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MIDDLE MIOCENE RECOVERY OF CARIBBEAN REEF CORALS: NEW DATA FROM THE TAMANA FORMATION, TRINIDAD

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ABSTRACT—Caribbean coral reef communities were restructured by episodes of accelerated biotic change during the late Oligocene/early Miocene and the late Pliocene/early Pleistocene. However, rigorous description of the effects of rapid biotic change is problematic because preservation and exposure of coral-bearing deposits is not consistent in all stratigraphic intervals. In the Caribbean, early and middle Miocene exposures are more rare than late Miocene and Pliocene exposures. One exception is the late early to early middle Miocene Tamana Formation of Trinidad, and old and new collections from this unit were studied to determine the timing of recovery after the Oligocene/Miocene transition. A total of 41 species of zooxanthellate corals were recovered from the unit, including 21 new records. Within these assemblages, species first occurrences outnumber species last occurrences by a factor of four (31 first occurrences and eight last occurrences). The extension of the stratigraphic ranges of species previously first recorded in Pliocene sediments has reduced an apparent Pliocene pulse of origination, indicating that the Pliocene/Pleistocene transition was largely a result of accelerated extinction against a background of near-constant origination. The fact that few species last occur in the Tamana fauna indicates that the Oligocene/Miocene transition was complete by the end of the early Miocene.

INTRODUCTION

TWO MAJOR episodes of biotic change characterize the post-Eocene history of Caribbean coral reef ecosystems. An early Miocene and later an early Pleistocene pulse of extinction and ecological change interrupted late Oligocene and Pliocene intervals of high regional diversity. Extensive Caribbean reef development coincided with high generic diversity during the Late Oligocene (Frost, 1972), and recent generic compilations suggest that the Caribbean Oligocene reef fauna included between 35 and 44 genera (Edinger and Risk, 1995; Budd, 2000). However, Vaughan (1919) recognized a period of increased extinction in Caribbean reef-corals during the early Miocene, and commented on the relatively poor development of Caribbean reef buildups during the Miocene. Nearly half the Oligocene genera disappear from Caribbean reefs during the early Miocene (Edinger and Risk, 1995), and few new genera appear. The exact timing of the post-Oligocene recovery of Caribbean coral species diversity remains uncertain, but regional species richness had achieved a new maximum by the late Pliocene. Although regional diversity was increasing throughout the middle to late Miocene, large-scale reefal buildups continued to be rare. Instead, corals occurred in off-reef or reef marginal environments (Frost, 1977). A large component of the increasing diversity is a distinct assemblage of free-living corals that inhabited non reef environments such as sea grass beds or shallow carbonate shelves (Johnson et al., 1995). Many of the dominant extant Caribbean species were also present by the beginning of the Pliocene, including members of the *Montastraea* “*annularis*” species group, *Acropora palmata*, *A. cervicornis*, *Diploria clivosa*, *D. strigosa*, and *Undaria agaricites*. However, these species did not assume the great abundance characteristic of Recent Caribbean reefs until after the regional mass extinction of corals at the end of the Pliocene.

Nearly half of the late Neogene reef coral species disappeared during the Plio-Pleistocene regional extinction (Budd et al., 1994). An initial increase in both the number of species last occurrences and the per-taxon extinction rates during the Early Pliocene culminated in a peak of extinction from 2 to 1 Ma. One-third of the total number of extinctions recorded from the Caribbean Neogene record ($n = 146$) are concentrated in this single million-year interval. All ecological groups and reefal environments were affected (Budd and Johnson, 1999b). During the Miocene and Pliocene, species of small corals exhibited higher rates of taxonomic turnover than species with large, long-lived colonies, but during

the Plio-Pleistocene extinction pulse all groups were strongly affected. Because extant species were already present, late Pliocene assemblages include a mix of extinct and extant forms. Extinct forms such as branching *Stylophora* species lived among species of *Acropora* that dominate in many living reef communities (Budd et al., 1998; Budd and Johnson, 1999b).

This detailed understanding of the Oligocene/Miocene and Pliocene/Pleistocene biotic transitions is a result of intensive sampling from the extensive coral bearing deposits preserved from these intervals. Frost and coworkers mapped late Oligocene and early Miocene reef deposits from fringing/barrier reef complexes in Chiapas (Frost and Langenheim, 1974) and Puerto Rico (Frost et al., 1983) and tracts of small patch reefs on carbonate platforms in Antigua (Frost and Weiss, 1979) and Texas (Frost and Schafersman, 1978). Similarly, large collections exist from numerous well-documented Late Neogene deposits from the Dominican Republic (e.g., Budd and Johnson, 1999a), Curaçao (Budd et al., 1998), and Costa Rica (Budd et al., 1999). In contrast, the early and middle Miocene recovery interval is less well known, in part due the relative lack of exposure and possibly resulting from the demise of extensive reef building associated with the Oligocene/Miocene transition. To date, rigorous study of early Miocene faunas have been completed from Anguilla (Budd et al., 1995) and Chiapas (Frost and Langenheim, 1974). Besides these examples, all knowledge of the early to middle Miocene fauna is based on limited collections from the Emperador Formation in Panama and the Chipola and Tampa Formations in Florida (Vaughan, 1919). This lack of coral-bearing deposits is probably a result of the demise of extensive reef building associated with the Oligocene/Miocene transition. Because of the limited exposure of late early and middle Miocene coral units, estimates of biotic change from this interval are highly sensitive to the quality of the limited available information. Some of the most diverse early to middle Miocene reef-coral assemblages have been described from the Tamana Formation of Trinidad. The goal of this work is to rigorously document the Tamana fauna through analysis of a combination of existing collections and extensive new collections within an up-to-date taxonomic framework. A thorough description of the coral fauna from these important sites is required to assess an apparent early Pliocene origination pulse and to more precisely determine the temporal and ecological pattern of recovery following the Oligocene/Miocene transition.

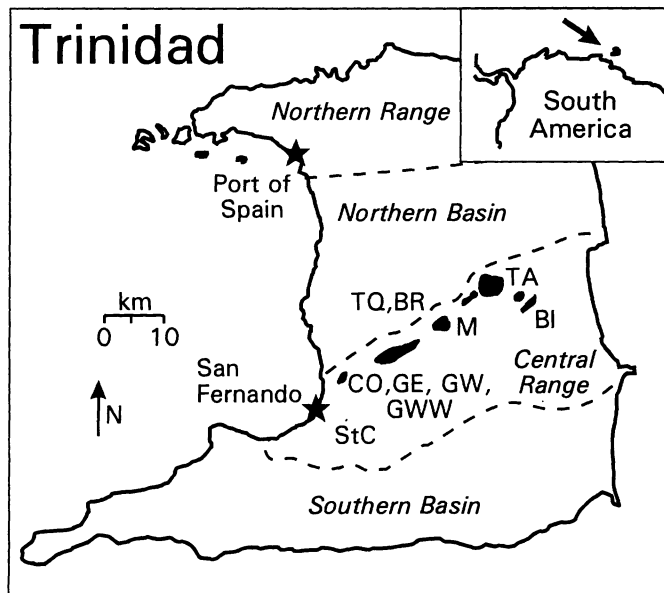


FIGURE 1—Locality map showing distribution of Tamana Limestones in the central range of Trinidad. Limestone units are indicated by the shaded areas. Abbreviations: BI, Biche Quarry; BR, Brasso Gorge; CO, Concord Quarry; GE, Gasparillo Quarry (East); GW, Gasparillo Quarry (West); GWW, Quarry West of Gasparillo Quarry (West); M, Machapoorie Quarry; StC, St. Croix Limestone; TQ, Tabaquite Quarry; TA, Tamana Cave.

