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ECOLOGY AND MORPHOLOGY OF THE CARIBBEAN MIO-PLIOCENE REEF-CORAL *SIDERASTREA*

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Small paucispecific banks constructed by the massive scleractinian *Siderastrea* occur along the northern margins of hermatypic coral distribution during the Miocene and Pliocene epochs. Quantitative studies of environmental variation in one bank-builder, *S. mendenhalli*, from sandstones north of the Gulf of California show that distinctively thin, closely spaced synapticulae form in turbid, nearshore habitats in the same manner as in modern *S. siderea* from Jamaica. Analysis of variation between *Siderastrea* species suggests that, like these nearshore populations, framework-building species have comparatively large corallite diameters; thin septa, columellae, and walls; and numerous synapticular rings. These results imply that skeletal configurations of Tertiary bank-building *Siderastrea* may have been uniquely adapted for rapid colony growth in turbid, protected environments with abundant suspended organic material.

Key words: corals, Scleractinia, environmental variation, multivariate analysis, Caribbean, Cenozoic.

Ann Budd Foster, Department of Geology, The University of Iowa, Iowa City, Iowa 52242, USA, *Received: January 1980.*

INTRODUCTION

During the Miocene and Pliocene epochs, Caribbean reefs consisted of small coral buildups constructed by a limited number of provincial scleractinian species (Frost 1977). Along the northern margins of hermatypic coral distribution, largely monospecific banks or thickets of *Porites*, *Goniopora*, or *Siderastrea* formed in protected embayments and in backreef lagoons (Vaughan 1900, 1917, 1919; Frost and Langenheim 1974; Foster 1979). The purpose of the present study is to describe and relate the ecology and morphology of one massive Mio-Pliocene species, *Siderastrea mendenhalli* Vaughan, 1917, which constructed small paucispecific banks on the north end of the Gulf of California. Intraspecific patterns of environmental variation and the overall morphology of *S. mendenhalli* are analyzed and compared with that of other *Siderastrea* species to determine which configurations of corallite structures in this genus are best adapted for building reef framework.

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In the text, the following abbreviations are used:

c — columella thickness
d — corallite diameter
nse — number of septa/corallite
nsy — number of synapticular rings/corallite
se — septum thickness
ss — synapticula spacing
st — synapticula thickness
w — wall thickness

THE ECOLOGY OF MIO-PLIOCENE *SIDERASTREA*

Reefs at the north end of the Gulf of California

Siderastrea mendenhalli has been found exclusively in early Pliocene sandstones of the lower Imperial Formation in the Coyote and Fish Creek Mountains approximately 30 km southwest of the Salton Sea in south-central California. Although *S. mendenhalli* usually occurs as isolated colonies, especially large colonies (1—2 m diameter) form reef-like structures or banks in sandstones along hillcrests west of Barrett Canyon in the Fish Creek Mountains (Foster 1979). These sandstones (Latrania Member of the Imperial Formation) were deposited under shallow marine conditions prior to the rifting of the Gulf of California 4 million years ago (Karig and Jensky 1972). They directly overlie Miocene volcanics (Alverson Formation) and grade upward into a yellow claystone (Burrobend Member of the Imperial Formation) deposited in the estuary of the Colorado River (Woodward 1963).

S. mendenhalli has been studied from two locations: Barrett Canyon (BC) and northeast Coyote Mountains (NCM). At the first locality, specimens were collected from a *Siderastrea* bank (500 m long, 20 m wide, 1—2 m thick). Although the centers of colonies from the bank are recrystallized, most corallites are well-preserved. Skeletal elements are replaced by a micritic envelope which retained their original size (± one micron) and configuration. Little or no evidence of mechanical or biological destruction or of calcareous algae was found (Foster 1979). Across the bank, six distinct facies can be recognized on the basis of molluscan composition and sedimentary textures (fig. 1). From oldest to youngest, these facies are: (1) a reddish-brown, calcareous muddy sandstone containing the bivalve *Miltha xantusi* and the corals *Dichocoenia merriami* and *Solenastrea fairbanksi* (Facies A); (2) a coralline limestone composed of large columnar and mound-shaped colonies of *S. mendenhalli* (Facies B); (3) a bioturbated light-colored siltstone containing abundant lucinid bivalves of the species *Pegophysema edentuloides* (Facies C); (4) a terrigenous sandstone containing some smaller bivalves and gastropods and scattered patch reefs of

