CHARACTER RELEASE FOLLOWING EXTINCTION IN A CARIBBEAN REEF CORAL SPECIES COMPLEX

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Abstract.—The Pleistocene extinction of the widespread organ-pipe *Montastraea* coral had measurable morphological and ecological effects on surviving lineages of the *Montastraea* "*annularis*" species complex. Extinction of the organ-pipe *Montastraea* occurred after more than 500,000 years of dominance in the shallow-water reef habitat of Barbados. Extinction resulted in a morphological shift of the columnar *Montastraea* lineage from thick to thin columns in modern reef environments. Pleistocene colonies of the columnar morphotype sympatric with organ-pipe *Montastraea* showed greater column widths than those in allopatry. We subjected our data to a number of criteria for interpreting the morphological shift as character release following lifting of competitive pressure after extinction. The morphological differences do not appear to be due either to chance or to physical properties of the marine environment. Differential local extinction and recolonization of four members of the species complex did not occur on Barbados, so that the species coexisted and appear to have coevolved between more than 600,000 and 82,000 years ago. The morphological shift is related to coral growth form and growth rate, and thus reflects the acquisition of a primary resource in corals— light. Character release occurred at the same oceanic Caribbean island (Barbados) where environments have fluctuated with similar variance throughout the period of coexistence. Not only has competition among living members of the *Montastraea* "*annularis*" species complex been convincingly demonstrated, but trends in relative abundance among fossil members of the species complex strongly suggest that a competitive hierarchy was operating during their Pleistocene coexistence on Barbados. We also observed an ecological analogue to character release on another Caribbean island, Curaçao. The distribution and abundance of living columnar *M. annularis* s.s. and massive *M. faveolata* from the leeward reef crest in Curaçao is greater now than in the Pleistocene, when organ-pipe *Montastraea* dominated this shallow-water reef habitat. Extinction of the faster growing, shallow-water organ-pipe *Montastraea* resulted in higher abundance of the columnar *Montastraea* lineage in shallow-water habitats, where it shifted its morphology to one adapted to high light levels. The species extinction released surviving lineages from a competitive network that had resulted in lower rank abundance in the Pleistocene community and enhanced abundance of both columnar *M. annularis* s.s. and *M. faveolata* in modern communities. Full validation of our interpretation of character release must await experiments that demonstrate whether phenotypic differences between populations have a genetic basis. However, we believe the results of this study point to the important, yet heretofore neglected, role that biological interactions have played in the evolution of closely related reef coral species.

Key words.—Biological interaction, character release, coral reefs, corals, evolution, Pleistocene, species complex.

Ever since Brown and Wilson (1956) promoted the evolutionary role of interspecific competition in generating divergence among closely related species, ecologists and evolutionary biologists have been interested in the relationship between coevolution and competition (Schoener 1989). Perhaps one of the most enigmatic of evolutionary phenomena, and one surrounded in serious debate, is the notion of character displacement and its complement, character release. Grant (1972, pp. 44–45) defined character release as "the process by which a morphological character state of a species changes under natural selection arising from the absence, in the same environment, of one or more species similar to it ecologically and/or reproductively." Essentially, character displacement occurs when allopatry (species occupy different places) turns into sympatry (species occupy the same place), perhaps at the border between two species ranges. Character release occurs when sympatry turns into allopatry, through either geographic range changes or local or global extinction (i.e., temporal change).

For some workers, character displacement/release is a dominant coevolutionary force brought about through inter-specific competition (Grant 1972, 1986, 1994; Schluter and McPhail 1992; Schluter 1994). Others argue that morphological patterns can be ascribed to a number of selective forces, including climate conditions, resource availability, and selection for better dispersers or competitors (Dayan and Simberloff 1998; for a review, see Taper and Case 1992). Such a bewildering array of possible selective pressures confounds simple interpretation of morphological change among taxa (Dayan and Simberloff 1998).

Recent efforts to approach the study of character displacement have entailed considerable quantitative rigor (Dayan and Simberloff 1998). Schluter and McPhail (1992) summarized six criteria that need to be met before morphological or other phenotypic differences between competing species can be interpreted as character shifts (displacement or release; Table 1). Aside from these criteria, there are also temporal components that are necessary, but are not often available in evolutionary and ecological studies of character shifts in living taxa. Specifically, it may not always be possible to determine which are original and which are derived populations or both the precontact and postcontact character states (Kel-

TABLE 1. Six criteria for morphological character release in the *Montastraea* "*annularis*" species complex. Criteria after Schluter and McPhail (1992).

1. Can morphological changes be explained by chance?	no
2. Do phenotypic differences between populations have a genetic basis?	probably
3. Did the species coexist prior to the extinction?	yes
4. Does the morphological shift reflect acquisition of a primary resource (in corals, light)?	yes
5. Were environments before and after release greatly different?	no
6. Has competition been convincingly demonstrated among living members of the *M.* "*annularis*" species complex?	yes

log 1975). For fossil organisms, these criteria can often be met and have formed the basis for several inquiries into character displacement in the fossil record (Eldredge 1968; Eldredge and Gould 1972; Kellog 1975, 1980; Schindel and Gould 1977).

Coral reefs display a bewildering array of biodiversity, and workers confronted with the origin of that diversity are perplexed at how so many apparently similar species have evolved. Although a great deal of ecological work has focussed on the idea of redundant species on reefs and their role in ecosystem function (Done et al. 1996), there is very little, if any, empirical data on the origin of that diversity (Palumbi 1992; Pandolfi 1992). The study of natural selection in reef corals is impeded by the fact that they are so slow growing (but see Potts 1984). Most evolutionary work has been undertaken on the genetic structure of living populations (Palumbi 1997; Benzie 1999), including hybridization studies (Wallace and Willis 1994; Veron 1995), the molecular phylogeny of supraspecific taxa (Romano and Palumbi 1996), and biogeography (Rosen 1984; McManus 1985; Potts 1985; Pandolfi 1992). However, the ways in which natural selection results in divergence among closely related species, leading to the large diversity of coral species, are essentially unknown.

Corals are particularly well suited to studies of the evolutionary implications of interspecific competition because many studies of corals confirm the hypothesis of widespread interspecific competition (Lang and Chornesky 1990; Van Veghel et al. 1996). In the Caribbean Sea, corals have been a conspicuous, diverse component of coral reefs for at least the past 600,000 years and their hard calcareous skeletons make comparative morphometric studies of fossil and modern forms possible. These robust skeletons are well represented in the Pleistocene fossil record.

In this paper we present a number of patterns that show, when taken together, that ecological character release following Pleistocene extinction resulted in morphological convergence in a surviving lineage of a reef coral species complex. We summarize the morphological and molecular data that show species boundaries within the complex, then present data on morphological convergence, coral growth rates, species abundance patterns, and competition. The morphological convergence was accompanied by the reorganization of dominance patterns within the complex, leading to very different species abundance patterns in shallow-water living reefs. There are few good examples of character shift (see discussions in Grant 1972, 1994; Schluter and McPhail 1992), but the changes in surviving species of the *Montastraea* "*an-*

nularis" complex appear to meet all of the criteria where data are available (Table 1). Our example of character release shows how vacated niches were occupied following background extinction (Raup and Sepkoski 1982; Jablonski 1986) and the role of biological interactions in the ecology and evolution of reef corals. The results suggest that biological interactions have played an important role in the evolution of closely related reef coral species. The degree to which such influence may be a general characteristic of speciose taxa needs further study.

Testing a Hypothesis of Character Release

In this paper we submit our data to the six tests of Schluter and MacPhail (1992), which shed light on whether to accept a hypothesis of character release. In our approach, any analysis favoring character release should pass all of the critical tests for which it is possible to obtain the data (Table 1): (1) morphological changes must not be able to be explained by chance; (2) the phenotypic differences observed among populations must have a genetic basis, otherwise selection cannot be implicated; (3) the species must have coexisted prior to the point at which character release is thought to have operated; (4) the morphological shift must reflect acquisition of a primary resource, such as food, light, or space; (5) environments before and after character release must not be greatly different, otherwise the morphological change could simply be a phenotypic response to changed environmental conditions; and (6) competition must be demonstrated in the taxa under study. Our analysis provides direct tests of all of the criteria except for point 2 (the genetic basis of phenotypic differences; Table 1).

Once these tests have been passed, further ambiguities must be resolved, because similar patterns can be obtained from other evolutionary processes. For example, both the niche-variation hypothesis (Van Valen 1965; Grant 1967) and an increase in sexual dimorphism may result in the kind of morphological shifts associated with character release (Dayan and Simberloff 1998). These and other alternatives, although not mutually exclusive with character release, will be discussed.

THE *MONTASTRAEA* "*ANNULARIS*" SPECIES COMPLEX

Montastraea "*annularis*" has long held the interest of coral reef ecologists because it is one of the most dominant corals of Caribbean reefs (Goreau 1959). For decades, this coral was considered the archetypal generalist (Connell 1978), with both a seemingly limitless ability for phenotypic plasticity in growth form and a distribution ranging from the intertidal to more than 80 m water depth (Goreau and Wells 1967). The extensive variability in colony morphology (columns, massive heads, and sheets/plates) exhibited over this range was believed to be an adaptive response to differing light levels (Graus and Macintyre 1976). More recently, a number of features were found to covary with the different types of colony morphologies, including allozymes, reproductive biology, aggressive behavior, ecology, growth rate, corallite structure, and stable isotope composition (Knowlton et al. 1992, 1997; Van Veghel and Bak 1993, 1994; Van Veghel et al. 1996; Lopez et al. 1999). This concordance led

Weil and Knowlton (1994) to conclude that modern *M.* "*an-nularis*" sensu lato, long thought to represent one species, consists of a complex of at least three sympatric species in shallow- to mid-reef depths in Central America that differ in overall colony shape and the shape of the growing edge.

The three species of the living *M.* "*annularis*" species complex can be readily distinguished in the field using non-traditional morphologic characters related to overall colony shape and the colony growing edge. *Montastraea annularis* s.s. forms columns; *M. faveolata* forms smooth, skirted, massive mounds; and *M. franksi* forms bumpy, irregular mounds and plates. Initial morphological analyses of corallite measures revealed only minor differences among species in three key characters traditionally used to distinguish species of *Montastraea* (number of septa per corallite, calice diameter, and calice spacing; Knowlton et al. 1992; Weil and Knowlton 1994). However, morphometric analyses of nontraditional skeletal characters including septal relief and corallite structure show that the species are morphologically distinct (Budd and Johnson 1996; Knowlton and Budd 2001). It is presently unknown whether other modern growth forms from deeper water and more northern Caribbean localities will also show species-level differences.

Quantitative surveys of Pleistocene coral communities undertaken during the past 6 years have also yielded a number of growth forms of the *M.* "*annularis*" species complex in shallow-water deposits of the Caribbean Sea (Pandolfi and Jackson 1997, 2001, in press; Pandolfi 1999, 2001; Pandolfi et al. 1999). These include not only the massive, columnar, and sheet (plate) growth forms characteristic of *M. faveolata*, *M. annularis* s.s., and *M. franksi*, respectively, in the modern, but also one additional form that does not live today, the organ-pipe growth form.

Fossil Record and Phylogeny

The three modern species of the *M.* "*annularis*" complex arose prior to the high extinction peak at 2–1.5 million years ago, which occurred at the end of Late Pliocene to Early Pleistocene faunal turnover in Caribbean reef corals (Budd and Klaus 2001). Specifically *M. faveolata* and *M. franksi* are estimated to have originated between 4–3 million years ago. The entire complex consists of more than 10 species and extends back to at least late Miocene time. It is distinguished by circular corallites having three complete septal cycles (sometimes an incomplete fourth cycle) and corallite diameters less than 3.2 mm. Primary and secondary septa are generally equal in thickness, and if present, paliform lobes are weak. Preliminary phylogenetic analysis of morphotypes collected from the Early Pliocene to Early Pleistocene of the Dominican Republic, Costa Rica, and Panama (fig. 11 in Budd and Klaus 2001) indicates that the three modern species belong to different subclades within the complex, which appear to have diverged more than 4 million years ago. The analysis is based on eight characters examined in transverse thin section: corallite diameter, number of septa per corallite, corallite wall thickness, corallite wall structure, extension of costae beyond the wall, shape of tertiary costoseptae, paliforms lobes, and tertiary septum length (Budd and Klaus 2001). A subsequent analysis of 10 morphotypes (including

TABLE 2. Thirteen shape coordinates associated with the structure and development of the costoseptae and corallite wall were selected for morphometric analysis of two-dimensional characters from living colony surfaces of the *Montastraea* "*annularis*" species complex. Size and shape coordinates were calculated using two baselines (1–14, 1–12).

