). Throughout the present study, we define ''characters'' as independent and discrete morphologic structures that can be identified using topographic criteria (i.e., similarity of position). First, we have explored calical relief by analyzing 3-D landmark data on calical surfaces using a Reflex microscope. We have begun by obtaining Cartesian coordinates (x-y-z) for 25 landmarks along three adjacent costosepta on six mature calices from the top and six mature calices from the edge of each of the 30 colonies. The landmarks consist of spatially homologous points designed to reflect the shape of the septal margin (the uppermost growing edge) and costal extensions between corallites. They include juxtaposition of skeletal structures, maxima of curvature, and extremal points. Size and shape coordinates (Bookstein, 1991) were determined using the computer program GRF-ND (Generalized rotational fitting of n-dimensional landmark data, 1994, written by Dennis E. Slice available at http://life.bio.sunysb.edu/morph/). Centroid size was calculated in three dimensions by summing the squared distances from each of the 25 landmarks to a common centroid. Shape coordinates were calculated using triangles formed by triplets of the 25 points. Two corners of each triangle were defined by a common pair of points, which served as a fixed baseline. The third corner was defined by each of the remaining 23 landmarks. To calculate shape coordinates, the 23 triangles were translated, rotated, and rescaled

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FIGURE 2—SEM photos of representative calices of the three living species within the *Montastraea* ''*annularis*'' complex. Calices of *M. franksi* (1) have less relief; the costae are thicker and better developed. In contrast, the septa of *M. faveolata* (3) are highly exsert, and slope steeply toward the columella; the costae are short and thin; septal teeth are long and distinct. Calices of *M. annularis* s.s. (2) have morphologies that are between the two extremes but are closer to *M. franksi*; costal development is highly regular, and primary septa are often prominent. CL, columella; CN, coenosteum; PC, primary costa; PS, primary septum; T, septal tooth; TC, tertiary costa; TS, tertiary septum. Scale bar = 1 mm. 1, *M. franksi* (SUI 95221); 2, *M. annularis* s.s. (SUI 95200); 3, *M. faveolata* (SUI 95229).

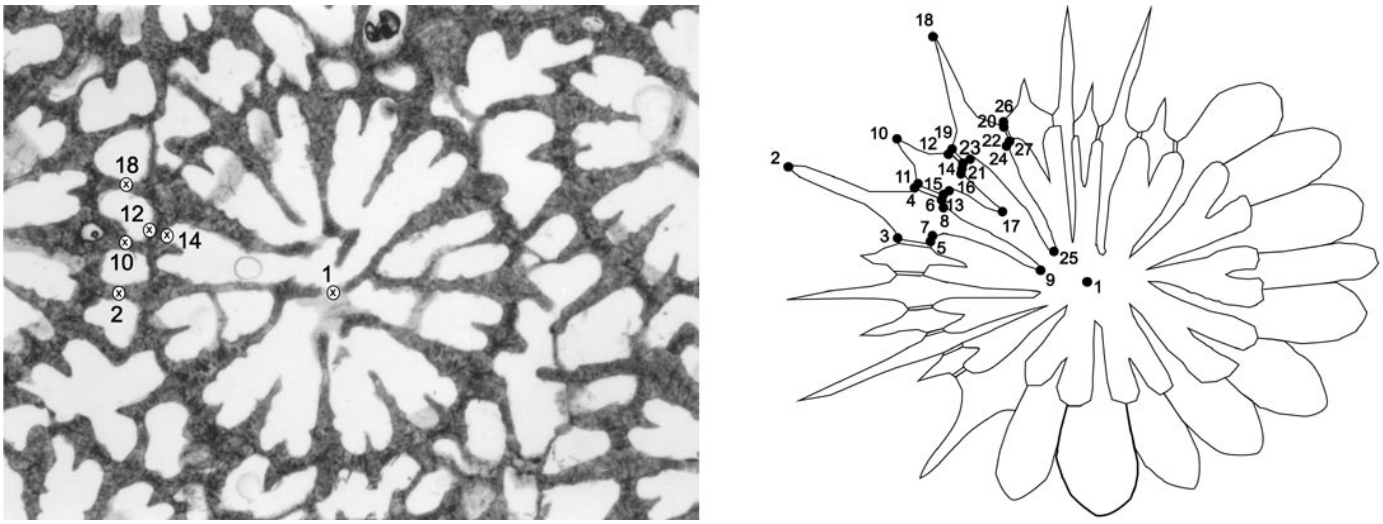

FIGURE 3—Two-dimensional Cartesian coordinates collected for 27 landmarks on transverse thin-sections of corallites. Only extremal landmarks are indicated in the thin-section on the left. Point numbers 1 and 14 and point numbers 1 and 12 were used as baselines. These landmarks were selected to characterize the development and structure of the corallite wall and costosepta.

relative to the baseline. The resulting coordinates of the third point, termed ''shape coordinates,'' serve as variables in subsequent statistical analyses (see Budd et al., 1994b, and Budd and Johnson, 1996, for details). By registering two points on a common baseline, shape coordinates contain all the information about a given triangle's shape, independent of its size, so that the size and shape coordinates of a triangle are not correlated.

Size and shape coordinates were used to calculate Mahalanobis distances among colonies, which were input into an average linkage cluster analysis (unweighted pair-groups method using arithmetric averages, UPGMA). As in Budd et al. (1994b) and Budd and Johnson (1996), we used Mahalanobis distances instead of the more commonly used squared Euclidean distances, because we wanted to maximize between-group relative to within-group variation (Klecka, 1980). We thereby emphasize genetically based differences among colonies over non-genetic, phenotypic variation within colonies.

Although the data set focuses on non-traditional corallite features related to costal and septal relief, the resulting cluster dendrogram (Fig. 1) clearly shows the three species in the complex to be distinct, with *M. annularis* s.s. and *M. franksi* being most similar. The pattern of similarity among species matches that found using the genetic data described above. Canonical discriminant analysis indicates that the most important variables distinguishing species consist of coordinates related to the elevation and length of the costae, the shape of the septal margin, and the length of the tertiary septa (see also Budd and Johnson, 1996; Knowlton and Budd, in press). As shown in Figure 2, calical relief is high in *M. faveolata,* and the septa and costae are thin and exsert. In contrast, calices of *M. franksi* have low relief; the costae are thicker and better developed, and the tertiary septa are longer. Calices of *M. annularis* s.s. are intermediate in relief and have regular, moderately thick septa and costae.

Two-dimensional morphometric analyses.—Unfortunately, calical surfaces are often worn in fossil material, and samples providing 3-D data on calical surfaces are not available in large enough quantity to distinguish species using a statistical population approach. We have therefore explored 2-D morphological features that reflect the 3-D features described above. Our initial emphasis has been on thickening of skeletal structures observed in transverse thin-sections, especially the corallite wall and associated costosepta. We have begun by digitizing 27 landmarks on mature corallites as shown in Figure 3, and described in Table 1. Data were collected on six corallites from the tops and on six from edges of the same 30 colonies of the *M.* ''*annularis*'' complex as analyzed above. Size and shape coordinates were calculated for the two dimensional data using two baselines (points 1 to 14; points 1 to 12) and the previously mentioned computer program GRF-ND.

To facilitate interpretation, twelve shape coordinates associated with the structure and development of the corallite wall and costosepta (Table 2) were selected for analysis. Top priority was given to coordinates that define a single morphologic structure and do not combine several different structures into one variable. As in the 3-D analyses, the selected shape coordinates and centroid size were used to calculate Mahalanobis distances among colonies, and the distance matrix was analyzed using average linkage cluster analysis.

Although the similarities among species do not conform to the pattern found using genetic data (i.e., in this case, *M. annularis* s.s. and *M. faveolata* are more similar), three distinct clusters were detected (Fig. 4), which each correspond with a modern species. *M. franksi* is highly variable, and forms a loosely structured group. Canonical discriminant analysis indicates that the most important variables discriminating species consist of coordinates related to the thickness of the corallite wall (x14, x21) and the length of the costae beyond the corallite wall (-x10, -x18, csize). As illustrated in Figure 5, corallite walls are thick in *M. franksi,* intermediate in *M. annularis* s.s., and thin in *M. faveolata.* The costae have longer, more prominent extensions beyond the wall in *M. annularis* s.s. than in *M. franksi* or *M. faveolata.*

In sum, comparisons with genetic data show that the new morphologic measures related to the thickness and relief of the costosepta and the structure of the corallite wall are significantly more effective at distinguishing species within the *M.* ''*annularis*'' complex than are traditional characters. However, the new measures are not without problems, the most important being: 1) overlapping variation among species, and 2) differing patterns and amounts of variation within species. Distinct clusters can be recognized on dendrograms, but consistent cutoff levels cannot be

TABLE 1—Landmarks on transverse thin-sections of corallites of *Montastraea.* Types are: 1 = juxtaposition of structures; 2 = maxima of curvature; 3 = extremal points.

Number	Type	Description
1	3	Center of corallite
2	3	Outermost point on secondary costa
3	1	Outer left junction of secondary costoseptum with wall dissepiment
4	1	Outer right junction of secondary costoseptum with wall dissepiment
5	1	Inner left junction of secondary costoseptum with wall dissepiment
6	1	Inner right junction of secondary costoseptum with wall dissepiment
7	2	Left point of maximum curvature associated with secondary septal thinning
8	2	Right point of maximum curvature associated with secondary septal thinning
9	3	Innermost point on secondary septum
10	3	Outermost point on tertiary costa
11	1	Outer left junction of tertiary costoseptum with wall dissepiment
12	1	Outer right junction of tertiary costoseptum with wall dissepiment
13	1	Inner left junction of tertiary costoseptum with wall dissepiment
14	1	Inner right junction of tertiary costoseptum with wall dissepiment
15	2	Left point of maximum curvature associated with tertiary septal thinning
16	2	Right point of maximum curvature associated with tertiary septal thinning
17	3	Innermost point on tertiary septum
18	3	Outermost point on primary costa
19	1	Outer left junction of primary costoseptum with wall dissepiment
20	1	Outer right junction of primary costoseptum with wall dissepiment
21	1	Inner left junction of primary costoseptum with wall dissepiment
22	1	Inner right junction of primary costoseptum with wall dissepiment
23	2	Left point of maximum curvature associated with primary septal thinning
24	2	Right point of maximum curvature associated with primary septal thinning
25	3	Innermost point on primary septum
26	1	Outer left junction of tertiary costoseptum with wall dissepiment
27	1	Inner left junction of tertiary costoseptum with wall dissepiment

routinely applied in species recognition. Although errors in cluster assignment are less than 10 percent, they do occur. Moreover, when relief of the costosepta is not included in the analysis, as in 2-D analyses, relationships inferred among species do not match genetic results. Furthermore, the new measures are morphometric in nature, and many appear inadequate for use as homologous characters in phylogenetic analyses, because they sometimes confound two or more separate morphologic structures in one measure. Additional studies of growth are required to recognize discrete structures that are produced by different growth processes.

