A MULTI-CHARACTER ANALYSIS OF THE CARIBBEAN CORAL *MONTASTRAEA ANNULARIS* (ELLIS AND SOLANDER, 1786) AND ITS TWO SIBLING SPECIES, *M. FAVEOLATA* (ELLIS AND SOLANDER, 1786) AND *M. FRANKSI* (GREGORY, 1895)

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ABSTRACT

Wide variability in colony morphology of *Montastraea annularis* has traditionally been viewed as a largely phenotypic response to variation in environmental conditions. This perspective is challenged, however, by the coexistence of discrete colony morphologies at the same sites, often with little evidence of intermediate forms. Differences among colony morphotypes in proteins, aggressive reactions, and corallite morphology define three broadly sympatric shallow-water species. We redescribe the species that corresponds to the type specimen of *M. annularis* and two previously synonymized species, *M. faveolata* and *M. franksi*. *Montastraea franksi* is distinguished by larger, unevenly arrayed polyps that give the colony its characteristic irregular surface. Colony form is variable, and the skeleton is dense with poorly developed annual bands. *Montastraea faveolata* grows in heads or sheets, the surface of which may be smooth or have keels or bumps. Septa are highly exsert, and the skeleton is much less dense than in the other two species. *Montastraea annularis* grows in columns that exhibit rapid and regular upward growth. In contrast to the other species, margins on the sides of columns are typically senescent. A dominance hierarchy characterizes short-term aggressive reactions and can be used to identify these species in the field; *M. annularis* is the least aggressive and *M. franksi* the most aggressive. The species overlap broadly at intermediate depths, although *M. faveolata* has the shallowest distribution and *M. franksi* the deepest. *Montastraea faveolata* is the most distinctive species biochemically. Substantial biological differences among the species require that they be distinguished in future studies.

"From the study of the life of the colony in different surroundings, and from the repair of injury, and death in unsuitable habitats, I think it will be seen that the number of the true species of corals is by no means so great as is at present supposed" (Wood Jones, 1907).

"One such species is *Montastrea annularis*, which has a massive colony form . . . and a multilobate colony form. . . . Because these forms coexist and there are no structural intermediates, one could argue that they are really separate species" (Graus, 1977).

Montastraea annularis sensu lato is often considered the most important coral of modern western Atlantic reefs (Goreau, 1959; Hoffmeister and Multer, 1964). Its biogeographic distribution extends from Bermuda (Logan, 1988) to throughout the Caribbean and perhaps to Brazil (Laborel, 1969), and it ranges in depth from the intertidal to over 80 m (Goreau and Wells, 1967; Reed, 1985). Moreover, it is the most abundant coral at many locations, exposures and depths, at times approaching a monoculture (Scatterday, 1977).

Not surprisingly, colonies of *M. annularis* show marked variation in form across different environments (Barnes, 1973; Dustan, 1975b). Such variability could originate from genetic or environmental differences influencing corals directly or indirectly via their zooxanthellae. Empirical and theoretical studies aimed at elucidating these processes (Barnes, 1973; Dustan, 1979, 1982; Graus and Macintyre, 1976, 1982; Foster, 1979, 1980, 1983, 1985; Battey and Porter, 1989) provide no clear consensus on their relative importance, in part because variability across depth may not be driven by the same forces as variability across habitat.

Table 1. Locality (see Fig. 1), total number of colonies of each species, and depths [sample mean ($\bar{x}$) and standard deviation (SD)] from which specimens were collected

Reef	Species	N	Depth, m $\bar{x}$ (SD)
Salar	*annularis*	14	9.0 (3.5)
Salar	*faveolata*	13	4.8 (2.9)
Salar	*franksi*	12	12.0 (3.7)
Aguadargana	*annularis*	30	5.6 (1.4)
Aguadargana	*faveolata*	28	6.4 (2.7)
Aguadargana	*franksi*	26	13.4 (4.7)
Ulagsukun	*annularis*	13	5.9 (2.3)
Ulagsukun	*faveolata*	12	5.0 (1.8)
Ulagsukun	*franksi*	12	11.3 (4.2)
Limones	*annularis*	6	8.8 (0.9)
Limones	*faveolata*	11	10.5 (1.2)
Limones	*franksi*	11	12.7 (5.9)

Much less studied is the considerable variation in colony form within single sites in shallow water (Barnes, 1973; Dustan, 1975a; Graus and Macintyre, 1982; Tomascik, 1990). Microhabitat differences in light, competition, and bioerosion (Lewis, 1960; Dustan, 1975b; Graus, 1977; Graus and Macintyre, 1982; Frydl, 1979) appear inadequate to explain the extensive variation routinely observed over small spatial scales (Dustan, 1975a; Graus and Macintyre, 1982; Tomascik, 1990; Knowlton et al., 1992). This problem of coexisting colony morphologies in *M. annularis* inspired an earlier paper (Knowlton et al., 1992), in which we briefly documented the biochemical, behavioral, and morphological evidence pointing to the existence of at least three sibling species (sensu Mayr, 1963) in shallow water. Similar patterns have also been reported for three morphotypes in Curaçao and Bonaire (Van Veghel and Bak, 1993). Here we 1) redescribe the species corresponding to the type specimen, 2) resurrect and redescribe two additional species, 3) present in greater detail the behavioral, biochemical, morphological, and distributional differences among the species, and 4) consider the ecological, evolutionary and practical significance of our findings.

Methods

Collections.—Species were identified in the field on the basis of colony-level characters (Knowlton et al., 1992, see below). We collected from a total of 188 colonies (Table 1) comprising the three species from four areas in the San Blas archipelago, Panama (Fig. 1) in May 1990. Of these samples, all but two came from depths less than 18.5 m and 75% from depths of 3.5 to 12 m, where the three species overlapped. Whenever possible, we removed samples from large, subdivided colonies without injuring live tissues.

Aggression.—Contact-induced mortality (here termed "aggression," but see Lang and Chornesky, 1990) was compared for the six possible intraspecific and interspecific pairings. For each of these, we paired corals from the same reef and corals from different reefs, yielding a total of 12 classes of interactions. Paired colonies were placed in one of 10 nearby locations on Aguadargana Reef at a depth of 10 m, with the 4 to 15 replicates of the different classes distributed among locations to avoid confounding locality with class of interaction. The experimental area consisted of dead coral covered by a thick algal turf that reduced sediment resuspension and minimized disturbance by fishes. Colonies in each interacting pair were separated by a distance of 1–2 mm along healthy margins, and observed daily for 6 days. We counted the number of polyps killed each day and measured the total area affected (estimated by maximum length × width of dead area) on day 6. We used Mann-Whitney *U*-tests of SPSS-X (1987) to analyze the data.

Protein Electrophoresis.—At the end of the aggression experiment we brought colonies to the vicinity of the Smithsonian San Blas station and processed them within 36 h. We also collected samples of various growth forms of *M. cavernosa* for comparative purposes. Tissue (together with some under-

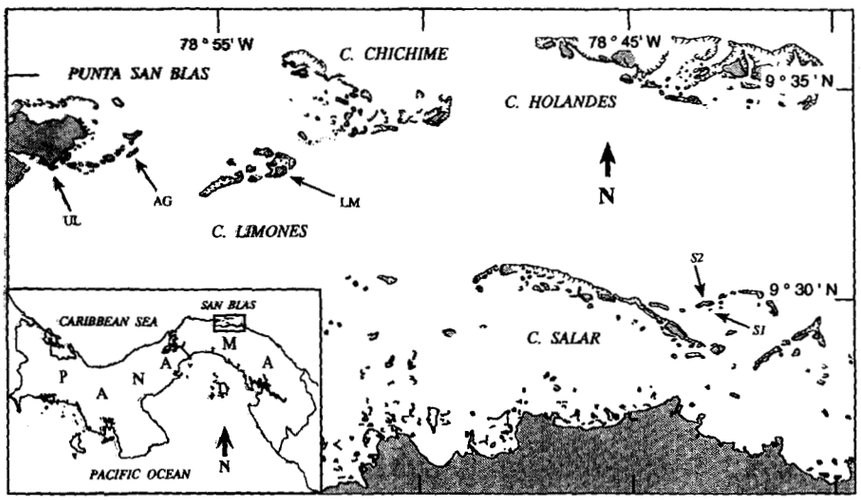


Figure 1. Collecting and census localities in the San Blas Archipelago, Panama. The initials on the figure correspond to the following names, moving from west to east: UL = Ulagsukun, AG = Aguadargana, LM = Limones, S2 = Salar-2, S1 = Salar-1. Five minutes latitude = 9.26 km.

lying skeleton) was removed with a spatula, placed in liquid nitrogen (1 to 2 ml of tissue plus 4 drops of stabilizing buffer in a cryogenic vial; Stoddart, 1983; Weil and Weigt, in press), and subsequently stored at −80°C until electrophoresis 2 to 3 weeks later. We used standard protein electrophoresis and staining techniques (Richardson et al., 1986; Murphy et al., 1990) slightly modified where necessary for corals (Weil and Weigt, in press). Tissue samples were homogenized on cold grinding plates with six to ten drops of grinding buffer. Filter paper wicks were separated from the homogenate by a piece of Miracloth (Calbiochem, La Jolla, California) to prevent mucus adhesion to the wicks. Horizontal starch gels (500 ml, 15%) were run for 4 to 6 h, sliced and stained. Gels were scored within 24 h, photographed, and stored in the refrigerator. Eighteen loci were screened, of which nine (all polymorphic) could be reliably scored. We analyzed the data with BIOSYS-1 (Swofford and Selander, 1981) and calculated probabilities of misidentification using the method of Ayala (1983).