MATERIAL AND METHODS

The Tamana Formation includes white to yellow impure limestones with discontinuous exposure along the flanks of the Central Range of Trinidad (Fig. 1; Donovan, 1994). This unit comprises shelf carbonates deposited on the margins of thrust-bounded uplift of the northern half of Trinidad and represents shallow facies equivalent to the deeper and more shallow calcareous silts and shales of the Brasso Formation (Carr-Brown and Frampton, 1979; Ehrlich et al., 1993). In the southern basin, the Herrera Member of the Cipero Formation may also represent a deeper water facies equivalent of Brasso/Tamana unit. Although corals are locally abundant, no extensive reef development is recognized in the unit. Instead, small coral patches and carbonate shoals developed in high energy nearshore environments. Local reef development might have been restricted by input of siliciclastics, and the development of channels in the upper parts of the carbonate rich units suggests that carbonate production ceased due to shallowing and increased input of fluvially derived sediments (Ehrlich et al., 1993). Regional carbonate production was greatly slowed by the eastward deflection of the Oronoco River from the Falcon Basin increasing the sediment load into the waters off the northeast coast of South America (Díaz de Gamero, 1996), and increased planktonic productivity associated with coastal upwelling (Edinger and Risk, 1995). Significant carbonate production has not occurred along the coast of Trinidad since the deposition of the Tamana Formation.

A combination of new and existing collections were used to determine species distributions within the Tamana Formation (Appendix 1). Material described by Duncan (1868) and Vaughan and Hoffmeister (1926) were examined as well as previously undescribed collections (Table 1). This material was complemented by extensive new collections including over 700 specimens from both new and previously studied localities. Detailed locality information was not always available, and some old localities could not be located for further sampling. Because it was not always

TABLE 1—List of zooxanthellate coral faunules from the Tamana Formation. See Appendix 1 for a full listing of sample localities.

Faunule	Taxa	Code	Collections ¹
Biche	2	BI	NMB
Brasso	13	BR	BM(NH)
Concord	13	CO	NMB
Cumuto	10	CU	BM(NH), USNM
Gasparillo (E)	14	GE	NMB, USNM
Gasparillo (W)	16	GW	SIO, NMB
Gasparillo (WW)	10	GWW	SIO
Machapoorie	9	M	BM(NH), NMB, USNM
St. Croix	9	StC	BM(NH)
Tabaquite	18	TQ	NMB, USNM
Tamana Cave	2	TA	USNM

¹ BH(NH) = Natural History Museum London, NMB = Naturhistorisches Museum Basel, USNM = United States National Museum of Natural History, SIO = Scripps Institution of Oceanography.

possible to ensure that new and old collections were produced from the same horizon, all collections were merged into a set of 11 faunules representing local assemblages from sections no more than 30 m thick (Table 2). This relatively coarse scale of analysis reflects the discontinuous preservation of corals within the local sections, and the merging of samples into faunules allows increased confidence in the sampling completeness of local paleo-communities at the cost of potentially combining collections from widely disparate times or paleoenvironments. Collections without adequate locality documentation did not yield unique taxa and were not included in any of the faunules.

Stratigraphic relationships among the limestone units within the Tamana Formation are not well understood because of complex facies relationships and poor exposures, but detailed biostratigraphic and facies analysis of a subset of the units suggests that carbonates exposed in Gasparillo, Guaracara, Brigand Hill, and Biche are roughly equivalent in age (Ehrlich et al., 1993). Analysis of planktonic foraminifera assemblages from these localities indicates deposition between the *Praeorbulina glomerosa* and *Globorotalia fohsi lobata* zones (Bolli and Saunders, 1985; Ehrlich et al., 1993), corresponding with the N8 to early N12 zone (Blow, 1969), or early middle Miocene (Langhian) to late middle Miocene time (16.4 Ma to 12.3 Ma, Berggren et al., 1995). Similar high-resolution biostratigraphic data are not available for the Machapoorie, Cumuto Road, Tabaquite, and Brasso faunules from the northern flank of the Central range or the St. Croix faunule from the southern Central Range, but all of these units have been previously correlated to better-constrained Tamana limestone exposures (Kugler, 1953, 1956).

Scleractinian species were identified using the taxonomic framework of Budd et al. (1994), and a standard set of diagnostic characters and illustrations of each species are available from the Neogene Biota of Tropical America project (NMITA: <http://nmita.geology.uiowa.edu>). Some identifications have been left in open nomenclature pending a formal taxonomic revision that is beyond the scope of the present work. Azooxanthellate taxa (*Asterosmilia* sp., *Oculina* sp., and *Sphenotrochus* sp.) were not included in the analysis. Common species are illustrated in Figures 2 to 4. All new collections are deposited at the United States National Museum of Natural History (Smithsonian Institution) or at the Scripps Institution of Oceanography. A complete list of specimens examined is available at the Journal of Paleontology world wide web site at <http://www.journalofpaleontology.org>.

The Tamana fauna was compared with assemblages obtained from the Caribbean Coral database (version 1999; Budd et al., 1994; Budd and Johnson, 1999b), a specimen-based compilation of all known Neogene occurrences of Caribbean zooxanthellate corals. This data set includes records of 208 species from 498

TABLE 2—Relative abundance of zooxanthellate coral species within the eleven faunules. New records and species that first or last occur in the Tamana Formation are also indicated. Abbreviations for each faunule are listed in Table 1.

Species	BI	BR	CO	CU	GE	GW	GWG	M	StC	TQ	TA	New	First or last
<i>Stephanocoenia intersepta</i>		R							R			Y	F
<i>Stylophora affinis</i>							R		R			Y	F
<i>Stylophora granulata</i>						R				C		Y	F ¹
<i>Stylophora imperatoris</i>				R				C		R			
<i>Stylophora minor</i>							R					Y	F ¹
<i>Stylophora undata</i>		C				R			R			Y	
<i>Pocillopora arnoldi</i>								R				Y	
<i>Madracis</i> sp.		R								R			
<i>Agaricia undata</i>		R			R	C			R				F ¹
<i>Undaria crassa</i>		R	R		R	C	R			R		Y	F
<i>Pavona machapooriensis</i>								R				Y	F, L
<i>Pavona pennyi</i>				R		R			R				F, L
<i>Pavona trinitatis</i>				R				R					F ¹ , L ¹
<i>Leptoseris gardineri</i>						R						Y	F ¹ , L ¹
<i>Leptoseris walli</i>				R									F ¹ , L ¹
<i>Psammocora trinitatis</i>				R	R	C			R	R			F ¹
<i>Psammocora gasparillensis</i>			R		R					R			F, L
<i>Siderastrea siderea</i>			R		R					R			F ¹
<i>Porites-I astreoides</i>			R									Y	F
<i>Porites-I aff. astreoides</i>		C		R	R					R		Y	F ¹
<i>Porites-I trinitatis</i>				R	C	C	C			C	R		F, L
<i>Porites-I waylandi</i>		R	R		R	C	R			R	R		F ¹
<i>Porites-II baracoensis</i>					R			R		R			
<i>Goniopora hilli</i>						R	R			R		Y	F ¹
<i>Caulastrea portoricensis</i>			R		C	C	C			C		Y	F
<i>Favia dominicensis</i>			R							R		Y	F ¹
<i>Goniastrea trinitatis</i>									R			Y	F, L
<i>Diploria zambensis</i>		R										Y	F
<i>Colpophyllia</i> sp.					R	R						Y	
<i>Montastrea-I brevis</i>			C			R				R		Y	F
<i>Montastrea-I limbata-2</i>		C	C		C	C	C			R		Y	F ¹
<i>Montastrea-I</i> sp. A							R					Y	F
<i>Montastrea-I trinitatis</i>	R	R	R	R	R	R	R			R		Y	F ¹
<i>Montastrea-II canalis</i>		C	R			R						Y	F ¹
<i>Montastrea-II cylindrica</i>		R			R							Y	F ¹
<i>Montastrea-II endothecata</i>		R							R			Y	F ¹
<i>Solenastrea bournoni</i>			R							C		Y	F ¹
<i>Trachyphyllia bilobata</i>								R					
<i>Antillophyllia sawkinsi</i>	R			C				C					
<i>Placocyathus trinitatis</i>								C					F
<i>Mycetophyllia bullbrooki</i>			R	R									F ¹