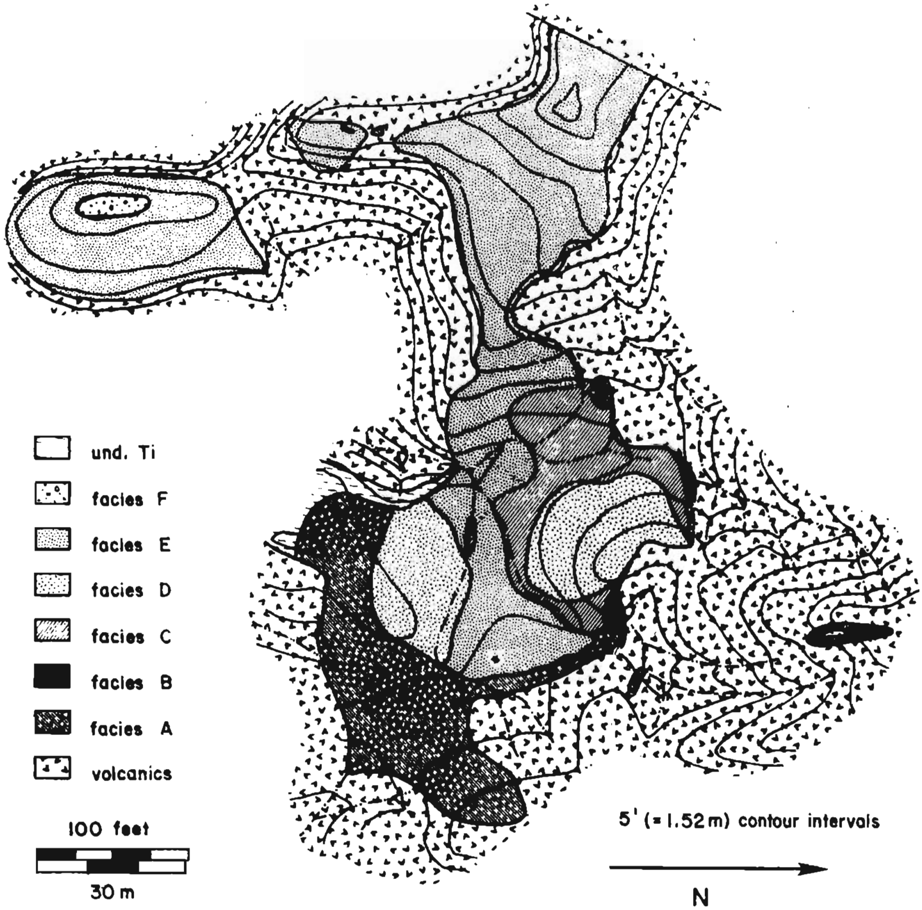

Fig. 1. Map showing distribution of facies in Latrania Member of the Imperial Formation at the Barrett Canyon locality.

the coral *Solenastrea fairbanksi* (Facies D); (5) a moderately coarse sandstone with abundant large casts of the venerid bivalve *Periglypta multicostata* (Facies E); (6) a very coarse sandstone with fragments of the epifaunal bivalves *Ostrea heermani* and *Pecten keepi* (Facies F). Corals occur in Facies A, B, and D. In Facies A, colonies of *D. merriami* and *S. fairbanksi* have small (10 cm diameter) mound shapes, and colonies of *Diploria bowersi* and *Eusmilia solida* have smaller (5 cm diameter), irregular shapes. The reef facies (Facies B) is composed almost entirely of *S. mendenhalli* (1—2 m diameter). Smaller (5—10 cm) colonies of *Porites carrizensis*, *Siderastrea californica*, and *S. fairbanksi* occur sporadically interspersed between the large *S. mendenhalli* colonies. The lagoon facies (Facies D) contains scattered mound-shaped colonies (10 cm diameter) of *S. fairbanksi*, *D. merriami*, and *P. carrizensis* and patch reefs (10 m × 3 m × 50 cm) constructed by larger (1 m diameter), columnar colonies of *S. fairbanksi*.

Comparisons of the molluscan compositions of each facies with those in modern

Gulf of California environments suggest that the facies were deposited under shallowing marine conditions in progressively nearshore environments (Foster 1978). The hemispherical coral shapes indicate that the *Siderastrea* bank (Facies B) was formed initially in a protected setting in shallow (5—10 m depth) clear water. Facies A formed seaward of the bank in deeper (10—20 m depth), more exposed positions having little terrigenous sediment influx. Facies D formed immediately shoreward of the bank in shallow (0—10 m depth) backreef areas with high sedimentation rates. Facies C formed in deeper (10—20 m depth), more turbid portions of the backreef lagoon. Facies E and F formed after the bank had been buried by sediment in very shallow (0—5 m depth) nearshore sand flats and sand channels.

No reef-structure or facies patterns occur at the second location (NCM). The coral fauna consists of a diverse assemblage of isolated, small (5—10 cm diameter) mound-shaped colonies of *S. fairbanksi*, *P. carrizensis*, *D. merriami*, *E. solida*, *S. mendenhalli*, *S. californica*, and *D. bowersi*. As suggested by the molluscan fauna, the depositional environment was probably a deep (10—20 m), low turbidity, hard rock platform similar to that represented by Facies A at Barrett Canyon (Foster 1979).