RECOGNITION OF SPECIES WITHIN UPPER PLIOCENE TO LOWER PLEISTOCENE SEQUENCES IN COSTA RICA AND PANAMA

Material and data.—Because of their unusual effectiveness in distinguishing modern species within the *Montastraea* ''*annularis*'' complex, we applied the 2-D morphometric approach to distinguish morphologically similar species in collections of *M. annularis*-like corals made in the Limón Group of Costa Rica and the Bocas del Toro Group of Panama. The collection localities include 21 sites in Costa Rica (seven in the Quebrada Chocolate Formation, 14 in the Moín Formation) and 11 sites in Panama (three on Isla Colón, six on Isla Bastimentos, and one on Swan Cay); they are listed in Table 3 and described in detail in Coates et al. (1992), Coates (1999), Budd et al. (1999), and McNeill et al. (2000). High-resolution age-dates for the localities have been

TABLE 2—Shape coordinates used in cluster and discriminant analyses of 2-dimensional landmark data collected on corallites in transverse thin-section.

Shape coordinates	Baseline	Definition
x2	1–12	extension of secondary costa
x9	1–14	length of secondary septum
x10	1–12	extension of tertiary costa
x14	1–12	wall thickness
x16	1–14	width of tertiary septum
x17	1–14	length of tertiary septum
x18	1–12	extension of primary costa
x21	1–12	wall thickness
y11	1–12	outer width of tertiary wall costoseptum
y19	1–12	outer width of wall dissepiment
y21	1–14	inner width of wall dissepiment
y22–y21	1–12	inner width of primary wall costoseptum

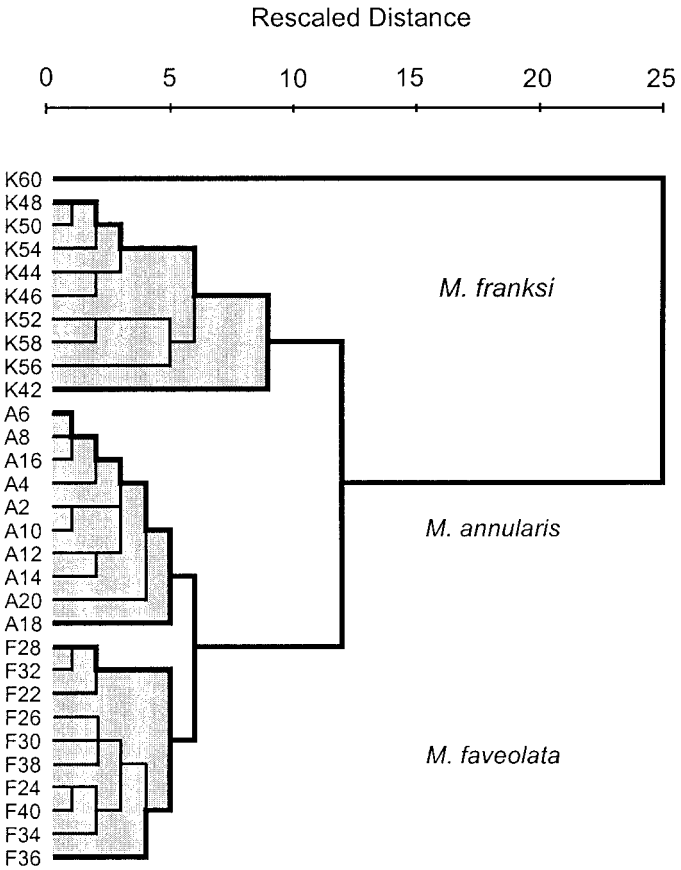

FIGURE 4—Cluster analysis of 2-D landmark data on corallites of living species of the *Montastraea* ''*annularis*'' complex. Each branch of the dendrogram represents one colony. Colony numbers are indicated for each colony; corresponding museum catalog numbers are given in Appendix I. A's indicate colonies of *M. annularis* s.s., K's indicate colonies of *M. franksi*; and F's indicate colonies of *M. faveolata.* The dendrogram also shows the three species in the complex to be distinct, with *M. annularis* s.s. and *M. faveolata* being most similar. The most important variables in discriminating species consist of non-traditional morphologic characters related to the thickness of the corallite wall and the length of the costae beyond the wall.

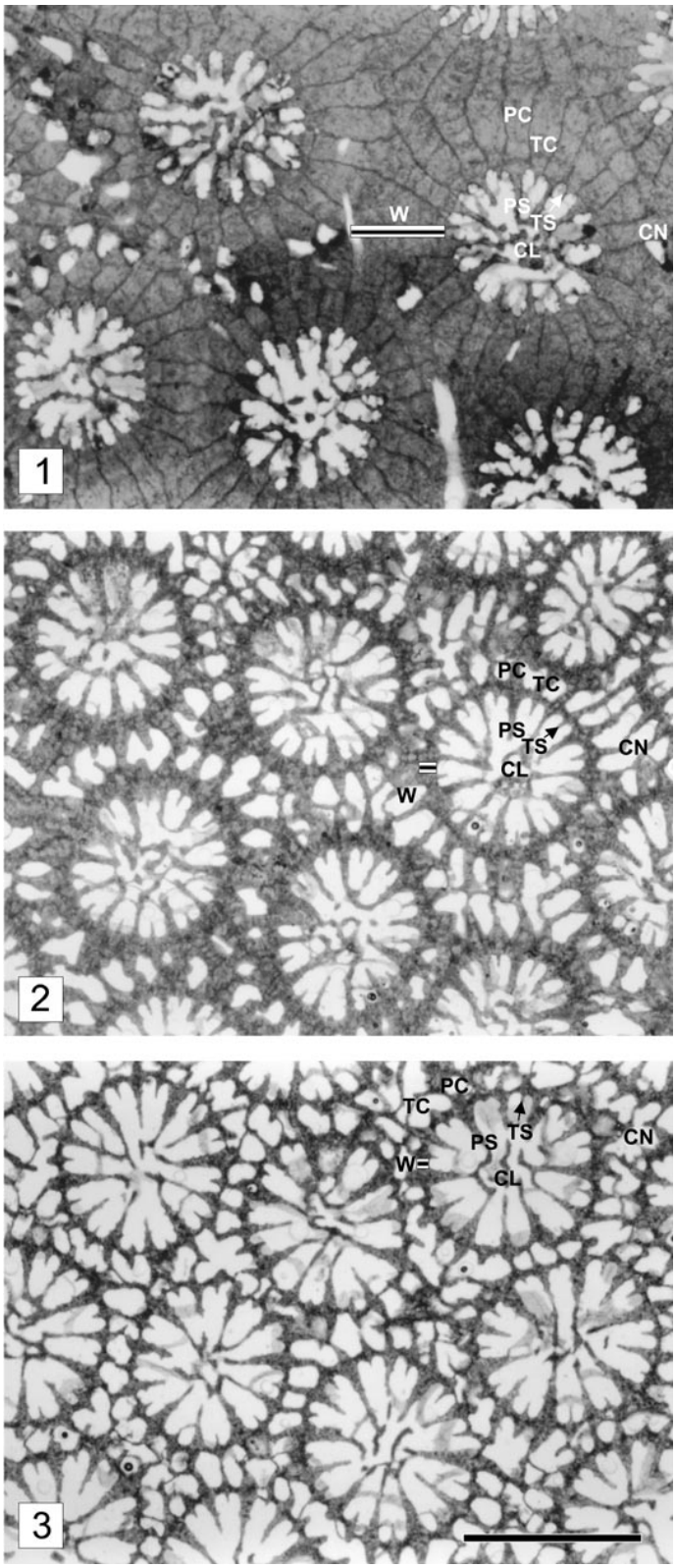

FIGURE 5—Transverse thin-sections of representative corallites of the three living species within the *Montastraea* ''*annularis*'' complex. Although corallites in the three species are similar in diameter and numbers of septa, distinct differences appear in wall structure. Corallites of *M. franksi* (1) have thick septothecal walls, formed by coalesced costosepta. Corallites of *M. annularis* s.s. (2) have thinner septothecal walls, but longer and better developed extensions of costae beyond the wall. Corallites of *M. faveolata* (3) have very thin walls that are partially parathecal and formed by dissepiments; extensions of costae beyond the wall are reduced. CL, columella; CN, coenosteum; PC, primary costa; PS, primary septum; TC, tertiary costa; TS, tertiary septum; W, wall. Scale bar = 3 mm. 1, *M. franksi* (SUI 95228); 2, *M. annularis* s.s. (SUI 95206); 3, *M. faveolata* (SUI 95214).

determined by integrating biostratigraphic (microfossil), magnetostratigraphic, and strontium isotopic techniques (McNeill et al., 2000).

A total of 94 well-preserved specimens from the two sequences (Table 3, Appendix I) were selected for analysis. These specimens are included in the Cenozoic Coral Database (''CCD''; available at http://nmita.geology.uiowa.edu), and are deposited at the University of Iowa Paleontology Repository (''SUI''). The same 27 landmarks as in 2D analyses of the modern *M.* ''*annularis*'' complex (Fig. 3, Table 1) were digitized on 2–6 mature corallites within each specimen. As above, size and shape coordinates were calculated for two baselines (points 1 to 14, points 1 to 12) using GRF-ND, and centroid size and the 12 shape coordinates in Table 2 were input as variables in subsequent multivariate statistical analyses.

Recognizing morphotypes within stratigraphic subsets.—Because the differences between modern species within the *M.* ''*annularis*'' complex are more readily interpretable as barriers to gene flow in sympatry (Knowlton and Budd, in press), we began our analyses by breaking the data set up into four stratigraphic subsets (Table 3, Appendix I): 1) ''c1-2,'' the Moín Formation, 2.9–1.5 Ma, 47 specimens, 2) ''c3-4,'' the Quebrada Chocolate Formation, 3.5–2.9 Ma, 17 specimens, 3) ''p1-2,'' Isla Bastimentos and Swan Cay, 2.2–0.8 Ma, 27 specimens, and 4) ''p3,'' Isla Colón, 3.5–1.7 Ma, three specimens. As in Budd and Coates (1992), Mahalanobis distances were calculated separately among specimens within each stratigraphic subset, and the resulting distance matrices were analyzed using average linkage cluster analysis (Fig. 6).

1) Within subset ''c1-2,'' two distinct clusters were detected: Morphotype #1 and Morphotype #2 (Fig. 6). Canonical discriminant analysis indicates that the three initially unclassified specimens group most closely with Morphotype #1. This analysis also reveals that the most important variables distinguishing the two morphotypes consist of coordinates related to the thickness of the corallite wall (-csize, x14, x21). Morphotype #1 (Fig. 7.1, 7.2) has considerably thicker corallite walls than Morphotype #2 (Fig. 7.3, 7.4). Furthermore, the walls of Morphotype #1 are primarily septothecal and formed by coalesced costosepta, whereas the walls of Morphotype #2 are partially parathecal and formed by dissepimental tissue.

2) Within subset ''c3-4,'' three distinct clusters were detected: Morphotype #3, Morphotype #4, and Morphotype #5 (Fig. 6). Canonical discriminant analysis indicates that the most important variables distinguishing morphotypes consist of coordinates related to corallite size (csize) and length of costae beyond the wall (x18, x2, x10). Corallites of Morphotype #4 (Fig. 7.6) are small, corallites of Morphotype #3 (Fig. 7.5) are intermediate, and corallites of Morphotype #5 (Fig. 7.7) are large. Given that shape coordinates are, by definition, independent of size (Bookstein, 1991), costal extensions are relatively longer in Morphotypes #3 and #4 than they are in Morphotype #5.