¹ Indicates species that also occur in late early or early middle Miocene deposits from Curacao, Panama, or the Dominican Republic.

early Miocene to Recent collections, and includes samples from eight other Early and Middle Miocene reef units (Appendix 2). Early Miocene faunas include the three distinct depth assemblages from Anguilla Formation (Budd et al., 1995), the Emperador Limestone of the La Boca Formation from Panama (Vaughan, 1919; Woodring, 1957, 1964) and the Tampa member of the Arcadia Formation from Florida (Scott, 1988). Early to Middle Miocene units include the Baitoa Formation from the northern Dominican Republic (Saunders et al., 1986), and the Chipola Formation from northern Florida (Vokes, 1989). Middle Miocene records were obtained from the older units in the Seroe Domi Formation of Curaçao (Budd et al., 1998), and from new collections from the Valiente Peninsula of Panama ("unnamed volcanics" in Coates, 1999; A. F. Budd, personal commun., December, 1999). Oligocene occurrences of Neogene species were added to this data set to identify spurious Neogene first occurrences (Budd, 2000). These data were taken from modified published lists from the Antigua and Central Plain Formation of Antigua (Frost and Weiss, 1979), the Lares Formation of Puerto Rico (Frost et al., 1983), the Rancho Berlin and La Quinta Formations of Chiapas (Frost and Langenheim, 1974), and the Anahuac Formation of Texas (Frost and Schafersman, 1978).

Neogene patterns of species turnover were estimated using standard methods previously applied to the Caribbean coral database (Budd et al., 1994, 1996; Budd and Johnson, 1996, 1999b;

Johnson and McCormick, 1999). Sample age resolution is not uniform (Fig. 5), so conservative estimates of species richness and taxonomic turnover were calculated. Each sample was assigned a "long" stratigraphic range extending from the lower age boundary of the sample in which the species first occurs to the upper age limit of the sample in which the species last occurs. This "long range" approach contrasts with the "midpoint ranges" commonly estimated from the midpoint age of the sample of first occurrence to the midpoint age of the sample in which the taxon last occurs. The true durations of taxa are always underestimated by stratigraphic ranges, so applying "long ranges" represents a conservative approach. Counts of range-through species richness and the numbers of first and last occurrences of species were then calculated from the stratigraphic ranges for a set of one-million-year subintervals extending from Miocene to Recent. Age resolution for 48 percent of the samples exceeds one million years, so the numbers of first and last occurrences in each temporal subinterval was weighted with respect to age resolution. For example, if a sample age resolution spanned three subintervals, then each first occurrence in that sample would contribute one-third of a first occurrence to each subinterval. This convention will tend to smooth peaks that might result from using midpoints of sample age ranges to associate samples with a single subinterval in absence of evidence that the true age of that sample was restricted to that subinterval.

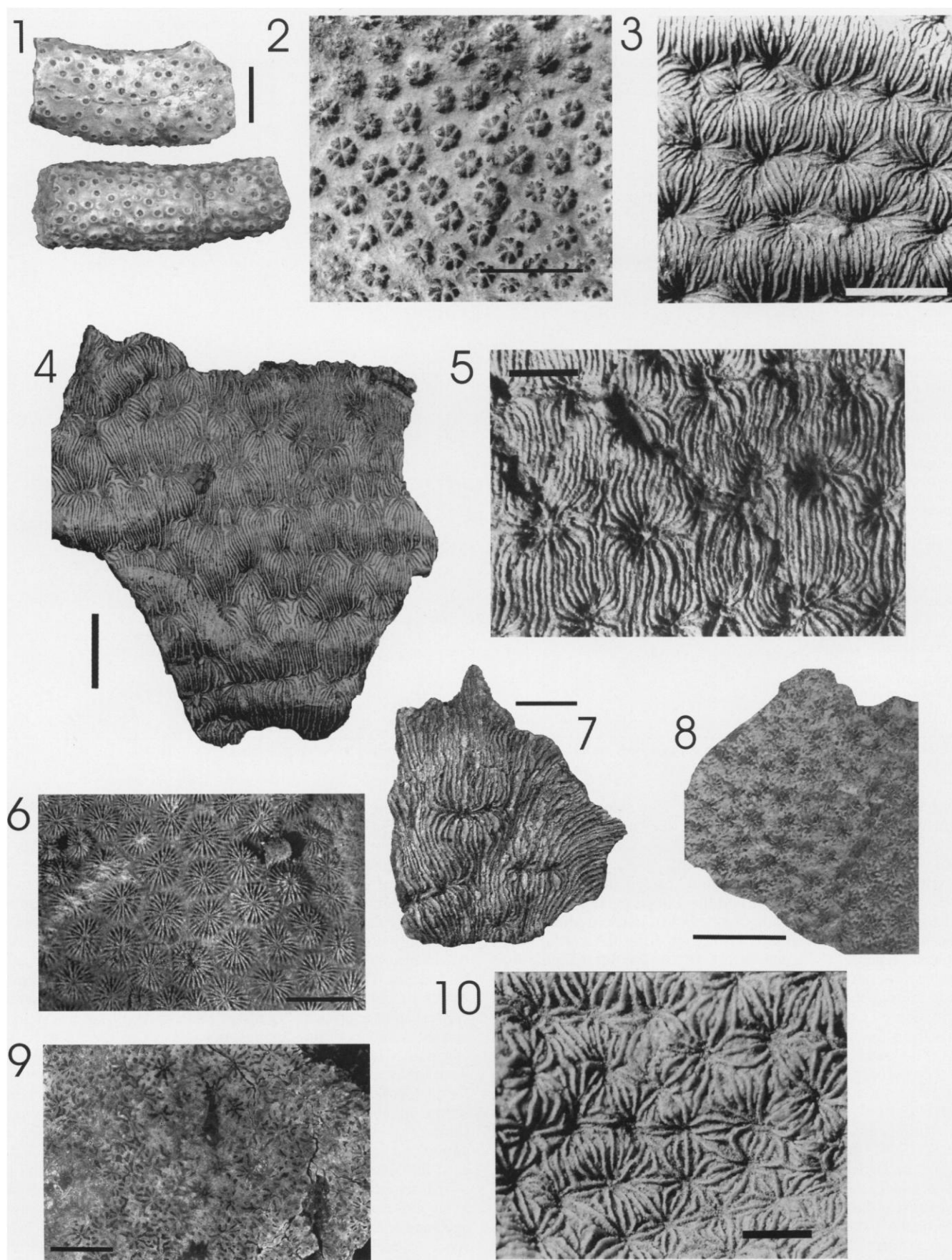


FIGURE 2—Calical surfaces of common species of reef corals collected from the Tamana Formation. All scale bars are 5 mm long. 1, *Stylophora granulata*, USNM 100583. 2, *Stylophora imperatoris*, NMB D6397. 3, *Undaria crassa*, USNM 100584. 4, *Agaricia undata*, USNM 100585. 5, *Pavona trinitatis*, NMB D6387. 6, *Siderastrea siderea*, BM(NH) AZ 990. 7, *Leptoseris gardineri*, USNM 100586. 8, *Porites trinitatis*, USNM 100587. 9, *Psammocora trinitatis*, USNM 100588. 10, *Pavona pennyi*, USNM 100589.