Shape coordinates	Baseline	Definition
x02	1–12	extension of secondary costa
x09	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

the three modern species, the two Pleistocene morphotypes [columnar and organ-pipe], and five morphotypes [2, 6–9] from the Plio-Pleistocene of Costa Rica and Panama; after Budd and Klaus 2001) using the corallite characters listed in Table 2, confirms the distinctions among the three subclades and shows that the Pleistocene columnar and organ-pipe morphotypes are most closely related to *M. annularis* s.s. (Fig. 1). Unlike the other seven taxa in the analysis, the relationships between the three members of the *M. annularis* subclade are poorly resolved, and no apomorphies support either *M. annularis* s.s. or the Pleistocene columnar morphotype. The grouping of the two Pleistocene morphotypes is supported by possession of a thin corallite wall. The organ-pipe morphotype itself is supported by the possession of a parathecal wall. Both additional characters (e.g., longitudinal characters based on dissepiments and the columella and colony-level characters based on budding patterns and extension rates) and additional samples need to be included in the analysis to better determine the timing and pattern of divergence between *M. annularis* s.s. and the Pleistocene columnar and organ-pipe morphotypes. We view these relationships as preliminary; in fact, in this paper we treat the Pleistocene columnar *Montastraea* and *M. annularis* s.s. as a single lineage, despite their separation on the cladogram (see below).

Comparative Taxonomy and Morphometric Analyses of the Montastraea "annularis" Complex

Although species within complexes of scleractinian corals overlap considerably in traditional morphologic characters, work on the coral genus *Porites* has demonstrated that multivariate statistical analyses of three-dimensional landmark data are effective at teasing apart morphologically similar clusters of colonies (i.e., morphospecies) that are electrophoretically distinct (Potts et al. 1993; Budd et al. 1994; Johnson and Budd 1996; Budd and Johnson 1996). This result agrees with the findings of Jackson and Cheetham (1990, 1994) on bryozoans. Thus, morphometric approaches hold great promise for reconstructing phylogenies at the species level in colonial marine invertebrates

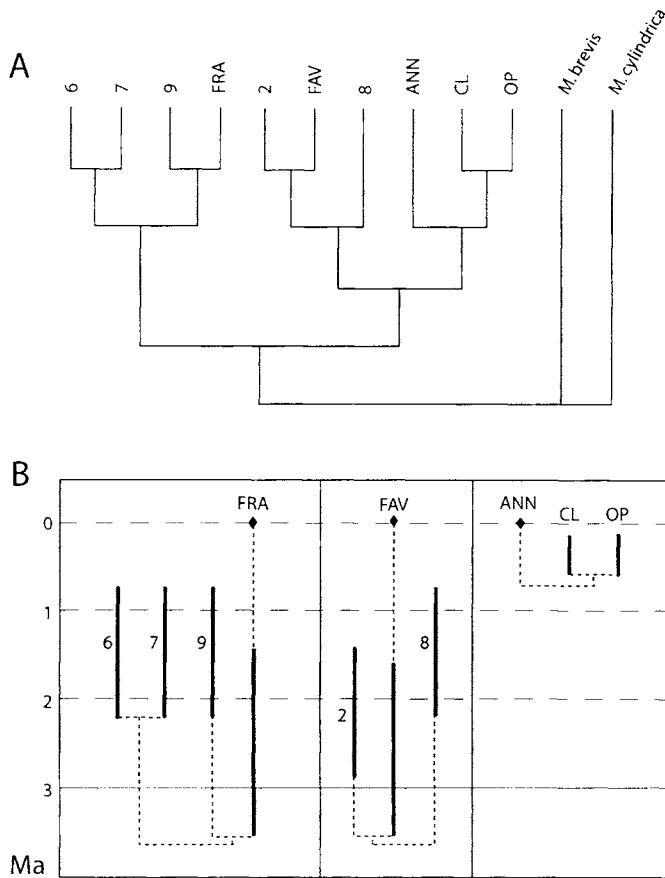Our first goal was to establish that the fossil and modern

FIG. 1. (A) Cladogram and (B) phylogenetic tree constructed by calibrating the cladogram with the known stratigraphic ranges of each taxon from the *Montastraea* "*annularis*" species complex. 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 refer to the Costa Rican and Panamanian morphotypes (Budd and Klaus 2001); ANN, modern *M. annularis* s.s.; FRA, modern *M. franksi*; FAV, modern *M. faveolata*; CL, Pleistocene columnar morphotype; OP, Pleistocene organ-pipe morphotype. The cladogram was constructed using a heuristic search in PAUP 4.0b6 for Microsoft Windows (Swofford 2000) and two Mio-Pliocene species, *M. brevis* and *M. cylindrica*, as outgroups. The search resulted in a total of two most parsimonious trees consisting of 27 steps each (CI = 0.667, HI = 0.333, RI = 0.743, RC = 0.495). The two trees differ in the placement of morphotype 9 within the *M. franksi* subclade.

species of the *M.* "*annularis*" complex could be distinguished morphologically. We began by obtaining three-dimensional Cartesian coordinates for 25 landmarks on calices of 30 living colonies collected in Panama (10 *M. annularis* s.s., 10 *M. faveolata*, and 10 *M. franksi*) using a three-dimensional Reflex (Reflex Measurement Somerset, U.K.) microscope. To account for intracolony variability, points along three adjacent costosepta were digitized from six calices on samples from the top and edge of each colony. Size and shape coordinates (Bookstein 1991) were calculated for a baseline defined by three points using the computer program GRF-ND (generalized rotational fitting of *n*-dimensional landmark data, 1994, written by D. E. Slice and available via http://life.bio.sunysb.edu/morph/). The resulting size and shape co-

ordinates were used to calculate Mahalanobis' distances among colonies, which were analyzed using average linkage cluster analysis (for multivariate statistical methods, see Marcus 1993). The resulting dendrogram clearly shows the three species in the complex to be distinct, with *M. annularis* s.s. and *M. franksi* being most similar (see Fig. 2A). Canonical discriminant analysis indicated that the most important variables in discriminating species consist of nontraditional morphologic characters related to the elevation and development of the costae and the shape of the septal margin (Budd and Johnson 1996; Knowlton and Budd 2001). Thus, three-dimensional landmark methods are capable of distinguishing among corallites of the three species (Fig. 2A). These results agree strongly with molecular analyses performed on the same specimens by Knowlton and Budd (2001).

Applying morphometric analyses of three-dimensional landmark data is difficult in fossil material, because many of the features that distinguish closely related species in three dimensions are worn or recrystallized. To determine if two-dimensional characters are diagnostic, we digitized 27 landmarks in two dimensions on transverse thin-sections of six corallites from the tops and six corallites from edges of the same 30 colonies of the *M.* "*annularis*" complex as above (Fig. 3). Size and shape coordinates (Bookstein 1991) were calculated for two baselines (1–14, 1–12) using the computer program GRF-ND. Thirteen shape coordinates (Table 2) associated with the structure and development of the costoseptae and corallite wall were selected for analysis. Results from the two-dimensional analysis again showed three distinct clusters with no overlap (Fig. 2B). Qualitative differences also appear to exist in wall structure. In *M. faveolata*, the septa do not thicken significantly and the wall is formed primarily by dissepiments. In contrast, in *M. franksi*, the wall is formed exclusively by septal thickening and coalesced thick costae extend variably between adjacent corallites. In *M. annularis* s.s., the wall structure is similar to *M. franski*, except the costae are less variable and not coalesced (Fig. 4).

Finally, we collected the same size and shape coordinate data for fossil specimens (10 organ-pipe *Montastraea* and 15 columnar *Montastraea*) from the 82,000-year-old reef on Barbados and added them to the dataset. Canonical discriminant analysis of two-dimensional landmark data on corallites of the three living species and Pleistocene organpipe and columnar *Montastraea* showed divergent morphology among all taxa and morphotypes (Fig. 5). The two-dimensional data for the Pleistocene organ-pipe species are most similar to living *M. annularis* s.s., whereas the two-dimensional data for the Pleistocene columnar morphotype are most similar to living *M. faveolata* (Fig. 4)

The Pleistocene Organ-pipe and Columnar Forms of Montastraea

Our evidence indicates that the extinct organ-pipe *Montastraea* was a distinct species from the living members of the species complex, insofar as species can be differentiated based on morphological criteria. Moreover, it appears that crucial differences exist between the extinct organ-pipe species and the Pleistocene columnar form, so the two are dif-
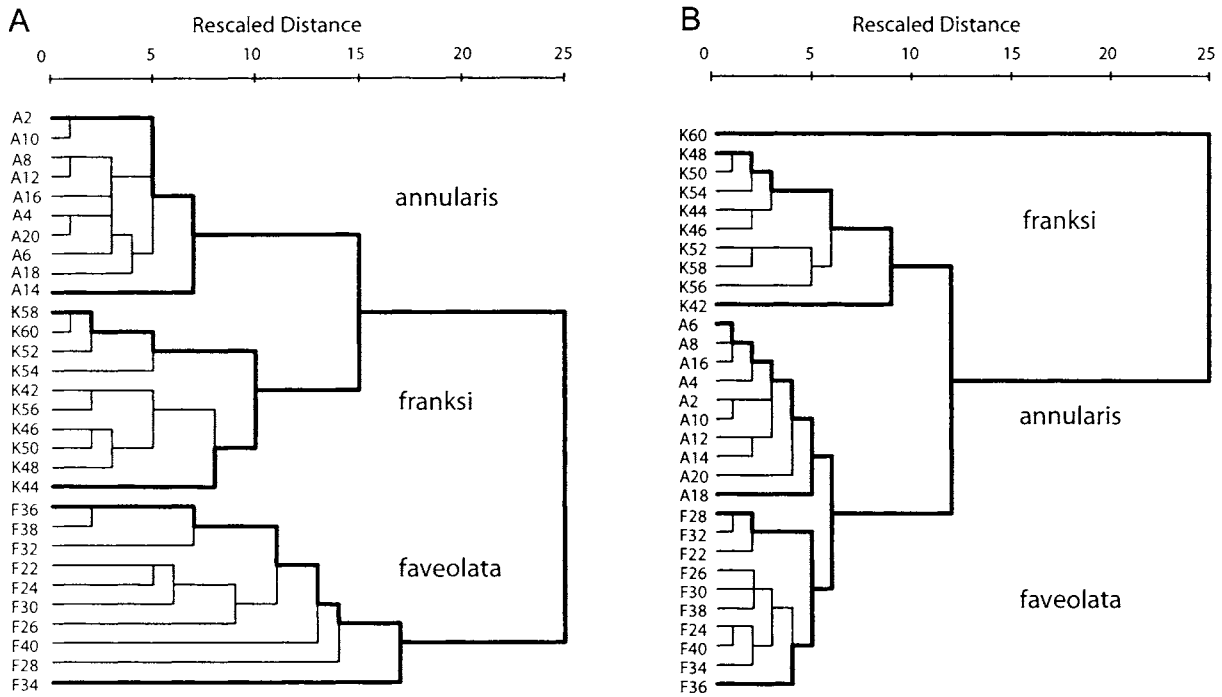
FIG. 2. (A) Cluster analysis of three-dimensional landmark data on calices of living species of the *Montastraea* "*annularis*" complex. (B) Cluster analysis of two-dimensional landmark data on corallites of living species of the *M.* "*annularis*" complex. Each branch of each dendrogram represents one colony. Both dendrograms clearly show the three species in the complex to be distinct. A, *M. annularis* s.s.; F, *M. faveolata*; K, *M. franksi*.
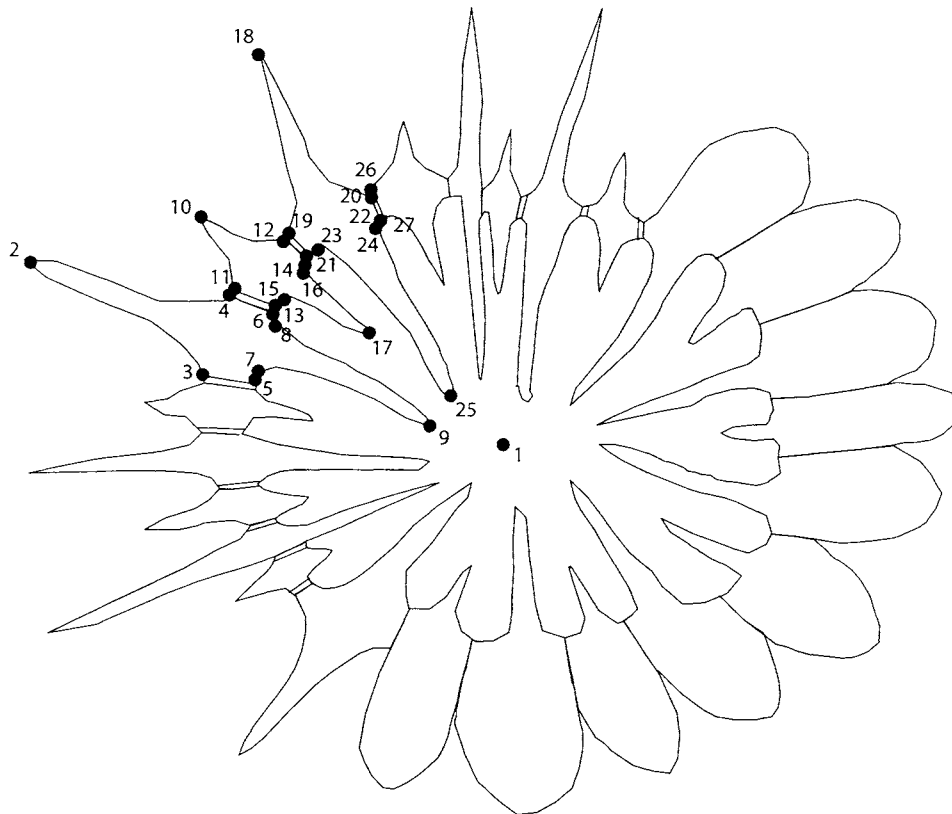