Corallite Morphometrics.—After collecting the tissue samples, all colonies were retagged, bleached (10% sodium hypochlorite in sea water), rinsed in fresh water, and dried. For each species, we chose 15 colonies representing a variety of forms for morphometric analysis. Five of each species came from Aguadargana Reef at depths of 7.5–12 m, five came from other depths on Aguadargana, and five came from various depths on other reefs.

Measurements and analyses were based on well established protocols for this genus (Foster, 1979, 1980, 1985; Budd, 1990, 1991). On each colony, we randomly selected five corallites along each of two transects placed 2 cm from the edge and 2 cm from the center of the sample. We measured 11 standard characters (Fig. 2) on each corallite from a computer screen image produced by a video image processing system (JAVA, Jandel Co., 1988) connected to a stereo microscope. Some character values for a single corallite were averaged from several measurements. Calice and columella diameters were the means of maximum and minimum diameters. Two primary and two tertiary septa were measured; these were the widest primary septa and its opposite, and a pair of opposing tertiary septa adjacent to the measured primary septa.

For each character we calculated a colony mean from the ten measured corallites. We then entered the means for each species into a canonical discriminant function analysis of SPSS/PC+ (1990) using stepwise variable selection ordered by minimizing Wilks' Lambda.

Distribution and Abundance.—We estimated the abundance of the three species on four San Blas reefs characterized by different conditions of exposure (Fig. 1). Salar-1 is a small patch reef and Ulagsukun is a fringing reef near the mainland. Both are situated in protected areas subject to sedimentation. Salar-2 and Aguadargana are in fore reef areas moderately exposed to high wave energy during storms and the Panamanian dry season, although neither forms part of the outer barrier. Salar-2 deepens very slowly, while Aguadargana has a steeply sloping profile.

Across each reef we repeatedly draped a 10-m unweighted line parallel to the reef crest (Loya and

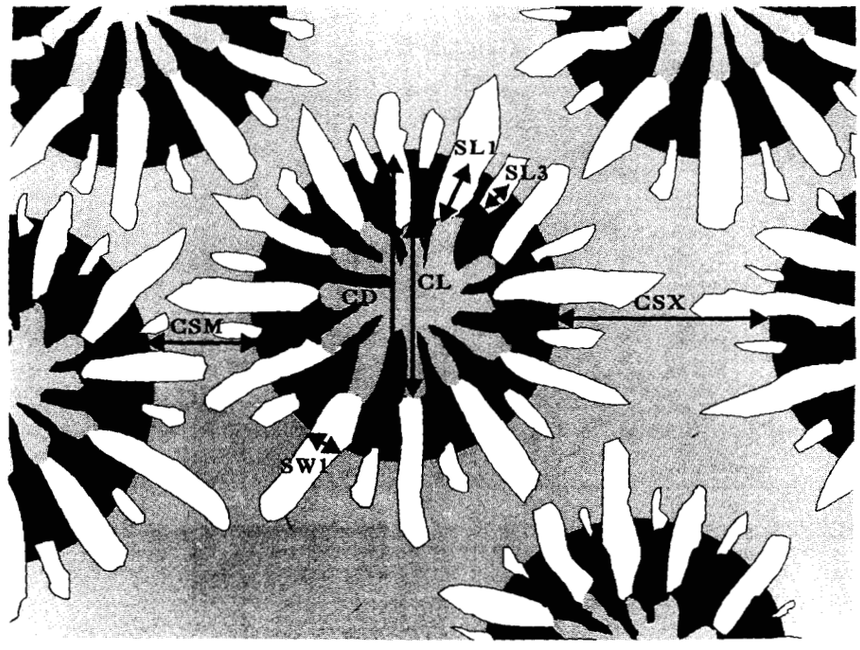


Figure 2. Measurements made on individual corallites for morphometric analyses. CD, calice diameter; CL, columella diameter; SL1, length of primary septa; SW1, width of primary septa; SL3, length of tertiary septa; CSM, distance from wall to closest calice; CSX, distance from wall to farthest neighboring calice.

Slobodkin, 1971), moving from deep to shallow. The origin of the deepest transect was chosen haphazardly, at a depth dictated by the profile of the reef or constraints on diving times. Shallower transects were placed by moving the origin of the line 5 m from the origin of the previous transect. On the Salar reefs, we made multiple sets of deep to shallow transects to have an adequate total number of transects. Depths surveyed on the different reefs ranged from 19 to 1 m (Salar-1), 14 to 2 m (Salar-2), and 24 to 1 m (Aguadargana, Ulagsukun). We placed a total of 53 transects on Salar-1 (both north and south sides of reef), 28 on Salar-2, 28 on Aguadargana, and 30 on Ulagsukun. We recorded the length and width along each transect of the colonies encountered.

To calculate percent cover, transects were assigned to one of eight 3-m depth intervals (0.1–3.0, 3.1–6.0, through 21.1–24.0 m) that were analysed separately, and the number of meters along the transects the species occupied was divided by the total number of meters censused for each depth interval. Size of the colonies was estimated by multiplying the maximum length by the maximum width.

Species Descriptions

We use the original spelling for the genus, following Wells and Lang (1973) and Budd (1991). Taxonomic literature was used to identify the earliest type material that could with reasonable confidence be assigned to the morphotypes recognizable on modern reefs. Dr. Ken Johnson then examined these type specimens and compared them with examples of the morphotypes from our collections. The assignments presented below reflect both the apparent growth form of the colony from which the type material was collected and measurements of the calices made by Dr. Johnson. In addition to the three species discussed below, we examined type material for two additional, currently synonymized species: *M. costata* (Duncan, 1863), whose identity relative to the three described species

remains uncertain (K. Johnson, pers. comm.) and *M. hispidula* (Verrill, 1901), which we synonymize with *M. franksi*. Synonymies are otherwise limited to several published photographs where species identification is unambiguous from the growth form of the colony. A quantitative comparison of the corallites of the three species (Table 2) supplements the largely qualitative descriptions that follow.

Montastraea annularis (Ellis and Solander, 1786)
Figures 3A; 4A, B; 5A; 6A; 7A, B

Madrepora annularis Ellis and Solander, 1786: 169, pl. 53, figs. 1, 2.
Montastrea annularis: Goreau, 1959: fig. 12 ("knobs"); Roos, 1964: pl. Vb; Barnes, 1973: fig. 1 bottom ("columnar-lobate"); Scatterday, 1974: figs. 6, 7; Dustan, 1975a: fig. 10 ("type 4, knobby-massive"); Graus and Macintyre, 1976: fig. 1b (natural habitat); Rützler and Macintyre, 1982: pl. 4 center left, center right; Colin, 1988: 243 bottom ("knobby"); Van Veghel and Bak, 1993: fig. 1c ("columnar").
Montastraea annularis: Foster, 1983: fig. 1b; Knowlton et al., 1992: fig. 1a ("morphotype 1").

Holotype.—A beachworn specimen of Recent age collected in the Antilles and deposited in the Hunterian Museum, Glasgow University, Scotland (Fig. 3A). Colony fragment conical in shape, with corallites growing from central axis. Corallites small, closely and uniformly spaced, with narrow septa. Upper surface smooth, with newly budded corallites distributed evenly. Corallite walls narrow, well defined and slightly raised. Coenosteum an open network; costae often confluent. Measurements (mean of 10 corallites, mm): corallite diameter (CD) 2.2, maximum spacing (CSX) 1.3, minimum spacing (CSM) 0.7.

Other Material.—USNM 94369 (length 9.6 cm, width 9.8 cm, height 8.4 cm) San Blas, Panama (Salar-1, depth 8.0 m) (Fig. 4A, B). USNM 94370 (length 10.5 cm, width 7.3 cm, height 6.4 cm) San Blas, Panama (Aguadargana, depth 4.0 m).