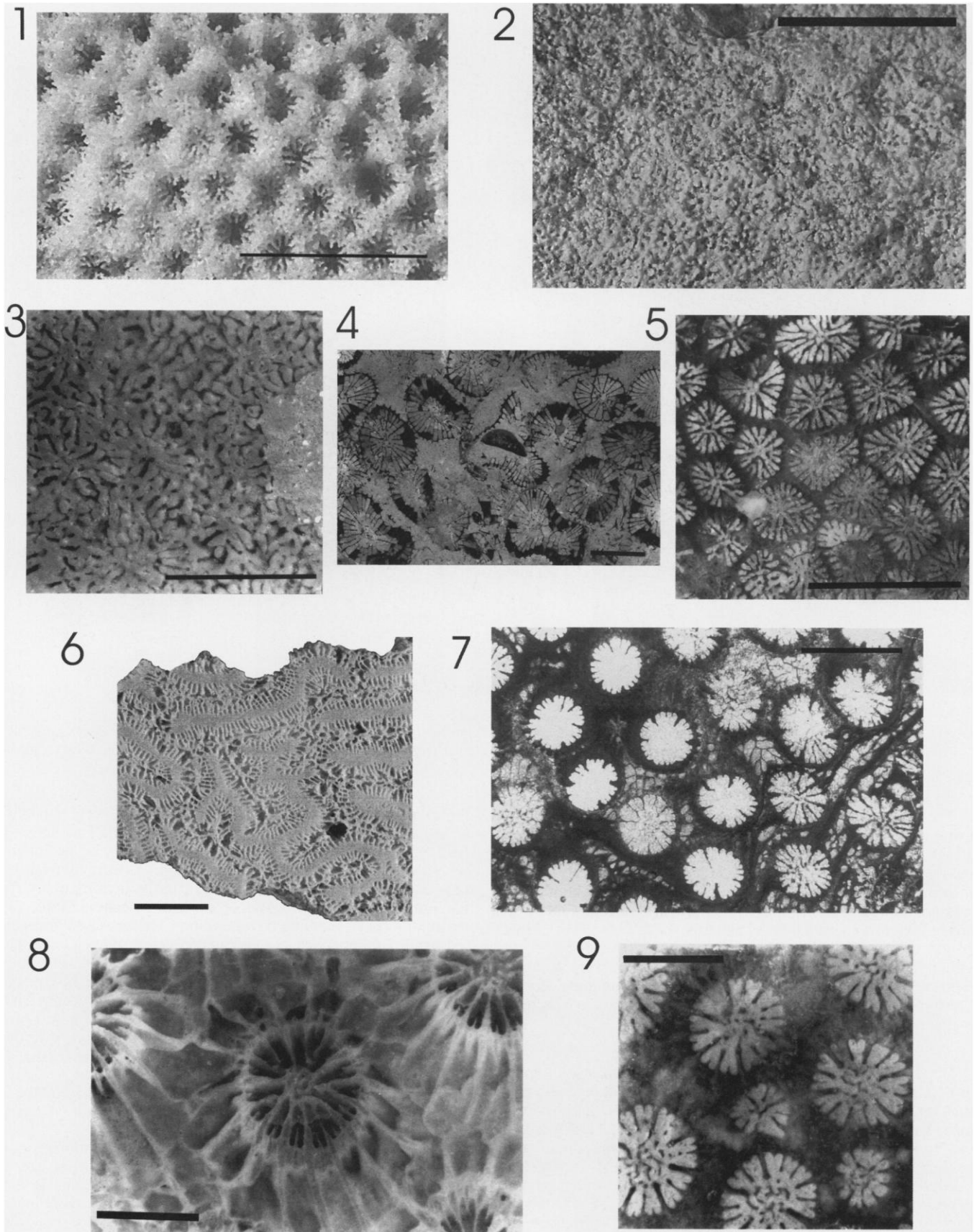


FIGURE 3—Calical surfaces of common species of reef corals collected from the Tamana Formation. 1, *Porites-I astreoides*, NMB D6393, scale bar is 5 mm. 2, *Porites-I waylandi*, USNM 100590, scale bar is 5 mm. 3, *Goniopora imperatoris*, USNM 100591, scale bar is 5 mm. 4, *Caulastraea portoricensis*, NMB D6389, scale bar is 10 mm. 5, *Goniastrea trinitatis*, USNM 353661, scale bar is 5 mm. 6, *Diploria zambensis*, BM(NH) R28970, scale bar is 10 mm. 7, *Montastraea-I* sp. A, USNM 100592, scale bar is 5 mm. 8, *Montastraea-I brevis*, NMB D6388, scale bar is 5 mm. 9, *Montastraea-I limbata*, USNM MO353654, scale bar is 5 mm.