SIDERASTREA in other reefs

Although no other occurrences of fossil or modern *Siderastrea* banks have been reported in the Gulf of California area, similar reefs have been reported from the Shoal River Marl of the mid-Miocene Alum Bluff Stage of northern Florida (Vaughan 1900, 1919). These Florida reefs are largely monospecific accumulations of *Siderastrea silecensis* (12 m thick). They occur within phosphatic sands and clays deposited in a warm, shallow brackish embayment during a marine transgression (Puri and Vernon 1964). Both *S. mendenhalli* and *S. silecensis* have limited temporal and geographic distributions. *S. mendenhalli* is restricted to the Pliocene sandstones of south-central California; whereas *S. silecensis* is restricted to Miocene sandstones of Florida. In contrast, other widespread Mio-Pliocene *Siderastrea* species do not exclusively build banks but occur on reefs in conjunction with other coral genera. For example, *Siderastrea siderea*, along with *Montastraea*, *Colpophyllia*, and *Porites*, is common on lower Miocene banks of the La Quinta Formation near Chiapas, Mexico (Frost and Langenheim 1974). *Siderastrea conferta* forms large (11 cm diameter) coralla on diverse Miocene reefs in Puerto Rico (Vaughan 1919, Coryell and Ohlsen 1929) and in Anguilla (Vaughan 1919). Three *Siderastrea* species (*S. siderea*, *S. dalli*, *S. pliocenica*) have been found in upper Pliocene sands and muds of the Pinecrest Member of the Tamiami Formation of southern Florida (Weisbord 1974, Meeder 1979) but were not important framework builders.

In modern reefs, *Siderastrea siderea* is a significant but secondary contributor to the framework. It is abundant in reef flat, rear zone, and backreef areas (Goreau 1959; Milliman 1973) and is especially important in the pioneering stages of reef development (Lewis 1960). *Siderastrea radians* commonly occurs as small (10—20 cm diameter) isolated colonies in inshore areas and on sand flats. It contributes negligibly to the reef framework.

THE MORPHOLOGY OF *SIDERASTREA MENDENHALLI*

Siderastrea has a colonial cerioid growth form, large corallite diameters, and well-defined corallite walls united by numerous synapticulae. Corallites bud extratentacularly and are non-polymorphic. Septa are numerous and are arranged in three or more cycles. Septal margins are dentate and the columella consists of numerous papillary trabeculae (Vaughan 1919; Wells 1956). Species within the genus are distinguished using characters such as septal number, corallite diameter, columella structure, wall structure, and spacing between septal teeth (Vaughan 1919). The species analyzed in the present report are illustrated in plates 30 and 31.

Description and analysis of environmental variation

Eight *S. mendenhalli* colonies from each location were analyzed numerically to determine the magnitude and pattern of intraspecific environmental variation. Eight characters (fig. 2) were measured on six corallites of each colony using transverse thin-sections prepared 5 mm from the colony surface. All characters were measured

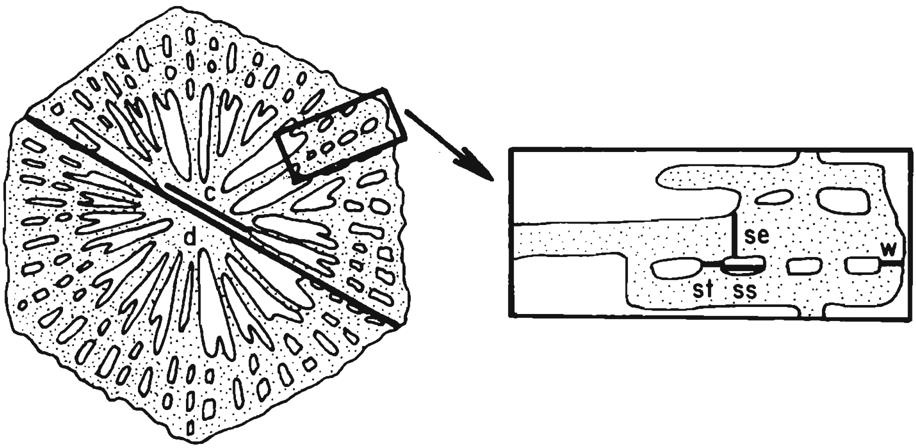

Fig. 2. Line diagrams illustrating six measurements taken on *Siderastrea* corallites. Two additional characters (*nse*, number of septa, and *nsy*, number of synapticular rings) were also analyzed numerically; *c* columella thickness; *d* corallite diameter; *se* septum thickness; *ss* synapticula spacing; *st* synapticula thickness; *w* wall thickness.

to the nearest 0.025 mm, except 'd' which was measured to the nearest 0.1 mm. Means and standard deviations for each population (SM (BC), SM (NCM)) are listed in Table 1. Analysis of variance (Barr *et al.* 1976) suggests that means of the two populations are equal in all characters except 'c', 'st', and 'ss'. The columella and synapticulae are generally thicker and the synapticulae are more closely spaced in the northeast Coyote Mountains (NCM) population (Table 1, pl. 30). Multivariate analysis (Barr *et al.* 1976) confirms that the two populations can be distinguished using a linear combination of characters (for the Hotelling-Lawley trace: $F(8.73) = 4.15$, Prob $< F = 0.0004$).