Diagnosis.—Branching colonies formed by long, thick columns. Living tissue restricted to tops of often clavate columns. Live colony surface usually lacking ridges or bumps. Corallites on tops of columns closely packed, uniformly distributed, and evenly exsert, with maximum diameters of mature corallites typically 2.1 to 2.6 mm. Sharp septocostal teeth usually inconspicuous in dorsal view. Coenosteum reduced and costae of neighboring corallites often confluent, at least basally. Sides of columns with few or no small corallites and generally not actively growing. Calices in this region larger (maximum diameters typically 2.3 to 2.8 mm), flattened, more widely spaced, with thicker septocostae whose lacerate margins have conspicuous lateral projections. X-radiographs of longitudinal sections with regular annual bands and growth tracks of corallites radiating distally. The least aggressive of the three sibling species.

Description.—Large, branching, lobate plocoid colonies formed by long, thick, disjunct columns (Fig. 5A). Columns formed by extratentacular budding of small polyps. Column often widening distally, ending in broad, nearly flat surface. Only top parts of the columns covered with living tissue (Fig. 4A). Sides of columns near tissue margin generally senescent with few small polyps (Fig. 4B), sometimes with small lip extending from part of column (Fig. 4A, left side). Below area of live tissue, columns typically fouled (Fig. 5A) and bioeroded (Fig. 6A). Colonies consisting of individual columns (usually a broken piece from another colony), small, low (<1 m) clusters of columns, or large, dense clusters up to 8 m wide, formed by long, thick columns, each of which can be over 2 m long, variable in diameter, and of irregular form. Fusion of live tissue sometimes seen between central columns of densely packed colonies. X-radiographs of longitudinal sec-

Table 2. Morphometric comparisons of the three species [sample means ($\bar{x}$) and standard deviations (SD)]. ANOVA P values indicate significance for differences among species means (based on univariate F ratio), and groups show significant ($P < 0.05$) pair-wise differences between species means (Student-Newman-Keuls). All characters with significant differences between pairs of species also showed significant differences among species using non-parametric tests (Kruskal-Wallis, all P's ≤ 0.033). DFA shows the order of entry of characters for the discriminant function analysis (P's for all entered characters <0.0001), and which discriminant function the entered character influenced most heavily.

	Diameter (mm)				Septa dimensions (mm)								Calice spacing (mm)			
	Calice CD		Columella CL		Width 1° SW1		Length 1° SL1		Length 3° SL3		Number of Septa NS		Maximum CSX		Minimum CSM	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Species																
annularis	2.29	0.15	1.02	0.09	0.20	0.02	0.79	0.07	0.28	0.03	24.30	0.79	1.93	0.26	1.14	0.13
faveolata	2.39	0.15	0.96	0.13	0.18	0.03	0.81	0.07	0.25	0.06	23.83	0.40	1.80	0.28	0.83	0.16
franksi	2.57	0.23	1.13	0.11	0.21	0.02	0.83	0.09	0.32	0.06	24.92	1.44	2.48	0.34	1.28	0.21
Statistics																
ANOVA P	0.0005		0.0004		0.0010		0.3187		0.0005		0.2798		0.0000		0.0000	
Groups	*fr* > *fa, an*		*fr* > *an, fa*		*fr, an* > *fa*		—		*fr* > *an, fa*		—		*fr* > *an, fa*		*fr* > *an* > *fa*	
DFA	3rd, DF2		6th, DF1		—		5th, DF2		4th, DF1		—		2nd, DF1		1st, DF1	

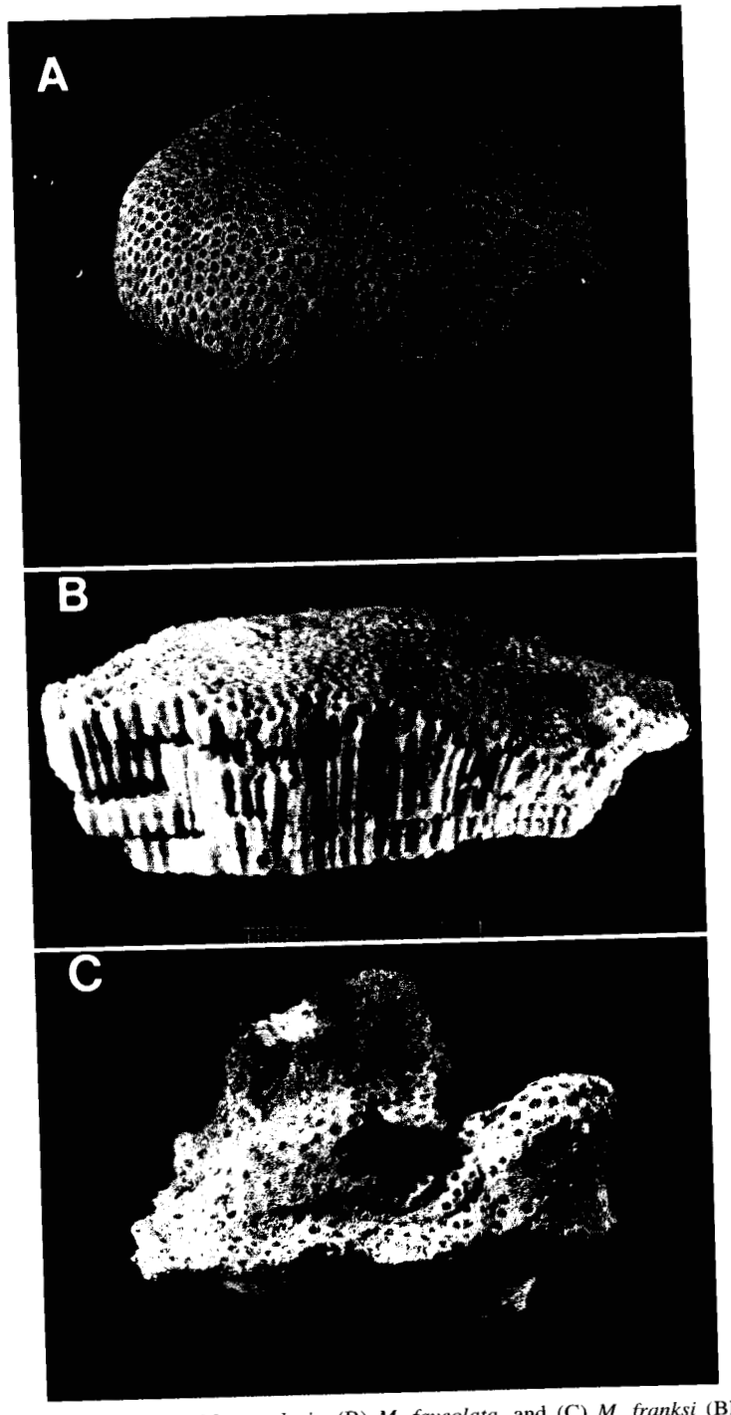


Figure 3. Holotypes of (A) *M. annularis*, (B) *M. faveolata*, and (C) *M. franksi* (BMNH R2514). Scale markings in mm. [Photographs by Photographic Department, British Museum (Natural History)].