(3) Within subset ''p1-2,'' four distinct clusters were detected: Morphotype #6, Morphotype #7, Morphotype #8, and Morphotype #9 (Fig. 6). Canonical discriminant analysis indicates that the most important variables distinguishing morphotypes consist of coordinates related to development of tertiary septa (-x17) and

TABLE 3—List of Costa Rica and Panama localities arranged in stratigraphic order from oldest to youngest (see Budd et al., 1999 for details).

Locality #	# Specimens	Country	Formation	Site name	Locality group	Ma start	Ma end	Age Grp
AB93-68	1	Costa Rica	Q. Chocolate	Q. Chocolate—road	QC4	3.5	3.2	c4
AB95-09	2	Costa Rica	Q. Chocolate	Rt. 32—Q. Chocolate	QC5	3.5	3.2	c4
AB93-06	7	Costa Rica	Q. Chocolate	Rt. 32—CTA Fence	BA2	3.1	2.9	c3
KJ-32-1	2	Costa Rica	Q. Chocolate	Rt. 32	BA6	3.1	2.9	c3
AB93-32	3	Costa Rica	Q. Chocolate	Moín Flat Field—sw	BA7	3.1	2.9	c3
AB93-31	1	Costa Rica	Q. Chocolate	Old Moín Rd—no	BA8	3.1	2.9	c3
AB95-03	1	Costa Rica	Q. Chocolate	Santa Rosa Rd	BA9	3.1	2.9	c3
AB95-16	1	Costa Rica	Moín	Rt. 32—Q. Chocolate	E2	2.9	1.9	c2
AB93-41	3	Costa Rica	Moín	Rt. 32—Stadium	SR3	2.9	1.9	c2
AB93-62	2	Costa Rica	Moín	Santa Rosa Rd	SR3	2.9	1.9	c2
AB93-57	1	Costa Rica	Moín	Rt. 32—Sta Marta Sda	SR4	2.9	1.9	c2
AB93-71	7	Costa Rica	Moín	Lomas del Mar	LE10	1.9	1.5	c1
CJ89-17	4	Costa Rica	Moín	Lomas del Mar	LE2	1.9	1.5	c1
KJ-LM(2)	11	Costa Rica	Moín	Lomas del Mar	LE5	1.9	1.5	c1
KJ-LM(1)	5	Costa Rica	Moín	Lomas del Mar	LE7	1.9	1.5	c1
CJ92-6(1)	4	Costa Rica	Moín	Lomas del Mar	LE8	1.9	1.5	c1
AB95-08	4	Costa Rica	Moín	Av. Barracuda	LW1	1.9	1.5	c1
AB93-23	3	Costa Rica	Moín	Apt. complex	P1	1.9	1.5	c1
KJ-P2	2	Costa Rica	Moín	Portete Reef #2	P2	1.9	1.5	c1
AB93-80	1	Panama	unnamed (Colón)	Hill Pt.—w	HP	3.5	1.7	p3
AB93-74	1	Panama	unnamed (Colón)	Paunch	PA	3.5	1.7	p3
AB93-75	1	Panama	unnamed (Colón)	Paunch	PA	3.5	1.7	p3
AB98-11	4	Panama	unnamed (Bastimentos)	Fish Hole—w	FH	2.2	1.8	p2
AB98-16	1	Panama	unnamed (Bastimentos)	Fish Hole—w	FH	2.2	1.8	p2
AB98-17	6	Panama	unnamed (Bastimentos)	Fish Hole—e	FH	2.2	1.8	p2
AB98-18	8	Panama	unnamed (Bastimentos)	Fish Hole—e	FH	2.2	1.8	p2
AB99-05	1	Panama	unnamed (Bastimentos)	Fish Hole—e	FH	2.2	1.8	p2
AB99-07	4	Panama	unnamed (Bastimentos)	Fish Hole—e	FH	2.2	1.8	p2
AB93-76	1	Panama	Swan Cay	Sway Cay	none	1.8	0.8	p1
AB99-12	2	Panama	Swan Cay	Sway Cay	none	1.8	0.8	p1

Total # specimens,	c1/c2	47
Total # specimens,	c3/c4	17
Total # specimens,	p1/p2	27
Total # specimens,	p3	3
GRAND TOTAL		94

corallite wall thickness (csize, -x14, -x21). Tertiary septa are relatively long in Morphotype #9 (Fig. 7.11), intermediate in Morphotype #7 (Fig. 7.9) and #8 (Fig. 7.10), and short in Morphotype #6 (Fig. 7.8). Corallite walls are relatively thick in Morphotype #7, intermediate in Morphotypes #6 and #9, and thin in Morphotype #8.

(4) Within subset ''p3,'' few statistically significant differences could be detected among specimens, suggesting that only one morphotype, Morphotype #10 (Fig. 7.12), is represented.

In summary, morphometric analyses of colonies within stratigraphic subsets indicate that 1–4 species may have co-occurred within any one stratigraphic horizon. These species are distinguished by five key characters: 1) wall thickness (x14, x21), 2) wall structure (y19, y21), 3) extensions of the costae beyond the wall (x2, x18, x10), 4) development of the tertiary septa (x17), and 5) corallite size.

Comparisons among stratigraphic subsets.—We then applied a similar morphometric approach to determine whether morphotypes from different stratigraphic horizons belonged to the same species. First, we performed a canonical discriminant analysis comparing the 10 Costa Rica and Panama morphotypes recognized in the four stratigraphic subsets. The data set consisted of the same 13 variables as used in the original cluster analyses. The results (Fig. 8) show that at least eight of the 10 morphotypes have statistically significant differences. Only Mahalanobis distances between Morphotypes #1 and #5 and between Morphotypes #3 and #10 were not statistically significant, due in part to their small sample sizes. Nevertheless, Mann-Whitney U-tests (Appendix II) suggest that statistically significant differences do exist between Morphotypes #1 and #5 in length of secondary septa (x9) and wall thickness (x14, x21), and between Morphotypes #3 and #10 in extension of costae (x2) and tertiary septum development (x16, x17). Morphotypes #2 and #9 also show overlap on plots of scores (Fig. 8), but Mann-Whitney U-tests (Appendix II) indicate that statistically significant differences exist between the two morphotypes in wall thickness (x14, x21), extension of costae (x18), width of tertiary costosepta (y11), and wall structure (y19, y21). Moreover, Mann-Whitney U-tests (Appendix II) indicate that there are also statistically significant differences in corallite diameter (estimated using the length of the baseline from landmarks 1 to 14). In the canonical discriminant analysis comparing the 10 Costa Rica and Panama morphotypes, centroid size is most strongly correlated with discriminant function 1, which accounts for 56.2 percent of the variance; wall thickness (x21, x14) is most strongly correlated with function 2, which accounts for 26.2 percent of the variance; and the extensions of costae beyond the wall (-x10, -x18, -x2) are most strongly correlated with function 3, which accounts for 5.7 percent of the variance.

We further used canonical discriminant analysis to compare: 1) morphotypes in the two younger stratigraphic subsets, with colonies of living species of the *M.* ''*annularis*'' complex; and 2) morphotypes in the two older stratigraphic subsets, with colonies that previously identified as *M. limbata* (see Budd, 1991). The colonies of ''*M. limbata*'' were collected at lower Pliocene localities (NMB localities 16818, 16823, and 16884 along Río Cana) in the Cibao Valley of the Dominican Republic (Saunders et al., 1986). In each case, the data set consisted of the same 13 variables as in previous cluster analyses of 2-D landmark data. Colonies of the living species of the *M.* ''*annularis*'' complex consist of the

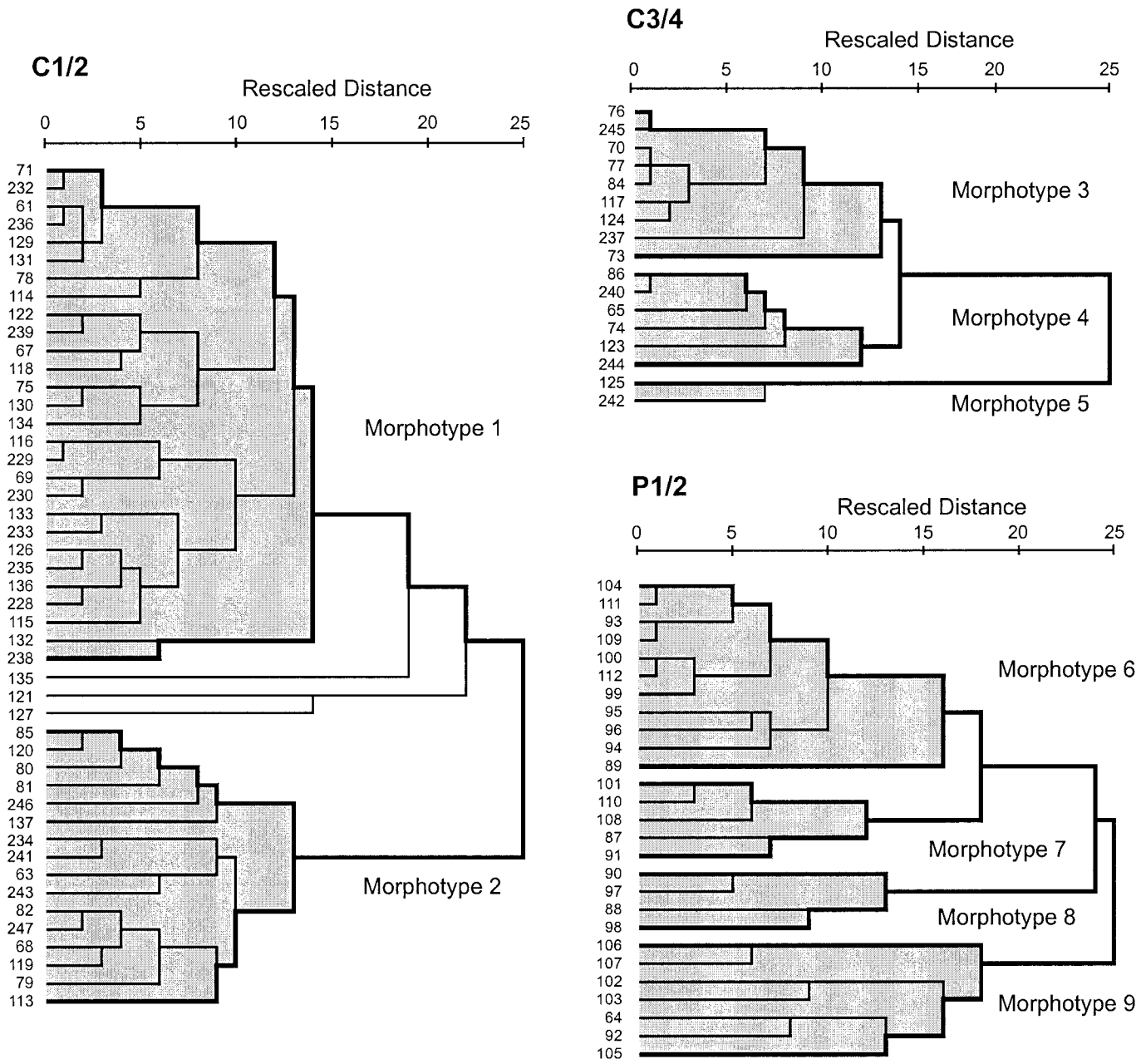

FIGURE 6—Cluster analysis of three stratigraphic subsets (c1-2, c3-4, p1-2) of *M. annularis*-like colonies from Costa Rica and Panama using 2-D landmark data. Each branch within each dendrogram represents one colony. Colony numbers are indicated for each colony; corresponding CCD numbers are given in Appendix I. A total of nine morphotypes were recognized in the three dendrograms. A tenth morphotype was recognized in stratigraphic subset p3. The most important variables in distinguishing morphotypes consist of the thickness and structure of the corallite wall (c1-2, p1-2), length of the costae beyond the wall (c3-4), corallite size (c3-4), and development of the tertiary septa (p1-2),

same as those analyzed above (Figs. 1, 4; Appendix I). The lower Pliocene Dominican Republic (''DR'') samples consist of two colonies collected at the Cañada de Zamba reef (NMB localities 16818, 16823; 5.6–4.5 Ma) and five collected in the Río Cana gorge through the Mao Adentro Limestone (NMB 16884, 4–3.7 Ma). These specimens are included in the Cenozoic Coral Database (''CCD''; available at http://nmita.geology.uiowa.edu), and are deposited at the Natural History Museum in Basel, Switzerland (''NMB''). Preliminary morphometric analyses, similar to those above for the Costa Rica and Panama stratigraphic subsets, indicate that the colonies from the Cañada de Zamba reef represent one species (''DR species #1''), and those from the Río Cana gorge represent two additional species (''DR species #2 and 3''). Of these three species, DR species #2 most closely resembles the holotype of *M. limbata* (Duncan, 1863), figured in Budd (1991) on plate 18, figure 1.