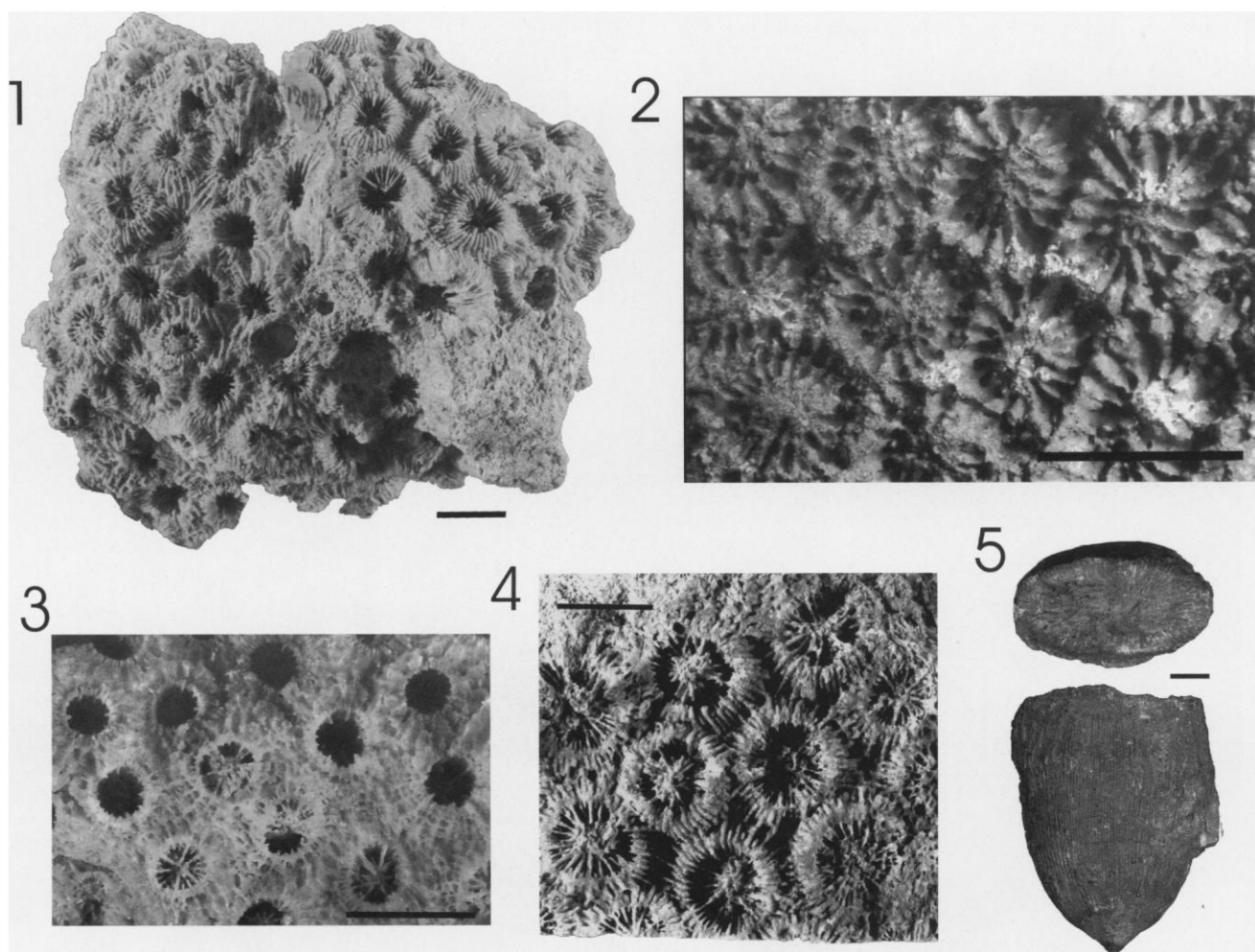


FIGURE 4—Calical surfaces of common species of reef corals collected from the Tamana Formation. 1, *Montastraea-II canalis*, BM(NH) R28960, scale bar is 10 mm. 2, *Montastraea-II trinitatis*, USNM MO353678, scale bar is 5 mm. 3, *Montastraea-II cylindrica*, BM(NH) R28967, scale bar is 10 mm. 4, *Montastraea-II endothecata*, BM(NH) R28967, scale bar is 10 mm. 5, *Antillophyllia sawkinsi*, NMB D6399, scale bar is 10 mm.

The early and middle Miocene faunules were also compared using detrended correspondence analysis (McCune and Mefford, 1997) of presence/absence data including only species that were recovered from at least three faunules. Sampling schemes were not consistent among the units so abundance data within faunules was not comparable, but previous work suggests that binary data are sufficient to extract main patterns of species co-occurrence (Budd et al., 1998; Pandolfi and Jackson, 2000; Pandolfi, this volume). Faunules from the Tamana Formation were compared with merged species lists from the other Miocene units. Low diversity lists from the Biche Quarry and Tamana Cave were not included in the ordination analysis.

RESULTS

Duncan (1868) reported 18 species from a limestone exposed at St. Croix on the southern flank of the Central Range and noted that the assemblage was dominated by massive shallow water taxa. Vaughan and Hoffmeister (1926) considered 11 of these species to be valid and added another 21 forms from additional localities, including five azooxanthellate species. This increased diversity was a result of new collections from a wider range of depositional settings. Following re-examination of existing collections and extensive taxonomic revision of the Agariciidae, Poritidae, and Faviidae, Budd et al. (1994) recognized 16 zooxanthellate species from the Miocene rocks of Trinidad. Eleven of

these species were recorded from samples that were thought to be collected from the middle Miocene Manzanilla Formation, but field verification indicated that these localities can be included within the Tamana Formation. New large collections from both new and old localities have increased the known diversity from the Tamana Formation to 41 species from 24 genera (Table 2). A collector's curve showing the rate of new species discoveries plotted against numbers of specimens recovered indicates that sampling is nearly saturated for the Tamana Formation (Fig. 6), although additional collecting is likely to result in the discovery of new taxa, especially after future discoveries of exposures from a wider range of paleoenvironmental settings. New records from the Tamana Formation include two species of extinct *Stylophora* and large numbers of the agariciid species *Undaria crassa*. The diversity of faviid species also increased, with new records of species of *Montastraea*, *Solenastrea*, *Favia*, *Diploria*, and the important early Neogene phaceloid species *Caulastrea portoricensis* (Table 2).

The 41 species recovered from the Tamana Formation represent 46 percent of the 90 known early to middle Miocene zooxanthellate coral species (Appendix 2). The Tamana fauna is richer than faunas from contemporaneous units, but this difference is probably caused by differences in sampling intensity. For example, the Seroe Domi Formation in Curaçao has also been extensively sampled, and the recovered fauna is as rich as that from

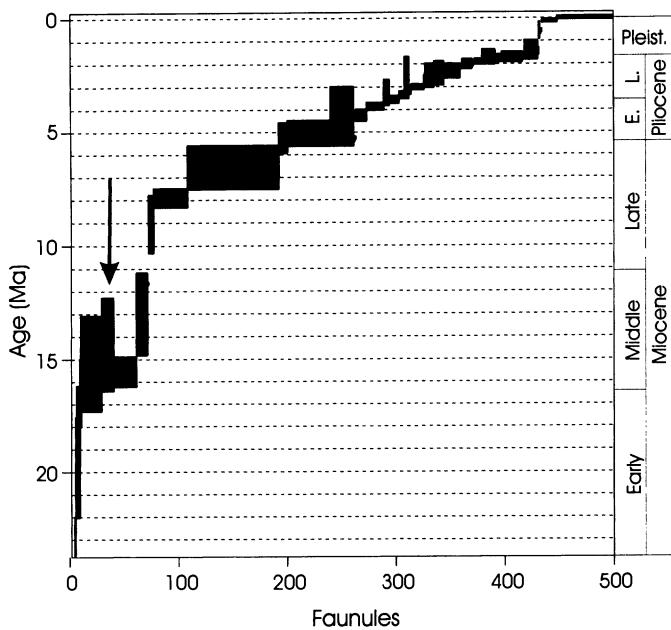


FIGURE 5—Stratigraphic ranges of 489 Neogene Caribbean coral faunules included in the 1999 version of the Caribbean coral database. The width of individual blocks indicate the number of collections from each stratigraphic interval. The Tamana collections are highlighted with an arrow.

the Tamana Formation. If the regional distribution of species is similar to that observed on modern Caribbean reefs, then the less well-sampled units are likely to hold significant undiscovered diversity. This sampling deficit is also evident in the observation that 51 percent of the early and middle Miocene species were recovered from only one unit, and only ten species (11 percent) were recorded from more than four units. This result contrasts with the observation that most extant Caribbean coral species have broad geographic distributions.