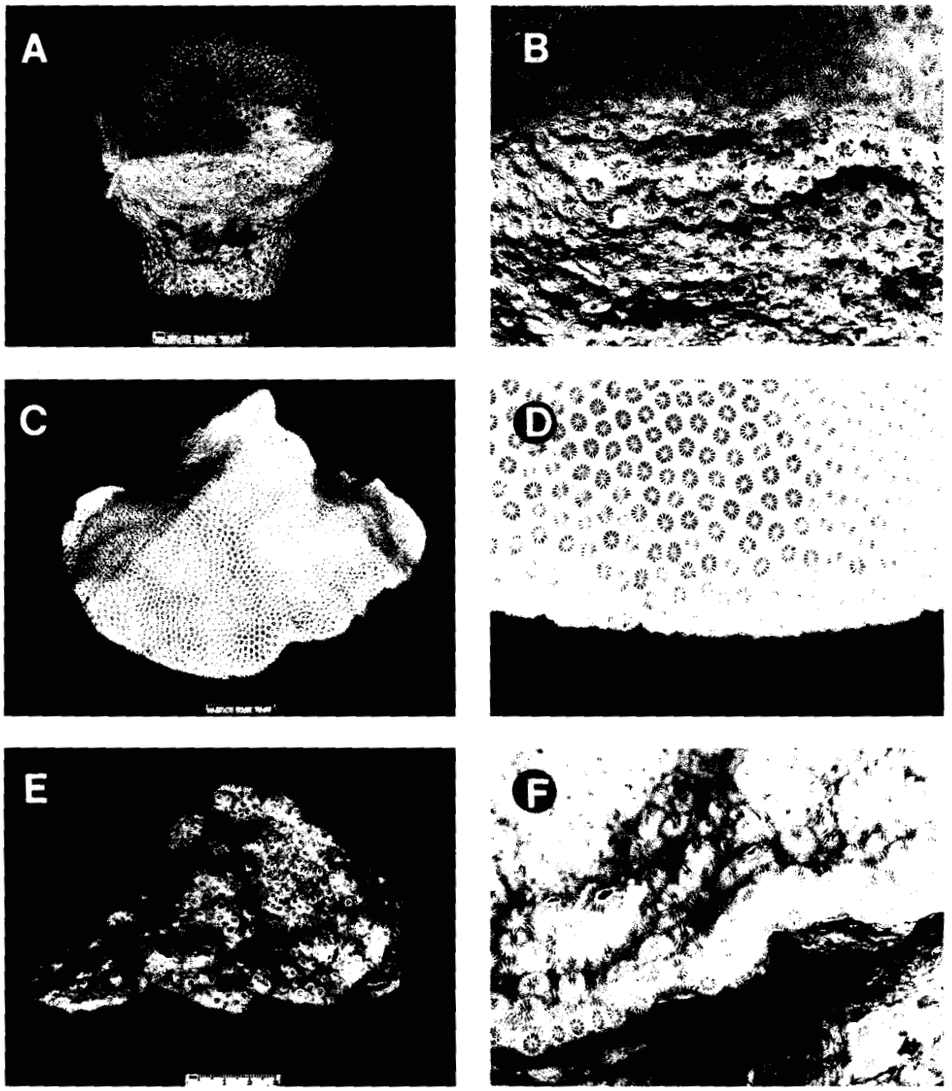


Figure 4. The three members of the *M. annularis* species complex, showing differences in colony shape and margins. (A–B) *M. annularis* (USNM 94369), (C–D) *M. faveolata* (USNM 94371), (E–F) *M. franksi* (USNM 94373). Scale bar is 3.0 cm. (Smithsonian photographs, Antonio Montaner).

tions (Fig. 6A) with highly regular, clear annual bands; tracks of corallites radiating distally.

Corallites on tops of columns (Fig. 7A) small (Table 2), little and evenly exsert, closely packed, and uniformly distributed, giving tops of individual columns a very smooth, uniform appearance. Septa thin, hexagonally arranged, and in three complete cycles (=24 septa), with first two usually reaching the spongy and well developed columella. Septocostal teeth arranged in a fan system (Wells, 1956), with few projections conspicuous in dorsal view. Coenosteum reduced, typically

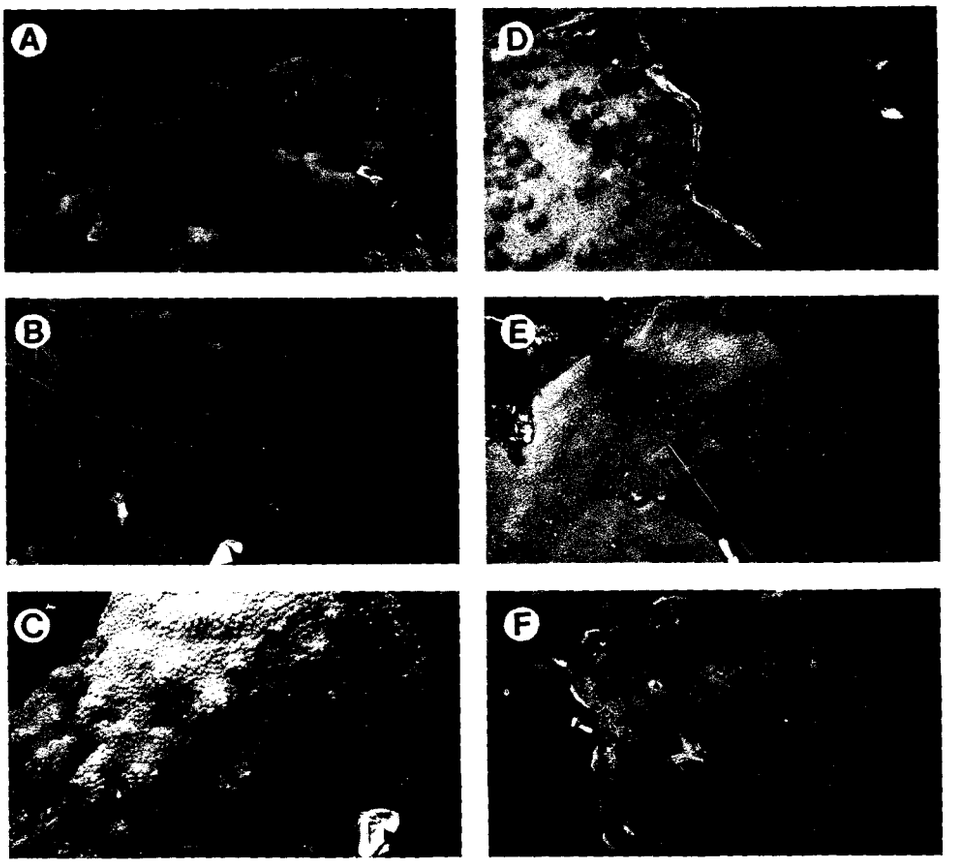


Figure 5. Field photographs of (A) *M. annularis*, (B) *M. faveolata*, (C) *M. franksi*, (D) aggressive interaction between two colonies of *M. faveolata*, (E) non-aggressive interaction between two colonies of *M. faveolata*, and (F) aggressive interaction between *M. franksi* (center) and *M. faveolata* (sides). (A–C) Salar-1, 7–8 m; (D–F) reef east of Salar-1 (78°40′30″W, 9°29′30″N), 9.5–10.5 m. Photographs by M. Lang.

blade-like costae often confluent with costae of neighboring corallites. In comparison, corallites at margins of living areas (Fig. 7B) somewhat larger, flatter, and more widely spaced. Septocostae thicker, with lacerate teeth bearing lateral projections conspicuous in dorsal view.

Color of living colonies usually golden brown to tan, occasionally approaching gray or green. Oral disks, tentacles and coenosarc generally uniform in color.

Distribution.—*Montastraea annularis* is found at shallow and intermediate depths (1–20 m). Published photographs and personal observations confirm its presence on reefs of Panama, Venezuela, Bonaire, Curaçao, the Bahamas, and Jamaica, and it is likely found throughout the region. The absence of columnar-lobate morphologies in Bermuda (Logan, 1988), however, suggests that *M. annularis* sensu stricto is absent there.

Remarks.—In shallow water the shape and size of the columns can be quite variable, ranging from round to U-shaped. In deeper areas columns are less often clavate and may narrow distally.

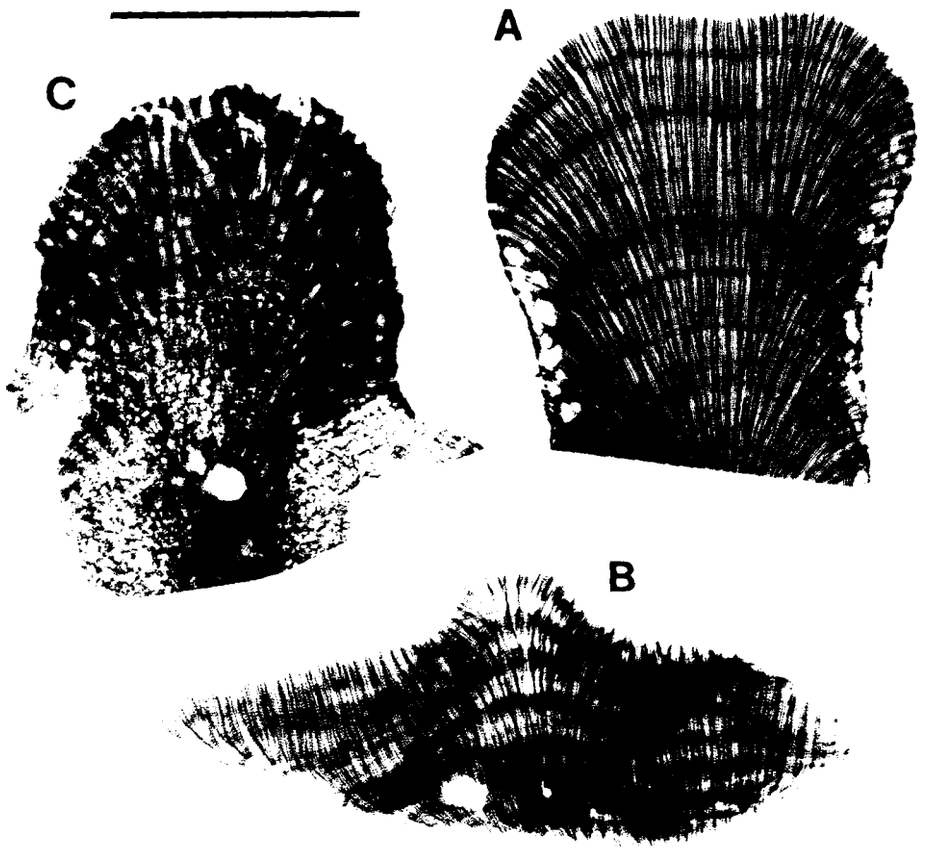


Figure 6. X-radiographs of (A) *M. annularis*, (B) *M. faveolata*, and (C) *M. franksi*. Scale bar is 5.0 cm. X-radiographs by H. M. Guzmán.