The results comparing the six younger morphotypes (#1, 2, 6–9) and the three modern species (Fig. 8) show that the nine groups have statistically significant differences. However, Morphotypes #1, 6, and 7 overlap with *M. franksi*, and Morphotype #8 overlaps

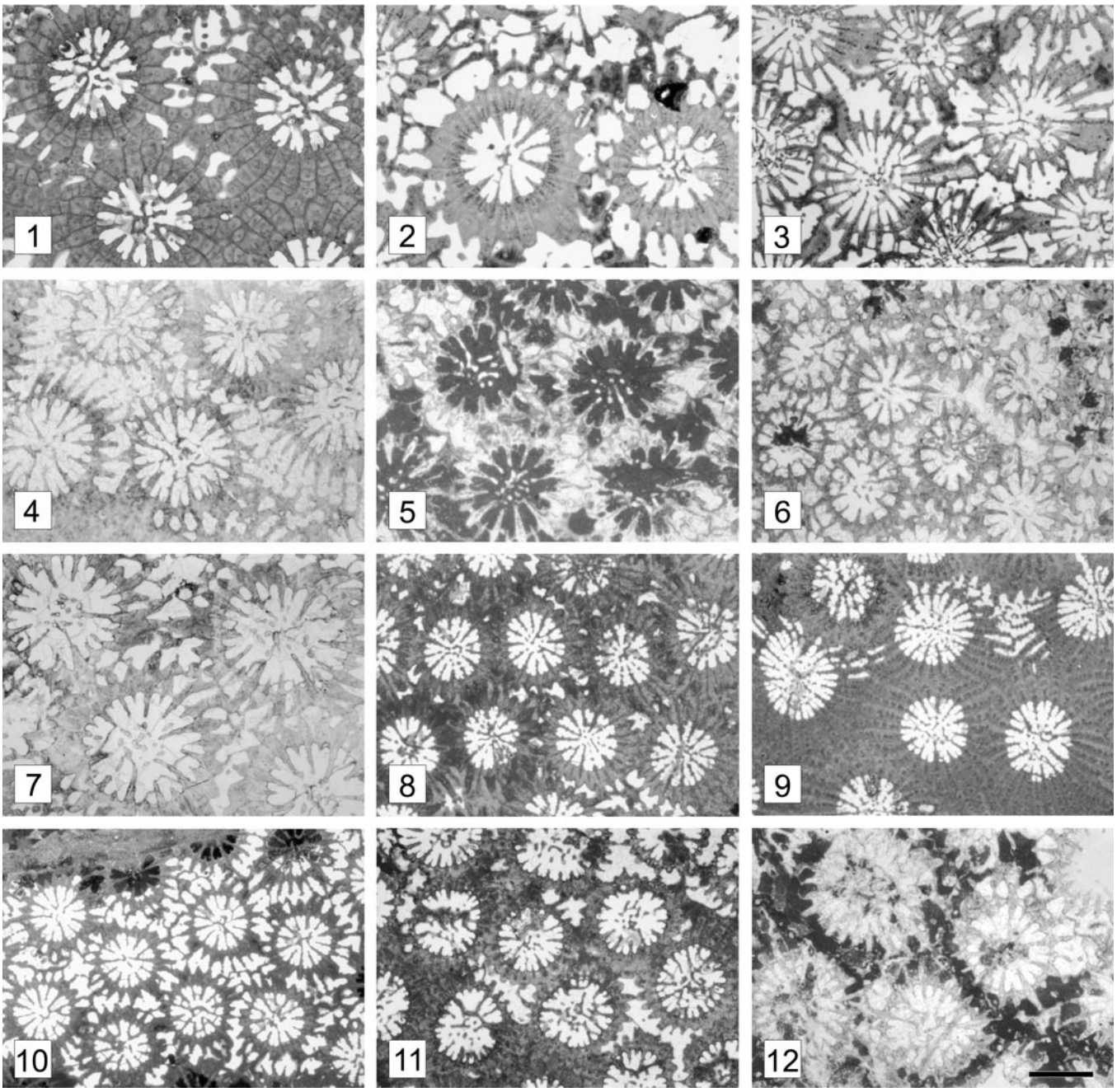

FIGURE 7—Transverse thin sections of representative corallites of 10 fossil morphotypes of *M. annularis*-like colonies from Costa Rica and Panama. Key characters distinguishing morphotypes include wall thickness, wall structure, extensions of the costae beyond the wall, development of the tertiary septa, and corallite size. Scale bar = 2 mm. 1, 2, Morphotype #1 (SUI 95121, 95126); 3, 4, Morphotype #2 (SUI 95137, 95141); 5, Morphotype #3 (SUI 95154); 6, Morphotype #4 (SUI 95166); 7, Morphotype #5 (SUI 95167). 8, Morphotype #6 (SUI 95179); 9, Morphotype #7 (SUI 95181); 10, Morphotype #8 (SUI 95188); 11, Morphotype #9 (SUI 95191); 12, Morphotype #10 (SUI 95198).

with *M. annularis* s.s. Nevertheless, Mann-Whitney U-tests (Appendix II) indicate that significant differences exist between these morphotypes and modern species in wall thickness (x14, x21), tertiary septum development (x16, x17), wall structure (y19, y21), and three additional costoseptal shape coordinates (x9, x10, y11). Wall thickness (x21, x14) and wall structure (y19) are most strongly correlated with discriminant function 1, which accounts for 54.6 percent of the variance; centroid size is most strongly correlated with function 2, which accounts for 25.2 percent of the variance; and costoseptum width (y22–y21) is most strongly correlated with function 3, which accounts for 10.4 percent of the variance.

The results comparing the older morphotypes (#3–5, 10) and the three DR species (Fig. 8) show that the seven groups have statistically significant differences. However, Morphotype #4 overlaps with DR species #3. Mann-Whitney U-tests (Appendix II) show no statistically significant differences between Morphotype #4 and DR species #3 in the 12 shape coordinates (Table 2),

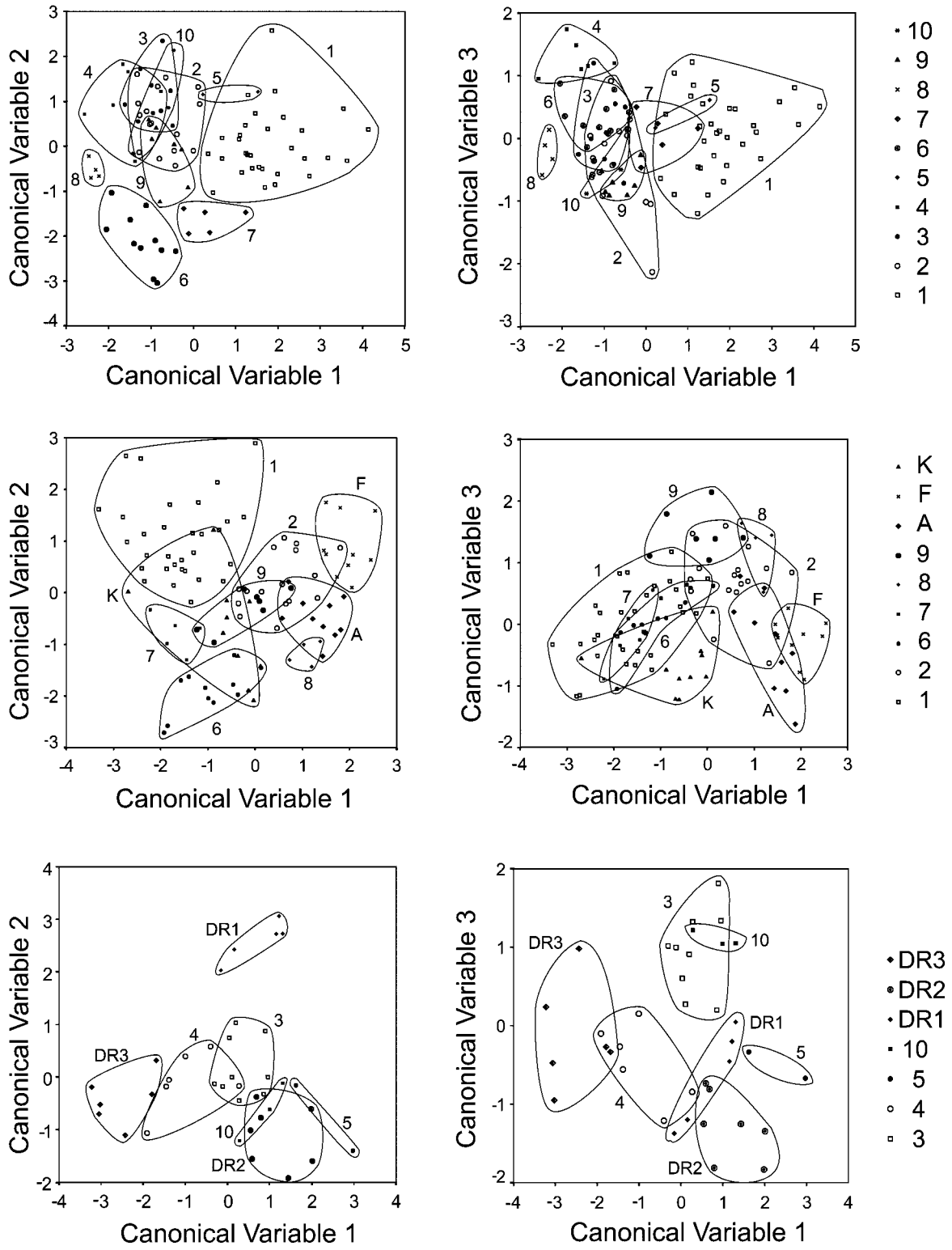

FIGURE *8*—Plots of scores in canonical discriminant analyses comparing: top, the 10 Costa Rica and Panama morphotypes; middle, the younger Costa Rica and Panama (c1-2, p1-2) morphotypes with the three modern species; bottom, the older Costa Rica and Panama (c3-4, p3) morphotypes with three lower Pliocene species from the Dominican Republic. Each point on the plots represents one colony; polygons enclose previously recognized morphotypes or species. Numbers without letters refer to the Costa Rica and Panama morphotypes, numbers with a DR prefix refer to the three DR species; A = *M. annularis* s.s., K = *M. franksi*; F = *M. faveolata.* In the first analysis (top), Morphotypes #1 and #5 and Morphotypes #3 and #10 did not significantly differ. All morphotypes and species in the second (middle) and third (bottom) analyses revealed statistically significant differences.