Tabulation of the number of first and last occurrences in the Tamana Formation and other early to middle Miocene coral faunas indicates significant species origination during the late early and early middle Miocene. Thirty-one of the species recovered from the Tamana Formation represent first occurrences, comprising 75 percent of the total fauna (Table 2). Thirteen of the 31 first occurrences are restricted to the Tamana Formation and the other eighteen were also recovered from other roughly contemporaneous units from Curaçao, Panama, and the Dominican Republic. Many of these first occurrences include taxa characteristic of the Caribbean Neogene shallow water *Porites/Montastraea* assemblage along with foliaceous agariciids characteristic of deeper or more turbid habitats. In contrast, only eight records represent species last occurrences from the Tamana Formation, and all eight of these species are endemic to the unit. Moreover, several of these endemic species are known only from a limited number of specimens and are within genera in need of taxonomic revision. For example, Vaughan and Hoffmeister (1926) described three species of *Pavona* from less than ten specimens. Oligocene hold-over species are present in the Tamana Formation, but rarely last occur in the unit. Although 11 Tamana species have also been identified from Oligocene units, 10 of these species persist until at least the late Miocene (Appendix 2). In summary, species' last occurrences are much less common than first occurrences in the early middle Miocene Tamana Formation.

The addition of the new records from the Tamana Formation changes the pattern of species turnover both by adding new taxa

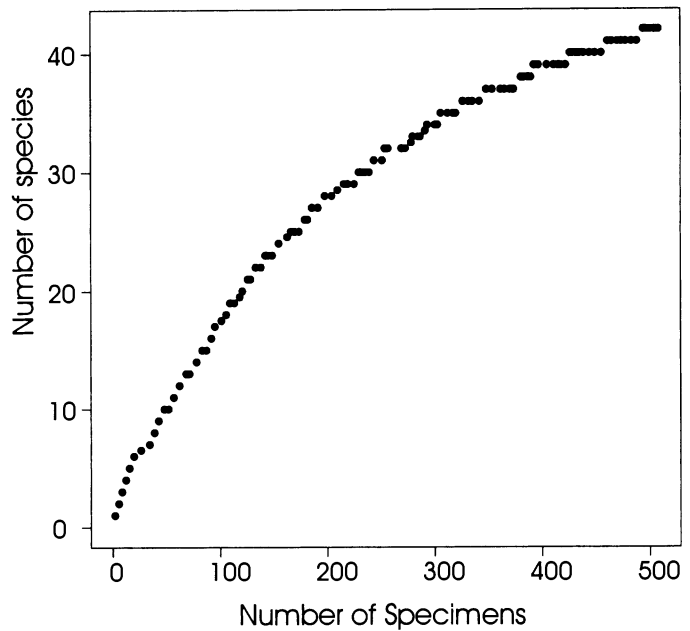


FIGURE 6—Collectors curve illustrating effect of addition of new specimens to the total number of species recovered from localities in the Tamana Formation. Because the shape of the curve is in part a function of the input order of records, this curve is constructed from the median distribution of 500 runs in which records were considered in random order.

and by extending the range of many species back to middle Miocene (Fig. 7). Estimates of species richness increase during middle to late Miocene time, decreasing the apparent early Pliocene diversification. This pattern is shown by changes in numbers of first occurrences, as range extension shifts many late Miocene or Pliocene first occurrences back into the middle Miocene. In contrast, the pattern of species disappearance is only slightly altered by addition of species endemic to the Tamana Formation, and no new extinctions of Oligocene species were recorded. These results suggest that much of the Neogene diversification of Caribbean reef corals occurred during the early or middle Miocene and not in the late Miocene or Pliocene, and recovery of species diversity following the early Miocene extinction was relatively rapid and well underway by the middle Miocene.

The Tamana faunules form a discrete group on an ordination plot (Fig. 8). The Machapoorie and Cumuto faunules are distinct from the other Tamana communities, because they are characterized by an assemblage of free living corals including *Trachyphyllia bilobata* and *Antillophyllia sawkinsi* along with the thin branching *Porites baracoensis* and the endemics *Pavona machapooriensis* and *Pavona trinitatis*. The early Miocene faunules form a cluster distinct from both the Tamana faunules and the late early to middle Miocene assemblages. These older units are characterized by assemblages including a larger proportion of species with Oligocene records. The Machapoorie faunule also contains a significant number of archaic species, suggesting that it may be miscorrelated with the other Tamana faunules, but further stratigraphic analysis is required to test this possibility. More likely the Machapoorie and Cumuto faunules were deposited in paleoenvironments distinct from the other Tamana assemblages. Although there is a clear time signal along the first axis of the ordination, the middle Miocene assemblages from the Valiente Volcanics and the Baitoa Formation do not have higher scores than the Tamana faunules, indicating that this time signal is confounded with other factors.

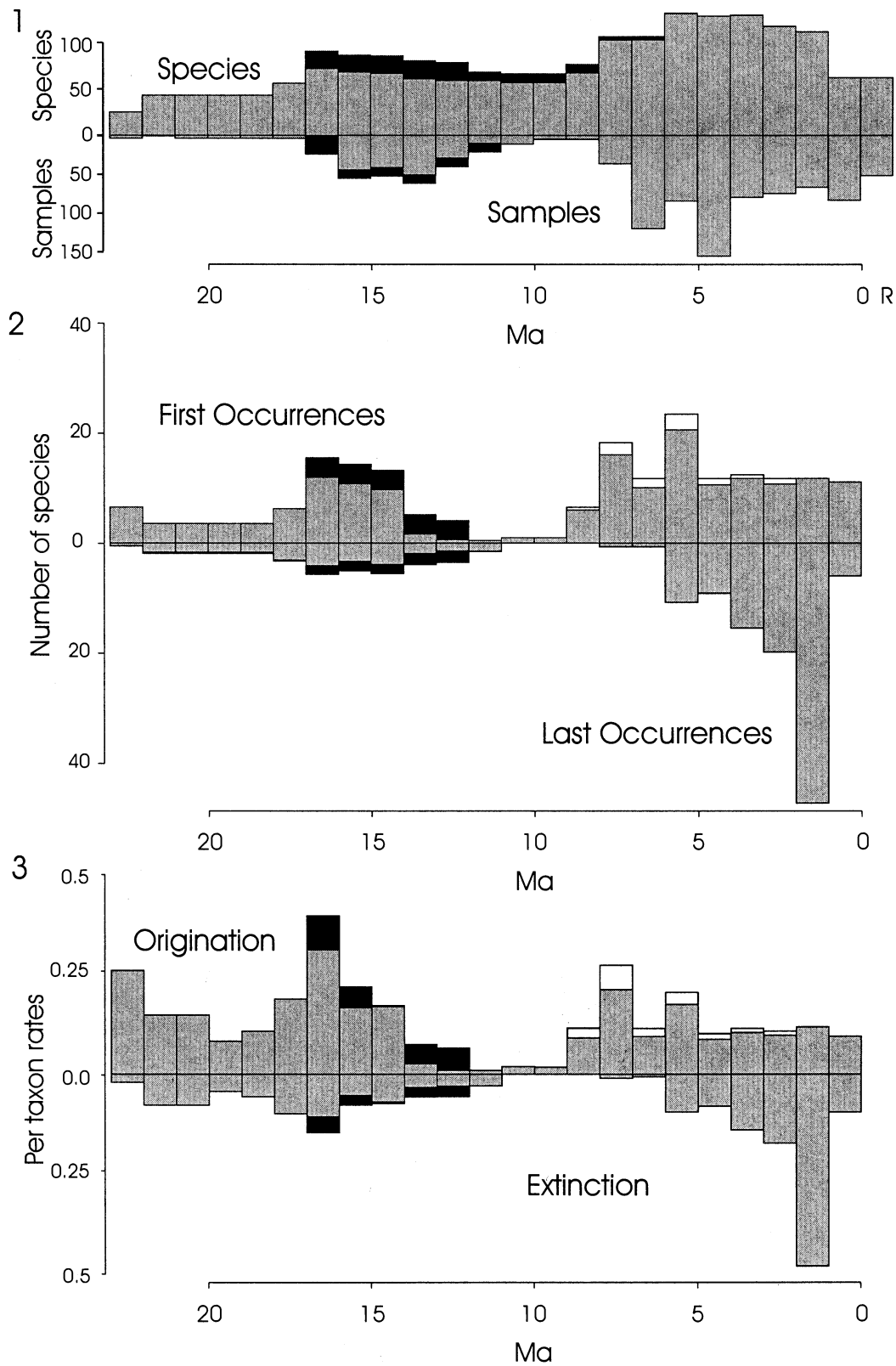


FIGURE 7—Measures of taxonomic turnover and sampling intensity for one million year time intervals from early Miocene to Recent. Black areas indicate increased estimates and the white areas indicate decreased estimates of taxonomic turnover resulting from the addition of the Tamana fauna. 1, Range-through species richness and numbers of samples. 2, Numbers of first and last occurrences in each million year subinterval. 3, Per taxon rates of species extinction and origination.