Montastraea faveolata (Ellis and Solander, 1786)
Figures 3B; 4C, D; 5B, D, E, F-left and right; 6B; 7C, D

Madrepora faveolata Ellis and Solander, 1786: 166, pl. 53, figs. 5, 6.
Montastrea annularis: Goreau, 1959: fig. 15 ("shingle-like"); Barnes, 1973: fig. 1 top; Dustan, 1975a: fig. 8 ("type 2, large skirted"); Graus and Macintyre, 1976: fig. 1a (natural habitat); Hudson, 1981: figs. 3, 5; Rützler and Macintyre, 1982: fig. 19 (foreground); Zlatarski and Estalella, 1982: pl. 29, figs. 1–3; Porter, 1974: cover; Van Veghel and Bak, 1993: fig. 1b ("massive").
Montastraea annularis: Knowlton et al., 1992: fig. 1b ("morphotype 2").

Holotype.—A highly recrystalized specimen, perhaps of Late Pleistocene age, collected in the Antilles and deposited in the Hunterian Museum, Glasgow University, Scotland (Fig. 3B). Fragment plate-shaped; upper and lower surfaces formed by splitting along parallel growth bands that have been emphasized during diagenesis. Corallite growth only slightly divergent; spacing uniform with few newly budded corallites visible. Calical walls persist but internal features of most corallites absent due to "honeycomb" preservation. Measurements (mean of 10 corallites, mm): corallite diameter (CD) 2.6, maximum spacing (CSX) 1.3, minimum spacing (CSM) 0.8.

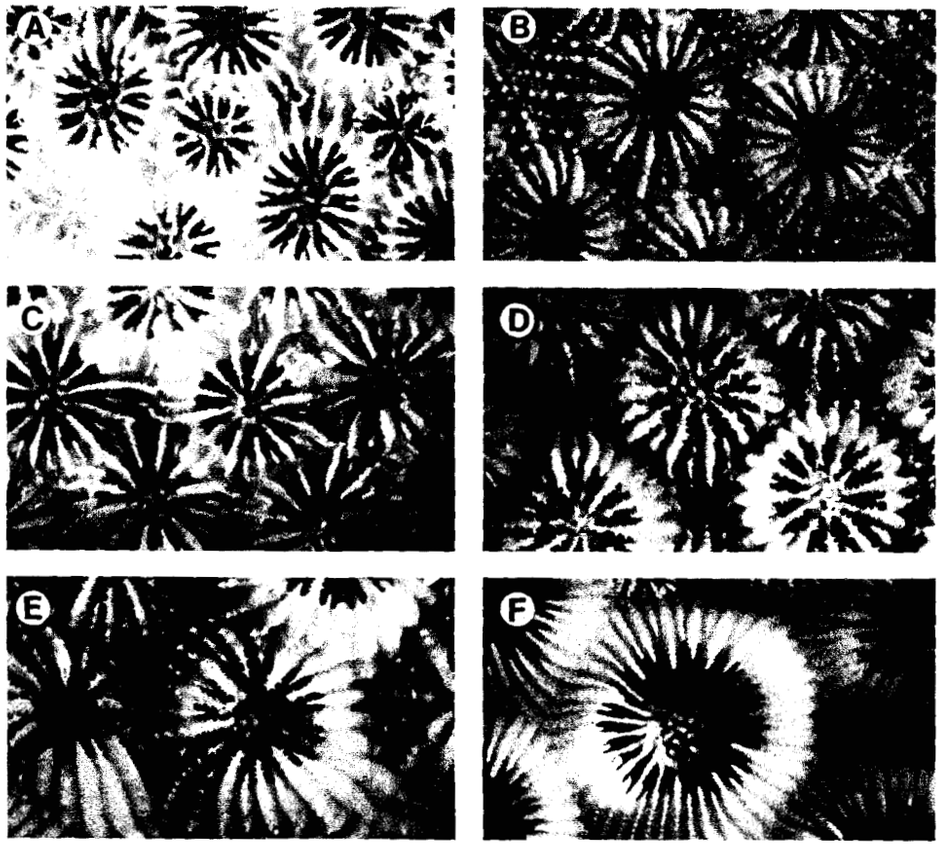


Figure 7. Close-up of corallite structure for (A) *M. annularis* (top of column), (B) *M. annularis* (side of column), (C–D) *M. faveolata,* (E) *M. franksi,* and (F) *M. cavernosa.* Scale of (A–E) is 1.5 that of (F). Scale bar is marked in mm.

Other Material.—USNM 94371 (length 23.2 cm, width 19.0 cm, height 8.4 cm) San Blas, Panama (Limones, depth 9.0 m) (Fig. 4C, D); USNM 94372 (length 18.5 cm, width 12.5 cm, height 12.0 cm) San Blas, Panama (Salar-1, depth 4.0 m).

Diagnosis.—Colonies crustose, massive-rounded, hemispherical, or massive and tall with shingle-like lateral extensions. Colony surface smooth or with long keel-like ridges or conical protrusions. Corallites uniformly distributed, closely packed, but sometimes unevenly exsert, with maximum diameters of mature corallites typically 2.2 to 2.7 mm. Septa thin and often highly exsert. Costae and lateral projections on septocostal teeth variable in size. Coenosteum reduced; costae of neighboring corallites, when blade-like, less often confluent than in *M. annularis.* Margins of colony actively growing, smooth in outline, with young and mature corallites intermingled. Corallum usually less dense than in other two species. X-radiographs showing fairly regular growth, usually with clear annual bands. Tracks of corallites often with regions of conspicuous parallel growth. More aggressive than *M. annularis,* but less aggressive than *M. franksi.*

Description.—Large, massive plocoid colonies formed by extratentacular budding. Colonies usually large, round heads, or big mounds with actively growing edges forming sheets, plates, shingles, or skirt-like lateral extensions (Fig. 5B). Coralla up to 10 m across and 3–4 m high. Crustose sheets sometimes covering large areas on exposed reefs (Fig. 5D, E, F-left and right). Shallow-water colonies (0–1 m) in protected areas massive and round, with smooth surface sometimes marked by inconspicuous ridges. In deeper (3–10 m) water, colonies often with well developed conical or keel-like protrusions (Fig. 5B, D-left, F-left and right) sometimes extending linearly as conspicuous ridges along the colony surface in parallel series running from center to margin. Active growth at edges of colonies, forming smooth outline with many small polyps (Fig. 4D). Corallum less dense than other two species. X-radiographs of longitudinal sections (Fig. 6B) with fairly regular growth, usually with well marked annual growth bands. Growth tracks of corallites often parallel, except below areas of active proliferation.

Corallites (Fig. 7C, D) small (Table 2), slightly exsert with a thin wall, and uniformly distributed with reduced coenosteum giving a smooth surface texture. Septa thin, in three complete cycles with first two usually reaching the spongy and well developed columella. First and second cycles of septa often highly exsert, giving surface of bleached and dried skeletons a distinctively translucent appearance. Septocostae dentate in fan system (Wells, 1956), with variation in extent to which teeth are lacerate and conspicuous in dorsal view. Costae blade-like, and where not confluent between neighboring corallites, creating small, open spaces between corallites (Fig. 7C); or thicker (Fig. 7D) and sometimes confluent as low ridges.

Color of living colonies generally brown, gray, or green, sometimes golden yellow in shallow water. Green oral disks and tentacles often contrasting with brown coenosarc.

Distribution.—Published photographs and personal observations confirm the presence of this species in Panama, Venezuela, Jamaica, Bonaire, Curaçao, the Bahamas, and Florida, and it probably occurs throughout the region. It broadly overlaps *M. annularis* in its depth distribution, but often extends to shallower or deeper habitats (but see Remarks).

Remarks.—Flattened deeper water colonies can be difficult to identify with information currently available, although the characteristically less dense skeleton and small, exsert corallites often remain recognizable. Chocolate brown colonies show biochemical differences that require further investigation.