TABLE 4—Characters used in the cladistic analysis.

#	Character	Related morphometric variables	Abbreviation	Character states
1	corallite diameter	csize	cd	1 = small (<2.2 mm), 2 = medium (2.2–2.6 mm), 3 = large (2.6–3.2 mm), 4 = 3.2–4 mm, 5 = >4 mm
2	number of septa per corallite	none	ns	1 = ~24 (3 complete cycles), 2 = 24–30 (incomplete 4th cycle), 3 = >30 (4 complete cycles)
3	corallite wall thickness	x14, x21	wt	1 = very thin, 2 = thin, 3 = intermediate, 4 = thick, 5 = very thick
4	corallite wall structure	y19, y21	ws	1 = mostly parathecal, 2 = moderately septothecal, 3 = mostly septothecal, 4 = septothecal
5	extension of costae beyond the wall	x2, x10, x18	cl	1 = short, 2 = medium, 3 = long, 4 = very long
6	shape of tertiary costoseptae	none	tct	1 = straight, 2 = expanding
7	paliform lobes	none	pl	1 = weak, 2 = well-developed
8	tertiary septum length	x16, x17	tsl	1 = short, 2 = medium, 3 = long, 4 = very long

but significant differences do exist between Morphotype #4 and DR species #3 in the traditional measure of corallite diameter (estimated using the length of the baseline from landmarks 1 to 14). Centroid size is most strongly correlated with discriminant function 1, which accounts for 41.9 percent of the variance; development of the tertiary septa (y11, x17) is most strongly correlated with function 2, which accounts for 25.3 percent of the variance; and the extension of costae beyond the wall (x10, x18) is most strongly correlated with function 3, which accounts for 17.8 percent of the variance.

In sum, morphometric comparisons between morphotypes in stratigraphic subsets and the modern and early Pliocene DR species reveal surprisingly few taxonomic equivalencies. A total of 8–10 species of *M. annularis*-like corals may indeed have existed in Costa Rica and Panama during late Pliocene to early Pleistocene faunal turnover. Another striking result is that the same five key ''characters'' distinguish species in each analysis: wall thickness and structure, extensions of the costae beyond the wall, development of the tertiary septa, and corallite size. As discussed above, these characters are correlated with different discriminant functions within each analysis, indicating that they may have been formed by independent growth processes.

INTERPRETING EVOLUTIONARY RELATIONSHIPS AND PATTERNS OF CHARACTER CHANGE

To determine if phylogenetic characters derived from these morphometric data are effective in interpreting evolutionary relationships among species, we performed a preliminary cladistic analysis using global parsimony. The taxa in the analysis include the 10 Costa Rica and Panama morphotypes, the three modern species, and the three early Pliocene DR species. Morphometric measures, such as Bookstein size and shape coordinates, may confound several different morphologic structures in one measure and not be homologous; therefore, they cannot serve directly as phylogenetic characters without careful consideration of their structural integrity and the processes by which they form (Wagner, 1994; Zelditch et al., 1995). For example, in the present study, centroid size combines the size of the corallite, wall, and costal extensions into a single measure. Therefore, for this preliminary cladistic analysis, we also used cursory observations of skeletal microstructure (e.g., Roniewicz and Stolarski, 1999) to select phylogenetic characters, so that the characters best reflect distinct structures formed by different growth processes. A total of eight characters (Table 4) were thereby selected. Four of the eight characters (#3, 4, 5, 8) consist of structures interpreted using the results of the above morphometric analyses. To avoid the confounding effects of centroid size, we estimated a fifth character, corallite diameter, using the length of the baseline from landmarks 1 to 14, and included it as the independent corallite size character. In addition to morphometrically-based characters, we also include three traditional corallite features that were used by Vaughan (1919) to distinguish species of *M. annularis*-like corals: number of septa per corallite, the presence of paliform lobes, and the shape of the tertiary costosepta.

Codes for the five quantitative characters (#1, 3, 4, 5, 8) were determined by examining frequency distributions summarized in the boxplots in Figure 9. These boxplots reveal the continuous and overlapping nature of the variation, that is characteristic of closely related scleractinian corals (Vaughan, 1907; Wallace and Willis, 1994; Veron, 1995; Knowlton and Budd, in press). In all five cases (characters #1, 3, 4, 5, 8), gaps in distributions do not occur between taxa. Codes were, therefore, determined using the results of Duncan's range tests (a multiple comparisons test performed as a ''One-way ANOVA Post Hoc test'' in SPSS for Windows, Release 8.0) as a guide. In cases where the taxa under comparison exhibited unequal variances, the results of Duncan's tests were confirmed using Dunnett's T3 multiple comparisons tests. Taxa whose differences were not statistically significant using these tests were given the same code; code numbers were assigned based on their rank order (Fig. 9). All five quantitative characters (#1, 3, 4, 5, 8) were treated as ordered in subsequent cladistic analyses. Although this method of coding does not directly preserve information about the values of means (Thiele, 1993), incorporating such information is unnecessary in this case, because of the extensive overlap among taxa and the roughly equalamounts of variation included within the codes for each character.

Codes for two (#6, 7) of the three non-morphometric characters are binary and determined qualitatively by visual examination. In the third non-morphometric character, number of septa per corallite (#2), the three codes reflect the categorization of the development of septal cycles in the genus *Montastraea* proposed by Vaughan (1919), and are treated as ordered. In general, in the three non-morphometric characters, the number of codes per character are fewer, and therefore, as presently defined, they lack the resolution of the morphometric characters.

A heuristic search was performed on the matrix using PAUP 4.0b4a for Microsoft Windows (Swofford, 1998) and two common late Miocene to early Pliocene species of *Montastraea*, *M. brevis* (Duncan, 1864) and *M. cylindrica* (Duncan, 1863) as described by Vaughan (1919) and Budd (1991), as outgroups. These two species have corallite diameters and number of septa that are intermediate between *M. annularis*-like corals and *M. cavernosa*-like corals, and thus are believed to represent a closely related sister group. The following settings were used in the heuristic

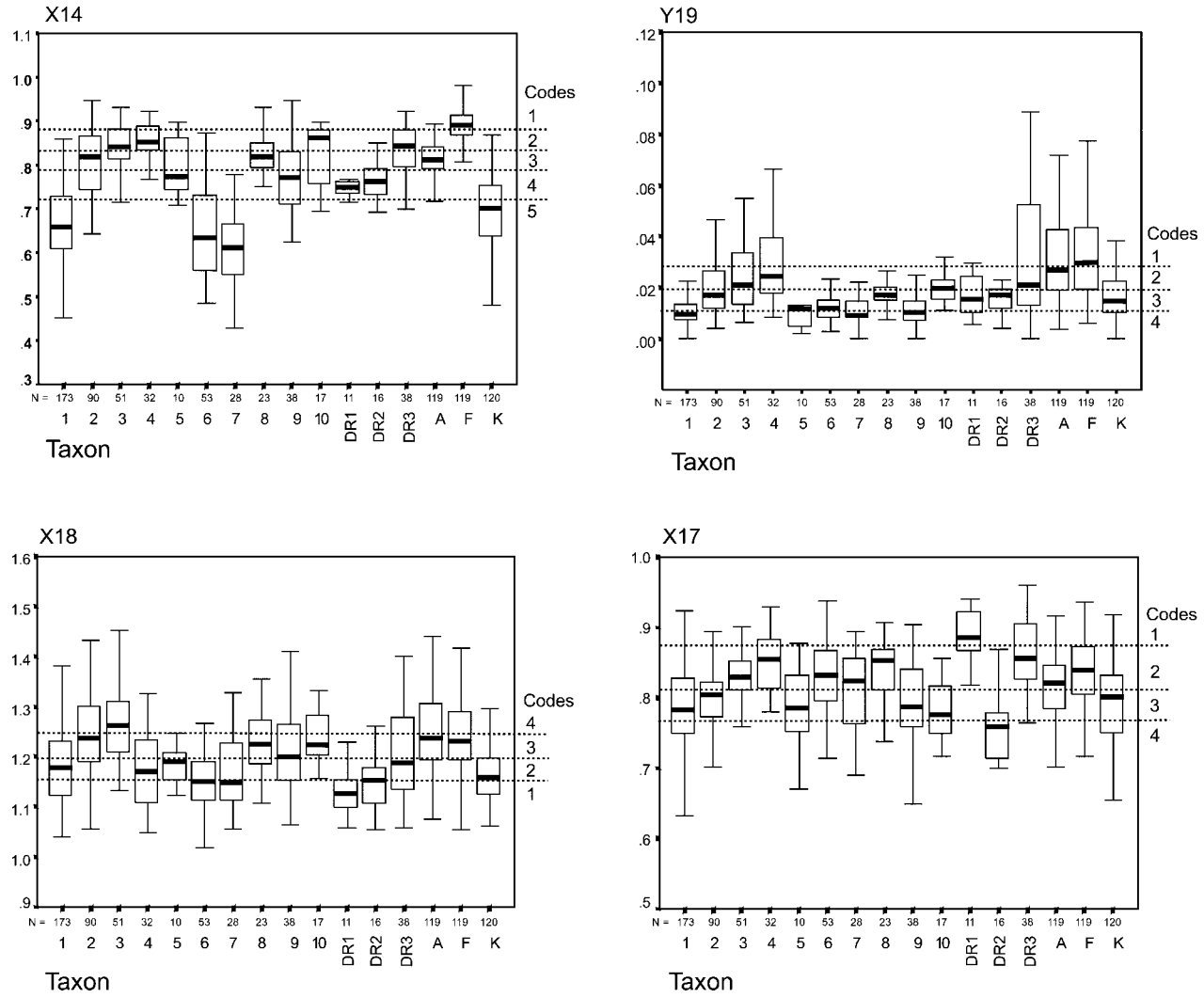

FIGURE 9—Boxplots based on the median, quartiles, and extreme values. The box represents the interquartile range containing 50 percent of the values. The whiskers represent the highest and lowest values, excluding outliers. The line across each box represents the median. Numbers without letters refer to the Costa Rica and Panama morphotypes, numbers with a DR prefix refer to the three DR species; A = *M. annularis* s.s., K = *M. franksi*; F = *M. faveolata.* Codes interpreted for these data are given in Table 5.

search: addition sequence random; number of replications = 100; tree-bisection and reconnection (TBR) branch swapping performed; MULPARS option in effect; steepest descent option not in effect. The search resulted in a total of three most parsimonious trees consisting of 37 steps each (CI = 0.568, HI = 0.432, RI = 0.754, RC = 0.428). The first two trees differ in topology, but not in patterns of character change. Specifically, in tree #1, Morphotype #2, Morphotype #8, and a 5-taxon clade (Morphotypes #3 and 4, DR species #3, *M. faveolata*, *M. annularis* s.s.) form a trichotomy; whereas, in tree #2, Morphotype #8 and the 5-taxon clade form a dichotomy (Fig. 10). The third tree differs from the first two trees in both topology and patterns of character change. Specifically, Morphotype #2 groups with Morphotype #10, instead of more distantly with Morphotype #8 and the 5-taxon clade. As a result, homoplasy is increased in two wall characters (#3, 4) and reduced in number of septa (character #2) and tertiary septum length (character #8; Table 5).