FIG. 3. Two-dimensional Cartesian coordinates collected for 27 landmarks on transverse thin sections of corallites of 30 living colonies (10 *Montastraea annularis* s.s., 10 *M. faveolata*, and 10 *M. franksi*) and 25 Pleistocene colonies (10 organ-pipe and 15 columnar *Montastraea*).
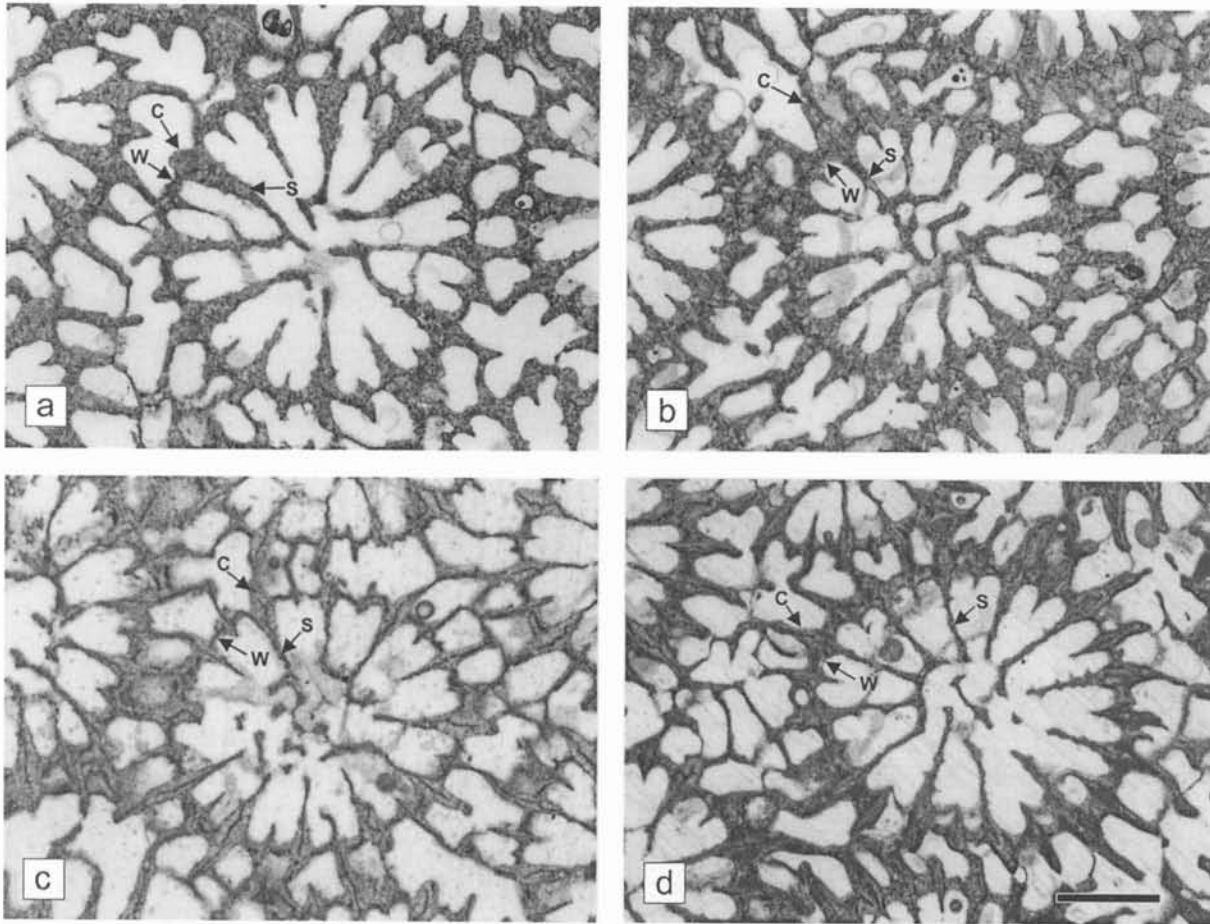
FIG. 4.   Transverse thin sections of representative corallites of similar living and Pleistocene lineages. (A) Modern *Montastraea faveolata* (96-16TM). (B) Modern *M. annularis* s.s. (95-39TM). (C) Pleistocene columnar morphotype (c71-1). (D) Pleistocene organ-pipe species (op92-1). Corallite morphologies of the two Pleistocene lineages (C, D) and the two closest living species (A, B) clearly differ, indicating either four distinct species or that corallite traits vary with growth form differences. The two Pleistocene lineages have generally thinner septae (s), and thinner and shorter costa (c) than the living species. The Pleistocene organ-pipe species (D) is similar to living *M. annularis* s.s. (B) in its moderately thick walls (w), and the Pleistocene columnar morphotype (C) is similar to living *M. faveolata* (A) in its thin walls, which are formed by dissepiment instead of coalesced costosepta. These qualitative observations are supported by the canonical discriminant analysis shown in Figure 5. Scale bar = 1 mm.

ferent morphospecies in the fossil strata (Fig. 5). The organ-pipe *Montastraea* can be distinguished from Pleistocene columnar *Montastraea* and living *M. annularis* s.s. in the field based on mode of branch formation and corallite senescence along column margins (Fig. 6). Pleistocene organ-pipe *Montastraea* have a very distinct growth form composed of slender branches, or pipes, that rise rom a common base. Both pipes and colonies may eventually reach a height of 2–3 m, and colonies are up to 8 m wide (Pandolfi et al. 2001). Hoffmeister and Multer (1968, p. 1491) noted that the mature colonies of the organpipe *Montastraea* "can be likened to a huge pincushion from which protrude numerous closely set club-shaped pins." The pipes are thin with a mean width of 7.8 cm in Barbados (SD 2.7 cm, $n = 426$ branches).

The extinct organ-pipe form has a very different morphology than other species of the *M.* "*annularis*" species complex. Both living columnar *M. annularis* s.s. and Pleistocene columnar *Montastraea* have much broader columns that diverge from one another throughout colony development (Fig. 6; Pandolfi et al. 2001). Living colonies commonly

attain diameters and heights of up to 3 m and have been described throughout the Caribbean (see references in Pandolfi et al. 2001). Narrow columns more suggestive of the extinct organ-pipe form than typical *M. annularis* s.s. can also develop, but their mode of formation is usually different. Such narrow branches usually form as a result of dying back of originally large columns and they do not extend very far back toward the base of the colony (Pandolfi et al. 2001). Scatterday (1974) described this process in *M.* "*annularis*" from Bonaire. Finally, based on comparative taphonomy, organ-pipe *Montastraea* had living corallites along the column or branch margins and sides (very little bioerosion along column margins), whereas living and fossil columnar *Montastraea* are characterized by sides of columns with dead and senescent corallites (heavily bioeroded in fossil specimens; Fig. 6).

Although we are confident that the organ-pipe growth form is a separate, extinct species of the *M.* "*annularis*" species complex, we are more hesitant to interpret Pleistocene columnar *Montastraea* as a separate species, even though it is
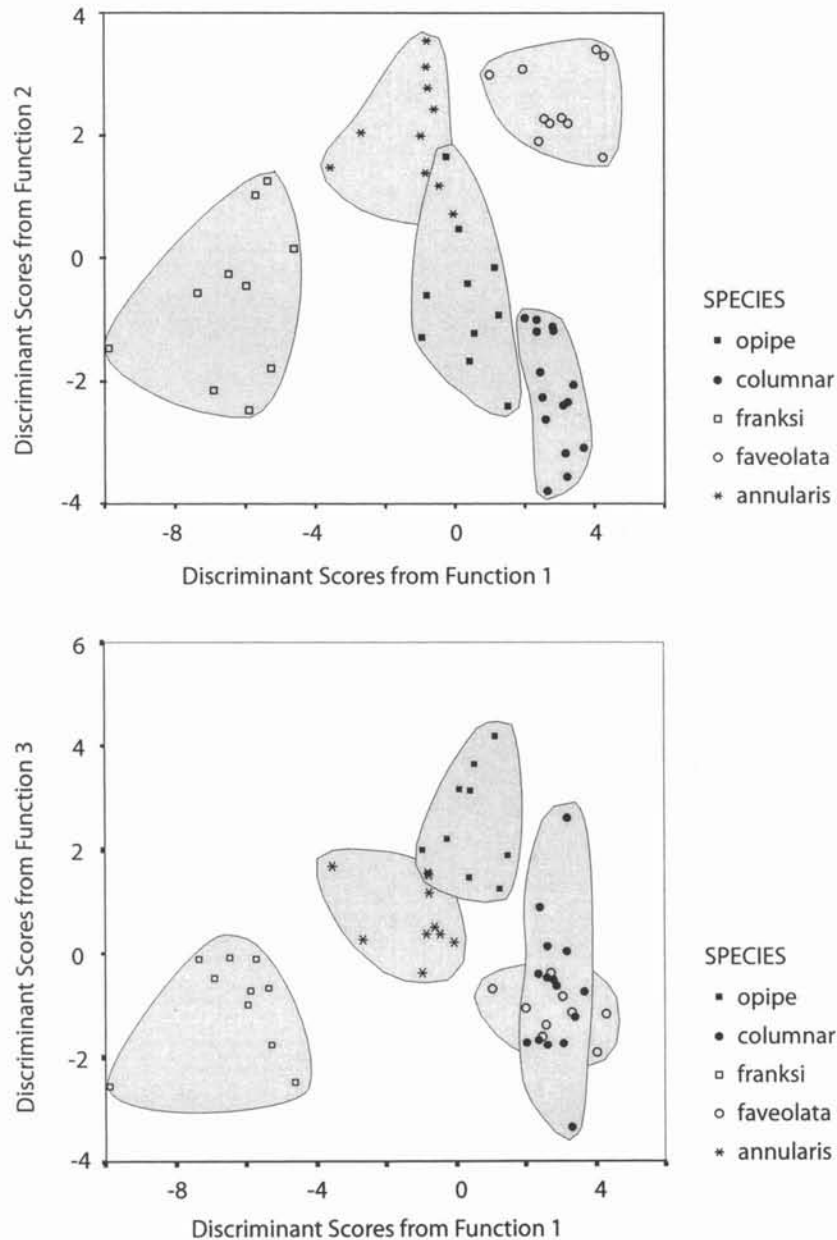
FIG. 5. Canonical discriminant analysis of two-dimensional landmark data on corallites of the three living species and Pleistocene organ-pipe (opipe) and columnar *Montastraea*. Each point on the two plots represents one colony. The five lineages are clearly distinct. The first four discriminant functions in the analysis were statistically significant; function 1 accounts for 66.7% of the variance, function 2, 20.0%, and function 3, 10.2%. Two coordinates associated with wall thickness (x21, x14) are significantly correlated with function 1; three coordinates associated with costoseptum width and length (x16, y22–y21, x2) with function 2; and three coordinates associated with wall dissepiments (y19, y21, y11) with function 3.

clearly distinct in the canonical discriminant analysis (Fig. 5, top panel). First, column widths and colony growth (astogeny) are very similar to living columnar *M. annularis* s.s. Second, the relationships between colony form and corallite architecture are poorly understood. The shift in corallite morphology observed between Pleistocene and living columnar morphotypes in the canonical discriminant analysis (Fig. 5) may have been linked to the shift in column width after the extinction of organ-pipe *Montastraea*. We are currently exploring the relationships between corallite characters (documented in the present study using transverse thin sections)

and features associated with upward colony growth (longitudinal thin sections) to decipher possible linkages and constraints between morphology at the corallite and colony levels. Third, our morphometric analysis is based on specimens collected from a single place, Barbados, so unlike the organ-pipe form that has been recorded across the Caribbean region, we do not yet have a clear indication of the biogeographic variability associated with the Pleistocene columnar growth form. For the remainder of this paper, we refer to living *M. annularis* s.s. and Pleistocene columnar *Montastraea* together as "the columnar *Montastraea* lineage."
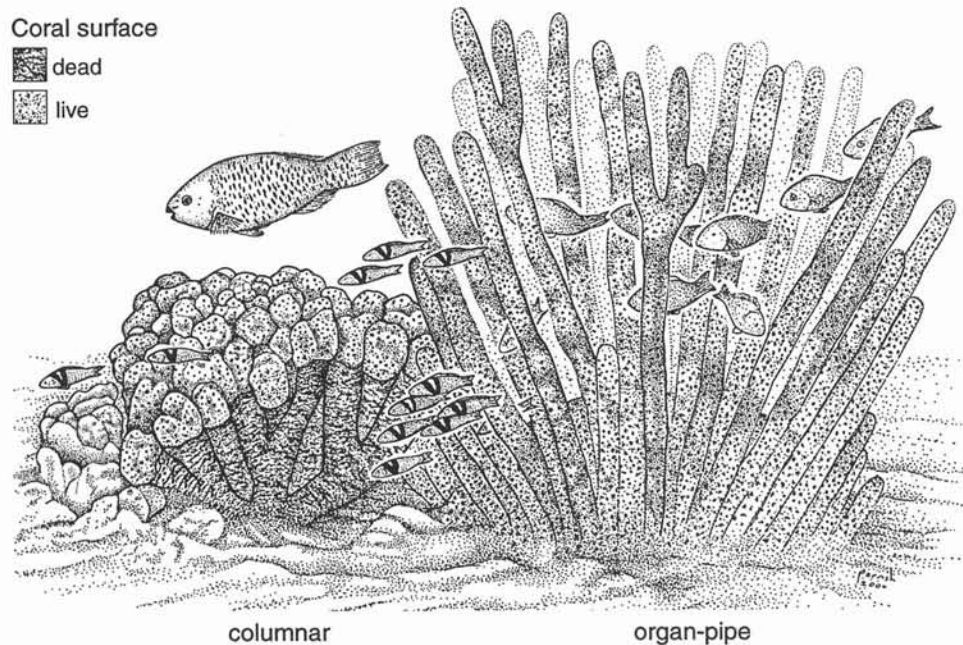
FIG. 6. Representation of a portion of a Pleistocene reef. Organ-pipe *Montastraea* grew fastest in shallow water, had columns that usually extended most of the length of the colony, and maintained living corallites along the entire length of their thin columns. The columnar *Montastraea* lineage grew more slowly, had columns that continually diverged during colony development, and maintained living corallites only on the top and periphery of the columns. (Figure drafted by M. Parrish.)