Montastraea franksi (Gregory, 1895)
Figures 3C; 4E, F; 5C, F-center; 6C; 7E

Echinopora franksi Gregory, 1895: 274, pl. 11, figs. 2, 3.
Orbicella hispidula Verrill, 1901: 100, pl. 15, figs. 3, 3a, 3b.
Montastrea annularis: Barnes, 1973: figs. 2-bottom, 3-top ("irregular-massive"); Dustan, 1975a: fig. 13 ("type 7, flat . . . lumpy"), fig. 51 (left); Zlatarski and Estalella, 1982: pl. 31, fig. 1; Van Veghel and Bak, 1993: fig. 1a ("bumpy").
Montastraea annularis: Knowlton, 1992: fig. 1c ("morphotype 3").

Holotype.—Well preserved colony from the Pleistocene of Barbados, deposited in the British Museum (Natural History), London (BMNH R2514) (Fig. 3C). Irregular encrusting and columnar growth form, perhaps related to shape of underlying substratum. Corallites large, exsert, with thick septa; spacing wide and irregular. Newly budded corallites more common along margin of colony. Coenosteum dense, very well developed, and poorly differentiated from wall. Costae

confluent, with large teeth. Measurements (mean of 10 corallites, mm): corallite diameter (CD) 2.4, maximum spacing (CSX) 2.5, minimum spacing (CSM) 0.9.

Other Material.—USNM 94373 (length 16.2 cm, width 16.8 cm, height 7.3 cm) San Blas, Panama (Salar-1, depth 12.0 m) (Fig. 4E, F); USNM 94374 (length 16.5 cm, width 10.7 cm, height 11.5 cm) San Blas, Panama (Limones, depth 8.0 m).

Diagnosis.—Irregular-massive, encrusting, plate-forming or sub-columnar colonies exhibiting irregular live surface due to unevenly exsert and irregularly distributed corallites. Corallites larger, more variable in size (maximum diameters typically 2.4 to 3.4 mm), and more widely and irregularly spaced than in the other two species. Septocostae thicker, with row of lacerate teeth down midline. Costae of neighboring corallites usually confluent, often as low ridges. Areas of active proliferation of polyps, with an intermingling of small and large polyps, along irregular colony margins and in central nodular outgrowths. Colony margins and scattered central polyps often without color. Corallum denser and harder than in the other two species. X-radiographs often with irregular growth and lacking conspicuous annual bands. More aggressive than both *M. annularis* and *M. faveolata.*

Description.—Massive, encrusting, plate or subcolumnar plocoid colonies formed by extratentacular budding. Unevenly exsert and irregularly distributed corallites giving bumpy appearance to corallum (Fig. 4E). Shallower colonies usually crustose or submassive (Fig. 5C, F-center). Young colonies crustose and round, but characteristic larger, exsert and widely separated corallites present even in very small colonies. Deep (>15 m) colonies forming massive heads, crustose sheets, massive plates or stacks of wide plates attaining sizes comparable to shallower specimens of the other species. Corallum dense, heavy and extremely hard compared to the other two species. Growth margin often irregular, due to projection of large polyps (Fig. 4F). X-radiographs of longitudinal sections (Fig. 6C) also highly variable; corallites often with irregular growth tracks and annual bands often obscured. Growth of neighboring polyps less well coordinated than in the other two species.

Corallites (Fig. 7E) larger than in the other two sibling species (Table 2), although considerably smaller than in *M. cavernosa* (Fig. 7F, note scale change). Walls solid and separated by well developed coenosteum. Septa thick and in three complete cycles, with first two usually reaching the large and spongy columella. Teeth down septocostal midline lacerate and very conspicuous in dorsal view. Costae generally thick, sometimes rounded and separated by narrow grooves, and generally confluent between neighboring corallites as low ridges.

Coloration highly variable, ranging across shades of gray, green and brown. Coenosarc matching or contrasting with coloration of oral disk and tentacles in a variety of colors. Tops of raised areas and growing margins typically with polyps lacking pigmentation.

Distribution.—Published photographs and personal observations confirm the presence of this species in Panama, Venezuela, Jamaica, Bonaire, Curaçao, and the Bahamas, and it is probably distributed throughout the region. It has a wide but consistently deeper depth range than the other two species. Small colonies occur as shallow as 2 m, and maximum depths probably exceed 50 m (but see Remarks). Irregular, slowly growing plates found on shallow reefs in Bermuda (Garret et al., 1971, fig. 5; Fairbanks and Dodge, 1979) may also belong to this species.

Table 3. Intra- and interspecific contact-induced mortality (aggression) as measured by visible tissue loss. Pairs were from the same or different reefs (latter separated by 4–25 km). Median amount of tissue destruction is for subordinate colonies after six days (length × width of killed area), and median onset indicates time elapsed before first mortality was recorded. In only four cases did the dominant colony also suffer mortality. Differences between intra- and interspecific pairings in area killed and delay of onset are highly significant ($P < 0.001$ in all cases, Mann-Whitney U-tests) for all pairs (data not shown) and just aggressive pairs. Comparisons of pairings from the same versus different reefs showed no significant differences (P always >0.05, Mann-Whitney U-tests).

Pairing type	Reefs	Number of pairs	% of pairs aggressive	Dominant species	Median damage aggressive pairs only	
					Area (mm^2)	Onset (days)
Intraspecific						
annularis–annularis	Same	6	33%	—	10	5
	Different	14	21%	—	27	6
faveolata–faveolata	Same	5	20%	—	4	2
	Different	15	20%	—	4	6
franksi–franksi	Same	7	43%	—	44	4
	Different	13	69%	—	64	2
Interspecific						
annularis–faveolata	Same	6	100%	*faveolata*	168	1
	Different	6	100%	*faveolata*	127	1
annularis–franksi	Same	6	100%	*franksi*	398	1
	Different	4	100%	*franksi*	189	1
faveolata–franksi	Same	7	100%	*franksi*	264	1
	Different	5	100%	*franksi*	208	1

Remarks.—Confirmation of the identity of deep water (>30 m) specimens requires further study. The characteristic mottled appearance of most specimens of this species may represent a lag in buildup of zooxanthellae populations in actively growing areas, as is seen in apical polyps of *Acropora cervicornis.*

Species Comparisons

Aggression.—Four conclusions emerged from our experiments on aggression (Table 3; Knowlton et al., 1992). First, there were striking differences in aggression between interspecific and intraspecific interactions. Interspecific pairings always resulted in aggressive interactions. Mortality appeared rapidly (generally within 1 day), and by 6 days was extensive (median area damaged was 127–398 mm^2 for interspecific pairings). In contrast, intraspecific pairings generally did not show aggression; when present, it was delayed in onset and on average less severe. These differences in extent and timing of aggression between intraspecific and interspecific pairings are highly significant ($P < 0.001$ for all Mann-Whitney U-tests, comparing all pairs or just aggressive pairs). Second, the three sibling species showed a consistent and clear hierarchy in aggressiveness, with *M. franksi* the most aggressive and *M. annularis* the least aggressive. Third, aggression was generally unilateral over the time scale we studied; in only four of the 94 pairings did both members of the pair suffer partial mortality. Finally, there were no strong and consistent differences in timing or extent of aggression between pairs from the same reef and pairs from different reefs ($P > 0.08$ for Mann-Whitney U-tests, although inter-reef pairings for *M. franksi* showed a trend toward increased aggressiveness). These general patterns were confirmed in less extensive trials in both Venezuela and the Bahamas.

Naturally occurring contacts in the field suggest that intraspecific aggression is

generally elicited over longer time periods. During a haphazard survey of interactions in the Salar region, 15 of 16 interactions involving *M. faveolata* (Fig. 5D, E) and 7 of 7 involving *M. franksi* had a band of dead coral separating the colonies (no intraspecific interactions involving *M. annularis* were seen). The band of dead coral appears to be wider in interspecific interactions (Fig. 5F), however (2 of 23 bands <2 cm in width for intraspecific interactions, versus 7 of 9 bands ≥2 cm in width for interspecific interactions between *M. faveolata* and *M. franksi*).