Table 1

Means ($\bar{X}$) and standard deviations (s) in mm of measurements of skeletal characters in populations of six *Siderastrea* species, 'n' indicates number of colonies measured in each population

		SM (BC) n=8	SM (NCM) n=8	SSd (LAG) n=8	SSd (SC) n=8	SSi n=6	SC n=8	SR n=8	SP n=7
d	$\bar{X}$	4.08	4.16	4.27	4.46	5.30	3.85	4.16	5.05
	s	0.29	0.26	0.55	0.26	0.76	0.35	0.36	0.66
se	$\bar{X}$	0.132	0.140	0.111	0.129	0.119	0.142	0.220	0.176
	s	0.018	0.015	0.008	0.010	0.015	0.020	0.024	0.013
c	$\bar{X}$	0.559	0.601	0.579	0.670	0.619	0.625	0.694	0.719
	s	0.045	0.073	0.062	0.034	0.112	0.110	0.096	0.107
w	$\bar{X}$	0.134	0.130	0.088	0.099	0.101	0.131	0.167	0.150
	s	0.021	0.034	0.016	0.009	0.026	0.014	0.033	0.020
st	$\bar{X}$	0.110	0.122	0.100	0.133	0.092	0.105	0.127	0.089
	s	0.009	0.014	0.016	0.012	0.007	0.017	0.019	0.005
ss	$\bar{X}$	0.191	0.159	0.133	0.115	0.215	0.199	0.148	0.232
	s	0.026	0.018	0.019	0.010	0.012	0.031	0.021	0.028
nsy	$\bar{X}$	3.42	3.28	4.33	4.33	3.74	3.19	3.60	3.28
	s	0.42	0.53	0.90	0.50	0.23	0.23	0.41	0.32
nse	$\bar{X}$	47.5	48.1	48.9	49.8	52.2	42.9	30.7	46.3
	s	2.0	2.3	5.6	2.8	7.0	3.9	2.0	5.6

Comparisons with environmental variation in other species

Morphologic variation in *S. mendenhalli* is considerably less than that in *Solenastrea fairbanksi*, another Imperial Formation coral (Foster 1979). In *S. fairbanksi*, populations from Barrett Canyon and the northeast Coyote Mountains differed significantly in 14 of 16 analyzed characters. Discriminant function analysis showed that no overlap existed between populations. Unlike *S. mendenhalli*, the columella was thicker in the Barrett Canyon population. However, like *S. mendenhalli*, wall structures were thicker in the northeast Coyote Mountains population.

To compare the variation in *S. mendenhalli* with that in modern *S. siderea*, the two *S. mendenhalli* populations and two previously measured populations of *S. siderea* (Foster 1978) were analyzed multivariately using discriminant analysis (Dixon 1975). The *S. siderea* populations consisted of: (1) 8 colonies from a clear forereef sand channel (20 m depth) near Discovery Bay, Jamaica (SSd(SC)), and (2) 8 colonies from a quiet, turbid backreef lagoon (16 m depth) near Discovery Bay, Jamaica (SSd(LAG)). In the analysis, two characters, 'st' and 'ss', were used and the first two canonical variables accounted for 100% of the total variation (CV1 = 75.4%). (+) 'ss' was more heavily weighted on the first canonical variable. (+) 'st' was more heavily weighted on the second canonical variable. Results of comparisons between populations show: (1) the *S. mendenhalli* populations overlap, whereas the *S. siderea* populations are distinct; (2) the range of variation or spread of points is equivalent in the two species; (3) the population from the more turbid environment (B, L) is centered to the right of the population from the deep clear environment (N, S) in each species; (4) some overlap exists between the *S. siderea* lagoon population and the *S. mendenhalli* populations (fig. 3). Results (1) and (2) suggest that the two species express the same magnitude of variation but that *S. siderea* responds more consistently to its environment. This interpretation assumes that the habitats of the