The Extinction of Organ-pipe Montastraea

The organ-pipe *Montastraea* went extinct sometime between 82,000 and 3,000 years ago, well before human occupation of the Americas (consensus now at 13,000–14,000 years ago) could have made any difference (Meltzer 1997). The known range of the extinct form is more than 600,000 to 82,000 years ago, both oldest and youngest occurrences from Barbados. Although 3.5-in cores have been drilled, there are no reliable ecological surveys of Caribbean coral communities aged between 82,000 and 3,000 years. The species was abundant in local populations throughout the Caribbean and in Barbados throughout its entire 500,000-year existence. It was also one of the most dominant corals in Pleistocene shallow-water settings throughout the Caribbean. Moreover, the coral had a broad ecological range, from protected back reef areas behind barrier reef crests to leeward and windward reef crest habitats. We have so far recognized this species from the Pleistocene of the Florida Keys, Barbados, Curaçao, San Andrés, Grand Cayman Island, the Bahamas, and the Dominican Republic, almost all situated well away from continental areas, so it probably favored an insular distribution. It clearly had a major ecological role in the communities in which it lived (Pandolfi 1999; Pandolfi et al. 2001).

MATERIALS AND METHODS

We used a variety of techniques to investigate the morphological response of surviving lineages of the *M.* "*annularis*" species complex following extinction of the organ-pipe *Montastraea*. During our Pleistocene census of the species abundance patterns on Barbados (see next section below), we measured column widths of both the organ-pipe and columnar *Montastraea*. Measurements were taken when the

two species were both in allopatry and in sympatry. We also measured column widths in 78 living colonies of columnar *M. annularis* s.s. from shallow reefs around Barbados and 16 living colonies from shallow reefs around nearby St. Vincent Island.

Pleistocene Species Abundance Patterns

Barbados

Study site.—We chose Barbados to examine trends in Late Pleistocene abundance of four morphotypes of the *M.* "*annularis*" species complex over the past 600,000 years because the fossil record is more complete and better studied there than anywhere else in the Caribbean, where Late Pleistocene reefs older than 125,000 years can be observed. Most of Barbados is covered by a series of raised reef tracts represented as geomorphological terraces. Reef growth occurred from more than 600,000 to 82,000 years ago around more than half of the island, and abundant corals are well preserved throughout (Bender et al. 1979; Radtke et al. 1988; Bard et al. 1990; Humphrey 1997). The majority of the reef-building episodes preserve transgressive reefs that were deposited during glacioeustatic sea-level rise. In general, the reefs are youngest at the periphery of the island and progressively older toward the interior. The terraces preserve the original fossil reef geomorphology as well as the original zonation patterns of the corals with respect to water depth

The geochronology of the Barbados reef terraces is known comprehensively (Bender et al. 1979; Edwards et al. 1987; Banner et al. 1991; Gallup et al. 1994). The geochronology can be correlated to interglacial sea-level highstands found in the marine oxygen isotope record, especially for the younger terraces on the island. Detailed geologic and stratigraphic

studies also provide a general framework for the relative age and correlation of reef terraces around the island (Mesolella 1967, 1968; Mesolella et al. 1970; Ku et al. 1990; Taylor and Mann 1991; Gallup et al. 1994).

Mesolella (1967) used the distribution and abundance of corals living in Jamaica (Goreau 1959) as a guide to describing zonation patterns in the Pleistocene of Barbados, and in general found excellent correspondence between the Recent and fossil communities (see also Jackson 1992). Interpretations of paleoenvironments and paleodepths were made quasi-independently of the corals using the terrace geomorphology (tops of reef terraces as a datum), physical characteristics of the sediments, and facies relationships (Mesolella 1967, 1968; Mesolella et al. 1970; for discussion of paleoenvironmental interpretation in Pleistocene reefs of the Caribbean, see Pandolfi et al. 1999). Subsequent workers have refined and corroborated these environmental interpretations based on carbonate diagenesis (James 1974), refined age dating (Bender et al. 1979), sequence stratigraphy (Humphrey and Kimbell 1990), and epibionts (Martindale 1992).

The typical coral zonation with increasing depth is as follows: shallow reef crest (0–5 m) dominated by *Acropora palmata*, shallow to mid fore-reef slope (5–20 m) characterized by *Acropora cervicornis*, and deep fore-reef slope characterized by a diverse assemblage of head corals. Commonly a buttress zone is developed between the shallow reef crest and shallow to mid fore-reef zones. In 1996 we made a quantitative census of the relative abundance of coral species in each of these environments on the 125,000-year terrace at 58 localities around the island (J. Pandolfi, unpubl. data). The results supported Mesolella's (1967) zonation based on qualitative observations, which we therefore used as a general framework for our censuses of the relative abundance of the different Pleistocene lineages in the *M.* "*annularis*" complex.

We investigated the species distribution patterns of four fossil morphotypes of the *M.* "*annularis*" species complex (organ-pipe, columnar, massive, and sheet) in communities dated between 600,000 and 82,000 years ago on the raised reef terraces on Barbados. These four Late Pleistocene morphotypes are all common to abundant throughout the island during this interval

Sampling.—We made a quantitative census of the *M.* "*annularis*" complex along 49 transects that came from the shallow fore-reef "buttress zone" and 23 transects that came from the deep fore-reef environment "head coral zone" (terminology of Mesolella 1967). We chose localities for these transects by three strict criteria to assure that we were sampling reasonably intact communities with minimal transport. First, we sampled only transgressive reefs. A transgressive reef is built during rising sea level over older sediments and usually only contains corals that lived during the same reef building event. Regressive reefs are built during sea-level fall over a previous transgressive reef and therefore may contain corals that are stratigraphically indistinguishable from the underlying or adjacent transgressive reef. By sampling only transgressive reefs, we minimized the problem of including corals from different time periods in a single assemblage. Coral growth during regressive phases is distinguished from that during transgressive phases by two traits: (1) re-

gressive corals are generally ponded on top of or in surface depressions of the transgressive reef, and are easily separated from the transgressive reef surface; and (2) they occur in a fine-grained matrix characterized by terrigenous debris that represents land runoff during sea-level fall. In practice, distinguishing between the two is not generally difficult. Second, we only sampled reefs where the top of the geomorphological terrace was exposed to provide a clear sea-level datum with the entire reef zonation below. Exceptions were made only when incomplete sections could be stratigraphically correlated unambiguously with adjacent complete sections. Third, we only sampled where the majority of corals were in upright and growth position and usually whole. The overwhelming majority of corals in the transects were upright and whole (Pandolfi et al. 2001).

The age of Pleistocene reefs at Barbados increases with elevation for most reefs that have been dated by radiometric methods (Humphrey 1997). We therefore used elevation as a proxy for age in our analyses of temporal abundance. This allowed us to sample a much greater spatial and temporal range of localities than would have been possible if we had only sampled places where radiometric age dates were available. The assumption of a positive linear relationship between terrace age and elevation inevitably introduces some error due to the complex terrain and geological history of Barbados and the dense human settlement on the island that may obscure faults and other geological complexities. However, because these errors were confined to narrow temporal ranges relative to the total range of the study and involved very few of the transects, we judged them to be small for our purposes of analyses of overall temporal trends.

Censuses were made by laying a 40-m tape across the rock outcrop and recording the position and length along the transect of all colonies of the four morphotypes of the *M.* "*annularis*" complex using standard line intercept transect procedures (Loya 1972, 1978). If there was no colony directly intercepting the transect tape, colonies were recorded if they were within 50 cm above or below the tape. We analyzed our data on a per meter basis. Because of the high frequency of zero occurrences, individual morphotype abundance per meter was transformed using the $\arcsin\sqrt{\log(\text{abundance}/m + 1)}$, which provided the closest fit to a normal distribution. The transformed variable for each morphotype in each environment was plotted against time and a regression line was fitted. We used the Spearman rank correlation coefficient to assess the significance of association of each morphotype pair in each environment, using the raw (untransformed) abundance per meter of transect. Results are presented in tabular form.

We also censused the whole coral community, concentrating on the 125,000-year-old reef, in the major reef environments recognized on Barbados. This provided us with an understanding of the other corals that lived with the *M.* "*annularis*" species complex during the Pleistocene. These results are also presented in tabular form.

Curaçao

During the course of a separate study on the raised reef terraces of Curaçao, we gathered data on Pleistocene distribution patterns of the entire reef coral community from 40-
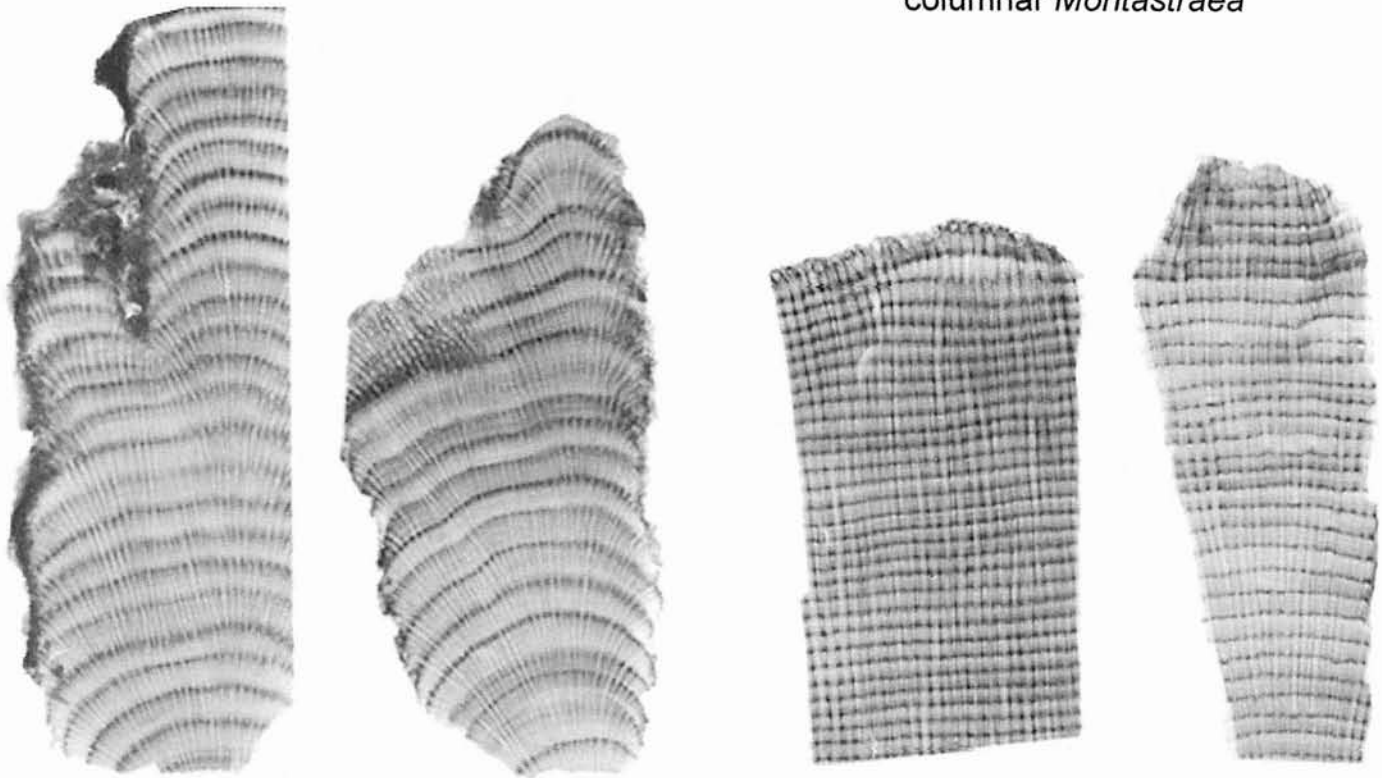
organ-pipe *Montastraea*

columnar *Montastraea*

Fig. 7. X-radiographs of slabs of the Pleistocene coral skeletons of organ-pipe *Montastraea* and columnar *Montastraea* from the same age and environment in the 82,000-year-old reef terrace in Barbados. Higher growth rates (thicker bands) existed in the organ pipe than the columnar form. Scale, from left to right: ×0.40, ×0.38, ×0.48, ×0.48.

m transects of the 125,000-year-old Hato Unit of the Lower Terrace (see methods in Pandolfi and Jackson 2001). The data on Pleistocene distribution patterns were compared with surveys taken on the adjacent modern reef (Van Veghel 1994a).