Protein Electrophoresis.—Biochemical data indicate that the three sibling species are closely related to each other but distinct (Table 4; Knowlton et al., 1992). All three members of the *M. annularis* species complex showed substantial differences from their sympatric congener *M. cavernosa,* with fixed or nearly fixed differences at five of nine loci. Nei's unbiased genetic distances between *M. cavernosa* and the three sibling species ranged from 1.04 to 1.13. Within the sibling species complex, *M. faveolata* was also quite distinct. This species differed strongly from *M. annularis* and *M. franksi,* with Nei's unbiased genetic distances of 0.24 and 0.26 respectively and strong differences at the malate dehydrogenase (MDHP1) locus. In contrast, *M. annularis* and *M. franksi* were very similar electrophoretically, with a Nei's unbiased genetic distance of only 0.06. Nevertheless, even at sites of sympatry the probability of misidentification (Ayala, 1983) between these two species was low ($P = 0.056$), when four loci were considered simultaneously (GTDH2, PGM1, LTY1 and LPP1) (Knowlton et al., 1992). Moreover, different populations of the same species were generally more similar than were different species from the same reef, so that populations of each species from different reefs clustered together using standard algorithms (Knowlton et al., 1992).

Corallite Morphometrics.—Univariate analyses showed highly significant differences (all pairwise P's < 0.001) in six characters: maximum and minimum spacing between calices, calicular diameter, columella diameter, primary septa length, and tertiary septa width (Table 2). The three species differed significantly in all pairwise comparisons of minimum spacing between calices, with *M. franksi* having the largest values and *M. faveolata* having the smallest values. Larger values for calice diameter, columella diameter, maximum spacing between calices, and tertiary septa length distinguished *M. franksi* from the others, while narrower primary septa distinguished *M. faveolata* from the others.

In a canonical discriminant analysis, six characters entered the analysis (Table 2). Large values for minimum and maximum calical spacing, tertiary septa length, and columella diameter contributed most heavily to positive scores for discriminant function 1. Large values for calice diameter and primary septa length contributed most heavily to positive scores for discriminant function 2. The analysis separated the three species with 87%, 87%, and 73% of *M. annularis, M. faveolata,* and *M. franksi* correctly assigned, respectively. There was little overlap among the polygons enclosing the canonical discriminant function scores for each species (Fig. 8). Colonies from a finite depth range on a single reef were just as often misclassified as colonies from other depths and reefs.

Distribution and Abundance.—All three species were abundant on the two protected and two semi-exposed reefs that we censused, and at intermediate depths (3–12 m) they were routinely found together. Nevertheless, percent cover data for these reefs (Fig. 9) revealed clear distributional differences among the species.

Montastraea annularis had the narrowest depth distribution, with the shallowest and deepest colonies on our transects found at 1 and 11 m respectively. *Montas-*

Table 4. Allele frequencies for the four Caribbean species of *Montastraea*

Locus Sample size Alleles	*annularis*	*faveolata*	*franksi*	*cavernosa*
TPI1 (Unidentified Isomerase, EC 5.3.1.–)				
(N)	53	51	56	32
A	0.094	0.020	—	—
B	0.906	0.980	1.000	1.000
TPI2 (Triose-phosphate Isomerase, EC 5.3.1.1)				
(N)	53	51	56	32
A	0.113	0.029	0.241	—
B	—	—	—	0.172
C	0.132	0.686	0.321	—
D	—	—	0.018	—
E	0.009	—	—	0.813
F	0.745	0.255	0.420	—
G	—	0.020	—	—
H	—	0.010	—	—
I	—	—	—	0.016
GPI1 (Glucose-6-phosphate Isomerase, EC 5.3.1.9)				
(N)	53	51	55	31
A	—	—	—	0.016
B	0.104	0.020	0.091	—
C	0.057	0.010	0.064	0.065
D	—	—	0.073	0.097
E	0.774	0.941	0.764	0.645
F	0.019	—	—	0.016
G	0.019	0.010	0.009	0.161
H	0.028	0.020	—	—
GTDH1 (Glutamate Dehydrogenase, EC 1.4.1.2)				
(N)	53	44	52	26
A	—	—	—	1.000
B	1.000	1.000	1.000	—
GTDH2 (Glutamate Dehydrogenase, EC 1.4.1.2)				
(N)	50	51	55	32
A	0.020	0.343	0.036	—
B	0.660	0.627	0.445	—
C	0.180	0.010	0.155	—
D	—	—	—	0.953
E	0.140	0.020	0.364	0.016
F	—	—	—	0.031
MDHP1 (Malate Dehydrogenase (NADP+), EC 1.1.1.40)				
(N)	52	50	51	32
A	—	—	—	0.063
B	—	—	0.049	0.125
C	—	0.010	0.098	0.094
D	0.933	0.070	0.853	0.391
E	0.048	0.850	—	0.219
F	0.019	0.070	—	0.109
PGM1 (Phosphoglucomutase, EC 5.4.2.2)				
(N)	48	49	47	31
A	0.021	0.010	0.277	0.435
B	0.250	0.082	0.170	0.387
C	0.094	0.112	0.096	0.177
D	0.563	0.347	0.223	—
E	0.073	0.296	0.234	—
F	—	0.133	—	—
G	—	0.020	—	—

Table 4. Continued

Locus Sample size Alleles	*annularis*	*faveolata*	*franksi*	*cavernosa*
LTY1 (Leucyl-tyrosine-peptidase, EC 3.4.11/13)				
(N)	48	45	50	31
A	0.010	—	—	1.000
B	0.479	0.411	0.800	—
C	0.500	0.522	0.200	—
D	0.010	0.067	—	—
LPP1 (Leucyl-proline-peptidase, EC 3.4.11/13)				
(N)	43	47	45	29
A	—	—	—	0.293
B	0.023	0.021	—	0.707
C	0.267	0.457	0.300	—
D	0.477	0.223	0.300	—
E	0.233	0.298	0.400	—

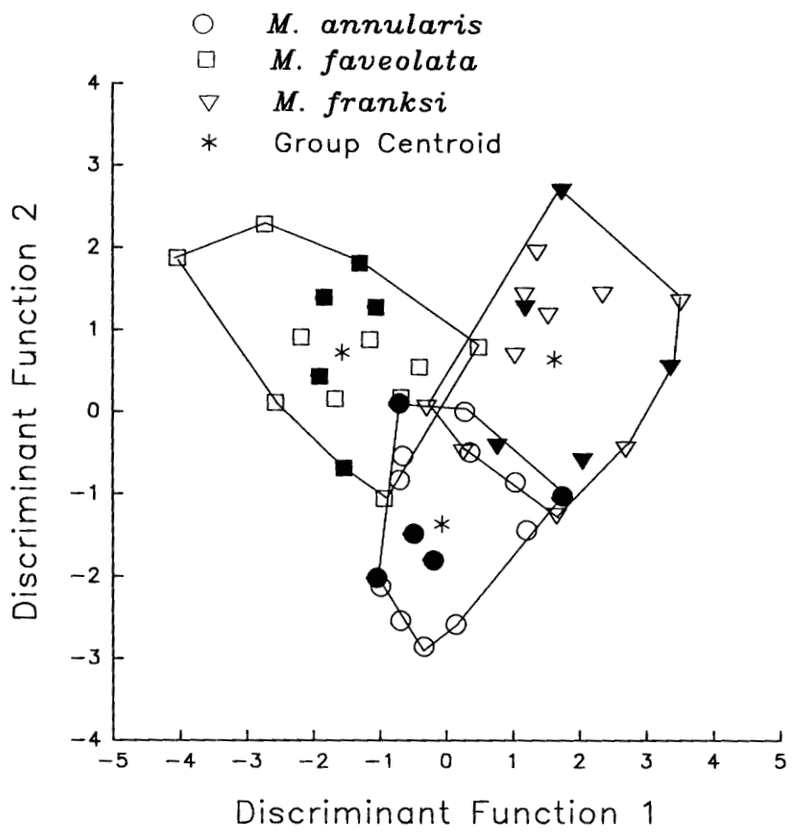
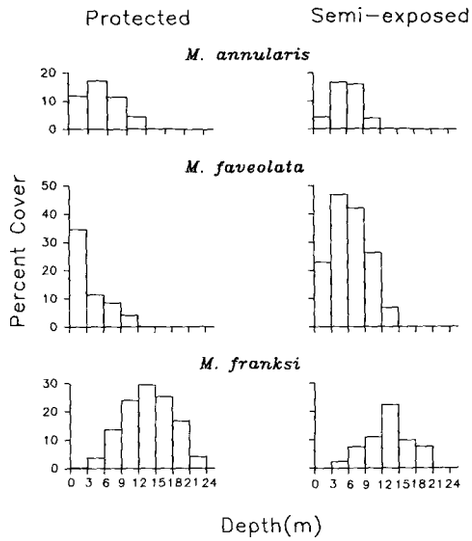


Figure 8. Canonical discriminant function scores for *M. annularis*, *M. faveolata* and *M. franksi*. Note that polygons enclosing all individuals of the same species show little overlap. Symbols for colonies from 7.5–12 m on Aguadargana reef are filled.