The three trees (Fig. 10) each contain two major groups of taxa: 1) Morphotypes #1, 5, 6, 7, 9; DR species #1, 2; *M. franksi* [''the *franksi* group''], and 2) Morphotypes #2, 3, 4, 8, 10; DR species #3; *M. faveolata* and *M. annularis* s.s. [''the *faveolata* group'']. The first group is characterized by thick corallite walls (character #4) and expanding costosepta (character #6); whereas the second group is characterized by three complete septal cycles (character #2) and long costae (character #5; Fig. 10). Each of the two major groups can be further subdivided into two subgroups or clades. The *franksi* group consists of one clade (''*franksi*-1'') containing *M. franksi* and three morphotypes (#1, 5, 9), and a second clade (''*franksi*-2'') containing two DR species (#1, 2) and two morphotypes (#6, 7). The first clade contains three plesiomorphic taxa (Morphotypes #1, 5, 9) and is characterized by septothecal walls (character #4) and long tertiary septa (character #8); whereas the second is characterized by short costae (character #5). The *faveolata* group consists of one clade (''*faveolata*-1'') containing *M. faveolata* and two morphotypes (#3, 10), which is characterized by large corallite diameters (character #1), and a second clade (''*faveolata*-2'') containing Morphotype #4 and DR species #3, which is characterized by shorter costae (character #5). DR species #3 is plesiomorphic. Three taxa (*M. annularis* s.s., Morphotype #8 and possibly Morphotype #2) appear to be isolated and more distantly related to the *M. faveolata* group. Of these three taxa, *M. annularis* s.s. is plesiomorphic.

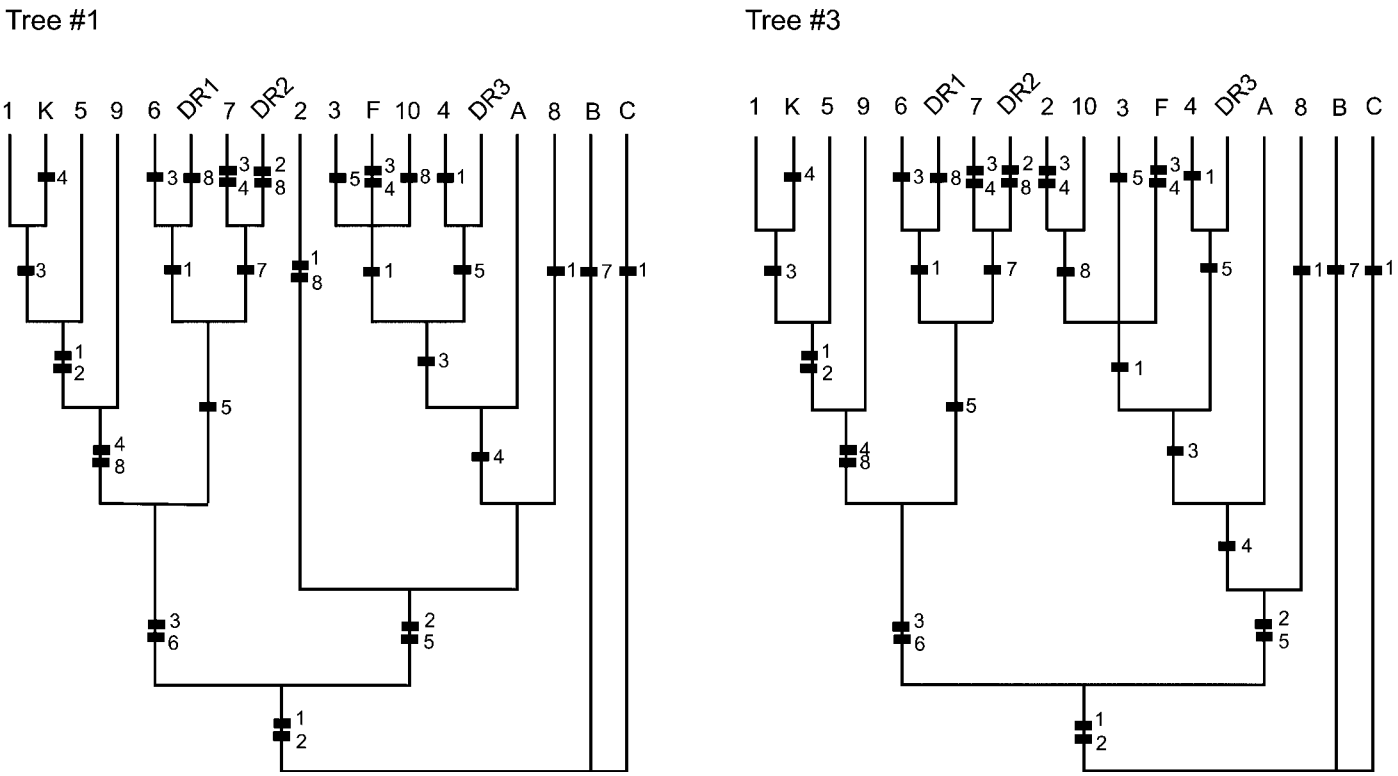

FIGURE *10*—Two of the three most parsimonious trees found using a heuristic search, the character matrix in Table 5, and *M. brevis* and *M. cylindrica* as outgroups. In the labels for each branch, numbers without letters refer to the Costa Rica and Panama morphotypes, numbers with a DR prefix refer to the three DR species; A = *M. annularis* s.s., K = *M. franksi*; F = *M. faveolata,* B = *M. brevis,* C = *M. cylindrica.* The trees contain two major groups of taxa: 1) Morphotypes #1, 5, 6, 7, 9; DR species #1, 2; *M. franksi* [''the *franksi* group''], and 2) Morphotypes #2, 3, 4, 8, 10; DR species #3; *M. faveolata* and *M. annularis* s.s. [''the *faveolata* group''].

As illustrated in the first tree (Fig. 10), few consistent trends emerge upon visual examination of patterns of character change within the four clades. Corallite diameter (character #1) shows patterns of parallel increases within the two younger clades (*franksi*-1, *faveolata*-1), but parallel decreases within the two older DR-associated clades (*franksi*-2, *faveolata*-2). Number of septa per corallite (character #2) reveals a similar pattern of both increase (*franksi*-1) and decrease (*franksi*-2). Wall thickness (character #3) and structure (character #4) show parallel increases within the *franksi* clades, but decreases within *faveolata*-1. Tertiary septum length (character #8) shows increases within *franksi*-2 and *faveolata*-1, but also a decrease within *franski*-2.

TABLE *5*—Character matrix (18 taxa, 8 characters) analyzed using global parsimony. *M. brevis* and *M. cylindrica* were designated as the outgroup. CI, consistency index. Abbreviations for characters are given in Table 4.

Taxon	(1) cd	(2) ns	(3) wt	(4) ws	(5) cl	(6) tct	(7) pl	(8) tsl
Morphotype #1	3	1	5	4	2	2	1	3
Morphotype #2	3	1	3	3	3	1	1	3
Morphotype #3	3	1	2	2	3	1	1	2
Morphotype #4	1	1	2	2	2	1	1	2
Morphotype #5	3	1	4	4	2	2	1	3
Morphotype #6	1	2	5	3	1	2	1	2
Morphotype #7	2	2	5	4	1	2	2	2
Morphotype #8	1	1	3	3	3	1	1	2
Morphotype #9	2	2	4	4	2	2	1	3
Morphotype #10	3	1	2	2	3	1	1	3
DR species #1	1	2	4	3	1	2	1	1
DR species #2	2	3	4	3	1	2	2	4
DR species #3	2	1	2	2	2	1	1	2
M. annularis s.s.	2	1	3	2	3	1	1	2
M. faveolata	3	1	1	1	3	1	1	2
M. franksi	3	1	5	3	2	2	1	3
M. brevis	4	3	3	3	2	1	2	2
M. cylindrica	5	3	3	3	2	1	1	2
tree #1, CI	0.444	0.500	0.667	0.600	0.750	1.000	0.500	0.500
tree #2, CI	0.444	0.500	0.667	0.600	0.750	1.000	0.500	0.500
tree #3, CI	0.500	0.500	0.571	0.500	0.750	1.000	0.500	0.600

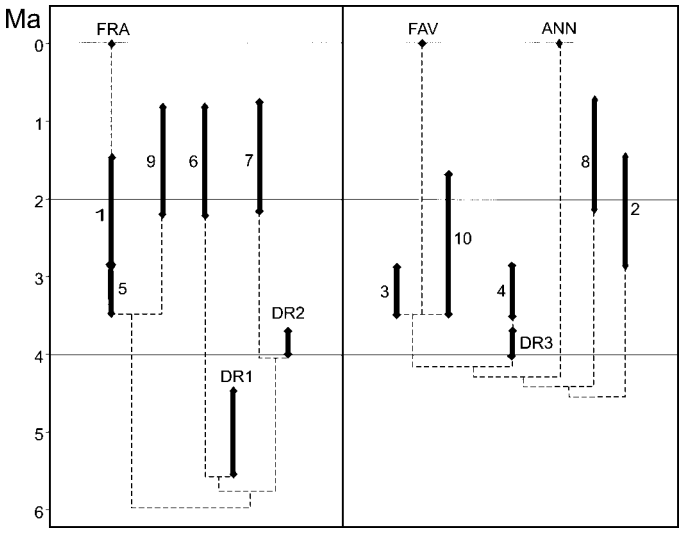

FIGURE *11*—Phylogenetic tree constructed by calibrating the first tree in Figure 10 with the known stratigraphic ranges of each taxon. Thick vertical lines for each morphotype or species correspond with the maximum age range reported for the localities in which they occur. Dotted lines indicate inferred relationships derived from the cladistic analysis. Numbers without letters refer to the Costa Rica and Panama morphotypes, numbers with a DR prefix refer to the three DR species; ANN = *M. annularis* s.s., FRA = *M. franksi*; FAV = *M. faveolata.* The three modern species of the *M. ''annularis''* complex all arose prior to accelerated extinction during the early Pleistocene (~2–1.5 Ma). Six or more previously unrecognized species also existed within the complex in Costa Rica and Panama between 4–2 Ma, and so did *M. limbata* (DR species #2).