Coral Growth Rates

Living coral colonies

To understand the relationship between growth rate and growth form, we collected data from five published reports of growth rates of various growth forms of M. *"annularis"* (see the Appendix for a full description of the data). Growth rates were determined in these studies using marker dyes (Van Veghel and Bosscher 1995) and by measuring the width of annual density band couplets, termed "growth band," using X-radiographs (Dodge and Brass 1984; Hubbard and Scaturo 1985; Tomascik 1990; Hudson et al. 1994). Most of these studies were completed prior to the establishment of the different growth forms as different species, and there are surely errors associating a one-to-one correspondence between overall growth form and species identification (Weil and Knowlton 1994). However, there is no apparent reason to suspect an inherent bias in misidentification of species.

We included only those studies that reported linear extension rates on colonies that could be unambiguously attributed to the different growth forms of M. *"annularis."* Data for colonies that had transitional morphologies were omitted from our analysis. Many earlier pioneering reports of growth rates of M. *"annularis"* (e.g., Dustan 1975; Graus and Macintyre 1982; Dodge and Lang 1983; Huston 1985) could not be incorporated because, although these authors recognized differences in colony morphology with depth, they did not indicate colony morphology for the growth data. Moreover, our survey only used papers that reported specific depths and habitats for the measured colonies.

Pleistocene coral colonies

We measured growth rates from X-radiographs of slabs of Pleistocene coral skeletons in organ-pipe and columnar *Montastraea* from the 82,000-year terrace from a shallow-water back-reef environment on Barbados. This is the last known co-occurrence of these two morphotypes. Growth rates can be calculated by measuring the thickness of yearly growth bands over multiple cycles (see Fig. 7; Buddemeier and Kinzie 1976). We counted the number of yearly growth bands along the axis of maximum colony growth of 27 slabbed

Pleistocene organ-pipe *Montastraea* N = 426
Pleistocene columnar *Montastraea* N = 462
Living *M. annularis* s.s. N = 447
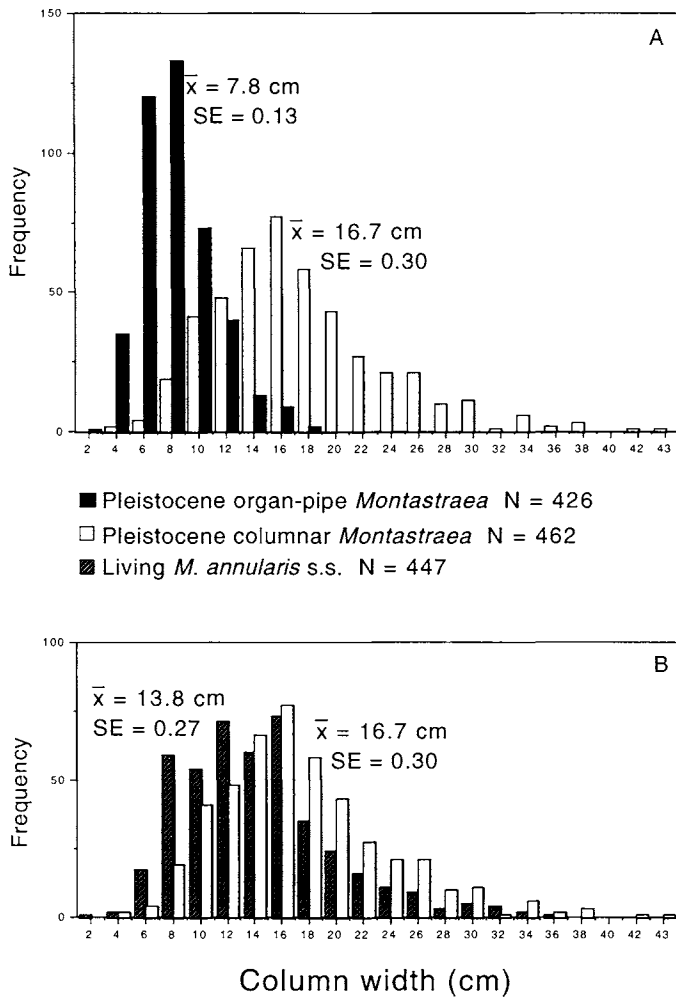

Column width (cm)

FIG. 8. Column width of living *Montastraea annularis* s.s., Pleistocene columnar *Montastraea*, and Pleistocene organ-pipe *Montastraea* from Barbados. (A) Pleistocene organ-pipe and columnar *Montastraea* show clear differences in column width. (B) Following the extinction of the organ-pipe form, living columnar *M. annularis* s.s. displayed more slender column widths than Pleistocene columnar *Montastraea*, but not as slender as the extinct organ-pipe species. SE, standard error on the mean.

columnar and 30 slabbed organ-pipe colonies to obtain an estimate of growth rate in these ancient corals. Mean length of colony surveyed was 9.00 cm (SD = 4.42) for the columnar morphotype and 10.83 cm (SD = 4.44) for the organ-pipe species.

RESULTS

The Pleistocene organ-pipe species had significantly thinner columns than both the Pleistocene columnar *Montastraea* and living *M. annularis* s.s. (see Fig. 8; Table 3). However, living *M. annularis* s.s. also had significantly thinner columns than Pleistocene columnar *Montastraea* (see Fig. 8; Table 3). Moreover, the width of Pleistocene columnar *Montastraea* columns was significantly greater when it was found in sympatry (along the same 40-m transect) with organ-pipe *Montastraea* (*N* = 366; mean = 17.2 cm; SD = 6.6) than when it was found in allopatry (organ-pipe *Montastraea* was not

TABLE 3. Student's *t*-test of mean column width among fossil columnar, living columnar, and fossil organ-pipe colonies of the *Montastraea* "*annularis*" species complex. Tests were completed on log-transformed data.

	Pleistocene organ-pipe	Pleistocene columnar	Living columnar
Pleistocene organ-pipe	—		
Pleistocene columnar	−31.36*	—	
Living columnar	−21.76*	−7.78*	—

*P < 0.005.

found along the 40-m transect) with this species (*N* = 62; mean = 15.2 cm; SD = 4.9; *t* = −2.76; *P* = 0.007).

Pleistocene Abundance Patterns

In a previous study we reported on the results of 79 40-m transects that gathered information on the relative abundance of four morphospecies within the species complex between 600,000 and 82,000 years ago on Barbados (Pandolfi et al. 2001). Briefly, in the shallow reef habitat (5–10 m water depth), the abundance of organ-pipe *Montastraea* increased throughout its duration, while abundance of the other morphotypes either remained the same or declined (see Fig. 9). Moreover, the only significant inverse correlations in abundance among morphotypes are between the extinct organ-pipe form and the massive and sheet forms (Table 4). In the deep reef habitat (20–30 m water depth), the organ-pipe and massive forms are relatively constant, whereas the columnar form decreases significantly in abundance per meter through time, and the sheet growth form is abundant until around 200,000 years, then dramatically falls in abundance (not shown; see Pandolfi et al. 2001). Significant negative correlations in abundance among species in the deep reef habitat occurred between extinct organ-pipe and the sheet and between the sheet and columnar forms (not shown; see Pandolfi et al. 2001).

Shallow coral communities in the Pleistocene leeward reef-crest environment in Curaçao were dominated by *Acropora palmata* and the organ-pipe *Montastraea*. Within the *M.* "*annularis*" complex, columnar *Montastraea* was much less abundant than the organ-pipe form (see Fig. 10). The organ-pipe species was also more abundant than all the other species of the *M.* "*annularis*" complex in the shallow-water Pleistocene windward reef crest and windward back reef environments at Curaçao (Pandolfi and Jackson 2001). Recent reefs at Curaçao exhibit a different pattern (see Fig. 10; Van Veghel 1994a). Although the data were collected differently, columnar *M. annularis* s.s. and massive *M. faveolata* are more abundant within the species complex in Recent shallow-water environments now than they were 125,000 years ago in the Pleistocene. Today, columnar *M. annularis* s.s. has its highest abundance in shallowest water, massive *M. faveolata* at intermediate depths, and sheet *M. franksi* in the deepest water (Van Veghel 1994a; see Fig. 10).

Coral Growth Rates

Our literature survey of linear extension rates of living members of the *M.* "*annularis*" species complex show that
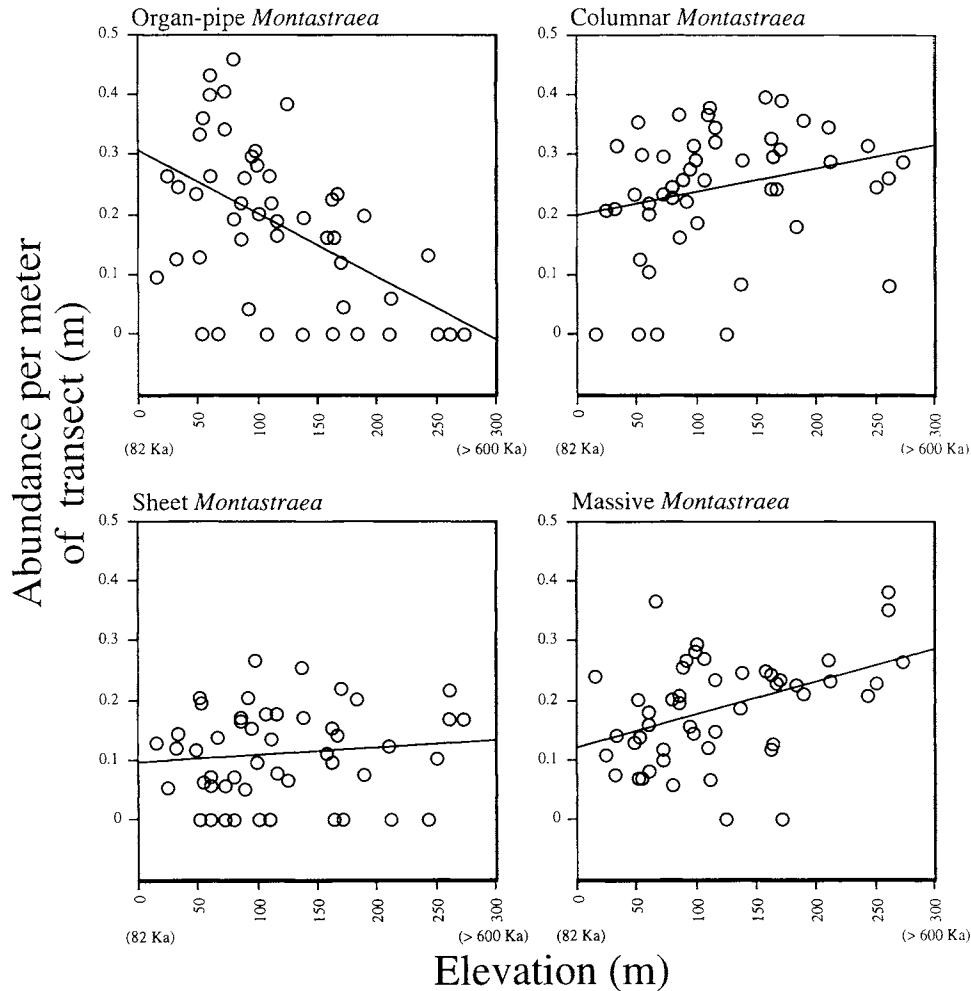
FIG. 9.   The transformed abundance per meter (arcsin-$\sqrt{\log[x + 1]}$, where x is abundance per meter of transect) in relation to terrace elevation for each individual morphotype of the *Montastraea* "*annularis*" species complex. Abundances were measured from the shallow fore-reef environment of the Pleistocene terraces of Barbados. Terrace elevation is used as a proxy for time with lower elevations denoting younger reef-building events. Ka, thousand years ago.

columnar *M. annularis* s.s. has higher growth rates than massive *M. faveolata* and this species has higher growth rates than sheet morphs of *M. franksi* (see Fig. 11). In general, this trend follows along depth gradients. However, along the gradient in water depth plotted, there is overlap in growth rate between adjacent growth forms. The range of growth rates and the decrease in growth rates with depth in Figure 11 are similar to those observed by Huston (1985) and Graus and Macintyre (1982). A Mann-Whitney U-test for differences in growth rates among massive and columnar colony morphologies was performed on corals in less than 15-m depth. Co-

lumnar forms had higher growth rates than massive forms within this depth range ($Z = -3.35$, $P < 0.0001$). Mean growth rate for massive forms was 0.85 cm/year (SE = 0.03, $N = 48$) and for columnar forms was 1.11 cm/year (SE = 0.06, $N = 17$).

In the fossil corals, growth rates were significantly higher ($t = -16.31$; $P < 0.0001$) in the organ-pipe *Montastraea* (mean = 1.27 cm/year; SD = 0.186; $N = 30$) than in columnar *Montastraea* (mean = 0.508 cm/year; SD = 0.113; $N = 27$) during their last known co-occurrence in the 82,000-year reef terrace on Barbados (see Fig. 12).