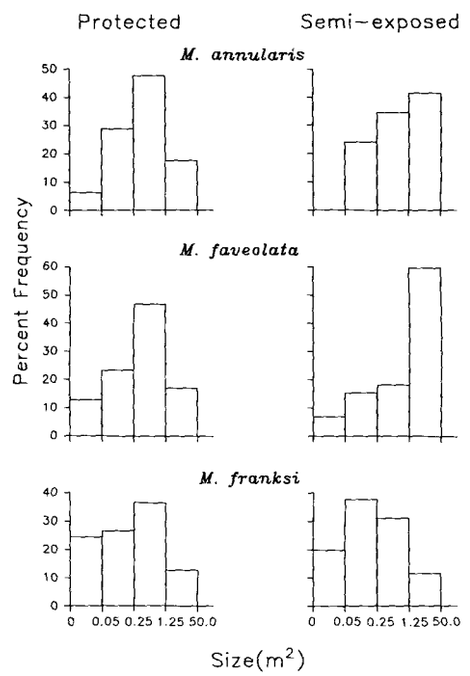


Figure 9. Interspecific variation in percent cover as estimated by linear transects, across a depth gradient for the two protected and two semi-exposed reefs.

Figure 10. Interspecific variation in distribution of size classes for colonies encountered on transects of the two protected and two semi-exposed reefs.

traea faveolata overlapped broadly with *M. annularis,* with minimum and maximum depths on the transects of 1 and 15 m. On the protected reefs, *M. faveolata* had its highest percent cover at 0–3 m, where it was the most abundant of the three species, while *M. annularis* was most abundant at 3–6 m and more abundant than *M. faveolata* at these depths. On the semi-exposed reefs, however, the zone of peak abundance for *M. faveolata* shifted downward and overlapped that of *M. annularis* (3–9 m). *Montastraea faveolata* was more abundant than *M. annularis* at all depths on these reefs. *Montastraea franksi* had the most distinctive depth distribution of the three species. On our transects it was found between 1.5 and 24 m, with a peak in abundance at 12–15 m, where it had the highest percent cover of the three species. *Montastraea franksi* was generally more abundant on the protected than semi-exposed reefs, while *M. faveolata* showed the reverse pattern.

On both protected and semi-exposed reefs, *M. franksi* had the greatest proportion of colonies in the smallest size categories, while *M. annularis* had the fewest (Fig. 10). Colony size distribution was markedly shifted to the largest size categories in semi-exposed habitats for *M. annularis* and *M. faveolata* but not for *M. franksi.*

Observations at other sites generally support the patterns seen on the reefs we transected. Nevertheless, the three species show considerable variability in relative abundance throughout their range, and on many reefs maximum depths are substantially deeper than those recorded on our transects.

DISCUSSION

Value of Multi-character Approach.—Many species of scleractinian corals are traditionally defined on the basis of corallite characters that often exhibit problematic variability within colonies and across habitats. Thus in recent years, several authors have argued for the utilization of other kinds of characters to separate closely related species (Lang, 1984; Willis, 1990). The strength of a multi-character approach is that debates over the adequacy of any particular character lose their importance in the face of a consistent pattern when all characters are considered together. When several unrelated character states reliably distinguish taxa from the same microhabitat, the argument for recognizing them as distinct species is particularly compelling (Wijsman-Best, 1974; see also Avise and Ball, 1990). This inference becomes even stronger when the same suites of characters can be found at a variety of sites.

Several independent lines of evidence—biochemical, behavioral, and morphological—consistently separate the three sibling species in areas of sympatry. Moreover, many of our results echo findings from other studies done elsewhere. A similar trio of morphotypes, with parallel differences in morphology, proteins and aggressive behavior, is found in Curaçao and Bonaire (Van Veghel and Bak, 1993). Several of Dustan's (1975a) Jamaican morphotypes can be unambiguously assigned to one of the three sibling species, and his comments concerning colony form, corallite morphology, color and depth distribution are entirely consistent with our observations. He also described a depth-related aggressive hierarchy (30 m > 1 m > 10 m; table 31, fig. 51) consistent with the aggressive hierarchy and depth distribution of the species described here. Tomascik (1990) showed that sympatric columnar and lobate colonies (*M. annularis* and *M. faveolata* respectively) in Barbados had consistent differences in growth rate across a variety of environmental conditions that parallel those we found (Knowlton et al., 1992). Hayes (1990), working elsewhere and independently in Panama, divided *M. annularis* sensu lato into three morphs based on colony form (lobate, plating, and irregular) that correspond to *M. annularis, M. faveolata* and *M. franksi* respectively (Hayes, pers. comm.). The existence of at least three widely distributed, often sympatric sibling species is the most parsimonious interpretation of these findings.

Nevertheless, the suites of covarying characters we have examined to date do not eliminate all potential confusion in identifying particular specimens. Morphological and biochemical characters have a range of ambiguity where species overlap. Rapid aggressive reactions that define species grade into more delayed, intraspecific histocompatibility reactions (our field surveys, see above; Logan, 1984; Lang and Chornesky, 1990), and could occasionally fail to develop altogether. Some specimens are likely to show ambiguity in several characters simply on the basis of chance, and occasional hybrids, whose existence is to be expected (Willis et al., 1992), will exacerbate this problem. Moreover, only skeletal characters are available from museum and fossil specimens, and those we used separate most but not all individuals.

These limitations, while hardly unique, point to the need for additional characters, analyses and experimental work. Our first priority is to develop more sensitive methods for distinguishing the species based on skeletal differences alone (Budd and Knowlton, in prep.), so that the large amount of already collected material can be reliably identified. Treating marginal and central corallites as separate characters may be particularly effective for non-fragmentary material because of the different growth patterns of these species. Analyses of mtDNA

(e.g., Holland et al., 1992) could provide better resolution than proteins, which are at their limit of usefulness in separating species pairs as closely related as *M. annularis* and *M. franksi.* Breeding studies may not, however, provide a clear-cut answer, because coral species often hybridize in the laboratory (or even occasionally in the field) (Willis et al., 1992).

Other Species in the M. annularis *Complex.*—As indicated previously (Knowlton et al., 1992), there may be additional species in the *M. annularis* complex in other environments and geographic regions, and perhaps in areas already explored by us.

Considerable uncertainty concerns the lower depth range of these species, since *M. annularis* sensu lato is reported from depths of 80 m (Goreau and Wells, 1967; Reed, 1985). *Montastraea faveolata* and particularly *M. franksi* appear to extend to greater depths than those we studied, but convergence to a flattened morphology at these depths makes it difficult to rule out the possibility of additional deep water species. Dustan (1975a), for example, describes the occurrence of flat plates ("type 6") and flat whorled colonies ("type 8") below 35 m in Jamaica, which may or may not represent additional species. Similarly, other habitats should be examined to see if they contain species with restricted environmental distributions.

Differences between corals from widely separated biogeographic regions also occur. For example, the very long columns of *M. annularis* in Barbados (Lewis, 1960, fig. 15) and Tobago (Lewis, pers. comm.) and the large lumpy colonies of *M. faveolata* from the Bahamas (Weil, pers. obs.) have not been observed in Panama or Venezuela. The significance of such differences is difficult to determine, for even if genetic differences between regions can be established, no hard and fast rule for distinguishing between geographic differentiation and speciation exists. Geographic subdivision of one or more of the species described here is conceivable, for example, northern and southern Caribbean species. Geographically narrow endemics may also occur, particularly in isolated regions such as Bermuda, the Flower Gardens, or Brazil. A multitude of geographically separated species within our described taxa seems unlikely in this non-brooding group, however.

Variability in aggressive response and color within our study areas also requires further study, although we found no clear evidence for other unrecognized species based on these characters. In shallow water, *M. franksi* shows the most variability in colony morphology, color, and intraspecific aggressive interactions. Of particular note were four pairs of *M. franksi* with an aggressive response comparable to that observed between species in timing and extent. These responses might represent an unusually well developed intraspecific histocompatibility reaction, however (Logan, 1985). There was no consistent relationship between color and aggressiveness in our experiments (some of the most aggressive intraspecific pairings of *M. franksi* occurred between pairs of the same color), and some natural, intraspecific contacts between gray and green morphs of both *M. annularis* and *M. faveolata* showed no signs of aggression (Fig. 5E). Electrophoretic analyses also failed to reveal any obvious pattern related to color differences or aggressive reactions within species (Van Veghel and Bak, 1993). The only exception was a chocolate brown morph of *M. faveolata* that showed minor biochemical and morphological differences whose significance remains unclear. Dustan (1975a) mentioned aggression between a dark brown and a grey/green colony, both with a "lumpy-round" morphology at 28 m in Jamaica, and Logan (1985) described consistent aggression between light and dark brown forms in Bermuda. The speed

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