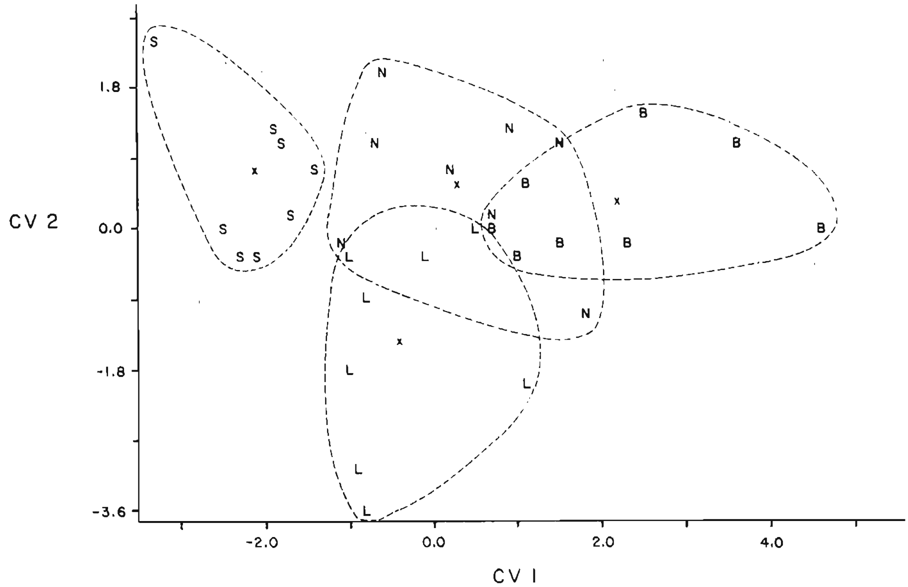

Fig. 3. Plot illustrating the results of discriminant analysis comparing two *S. mendenhalli* populations and two *S. siderea* populations. CV1 indicates the score for each colony on the first canonical variable, CV2 indicates the score for each colony on the second canonical variable. A dashed line outlines the approximate margin of each group. An 'x' marks the mean within each group. *C*, colonies of *S. siderea* from Jamaican forereef; *L*, colonies of *S. siderea* from Jamaica, lagoon; *N*, colonies of *S. mendenhalli* from northeast Coyote Mountains; *B*, colonies of *S. mendenhalli* from Barrett Canyon.

two populations of each species differ equally and that environmental heterogeneity is equivalent in all habitats. Result (3) confirms that *S. mendenhalli* is responding morphologically to turbid environments in the same manner as *S. siderea*. Result (4) suggests that *S. siderea* and *S. mendenhalli* have similar overall morphologies but that *S. mendenhalli* may be better adapted in general for turbid, lagoonal environments.

Since patterns of environmental variation within species appear to be related to sources of nutritive energy (Foster 1978), the similarities between *S. mendenhalli* and *S. siderea* suggest that *S. mendenhalli* may have derived its energy largely by ingesting suspended material trapped using mucus nets in the same manner as *S. siderea* (Lewis and Price 1975; Lewis 1976, 1977). The thinner, more widely spaced thecal and columellar structures in turbid environments may be related to faster upward growth in environments containing more suspended material. This faster upward growth has been documented for *S. siderea* (Foster 1978) and is presumed for *S. mendenhalli* because of the presence of numerous large coralla at the more turbid Barrett Canyon location. *S. fairbanksi*, on the other hand, grew more rapidly in the clear, platform environment of the northeast Coyote Mountains location and may have derived nutrition largely by tentacle feeding on zooplankton (Foster 1979). The differences between *S. fairbanksi* and *S. mendenhalli* in patterns of environmental variation support this hypothesis.

MORPHOLOGIC COMPARISONS BETWEEN *SIDERASTREA* SPECIES

Measurements (Table 1) were also made on 6 corallites in 8 colonies of *S. californica* (SC) from the Barrett Canyon locality, in 6 colonies of *S. silecensis* (SSi) from the Tampa Formation (Vaughan's loc. 4890), and in 7 colonies of *S. pliocenica* (SP) from the Pleistocene Caloosahatchee Formation (Vaughan's loc. 3206); and differences between species were analyzed using discriminant analysis (Dixon 1975). The first two canonical variables accounted for 96.9% of the total variation (CV1 = = 50.9%), and three characters 'd', 'se', and 'st' were used. (+) 'se' and (−) 'st' were more heavily weighted on the first canonical variable, whereas (+) 'd' and (−) 'se' were more heavily weighted on the second canonical variable. The results (fig. 4) show that: (1) the two Florida species (SSi, SP) are distinct from each other and

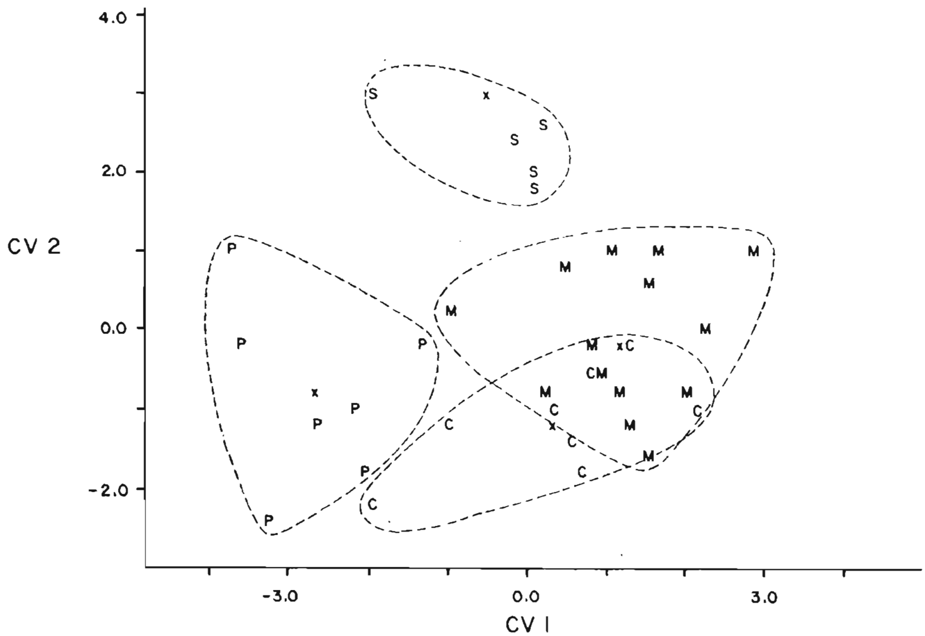

Fig. 4. Plot illustrating the results of discriminant analysis comparing four Pliocene *Siderastrea* species. CV1 indicates the score for each colony on the first canonical variable. CV2 indicates the score for each colony on the second canonical variable. A dashed line outlines the approximate margin of each group. An 'x' marks the mean within each group. *M*, colonies of *S. mendenhalli*; *C*, colonies of *S. californica*; *S*, colonies of *S. silecensis*; *P*, colonies of *S. pliocenica*.