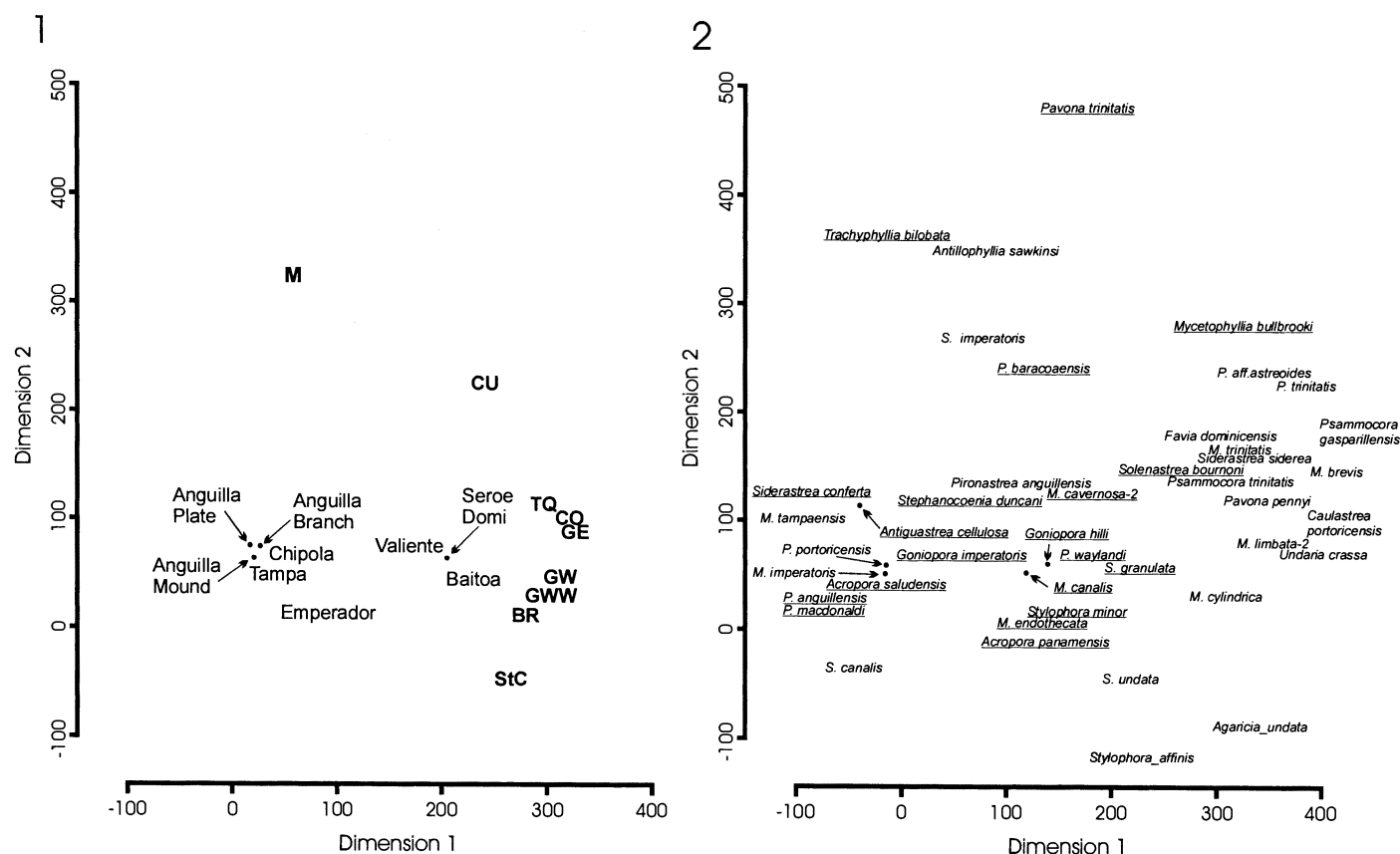


FIGURE 8—Results of Detrended Correspondence Analysis of nine Tamana faunules with nine other early to middle Miocene faunules. 1, Plot of faunule scores in the first two axes of the ordination space. Bold symbols indicate the Tamana faunules and abbreviations given in Table 1. 2, The distribution of species scores along the first two axes. Underlined species also occur in Oligocene units. Generic abbreviations are used for the common genera *Montastraea* (M), *Porites* (P), and *Stylophora* (S). Both plots show results from a single ordination, so similar positions of species and samples on the two plots indicates a correlation between those species and samples.

The distribution of species colony forms in the ordination (Fig. 8) suggests that the Tamana faunules are distinguished by more foliaceous species and the early Miocene units are dominated by ramose species. Seven of the 40 Tamana species grow as plates, including locally abundant agaricids such as *Agaricia undata* and *Undaria crassa*. In contrast, both older and younger faunas include abundant branching pocilloporid species (especially *Stylophora*) and branching *Porites*. This result reflects the range of environments sampled from the Tamana Formation, including several relatively deep water facies characterized by abundant platy coral species. In the Gasparillo (West) section, unifacial plates of *Agaricia undata* and *Porites trinitatis* were collected from bedded units interpreted to have formed as shallow carbonate material was washed into the deeper water facies of the Brasso Formation (Kugler, 1953). Similar plate coral facies are not known from the other early to middle Miocene units that have been extensively sampled. For example, corals from the early Miocene Anguilla Formation were deposited on a shallow wave-swept platform as a patchwork of coral thickets developed in a frequently disturbed environment (Budd et al., 1995). The middle Miocene Seroe Domi assemblages from Curaçao are similarly dominated by massive and branching corals preserved in bedded coralline grainstones characteristic of exposed paleoenvironmental conditions (Budd et al., 1998).