To further understand the relationships suggested by the cladistic analysis, tree #1 was calibrated using the known stratigraphic ranges for the 16 ingroup taxa (Fig. 11) following the methods of Smith (1994). Tree #1 was used in this procedure, because it involves less homoplasy in two wall characters (#3, 4) that played important roles in the above morphometric analyses distinguishing the three modern members of the *M. ''annularis''* complex. In this reconstruction, the plesiomorphic status of Morphotypes #1 and #5 and their cladistic grouping with *M. franksi* suggest that these three taxa may represent a metaspecies or, in other words, a single ancestral-descendant lineage. Similarly, the plesiomorphic status of DR species #3 and its cladistic grouping with Morphotype #4 suggest that these two taxa may also represent a metaspecies. The reconstruction (Fig. 11) shows range extensions of two million years or more in the relationships of Morphotypes #6 and 7 with DR species #1 and #2. A similarly long range extension is involved in the ghost lineage linking the *franksi*-1 (Morphotypes #1, 5, 9; *M. franksi*) and *franksi*-2 (Morphotypes 6, 7; DR species 1, 2) clades. The three relatively isolated taxa (*M. annularis* s.s., Morphotypes #2 and 8) also reveal long range extensions in their relationships with the *faveolata*-group.

DISCUSSION AND CONCLUSIONS

The present study shows that the recently discovered *M. ''annularis''* species complex consists of two or more diverse evolutionary groups of species, which each contain at least one modern species. Moreover, the three modern species within the complex appear to have been distinct for at least the past 2–4 m.y., and to have coexisted with clades containing pre-turnover taxa. Despite the high consistency indices and low number of equally parsimonious trees in the results of the cladistic analysis, questions still remain about the exact numbers of fossil species and the detailed patterns of divergence among species. The high number of plesiomorphic taxa (five of 16), the long range extensions found in calibrating the phylogenetic tree, and the low resolution in the cladistic relationships associated with *M. annularis* s.s. and Morphotypes #2 and 8 indicate that more data are needed before a final assessment of these taxa and their evolution can be made. Moreover, relationships between the three modern species in the cladogram do not agree with the analyses of genetic data, which suggest that *M. franksi* and *M. annularis* s.s. are more closely related. Two types of data would improve the match between the cladistic analysis and stratigraphy and the match between morphologic and genetic data: 1) sampling more stratigraphic units and increasing sample sizes and 2) adding more characters.

Sampling.—The present samples were taken from limited geographic locations and reef environments; only two neighboring upper Pliocene to lower Pleistocene sequences (Costa Rica, Panama), one early Pliocene sequence (Dominican Republic), and one modern reef complex (Panama) are represented. No species was found to occur in both the Costa Rica and Panama sequences, which appear to involve similar reef environments and communities (Budd et al., 1999). Morphotypes #3 (Costa Rica) and #10 (Panama) are the most similar, but they differ in tertiary septum length. This observed level of endemism contrasts strikingly with the Caribbean-wide distributions of species within the *M. ''annularis''* complex today. Nevertheless, the preliminary cladistic analysis suggests that most of the Costa Rica and Panama morphotypes are more closely related to one of the three modern species or the three DR species than they are to one another. Clearly, more populations need to be sampled in order to fully investigate geographic and environmental variation within species, and more effectively interpret the observed fine-scale differences among similar morphotypes. Both modern and fossil samples are needed as follows:

1) More sampling of genetically characterized colonies is needed in different modern reef environments at different geographic locations, so that direct comparisons can be made with the Recent in assessing morphologic differences among fossil populations collected in different stratigraphic units. For example, previous transplantation experiments (Foster, 1979, 1980) have shown that both skeletal growth and density of *M. faveolata* vary ecophenotypically in response to different environmental factors. Wall thickness, in particular, is affected by this variation. Samples representative of the range and nature of ecophenotypic plasticity within species of the *M. ''annularis''* complex are thus essential to better understanding species boundaries.

2) More sampling is also needed in other upper Miocene to lower Pliocene [e.g., the Dominican Republic (Budd, 1991)], Plio-Pleistocene [e.g., Jamaica (Budd and McNeill, 1998), Curaçao (Budd et al., 1998)], and upper Pleistocene units at scattered Caribbean locations, so that the observed narrow geographic distributions and long phylogenetic range extensions can be more thoroughly evaluated. Such sampling would also increase the size of the ingroup by adding taxa occurring elsewhere in the Caribbean, and thus improve the resolution of cladistic analyses. Finally, increased sample sizes within the studied Costa Rican and Panamanian sequences would improve resolution in the statistical comparisons among fossil populations.

Characters.—The new morphologic characters emphasizing the development of the corallite wall effectively distinguish the two major evolutionary groups. Differences occur within the two groups in traditional species-level characters such as corallite diameter, number of septa per corallite, costal extensions (i.e., coenosteum development), and the relative development of different septal cycles (in this case, the tertiary septa). Although capable

of distinguishing clades using coarser measures at higher taxonomic levels (e.g., *M. ''annularis''* from *M. ''cavernosa''*), corallite diameters and, to a lesser degree, numbers of septa per corallite exhibit homoplasy when examining fine-scale evolution within the complex.

Despite the effectiveness of the new morphologic characters in distinguishing clades, they alone do not provide adequate insight into the evolutionary relationships among clades, and the search for additional non-traditional morphologic characters continues, especially those applicable to the fossil record. The match in patterns of similarity between the 3-D morphometric and genetic analyses suggests that features related to calical relief and upward linear extension need to be included in the phylogenetic analyses. In worn and fragmentary material such as the fossils in the present study, the most promising features are best revealed in longitudinal thin-sections or vertical slabs, and involve the structure and formation of dissepiments (both endothecal and exothecal) and the columella (and associated paliform lobes). As mentioned above, the presence of distinct paliform lobes clearly distinguish DR species #2 and Morphotype #7 (''the *limbata* clade''), and visual examination also suggests that the metaspecies including *M. franksi* has thicker and more complex columellar structures.

In addition, as mentioned earlier, field observations reveal significant differences among the three living species of the *M. ''annularis''* complex at a higher level of homology, i.e., colony shape (Knowlton et al., 1992; Weil and Knowlton, 1994). These differences result from differences in: 1) maximum linear extension (''skeletal growth'') rates and patterns of variation in these rates across colony surfaces; and 2) rates and patterns of budding of new corallites within colonies (Graus and Macintyre, 1982). Morphometric studies and computer simulations of growth rates and budding patterns using x-radiographs of vertical slabs are needed to identify homologous characters at the colony level.

Another unexplored aspect of morphology involves septal microstructure. In transverse thin-section, relatively large, distinct trabecular centers can be seen along the mid-axis of the costosepta in the metaspecies including *M. franksi.* These structures contrast markedly with the more continuous centers of calcification observed in the rest of the study material. Study of trabeculae in longitudinal section may provide additional insight on the differences among species.

Even when characters are discovered that are effective at interpreting evolutionary relationships, the preliminary analyses in the present study suggest that they are likely to be quantitative in nature, and that the problems of overlapping variation among species and of differing amounts and patterns within species will persist. Although useful at higher taxonomic levels, diagnostic characters do not exist at the species level, even among species that are genetically distinct (*M. faveolata* vs. *M. annularis* s.s.). Quantitative differences in skeletal growth and density are the traits that distinguish closely related species. Delimiting states within characters will, therefore, continue to require a statistical population approach.

Evolutionary patterns.—In sum, the present study indicates the following evolutionary patterns within the *Montastraea ''annularis''* complex:

1) The three modern species of the *M. ''annularis''* complex arose prior to the high extinction peak at 2–1.5 Ma, which is associated with late Pliocene to early Pleistocene faunal turnover in Caribbean reef corals. Specifically, *M. faveolata* and *M. franksi* are estimated to have originated between 4–3 Ma. These species, therefore, survived the extinction episode.

2) Six possible new species (Morphotypes #2, 3 in Costa Rica; Morphotypes #6–9 in Panama) are represented in late Pliocene to early Pleistocene sequences in Costa Rica and Panama. At least one new species appears closely related to each of the three modern species and the three DR species. Additional data confirming the distinctiveness of these species (especially morphological data as indicated above, and ecological data as indicated in Pandolfi, 1999; Pandolfi et al., in press) are necessary before they can be formally named and described.

3) Each of the three early Pliocene Dominican Republic species belongs to a distinct clade, which includes late Pliocene to early Pleistocene morphotypes but not modern species. These three clades coexisted with clades containing modern species of the *M. ''annularis''* complex for at least 5 m.y. This coexistence was responsible for the high diversity of *M. annularis*-like corals during late Pliocene to early Pleistocene faunal turnover. The three modern species in the M. *''annularis''* complex originated in communities, whose compositions were quite different from those in which they live today.

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APPENDIX I

List of specimens analyzed. CCD, Cenozoic Coral database (http://nmita.geology.uiowa.edu); NMB, Natural History Museum, Basel, Switzerland; SUI, University of Iowa Paleontology Repository.