DISCUSSION

Character Release

The first aspect that needs consideration is whether the character shift we observed in species of the *M.* "*annularis*" complex passes the six tests summarized in Schluter and McPhail (1992; see Table 1) for the interpretation of character release to hold.

First, the morphological shift in the width of columns in

TABLE 4.   Spearman rank correlation of species abundance between morphotype pairs in the *Montastraea* "*annularis*" species complex from the Pleistocene shallow fore-reef of Barbados.

	Columnar	Massive	Sheet
Massive	−0.02	—	
Sheet	−0.03	0.38*	—
Organ-pipe	0.06	−0.52*	−0.49*

* $P < 0.05$.

Pleistocene

Modern

⊟ organ-pipe *Montastraea*   ■ *M. faveolata*
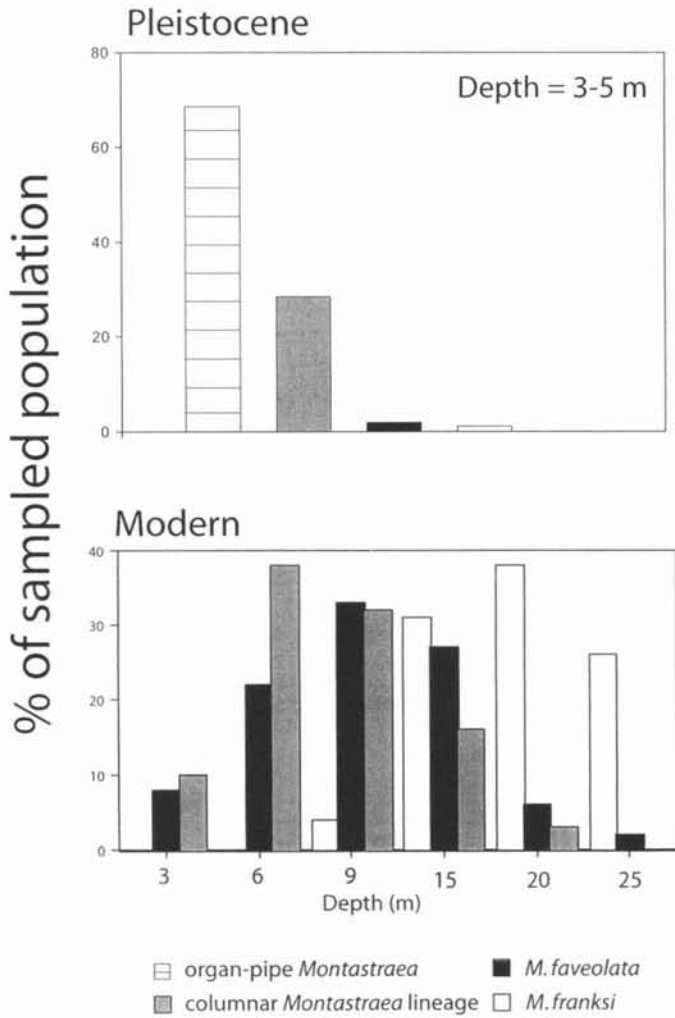▨ columnar *Montastraea* lineage   ☐ *M. franksi*

FIG. 10. Contrast between Pleistocene and modern relative species abundances of the *M.* "*annularis*" species complex only from the shallow leeward reef of Curaçao. In Pleistocene reefs of Curaçao (top), where the leeward reef crest is dominated by both *Acropora palmata* and the extinct organ-pipe *Montastraea*, the latter is the most abundant member of the species complex. Columnar *Montastraea* is much less abundant than the organ-pipe species, and the massive and sheet forms are not abundant. In contrast, living reefs of Curaçao show the greatest abundance of columnar *M. annularis* s.s. in the shallowest water, the greatest abundance of massive *M. faveolata* at intermediate depths, and the greatest abundance of sheet *M. franksi* at the deepest depths (bottom). Living data are from Van Veghel (1994a). Pleistocene data are percentage relative abundance of members of the species complex with respect to one another. Modern data are the frequency distributions of each species along a depth gradient. Top panel shows abundances for a depth zone of 3–5 m water depth, whereas bottom panel gives data for a range of water depths.

living *M. annularis* s.s. toward the organ-pipe *Montastraea* after the extinction (see Fig. 8; Table 3) would be difficult to explain by chance, especially as a significant shift away from organ-pipe *Montastraea* also occurred when the columnar *Montastraea* lineage was in sympatry with organ-pipe *Montastraea* before the extinction. Thus, the presence and later absence of the previously coexisting organ-pipe species is directly correlated with morphological changes in the columnar *Montastraea* lineage.
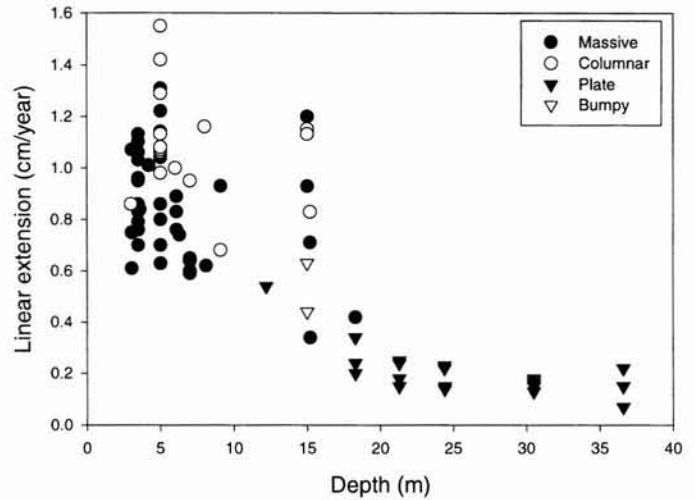

FIG. 11. Graph of published growth rates (linear extension) for growth forms of the *Montastraea* "*annularis*" species complex. Living columnar growth forms have higher growth rates than massive growth forms, and these have higher growth rates than bumpy or plate forms. Based on published growth rates in the modern species complex (see Appendix for data).

The second criterion is whether the phenotypic differences between populations have a genetic basis (Table 1). A number of very recent studies on the molecular and reproductive biology of the *M.* "*annularis*" complex suggest species differences are genetic—and thus colony growth form may be under genetic influence as well (Van Veghel 1994a; Knowlton et al. 1997; Lopez and Knowlton 1997; Lopez et al. 1999). Earlier work on allozymes (nine polymorphic loci) showed that *M. faveolata* was distinguished by a nearly fixed difference at one locus as well as frequency differences at others. Thus, rather large Nei's *D* values (e.g., 0.24–0.26 in Panama) separated *M. faveolata* from the other two species (Knowlton
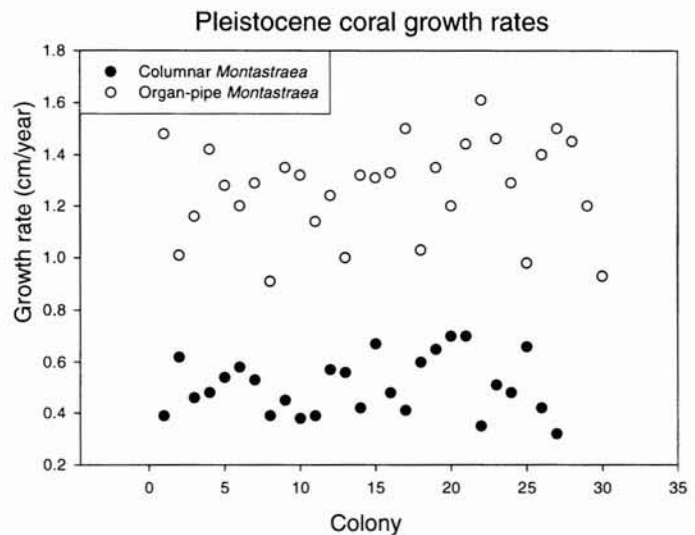

FIG. 12. Growth rates in the organ-pipe and columnar *Montastraea* during their last known coexistence in the 82,000-year-old reef terrace on Barbados. The Pleistocene data come from the windward side of the island in a shallow-water back-reef environment subject to sediment incursion.

et al. 1992; Van Veghel and Bak 1993; Weil and Knowlton 1994). *Montastraea annularis* s.s. and *M. franksi* are much more similar (Nei's $D = 0.06$), although individuals of the same species cluster together and can be statistically distinguished (Knowlton et al. 1992).

Recently, work has been done to develop DNA-based protocols for distinguishing the species. Because *Montastraea* gametes lack algal symbionts, Knowlton and coworkers have used gametes rather than somatic tissue and attempted various molecular genetic approaches. The most successful approach has been genomic fingerprinting with AFLP in which GAG and ATG extension primers indicate three or four genetic loci (band presence/absence) that distinguish *M. faveolata* from *M. franksi* (Lopez and Knowlton 1997). *Montastraea annularis* s.s. may also have diagnostic markers, but the differences between it and *M. franksi* were quantitative (band intensity) rather than qualitative. Thus, both allozyme and DNA sequence data collected to date support the hypothesis that *M. franksi* and *M. annularis* s.s. are more closely related to each other than either are to *M. faveolata*. This result agrees with reproductive studies showing that *M. faveolata* is unable to cross with either *M. annularis* s.s. or *M. franksi* (Knowlton et al. 1997). Interspecific fertilization success between *M. annularis* s.s. and *M. franksi* is comparable to intraspecific levels, but the two species differ by 1–2 h in the time of spawning (Knowlton et al. 1997). Whereas none of this absolutely proves that growth form, and thus column width, in the species complex has a genetic basis, it is certainly suggestive that it does.

The next criterion is whether species of the *M. "annularis"* species complex coexisted prior to the extinction, so that changes in morphology are indeed coevolutionary, or whether there were periods of extinction and recolonization (Table 1). The coexistence of the four Pleistocene morphotypes of the *M. "annularis"* species complex through more than 500,000 years has been well documented throughout the raised reef terraces at Barbados (Pandolfi 1999; Pandolfi et al. 2001). Moreover, the members of the complex coexisted throughout a southern Caribbean transect that extended from San Andrés in the west to Curaçao in the center to Barbados in the east during the last interglacial, 125,000 years ago (Pandolfi and Jackson 1997, 2001, in press; Pandolfi 2001). However, most of the raised reef terraces represent high sea-level stands when glacial meltwater raised global sea levels. The nature of low sea level stand reefs at Barbados and elsewhere is poorly known because the remains of these reefs are generally found today under the ocean, requiring drilling for analysis. Thus, there is a possibility that column width in the columnar *Montastraea* lineage was solely influenced by a restocking from low sea level, where genotypes with broad columns were favored, and these subsequently reestablished each time a new high stand reef was created. However, we consider this possibility remote because measured colonies found in sympatry spanned the same ages as those found in allopatry, indicating variation of morphology within similar reef-building episodes.

Next we ask whether the morphological shift reflects acquisition of a primary resource for the coral species complex (Table 1). The primary resources for corals that depend on symbiosis with photosynthetic dinoflagellates for growth are food and light (Barnes 1973; Sebens 1997). Their acquisition depends upon growth form, so growth form has long been thought to be adaptive in reef corals. Growth form differences have been related to differences in resource use such as light and space, and different growth forms display varying abundance of photoadaptive symbiont complexes, depending on light intensity at various points on the colony surface (Rowan and Knowlton 1995; Rowan et al. 1997). Because growth form is directly related to growth rate, we can think of resource use in terms of growth rate (see Chappell 1980). In general, growth rates of branching corals are much higher than massive corals, which in turn grow slightly faster than sheet- or platelike species (Jackson 1991).

Our literature survey shows that the same is true for the columnar, massive, and platelike growth forms of living colonies of the *M. "annularis"* species complex (see Fig. 11). Even though there is large variance within growth forms and broad overlap in growth rate among growth forms, living columnar *M. annularis* s.s. colonies have higher growth rates than massive *M. faveolata* colonies, and these have higher growth rates than plate colonies of *M. franksi* (Fig. 10). It is well known that growth rate decreases with depth as light attenuates in modern reefs (Dustan 1975; Hubbard and Scaturo 1985; Tomascik 1990; Van Veghel 1994a). Higher light levels in shallower water result in selfshaded, thin columns with emphasis on vertical extension (i.e., higher growth rates). So, as light attenuates with depth, first columns, then massive, and finally sheetlike forms predominate (Barnes 1973; Dustan 1975; Graus and Macintyre 1976, 1982). However, the differences in growth rates among the three living species also occur within the same depth range, so growth rate is not solely environmentally induced in these species (Fig. 11).

From the growth rates so far obtained from the living *M. "annularis"* species complex, we predict that the fossil organ-pipe *Montastraea* should have even greater growth rates than the fossil columnar form in shallow water, and it does. In sympatric Pleistocene *Montastraea* colonies, the columnar forms (mean = 0.51 cm/year) did not grow as fast as the organ-pipe forms (mean = 1.27 cm/year), and plot below the slowest growth rates measured in living *M. annularis* s.s. (Figs. 11, 12). (The depressed Pleistocene growth rates probably reflect the particular environment where they were collected: the turbid waters of a back-reef lagoonal environment that was subject to sediment incursion.) Thus, Pleistocene columnar *Montastraea* did not grow at the same rate as organ-pipe *Montastraea* 82,000 years ago while exploiting the same environment (Fig. 12). So resource use, as reflected in coral growth rate, was depressed in columnar *Montastraea* while in sympatry with organ-pipe *Montastraea*. By this line of reasoning, growth rates should be higher in living (thinner columns) than fossil (thicker columns) colonies of the columnar *Montastraea* lineage. Future work is needed to understand the variability in growth rate of Pleistocene and living colonies of the columnar *Montastraea* lineage in a number of reef environments before this question can be addressed.