from the two Gulf of California species (SM, SC), and (2) the two Gulf of California species (SM, SC) overlap considerably. F-matrices also suggest that *S. mendenhalli* and *S. californica* are not sufficiently distinct to warrant separation into two species. Result (1) suggests that *S. mendenhalli* and *S. silecensis* were distinct species which separately adopted the reef-building habit during Mio-Pliocene time at two extreme positions on the northern fringe of reef-coral distribution. Result (2) implies that *S. californica* may be merely a variant of *S. mendenhalli.*

Despite the differences between *S. mendenhalli* and *S. silecensis*, the morphology of numerous framework-building *Siderastrea* (*S. mendenhalli*, *S. silecensis*, *S. conferta*, and *S. siderea*) is remarkarbly similar (pl. 30, 31) and suggests that large corallites with thin columellae and numerous thin synapticulae may be better adapted for rapid colony growth and reef-building in *Siderastrea.* To test this hypothesis the morphology of three framework-builders (*S. mendenhalli*, *S. silecensis*, and *S. siderea*) has been compared with three non-framework-builders (*S. californica*, *S. pliocenica*, and *S. radians*). Measurements taken on six corallites in eight colonies of *S. radians* (SR, Table 1) from the forereef locality near Discovery Bay, Jamaica were added to the non-framework-building group. Analysis of variance (Dixon 1975) shows that framework-builders differ from non-framework-builders in all characters except 'd' and 'st'. Framework builders have thinner septa, columellae, and walls and more synapticular rows and septa per corallite than non-framework builders. Discriminant analysis (Dixon 1975) shows that the two groups also differed multivariately ($F(4, 56) = 30.2$, $p \ll .002$). The first canonical variable accounts for 100% of the total variation and five characters ('d', 'se', 'c', 'st', 'ss') were used. The most heavily weighted characters were (+) 'd' and (−) 'se'. The histogram (fig. 5) for the analysis shows that slight overlap occurs between the two groups. This result can probably be explained by the previously described overlap of *S. californica* with *S. mendenhalli.*

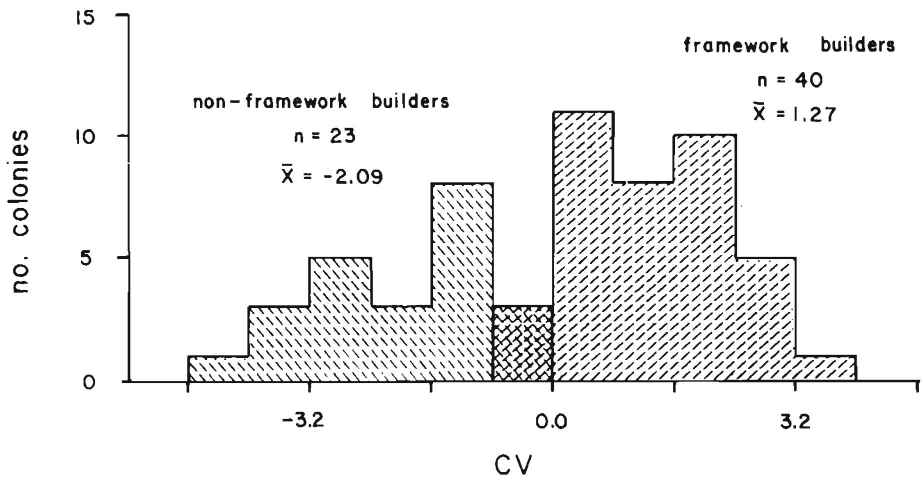

Fig. 5. Histogram showing the results of discriminant analysis comparing framework building and non-framework building coral morphologies. CV indicates the score on the canonical variable.

SUMMARY

(1) *S. mendenhalli* constructed banks in shallow, turbid environments along the north end of the Gulf of California during Pliocene time. The forereef contained a diverse assemblage of small, isolated mound-like coral colonies. Two reef coral species formed irregular-shaped colonies and patch reefs in backreef facies. The *Siderastrea* bank resembles reefs formed by *S. silecensis* in similar Mio-Pliocene Floridian embayments but differs in diversity from other larger Mio-Pliocene and modern central Caribbean reefs.