Taxon	Strat subset	CCD #	Museum catalog #	Colony #	Locality #	Country
Morphotype #1	c1/2	28	SUI 95105	228	CJ92-6(1)	Costa Rica
Morphotype #1	c1/2	76	SUI 95106	127	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	103	SUI 95107	229	CJ92-6(1)	Costa Rica
Morphotype #1	c1/2	125	SUI 95108	230	CJ92-6(1)	Costa Rica
Morphotype #1	c1/2	2202	SUI 95109	239	AB93-71	Costa Rica
Morphotype #1	c1/2	261	SUI 95110	232	CJ89-17	Costa Rica
Morphotype #1	c1/2	358	SUI 95111	129	CJ89-17	Costa Rica
Morphotype #1	c1/2	445	SUI 95112	233	CJ89-17	Costa Rica
Morphotype #1	c1/2	626	SUI 95113	130	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	630	SUI 95114	131	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	631	SUI 95115	132	KJ-LM(1)	Costa Rica
Morphotype #1	c1/2	632	SUI 95116	235	KJ-LM(1)	Costa Rica
Morphotype #1	c1/2	634	SUI 95117	133	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	636	SUI 95118	236	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	638	SUI 95119	134	KJ-LM(1)	Costa Rica
Morphotype #1	c1/2	848	SUI 95120	126	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	851	SUI 95121	135	KJ-LM(1)	Costa Rica
Morphotype #1	c1/2	863	SUI 95122	136	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	865	SUI 95123	238	KJ-LM(1)	Costa Rica
Morphotype #1	c1/2	2211	SUI 95124	61	AB93-71	Costa Rica
Morphotype #1	c1/2	2238	SUI 95125	67	AB93-71	Costa Rica
Morphotype #1	c1/2	2251	SUI 95126	69	AB93-71	Costa Rica
Morphotype #1	c1/2	2255	SUI 95127	71	AB93-71	Costa Rica
Morphotype #1	c1/2	2306	SUI 95128	75	AB93-41	Costa Rica
Morphotype #1	c1/2	2431	SUI 95129	78	AB93-71	Costa Rica
Morphotype #1	c1/2	3194	SUI 95130	114	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	3197	SUI 95131	115	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	3199	SUI 95132	116	KJ-LM(2)	Costa Rica
Morphotype #1	c1/2	6839	SUI 95133	118	AB95-08	Costa Rica
Morphotype #1	c1/2	6845	SUI 95134	121	AB95-08	Costa Rica
Morphotype #1	c1/2	6846	SUI 95135	122	AB95-08	Costa Rica
Morphotype #2	c1/2	496	SUI 95136	234	CJ92-6(1)	Costa Rica
Morphotype #2	c1/2	920	SUI 95137	137	KJ-LM(2)	Costa Rica
Morphotype #2	c1/2	2222	SUI 95138	63	AB93-57	Costa Rica
Morphotype #2	c1/2	2249	SUI 95139	68	AB93-71	Costa Rica
Morphotype #2	c1/2	2330	SUI 95140	241	AB93-71	Costa Rica
Morphotype #2	c1/2	2433	SUI 95141	79	AB93-41	Costa Rica
Morphotype #2	c1/2	2456	SUI 95142	80	AB93-23	Costa Rica
Morphotype #2	c1/2	2459	SUI 95143	243	AB93-62	Costa Rica
Morphotype #2	c1/2	2461	SUI 95144	81	AB93-23	Costa Rica
Morphotype #2	c1/2	2465	SUI 95145	82	AB93-62	Costa Rica
Morphotype #2	c1/2	2500	SUI 95146	85	AB93-23	Costa Rica
Morphotype #2	c1/2	3179	SUI 95147	246	KJ-P2	Costa Rica
Morphotype #2	c1/2	3193	SUI 95148	113	KJ-P2	Costa Rica
Morphotype #2	c1/2	3406	SUI 95149	247	AB93-41	Costa Rica
Morphotype #2	c1/2	6840	SUI 95150	119	AB95-08	Costa Rica
Morphotype #2	c1/2	6844	SUI 95151	120	AB95-16	Costa Rica
Morphotype #3	c3/4	853	SUI 95152	237	KJ-32-1	Costa Rica
Morphotype #3	c3/4	2252	SUI 95153	70	AB93-32	Costa Rica
Morphotype #3	c3/4	2261	SUI 95154	73	AB93-06	Costa Rica
Morphotype #3	c3/4	2314	SUI 95155	76	AB93-32	Costa Rica
Morphotype #3	c3/4	2339	SUI 95156	77	AB93-32	Costa Rica
Morphotype #3	c3/4	2477	SUI 95157	84	AB93-68	Costa Rica
Morphotype #3	c3/4	2507	SUI 95158	245	AB93-06	Costa Rica
Morphotype #3	c3/4	6835	SUI 95159	117	AB95-03	Costa Rica
Morphotype #3	c3/4	6849	SUI 95160	124	AB95-09	Costa Rica
Morphotype #4	c3/4	2226	SUI 95161	65	AB93-06	Costa Rica
Morphotype #4	c3/4	2286	SUI 95162	74	AB93-06	Costa Rica
Morphotype #4	c3/4	2292	SUI 95163	240	AB93-31	Costa Rica
Morphotype #4	c3/4	2502	SUI 95164	244	AB93-06	Costa Rica
Morphotype #4	c3/4	2531	SUI 95165	86	AB93-06	Costa Rica
Morphotype #4	c3/4	6848	SUI 95166	123	AB95-09	Costa Rica
Morphotype #5	c3/4	846	SUI 95167	125	KJ-32-1	Costa Rica
Morphotype #5	c3/4	2434	SUI 95168	242	AB93-06	Costa Rica
Morphotype #6	p1/2	30026	SUI 95169	89	AB98-11	Panama
Morphotype #6	p1/2	30076	SUI 95170	93	AB98-17	Panama
Morphotype #6	p1/2	30078	SUI 95171	94	AB98-17	Panama
Morphotype #6	p1/2	30079	SUI 95172	95	AB98-17	Panama
Morphotype #6	p1/2	30083	SUI 95173	96	AB98-17	Panama
Morphotype #6	p1/2	30196	SUI 95174	99	AB98-18	Panama
Morphotype #6	p1/2	30197	SUI 95175	100	AB98-18	Panama
Morphotype #6	p1/2	30405	SUI 95176	104	AB98-18	Panama
Morphotype #6	p1/2	30474	SUI 95177	109	AB99-07	Panama
Morphotype #6	p1/2	30476	SUI 95178	111	AB99-07	Panama
Morphotype #6	p1/2	30477	SUI 95179	112	AB99-05	Panama
Morphotype #7	p1/2	30002	SUI 95180	87	AB98-18	Panama

APPENDIX I

Continued.

Taxon	Strat subset	CCD #	Museum catalog #	Colony #	Locality #	Country
Morphotype #7	p1/2	30075	SUI 95181	91	AB98-17	Panama
Morphotype #7	p1/2	30323	SUI 95182	101	AB98-16	Panama
Morphotype #7	p1/2	30473	SUI 95183	108	AB99-07	Panama
Morphotype #7	p1/2	30475	SUI 95184	110	AB99-07	Panama
Morphotype #8	p1/2	30012	SUI 95185	88	AB98-11	Panama
Morphotype #8	p1/2	30032	SUI 95186	90	AB98-18	Panama
Morphotype #8	p1/2	30138	SUI 95187	97	AB98-11	Panama
Morphotype #8	p1/2	30139	SUI 95188	98	AB98-11	Panama
Morphotype #9	p1/2	2223	SUI 95189	64	AB93-76	Panama
Morphotype #9	p1/2	30073	SUI 95190	92	AB98-17	Panama
Morphotype #9	p1/2	30403	SUI 95191	102	AB98-18	Panama
Morphotype #9	p1/2	30404	SUI 95192	103	AB98-18	Panama
Morphotype #9	p1/2	30406	SUI 95193	105	AB98-18	Panama
Morphotype #9	p1/2	30471	SUI 95194	106	AB99-12	Panama
Morphotype #9	p1/2	30472	SUI 95195	107	AB99-12	Panama
Morphotype #10	p3	2218	SUI 95196	62	AB93-75	Panama
Morphotype #10	p3	2229	SUI 95197	66	AB93-74	Panama
Morphotype #10	p3	2472	SUI 95198	83	AB93-80	Panama
DR species #1	d4	12449	NMB D5622	153–154	NMB16818	Dom. Rep.
DR species #1	d4	13486	NMB D5626	155–157	NMB16823	Dom. Rep.
DR species #3	d5	13538	NMB D5654	167–170	NMB16884	Dom. Rep.
DR species #3	d5	13493	NMB D5655	171–173	NMB16884	Dom. Rep.
DR species #2	d5	13495	NMB D5656	174–176	NMB16884	Dom. Rep.
DR species #2	d5	13496	NMB D6416	177	NMB16884	Dom. Rep.
DR species #2	d5	12488	NMB D5652	178–179	NMB16884	Dom. Rep.
M. annularis	Recent	a455b/t	SUI 95199	2	San Blas Is.	Panama
M. annularis	Recent	a457b/t	SUI 95200	4	San Blas Is.	Panama
M. annularis	Recent	a464b/m	SUI 95201	6	San Blas Is.	Panama
M. annularis	Recent	a465b/t	SUI 95202	8	San Blas Is.	Panama
M. annularis	Recent	a95-10b/m	SUI 95203	10	San Blas Is.	Panama
M. annularis	Recent	a95-14b/m	SUI 95204	12	San Blas Is.	Panama
M. annularis	Recent	a95-18b/m	SUI 95205	14	San Blas Is.	Panama
M. annularis	Recent	a95-39b/m	SUI 95206	16	San Blas Is.	Panama
M. annularis	Recent	a95-07b/m	SUI 95207	18	San Blas Is.	Panama
M. annularis	Recent	a95-01b/m	SUI 95208	20	San Blas Is.	Panama
M. faveolata	Recent	f409b/m	SUI 95209	22	San Blas Is.	Panama
M. faveolata	Recent	f428b/t	SUI 95210	24	San Blas Is.	Panama
M. faveolata	Recent	f438b/m	SUI 95211	26	San Blas Is.	Panama
M. faveolata	Recent	f490b/m	SUI 95212	28	San Blas Is.	Panama
M. faveolata	Recent	f95-37b/m	SUI 95213	30	San Blas Is.	Panama
M. faveolata	Recent	f95-16b/m	SUI 95214	32	San Blas Is.	Panama
M. faveolata	Recent	f96-07b/m	SUI 95215	34	San Blas Is.	Panama
M. faveolata	Recent	f96-29b/t	SUI 95216	36	San Blas Is.	Panama
M. faveolata	Recent	f96-47b/m	SUI 95217	38	San Blas Is.	Panama
M. faveolata	Recent	f97-5b/t	SUI 95218	40	San Blas Is.	Panama
M. franksi	Recent	k312b/m	SUI 95219	42	San Blas Is.	Panama
M. franksi	Recent	k408b/m	SUI 95220	44	San Blas Is.	Panama
M. franksi	Recent	k417b/m	SUI 95221	46	San Blas Is.	Panama
M. franksi	Recent	k427b/m	SUI 95222	48	San Blas Is.	Panama
M. franksi	Recent	k95-13b/m	SUI 95223	50	San Blas Is.	Panama
M. franksi	Recent	k95-15b/t	SUI 95224	52	San Blas Is.	Panama
M. franksi	Recent	k95-04b/m	SUI 95225	54	San Blas Is.	Panama
M. franksi	Recent	k95-25b/m	SUI 95226	56	San Blas Is.	Panama
M. franksi	Recent	k95-03b/t	SUI 95227	58	San Blas Is.	Panama
M. franksi	Recent	k97-1b/m	SUI 95228	60	San Blas Is.	Panama

APPENDIX II

Shape coordinates having statistically significant differences among overlapping morphotypes and species. Z-statistics and *P*-values are derived from Mann-Whitney U tests.

Overlapping morphotypes and species	Shape coordinates	Morphologic character	Z-statistic	*P*-value
Morphotypes #1 vs. #5	x9	length of secondary septum	−2.910	0.004
	x14	wall thickness	−3.991	0.000
	x21	wall thickness	−3.988	0.000
Morphotypes #2 vs. #9	x14	wall thickness	−2.347	0.019
	x18	extension of costae	−2.451	0.014
	x21	wall thickness	−2.436	0.015
	y11	width of tertiary costoseptum	−2.237	0.025
	y19	wall structure	−4.037	0.000
	y21	wall structure	−2.858	0.004
Morphotypes #3 vs. #10	x2	extension of costae	−2.627	0.009
	x16	tertiary septum development	−2.981	0.003
	x17	tertiary septum development	−3.567	0.000
Morphotype #1 vs. *M. franksi*	x9	length of secondary septum	−2.716	0.007
	x10	extension of costae	−2.594	0.009
	x14	wall thickness	−3.015	0.003
	x16	tertiary septum development	−6.447	0.000
	x21	wall thickness	−3.055	0.002
	y19	wall structure	−5.964	0.000
	y21	wall structure	−7.033	0.000
Morphotype #6 vs. *M. franksi*	x14	wall thickness	−3.214	0.001
	x16	tertiary septum development	−3.869	0.000
	x17	tertiary septum development	−3.711	0.000
	x21	wall thickness	−3.323	0.001
	y19	wall structure	−2.926	0.003
	y21	wall structure	−3.547	0.000
Morphotype #7 vs. *M. franksi*	x14	wall thickness	−4.607	0.000
	x16	tertiary septum development	−3.594	0.000
	x21	wall thickness	−4.793	0.000
	y11	width of tertiary costoseptum	−2.580	0.010
	y19	wall structure	−3.589	0.000
	y21	wall structure	−2.095	0.036
Morphotype #8 vs. *M. annularis* s.s.	x16	tertiary septum development	−3.643	0.000
	x17	tertiary septum development	−2.284	0.022
	y11	width of tertiary costoseptum	−3.452	0.001
	y19	wall structure	−3.882	0.000
	y21	wall structure	−2.445	0.014
Morphotype #4 vs. DR species #3	none			