The next criterion is whether reef environments before and after release were greatly different (Table 1). If so, then phenotypic plasticity might be responsible for the observed char-

acter shift. There are three aspects to environmental change that need to be addressed: global, local, and biotic. Global environmental parameters, such as sea level, atmospheric CO_2, and benthic surface area available for reef growth, have varied throughout the past several hundred thousand years as a consequence of Milankovitch forcing of climate (Barnola et al. 1987). As a result, each new reef building episode that initiates and sustains growth as a response to sea-level rise grows under a different set of environmental variables. Environments are rarely, if ever, the same (Bell 1992). However, the range in values of the environmental variables has probably been similar for the past several hundred thousand years (Berger and Jansen 1994). Thus, environmental variables that the *M. "annularis"* species complex experienced before and after the extinction event were within the range experienced by the species group during the past 500,000 or more years.

Tectonic uplift of Barbados began more than 600,000 years ago and continues today (Broecker et al. 1968; Mesolella et al. 1969; Bender et al. 1973, 1979; Humphrey 1997). The paleoenvironmental reconstructions of the raised reef deposits, based on constituent composition and sedimentological analysis, show a striking continuity of reef habitats through time (Mesolella et al. 1970). Mesolella (1967) found remarkable similarity between these Pleistocene reef habitats from Barbados and those being described from the living reefs of Jamaica by Goreau (1959). This similarity was reflected not only in the physiography of the reef environments, but also in the biological constituents found within individual Jamaican habitats. Moreover, both the reef habitats and the coral constituents appeared to show similarity through time. Jackson (1992) tested this notion in a semiquantitative analysis of Mesolella's (1968) data and found constancy in coral community composition during the past 200,000 years. A more quantitative analysis of the *A. palmata* zone, relying on an ecological field sampling approach, has also shown marked persistence in coral community structure from 104,000 to 225,000 years ago (Pandolfi 2000). Thus, local abiotic and biotic environments were remarkably similar before and after the extinction event that resulted in character release. We believe that such constancy rules out any environmental interpretation for the observed character shift. A similar argument applies to the leeward coast of Curaçao, where constancy through time and space has been documented (Pandolfi and Jackson 2001).

Competition

The final criterion for understanding character displacement/release is to determine whether competition has been convincingly demonstrated (Table 1). We discuss this point for both living and fossil *M. "annularis."*

Living species.—The *M. "annularis"* species complex includes some of the fiercest space competitors on modern Caribbean reefs (Lang 1973; Lang and Chornesky 1990). Indeed, there is abundant evidence that similar phenotypes actually compete for space among modern members of the *M. "annularis"* species complex (Van Veghel and Bak 1993; Van Veghel 1994a; Knowlton et al. 1992; Van Veghel et al. 1996). Space competition occurs either by physical contact, whereby tentacles cause lesions in the tissue of spatially ad-

TABLE 5. Competitive outcomes within members of the *Montastraea "annularis"* species complex and competitive mechanisms observed in the species complex (from Van Veghel et al. 1996).

Intraspecies group competitive outcomes			
Morphotype	Outcome		
Bumpy (B)	100% dominant		
Massive (M)	62% subordinate		
Columnar (C)	57% subordinate		
Competitive mechanisms (%)			
	B (66)	M (167)	C (130)
Tissue lesions	75	69	50
Overgrowth[1]	8	11	22
Overshadowing[2]	6	6	23
Other	11	14	5

[1] Unilateral growth by one competitor spreading over the surface of the other.
[2] Imposition of reduced light intensity on an underlying individual without physical contact.

jacent colonies (allelopathy), or by overshadowing (imposition of reduced light intensity on an underlying individual without physical contact) and overgrowth (unilateral growth by one competitor spreading over the surface of the other).

Experimental assessment of competition within the complex has revealed strong interactions among morphotypes. Van Veghel et al. (1996) showed that slower-growing massive (*M. faveolata*) and bumpy (*M. franksi*) forms are better allelopathic competitors than the faster-growing columnar (*M. annularis* s.s.) forms (Table 5). In contrast, overshadowing and overgrowth are much more common in the columnar *M. annularis* s.s. morphotype than in the other morphotypes (Table 5).

We believe that the patterns in competitive ability observed among modern *Montastraea* and their relationship to living coral growth rates point to a vigorous competition in the *M. "annularis"* species group (Table 6). Both within the species complex (Knowlton et al. 1992; Weil and Knowlton 1994) and between species of the complex and other Caribbean species (Van Veghel et al. 1996), slower growers are better allelopathic competitors, inflicting greater tissue damage on adjacent colonies than faster-growing species. Apparently, faster growers compensate by growing above the substratum faster and having higher linear extension growth rates. Competitive outcome occurs as a trade-off between growth rate and severity of allelopathic injury, a pattern also shown by other corals (Lang 1973).

Ancient species.—Extinction occurred after more than 500,000 years of ascendancy of the organ-pipe *Montastraea* relative to the other forms of the species complex in the shallow-water reef habitat of Barbados (Fig. 9). Thus, it was not predicted by trends in individual species abundance patterns through time (Pandolfi 1999; Pandolfi et al. 2001). In shallow water, organ-pipe *Montastraea* increased through time while columnar and massive forms decreased and the sheet growth form remained at a constant, much lower abundance, possibly occupying more shaded habitats. These abundance patterns, when taken together with negative abundance correlations between organ-pipe *Montastraea* versus the massive and sheet growth forms, suggest a competitive hierarchy from organ-pipe to columnar to massive to sheet growth form in the Pleistocene shallow fore-reef environment of Barbados

TABLE 6. Percent abundance in the Pleistocene of Barbados and competitive ranking of coral species coexisting with the *Montastraea* "*annularis*" species complex. Percent abundances are for coral species censused along eight transects from the buttress zone and seven transects from the deep fore-reef zone of the 125,000-year-old reef on the leeward coast of Barbados. Competitive hierarchy based on empirical results of Lang (1973) from Jamaica: S, scleractinian corals competitively subordinate to *M.* "*annularis*"; D, scleractinian corals competitively dominant to *M.* "*annularis*"; U, competitive ranking unknown; F, species that grow an order of magnitude faster than members of the *M.* "*annularis*" species complex. Results of Van Veghel et al. (1996) given as percent of *n* observed interactions in which *M.* "*annularis*" was subordinate to another coral species over a number of depths at Curaçao.

Species abundance in the buttress zone (8–12 m depth), 125,000-year-old reef, Barbados (%)				Species abundance in the deep fore-reef zone (20–30 m depth), 125,000-year-old reef, Barbados (%)			
Species	%	Competitive hierarchy	% subordinate (*n*)	Species	%	Competitive hierarchy	% subordinate (*n*)
columnar *Montastraea*	26.92			*Acropora cervicornis*	15.49	S, F	
Acropora cervicornis	21.53	S, F		columnar *Montastraea*	14.00		
Acropora palmata	15.11	S, F	100 (1)	*Siderastrea siderea*	13.78	S	0 (5)
organ-pipe *Montastraea*	11.27			*Colpophyllia natans*	12.44	S	15 (13)
				massive *Montastraea*	10.95		
massive *Montastraea*	8.39			*Porites astreoides*	5.35	S	0 (1)
Siderastrea siderea	2.71	S	0 (5)	sheet *Montastraea*	4.72		
Diploria labyrinthiformis	2.56	S	0 (6)	*Colpophyllia* spp.[1]	3.90	S	
Colpophyllia spp.[1]	1.97	S		*Diploria labyrinthiformis*	2.31	S	0 (6)
Diploria strigosa	1.62	S		*Porites furcata*	2.23	S	
sheet *Montastraea*	1.62			*Stephanocoenia intersepta*	2.00	S	0 (24)
Colpophyllia natans	1.55	S	15 (13)	*Acropora palmata*	1.97	S, F	100 (1)
Montastraea cavernosa	2.18	S	67 (15)	*Diploria strigosa*	1.42	S	
Porites astreoides	1.37	S	0 (1)	*Meandrina meandrites*	1.26	D	20 (5)
other *Montastraea* "*annularis*"	0.30			*Montastraea cavernosa*	2.51	S	67 (15)
Stephanocoenia intersepta	0.30	S	0 (24)	*Porites divaricata*	0.89	S	
Mussa angulosa	0.19	D		*Siderastrea radians*	0.74	S	
branching *Porites* fragments	0.08	S		organ-pipe *Montastraea*	0.66		
Meandrina meandrites	0.07	D	20 (5)	*Eusmilia fastigiata*	0.61	S	27 (22)
Agaricia agaricites	0.06	S	14 (42)	tophat *Montastraea* "*annularis*"	0.55		
Siderastrea radians	0.05	S		*Madracis mirabilis*	0.43	S	15 (20)
Isophyllastrea rigida	0.04	D		branching *Porites* fragments	0.39	S	
Dichocoenia	0.03	U		other *Montastraea* "*annularis*"	0.37		
Pocillopora cf. *palmata*	0.02	extinct		*Agaricia agaricites*	0.29	S	14 (42)
Porites furcata	0.02	S				S	
				Porites porites	0.25	S?	0 (4)
				Cladocora	0.18	D	
				Mussa angulosa	0.10	U	
				Favia fragum	0.07	U	
				Dendrogyra cylindricus	0.06	S	0 (2)
				Madracis decactis	0.03	Hydro-	25 (4)
				Millepora squarrosa	0.03	zoan	

[1] Includes instances of *Colpophyllia* that were not equivalent to *C. natans*.

throughout the more than 500,000-year history. We believe that intense competition for space under high light conditions apparently constrained the abundance of Pleistocene columnar, massive, and sheet *Montastraea* in the highly productive shallow fore-reef environment of Barbados while sympatric with organ-pipe *Montastraea*. These data support growth rate as a primary determinant of competitive outcome over long time periods, so that allelopathic interactions may not have been as important in shallow, high-light environments. Throughout this interval, as in modern reefs, none of the four morphotypes were physiologically limited to a particular depth and all survived (albeit in different abundances) in the shallow-water environment (Fig. 9). It is likely that the faster growing organ-pipe *Montastraea* was a fierce competitor at high light levels, overtopping other species within the *M.* "*annularis*" species complex and other reef coral species and reef inhabitants.

In summary, both the direct data from living communities and the indirect data from the fossil record suggest a long history of competition among species of the *M.* "*annularis*"

complex. Divergent selection for different ways of exploiting space and light minimized interspecific competition for these resources, enabling a long period of coexistence. Moreover, genotypes of the organ-pipe *Montastraea* in shallow water may also have gained from asexual propagation in disturbed shallow-water settings, where storms can break organ-pipe colonies more easily than other growth forms in shallow water and other corals living in deeper environments (Hughes and Jackson 1980).

Competition with other corals.—Our emphasis on competition within the *M.* "*annularis*" species complex in no way diminishes the probable strong competition between the species complex and other reef corals, especially elkhorn *A. palmata* and staghorn *A. cervicornis*, two species that were also abundant in the shallow reef habitats of the Pleistocene. Both the organ-pipe *Montastraea* and the two *Acropora* spp. exhibited high growth rates, were branching, and allocated resources within the colony to branch tips, where growth was most concentrated. Weil and Knowlton (1994, p. 171) noted that the branching morphology, commitment to upward

growth, and basal senescence "seem to be *Montastraea*'s best attempt at a staghorn-like lifestyle. . . . Competition between them appears to be mediated by the relative frequency of major storms and predators, both of which favor *M. annularis.*"

Is it possible that competition with the acroporids might have caused the pattern of convergent evolution? Morphological change in the columnar *Montastraea* lineage may have been induced not by competition with the organ-pipe species, but with other species outside of the *M. "annularis"* species complex. For example, after extinction of organ-pipe *Montastraea*, the columnar *Montastraea* lineage may have come into more contact with the faster-growing *A. palmata*, a species with very broad, palmate branches. Perhaps the columnar *Montastraea* lineage evolved thinner, faster-growing columns in response to greater proximity to extremely fast-growing *A. palmata* in an effort to avoid competition for light after it was able to invade the shallow water niche left vacant by the extinction of the organ-pipe *Montastraea*.

However, two factors argue against the *Acropora* spp. influencing the observed convergent evolution. First, both *A. cervicornis* and *A. palmata* existed in high abundance with the *M. "annularis"* species complex in both the 125,000-year-old (and actually extending back to more than 500,000 years ago; Mesolella 1967) Pleistocene environments of Barbados (Table 6) and in living coral reefs. For example, *A. palmata* was not only a dominant shallow-water coral for hundreds of thousands of years in the Pleistocene (Pandolfi 2000), but also in living Caribbean reefs until recent habitat degradation led to its decline (Jackson 1992, 1997; Hughes 1994). Thus, competition among the acroporids and the *Montastraea* species complex occurred both well before and well after the extinction and associated morphological shift. Second, both species of *Acropora* grow an order of magnitude faster than the *M. annularis* complex, so even if the columnar growth form increased its growth rate to match that of the extinct organ-pipe form (from 0.5 to 1.3 cm/year), which it did not, it would not seem to be enough to compensate for the competitive growth advantage of *Acropora*. Thus, we believe it unlikely for the morphological patterns shown to be a function of competition with *Acropora*.