(2) The pattern and magnitude of environmental variation in *S. mendenhalli* is similar to that observed in *S. siderea.* Both species have thin, closely spaced synapticulae in turbid environments. These similarities suggest that the two species may have used similar energy sources. *S. siderea* appears to have responded more consistently to its environment.

(3) The morphology of *S. mendenhalli* differs from that of the Floridian framework-builder *S. silecensis*; however, both species have large corallites with thin septa, columellae, and walls and numerous synapticular rings. This morphology is significantly different from that of non-framework building *Siderastrea* and may be specially adapted for more rapid colony growth in environments with abundant suspended organic material.

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EXPLANATION OF THE PLATES 30 AND 31

Plate 30

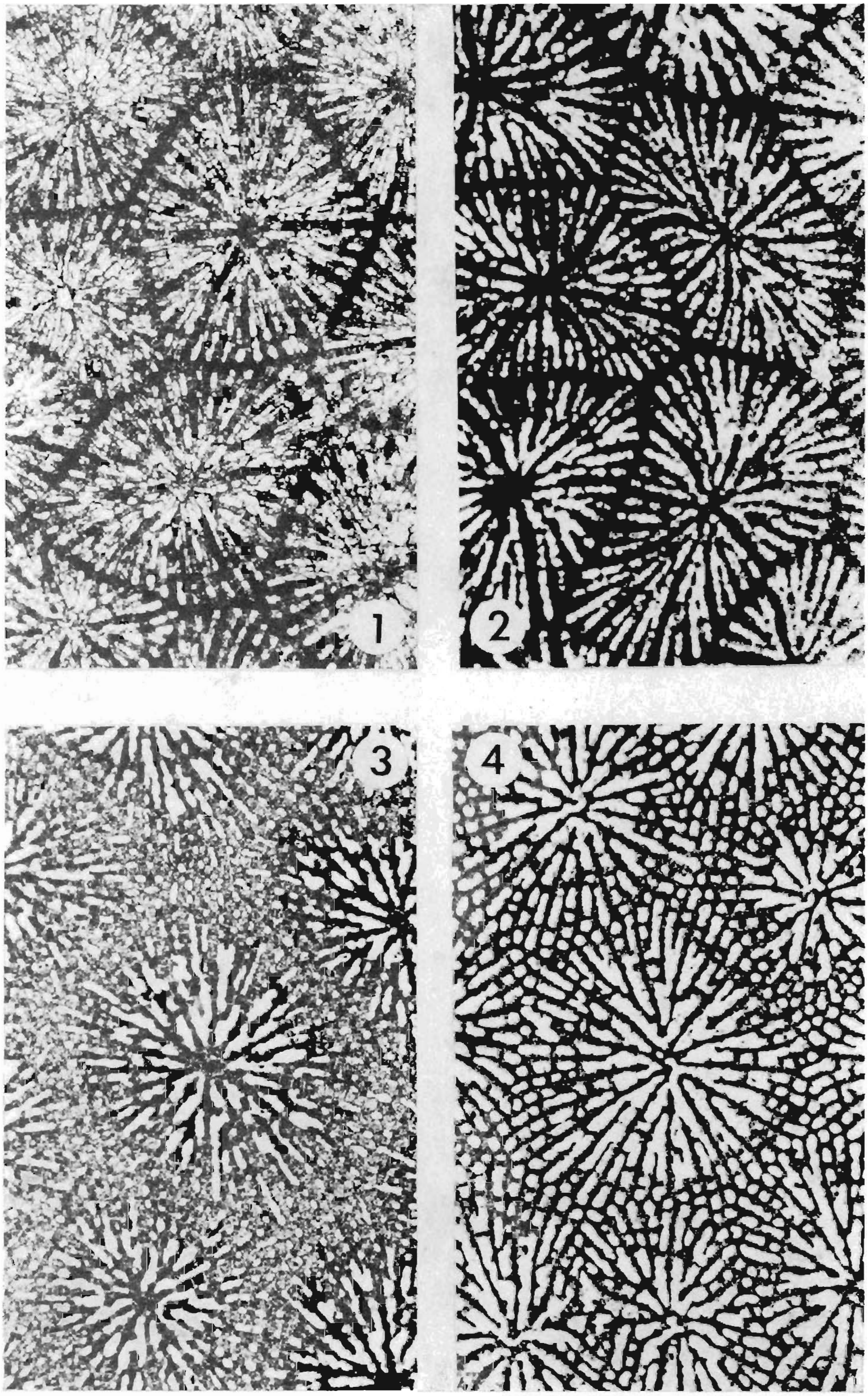
Thin sections showing environmental variation in *S. mendenhalli* and *S. siderea*. Colonies from turbid environments (2,4) have thinner columella and thinner, more closely spaced synapticulae than colonies of the same species from clear environments (1,3).