In fact, the coral species composition of habitats where the *M. annularis* species complex lived were essentially the same before and after the extinction of organ-pipe *Montastraea* (Pandolfi and Jackson 2001). Quantitative surveys of Pleistocene coral communities from Barbados yield a detailed view of the composition of coral communities from the buttress zone (8–12 m water depth) and the deep fore-reef zone (20–30 m water depth; Table 6). Almost all of the coral species that coexisted with the *M. "annularis"* species complex are competitively subordinate to it in both Lang's (1973) original surveys from Jamaica and more recent studies from Curaçao (Van Veghel et al. 1996; Table 6). Moreover, except for *Pocillopora* cf. *palmata* (see below), every species with which members of the *M. "annularis"* species complex coexisted prior to the extinction also coexist with them in living reefs (i.e., they are all extant). Thus, the character shift we observed cannot easily be ascribed to competition with any other coral taxa.

Are there other, now-extinct species that might have been intense competitors with the *Montastraea* species complex? The only species that existed with the *M. "annularis"* species complex before the extinction of organ-pipe *Montastraea* and not after is the now-extinct *P.* cf. *palmata*. This species had a similar stratigraphic distribution as organ-pipe *Montastraea* since 125,000 years ago, and we have speculated that it went extinct at the same time as organ-pipe *Montastraea* (Pandolfi 1999; Pandolfi et al. 2001). Our data from the Pleistocene of Barbados suggests that abundance of *P.* cf. *palmata* was low in the presence of the *M. "annularis"* species complex (Table 6). Thus, it appears that this species did not exert a great deal of influence over members of the complex before extinction of the organ-pipe *Montastraea*.

In sum, it is apparent that the changes we observed in the columnar *Montastraea* lineage explicitly meet five of the six criteria outlined by Schluter and McPhail (1992). There are no data that confirm or deny that the phenotypic differences between populations had a genetic basis (criterion 2). However, we strongly suspect that this is the case. Thus, there appears to be no reason to reject the hypothesis that convergent evolution was brought about through character release. If future work shows that Pleistocene columnar *Montastraea* is indeed a distinct species, character release may have been the first morphological response to a changed selective regime that ultimately led to the formation of a new species. Alternatively, growth form and corallite morphology may be linked, so that thinner columns led to corallite traits more similar to organ-pipe *Montastraea* with its thinner columns. Regardless, extinction resulted in morphological change in surviving lineages, so the influence of closely related species may have been important in the evolution of the *M. "annularis"* species complex.

Alternative Explanations

Given our interpretation of ecological release in the evolutionary history of the *M. "annularis"* species complex and its importance for the role of biological interaction in the evolution of reef corals, it is prudent to entertain alternative explanations for the temporal patterns. Thus, the second aspect that needs consideration is whether the character shift we observed in species of the *M. "annularis"* complex can be explained by some other evolutionary or selective process.

First, it is possible that the differences in column width displayed in living *M. annularis* s.s. are somehow related to variable resource availability over the more than 500,000-year history on Barbados. Such availability may be related to climatic or other environmental factors. However, climate has varied within the same boundaries for at least the past 400,000 years (Berger and Jansen 1994), and today's climate falls well within this variance, even with supposed global warming (Pittock 1999). It is interesting to note here a very recent modeling study that concluded that character displacement is even less likely to occur where spatial heterogeneity in resources occurs (Day 2000). More recently, deforestation and the ubiquity of sugar plantations on Barbados (Lewis 1984) has led to increased turbidity and pollution, perhaps decreasing light levels in nearshore surface waters. However, such a decrease in light levels would probably translate into

slower-growing broad columns, instead of the more narrow columns found in living *M. annularis* s.s.

A related point is that disturbance affects selective pressure in reef corals. Corals are thought to be adapted to various disturbance regimes (Huston 1994). Thus, it is possible that the morphological differences observed in *M. annularis* s.s. could be due to different disturbance regimes between 600,000 and 82,000 years ago versus the present. Because disturbance regimes are tied to environmental parameters on coral reefs, and environments appear to be similar in sympatry (> 600,000–82,000 years ago) and allopatry (Modern), this is probably unlikely.

A second alternative explanation is that coevolution indeed took place, but the mechanism was not competition. Schluter and McPhail (1992, p. 102) envisioned that "selection against interspecific hybrids might give extreme phenotypes a reproductive advantage if they are less likely to mate with the opposite species. Divergence would be favored by reproductive rather than ecological character displacement." However, it is difficult to see how column width in the organ-pipe *Montastraea* or the columnar *Montastraea* lineage could influence mate choice in corals that spawn their gametes into the water column on the same night every year (Van Veghel 1994b). Still, as Schluter and McPhail (1992) point out, there remains the possibility that the morphological trait is somehow highly genetically correlated with traits selected for mating.

There are also two other factors unrelated to character release that may generate morphological change in the absence of a competitor (Dayan and Simberloff 1998). The first is the niche-variation hypothesis that states the amount of variation in a given population is proportional to the size of the niche exploited by the population (Van Valen 1965; Grant 1967). One prediction of this hypothesis is that morphological variation should increase when a competitor is absent (phenotypes that had been selected against because of competition will no longer be at a disadvantage). Thus, coefficients of variation (CV) should rise in the absence of a competitor. Indeed, fossil columnar *Montastraea* showed a CV of 0.378 and that of living *M. annularis* s.s. showed a CV of 0.406, a rise of 7.4%.

A second factor is morphological change brought on by an increase in sexual dimorphism in the absence of a former competitor. However, all of the corals of the *M. "annularis"* species complex are hermaphroditic broadcast spawners, releasing their gametes on the same night of every year. All of their premating characteristics such as reproductive mode, development and maturation of gametes, and spawning behavior (except for a 2-h delay between *M. annularis* s.s. and *M. franksi*; Knowlton et al. 1997) are invariant among the living members of the species complex. Thus, it is unlikely that this mechanism was responsible for the morphological differences.

Ecological Analogue of Character Release

The morphological shift was accompanied by an ecological shift into shallower water by living colonies of the columnar *Montastraea* lineage (*M. annularis* s.s.) and massive *M. faveolata* at Curaçao (Fig. 10). Compared to their Pleistocene counterparts, *M. annularis* s.s. has taken over from the extinct organ-pipe *Montastraea* as the dominant member of the species complex in shallow water and *M. faveolata* has a higher abundance in the shallow fore-reef slightly deeper than the columnar form (Fig. 10). Likewise, the sheetlike species of the *M. "annularis"* complex in Barbados declined dramatically in abundance in the deep fore-reef environment for 500,000 years (Pandolfi et al. 2001), but sheetlike species (e.g., *M. franksi*) are the dominant form of *M. "annularis"* today in deeper water throughout the Caribbean (Goreau 1959; Dustan 1975; Grauss and Macintyre 1976; Bak and Luckhurst 1980), including Curaçao (Fig. 10). Thus, both columnar and massive species appear to have filled the ecological space left vacant in shallow water by the extinction of the organpipe species, and plate- or sheetlike species have correspondingly increased in deeper water. Apparently ecological space was vacated when the organ-pipe *Montastraea* went extinct, allowing for ecological sprawl of other members of the *M. "annularis"* species complex.

We suggest that self-shading in organ-pipe *Montastraea* limited their distribution in deeper water (15–30 m), so they were most abundant in shallow water (3–12 m), where they also shaded out and excluded columnar, massive, and sheetlike forms. By this scenario, extinction of the competitively superior (by high growth rates) species opened up shallow habitat for living columnar *M. annularis* s.s. and massive *M. faveolata*, whose Pleistocene morphotypes had been at least partially excluded by the faster- and taller-growing colonies with narrower branches of the organ-pipe species. For example, in the Pleistocene shallow-water windward reef crest on Curaçao, massive *Montastraea* never coexisted with columnar *Montastraea* and had a significantly different distribution from that of organ-pipe *Montastraea* (Pandolfi and Jackson 2001).

In summary, the patterns we have documented from Pleistocene sequences where fine resolution is available provide insight into the possible role of biological interaction in coral reef evolution. Our results indicate that experimental studies of the role of competition in natural selection in living organisms may reveal much about evolutionary mechanisms in species complexes, even though such study may be difficult and time-consuming with relatively slow-growing organisms like corals that have long generation times. Evolutionary studies of living taxa with a well-developed fossil record should provide the greatest potential for integrating experimental results over long temporal scales.

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APPENDIX

Data on which Figure 11 is based. For growth form: M, massive; C, columnar; B, bumpy; P, platelike morphotypes. N, number of growth bands counted. Notes include site information and sampling details.

Author	Location	Method	Notes	Growth form	Depth (m)	Linear extension (cm/year)	N	Environment
Van Veghel and Bosscher (1995)	Curaçao	Stain alizarin red-S	Average N per colony counted 10.8	B	15	0.63	54	back reef (leeward side of the island
			14.2	B	15	0.44		back reef
			13.6	M	5	1.14	71	back reef
			12.6	M	15	1.20	68	back reef
			27.8	M	5	1.31	63	back reef
			8.4	M	15	0.93	139	back reef
			14.6	C	5	1.06	42	back reef
			19.0	C	15	1.15	73	back reef
			14.4	C	5	1.29	95	back reef
			15.6	C	15	1.13	72	back reef
Dodge and Brass (1984)	St. Croix	X-ray	site CHF	C	7	0.95	70	fore-reef
			site BI	C	8	1.16	90	fore-reef
			site A	C	6	1.00	80	back reef
			site H	C	3	0.86	80	back reef
Tomascik (1990)	Barbados	X-ray	spur and groove region of fringing reefs on leeward side of Barbados	C	5	1.07	258	back reef
				C	5	0.98	286	back reef
				C	5	1.13	141	back reef
				C	5	1.42	209	back reef
				C	5	1.08	198	back reef
				C	5	1.55	219	back reef
				C	5	1.55	172	back reef
				M	5	0.70	136	back reef
				M	5	0.63	146	back reef
				M	5	0.80	120	back reef
				M	5	1.07	96	back reef
				M	5	0.86	130	back reef
				M	5	1.04	106	back reef
				M	5	1.22	103	back reef
Hubbard and Scaturo (1985)	St. Croix	X-ray	individual colonies	M	3.05	1.07	44	fore-reef
				M	6.1	0.83	240	fore-reef
				M	18.3	0.42	134	fore-reef
				P	21.3	0.25	30	fore-reef
				P	24.4	0.15	42	fore-reef
				P	30.5	0.15	69	fore-reef
				P	36.6	0.15	75	fore-reef
				C	9.1	0.68	95	fore-reef
				M	15.2	0.34	105	fore-reef
				P	18.3	0.24	150	fore-reef
				P	21.3	0.18	45	fore-reef
				P	30.5	0.16	70	fore-reef
				P	36.6	0.22	107	fore-reef
				M	3.05	0.61	50	fore-reef
				M	6.1	0.76	90	fore-reef
				M	15.2	0.71	201	fore-reef
				P	21.3	0.24	120	fore-reef
				P	24.4	0.23	85	fore-reef
				P	30.5	0.18	80	fore-reef
				P	36.6	0.07	16	fore-reef
				M	3.05	0.75	84	fore-reef
				M	6.1	0.89	25	fore-reef
				M	9.1	0.93	64	fore-reef
				P	12.2	0.54	33	fore-reef
				P	18.3	0.34	13	fore-reef
				P	21.3	0.18	75	fore-reef
				P	24.4	0.22	75	fore-reef

APPENDIX. Continued.

Author	Location	Method	Notes	Growth form	Depth (m)	Linear extension (cm/year)	N	Environment
				P	30.5	0.17	90	fore-reef
				C	15.2	0.83	18	fore-reef
				P	18.3	0.20	70	fore-reef
				P	21.3	0.15	35	fore-reef
				P	24.4	0.14	25	fore-reef
				P	30.5	0.13	51	fore-reef
Hudson et al. (1994)	Biscayne Bay	X-ray	depth between 2 and 5 m, individual colonies	M	3.5	0.76		patch reef
				M	3.5	0.833		patch reef
				M	3.5	0.96		patch reef
				M	3.5	0.83		patch reef
				M	3.5	0.95		patch reef
				M	3.5	0.70		patch reef
				M	3.5	0.79		patch reef
				M	3.5	1.06		patch reef
				M	3.5	0.86		patch reef
				M	3.5	1.10		patch reef
				M	3.5	1.03		patch reef
				M	3.5	0.79		patch reef
				M	3.5	1.13		patch reef
				M	3.5	0.96		patch reef
				M	3.5	0.95		patch reef
				M	4.2	1.01		back reef
				M	3.6	0.84		back reef
				M	3.5	0.76		back reef
				M	3.5	0.83		back reef
				M	3.5	0.86		back reef
				M	7	0.64		bank reef
				M	7	0.65		bank reef
				M	7	0.60		bank reef
				M	7	0.59		bank reef
				M	8.1	6.20		bank reef
				M	6.3	7.40		bank reef