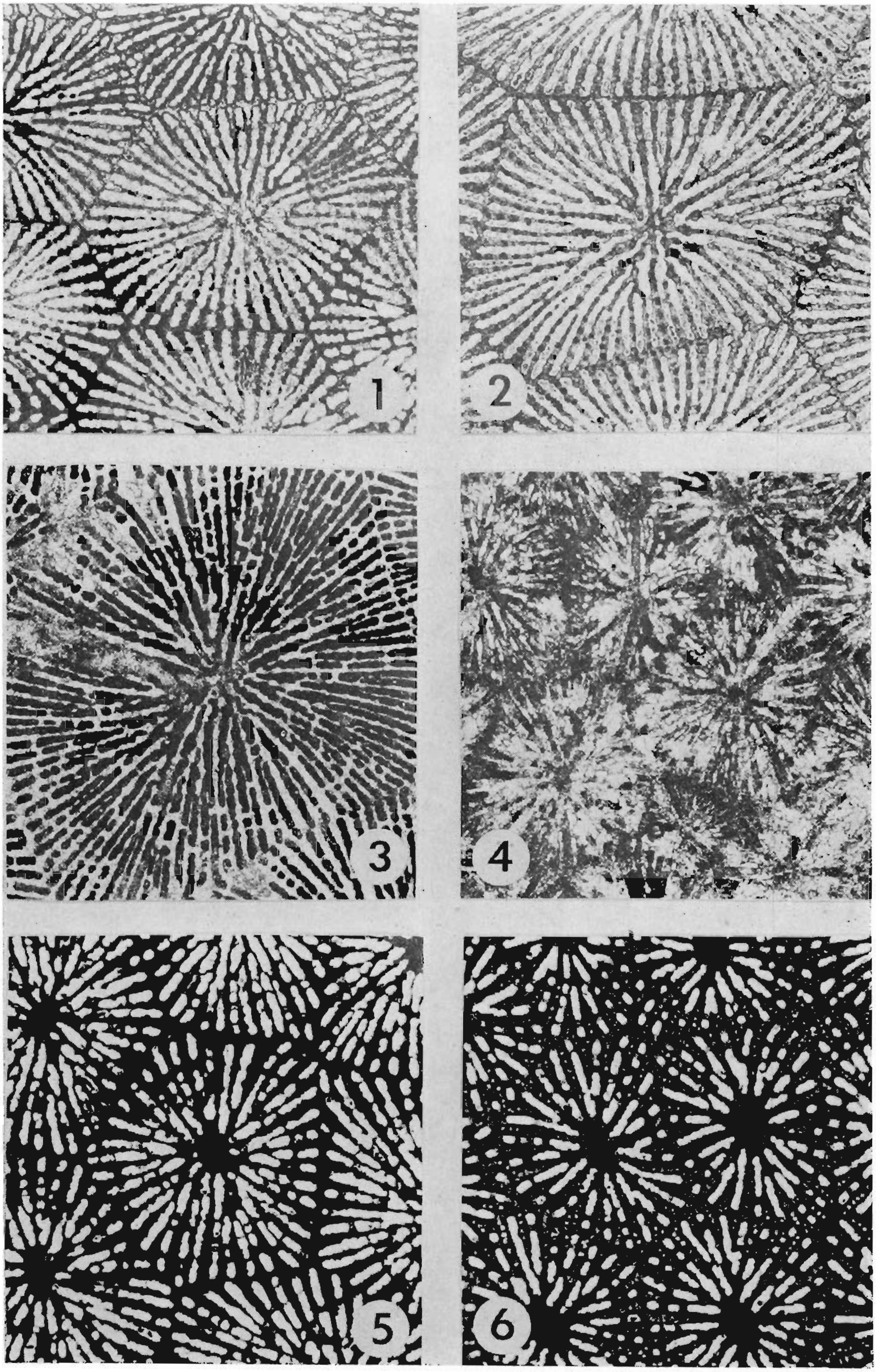
1. *Siderastrea mendenhalli*, northeast Coyote Mountains, California (SUI4566OA), trans. sect., ×10.
2. *Siderastrea mendenhalli*, Barret Canyon, California (SUI45628B), trans. sect., ×10.
3. *Siderastrea siderea* from forereef sand channel, Discovery Bay, Jamaica SUI45511D), trans sect., ×10.
4. *Siderastrea siderea* from forereef sand channel, Discovery Bay, Jamaica SUI45491D), trans. sect.. ×10.

Plate 31

Thin-sections of framework building (1—3) and non-framework building (4—6) *Siderastrea*. Framework builders have larger corallites, more septa, thinner columellae, and more synapticulae than non-framework builders.

1. *Siderastrea silecensis*, Tampa, Florida (USNM325142-6A) trans. sect., ×8.
2. *Siderastrea silecensis*, Tampa, Florida (USNM325142-5A) trans. sect., ×8.
3. *Siderastrea conferta*, Cocos Bay, Anguilla (USNM325166-1A), trans. sect., ×8.
4. *Siderastrea californica*, Barrett Canyon, California (USNM7616-4A), trans. sect., ×8.
5. *Siderastrea pliocenica*, Caloosahatchee, Florida (USNM3206-7A) trans. sect., ×8.
6. *Siderastrea radians*, Discovery Bay, Jamaica (SUI45701A), trans. sect., ×8.


1
2
3
4


1
2
3
4
5
6