DISCUSSION

New data from Trinidad and Curaçao require a reassessment of the nature of the Pliocene/Pleistocene transition on Caribbean

reefs. Previous analysis of the Neogene history of reef corals has identified a period of accelerated faunal change during the late Pliocene and early Pleistocene (Budd et al., 1994, 1996). However, within the interval between 4 and 1 Ma, taxonomic turnover was not synchronous, because species origination rates increased prior to a relatively rapid late Pliocene or early Pleistocene extinction pulse. This asymmetry resulted in an increase in species richness during the late Pliocene, now recognized as the acme of Cenozoic Caribbean coral species diversity. However, improved sampling of Miocene deposits has extended the range of many species back to the early and middle Miocene, smoothing an apparent Pliocene peak in species origination (Fig. 7). The median age of extant Caribbean coral species ($n = 62$) is 4.3 Ma, suggesting that over half of the species that were destined to dominate Pleistocene and Holocene reefs first appeared prior to the early Pliocene and before the extinction of the Mio-Pliocene assemblages. These results indicate that the transition from the early Neogene to modern coral fauna was not a nearly synchronous taxonomic turnover pulse but rather the accumulation of species from late early Miocene to late Pliocene followed by an extinction during early Pleistocene time. The temporal pattern of species origination remains unclear, but the new data presented here indicate substantial origination during the late early and early middle Miocene, with two-thirds of the species recorded from the Tamana Formation first occurring at that time. Whether these Miocene originations were clustered in time and represent an origination pulse remains to be tested because any real pulse will

appear spread forward in time as a result of the inadequate record. Future study of key deposits from the Lares Formation of Puerto Rico will address this issue.

In contrast, patterns of extinction show clear peaks. Although a one-million-year early Pleistocene sampling gap limits determination of the exact timing and duration of the Pliocene-Pleistocene extinction episode, the existence of an essentially modern fauna from the middle Pleistocene terraces of Barbados (Mesolella et al., 1970) indicates that extinction rates had declined to near zero before 500 Ka. Only five species have been shown to become extinct during the past one million years (Pandolfi et al., 2000; Jackson and Johnson, 2000; unpub. data). Although an adequate species-level data compilation is not yet available, the Miocene/Pliocene extinction pulse seems to have been similar in magnitude and duration (Edinger and Risk, 1995; Budd, 2000). Accelerated extinction had ceased by the early Miocene because only ten last occurrences have been recorded in from early Miocene deposits, including *Alveopora tampae*, *Astrocoenia incrustans*, *Astreopora goethalsi*, *Pavona panamensis*, *Goniopora panamensis*, *Goniastrea canalis*, *Leptoseris anguillensis*, *Siderastrea conferta*, *Porites-I anguillensis*, and *Montastraea-II tampaensis*. But sampling of this interval is sparse, and addition of records from the latest Oligocene and early Miocene deposits of Puerto Rico and Chiapas may slightly increase estimates of species extinction during the early Miocene. For example, Edinger and Risk (1995) list the genus *Actinacis* with a last occurrence in the Lares Formation of Puerto Rico. Although extinction rates were elevated for brief periods within the Cenozoic, there is no evidence that the Pliocene/Pleistocene and the Oligocene/Miocene extinctions were geologically instantaneous. Both transitions probably involved several million years of increased extinctions, and they clearly fit the model of press extinctions in which changing environmental conditions gradually decrease regional diversity by reduction of local diversity or through habitat removal (Erwin, 1996; Budd and Johnson, 1999b).

Rates of species appearance and disappearance combine to produce patterns of changing taxonomic diversity, therefore comparing patterns of taxon first and last occurrences can provide significant clues to the potential mechanisms underlying biotic change. Geologically rapid pulses of species first and last occurrences have been reported from many studies of regional biota (e.g., Ivany and Schopf, 1996). However, before these patterns are interpreted as real biological transitions the potential for sampling artifacts must be considered and ruled out (Vrba, 1995; Behrensmeyer et al., 1997; Holland and Patzkowsky, 1999). For Neogene Caribbean corals, the observed temporal correlation of origination and extinction probably results from the uneven distribution of samples. In the current data set, a poorly sampled early and middle Miocene interval precedes a late Miocene to Recent interval of more complete sampling.

The overall pattern of pulsed extinction and continuous origination suggests that Neogene Caribbean coral evolution consists of slow accumulation of diversity that is episodically restructured by accelerated extinction (Gould, 1985). On a regional scale, these extinction pulses are likely tied to changing physical environments. Abundant mechanisms exist that are capable of altering regional oceanographic conditions and changing the rate and ecological selectivity of extinction. Patterns of extinction selectivity and the distribution of endolithic organisms across the Oligocene/Miocene boundary in Puerto Rico suggest that the Early Miocene parallel decline in reef diversity and reef development was associated with eutrophication (Edinger and Risk, 1994), possibly related to increasing development of a strong thermocline (Gasperi and Kennett, 1993) following intensification of southern hemisphere glaciation. Potential factors implicated in the Pliocene/

Pleistocene extinction include environmental changes associated with the final uplift of the Isthmus of Panama, intensification of northern hemisphere glaciation, and the switch from high planktonic to primarily benthonic primary production that apparently strongly affected the Caribbean region at the end of the Pliocene (Hallock and Schlager, 1986; Stanley, 1986; Hallock, 1988; Allmon et al., 1993, 1996; Collins et al., 1996). Because extinction rates were elevated over a relatively long period, the relationship between environmental changes and biotic response is likely to be complex. This pattern may have resulted from either slow environmental change or lagged response to more rapid environmental changes. Parallel analyses of taxonomic groups with ecological requirements different from reef-corals or analysis of independent paleoenvironmental proxies is required to detangle these effects.

SUMMARY

1) New collections from the Tamana Formation in Trinidad contain 41 species of zooxanthellate corals.

2) Two thirds of these species first occur during the latest early or early middle Miocene time, but less than 20 percent of the records represent species last occurrences. Most of the species that last occur within the unit are endemic and may require taxonomic revision. Only one species that occurs in late Oligocene units last occurs in the Tamana Formation.

3) These additional data and new records from Curaçao indicate that the previously observed peak of species origination during late Miocene time is likely to be an artifact of incomplete sampling of older faunas. Therefore recovery from the Oligocene/Miocene extinction was well underway by the end of the early Miocene.

4) The Neogene history of Caribbean corals consists of constant diversification, with communities restructured by episodic extinction in response to environmental change. These extinction episodes are not geologically instantaneous but extend over several million years. This slow rate of change may reflect low rates of environmental change or may reflect lagged response to changes that occurred on shorter time scales.

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APPENDIX 1

List of collections including material from the Tamana Formation. The locality codes and names are taken from specimen labels. Museum abbreviations are listed in Table 1.

Locality code	Locality name	Faunule	Museum code	Notes
Biche	Biche Quarry	Biche	NMB	Mile 16.5, Cunapo Southern Road.
St. Croix	St. Croix	Brasso	BM(NH)	Duncan (1868), near Savanna Grande
Brasso Cong.	Brasso Conglomerate	Brasso	BM(NH)	Brasso Conglomerate, Brasso Fm; 460 links east, 327 links North.
Brasso	Brasso Gorge	Brasso	BM(NH)	Navarro River ("Brasso") and clay "crab claw" beds, central Range, 435 links E 295 links North.
25-1-1945	Concord Quarry 1	Concord	NMB	Guaracara Limestone
CQ1	Concord Quarry 1	Concord	NMB	
CQ2	Concord Quarry 2	Concord	NMB	
PP	Pointe a Piere-Guaracara Ls.	Concord	NMB	
Cumuto Road (S+N)	Cumuto Road	Cumuto	BM(NH)	
Cumuto Road (P)	Cumuto Road	Cumuto	BM(NH)	Mile 17 Cumuto Road.
USGS 8299, USGS 9217	Cumuto Road	Cumuto	USNM	Vaughan and Hoffmeister (1926), Cumuto Road mile 17, latitude 10°28'30"N, longitude 61°13'25"W.
KJ4, KJ5, KJ14	Gasparillo (East)	Gasparillo (East)	SIO	
JS 2826	Gasparillo Quarry	Gasparillo (East)	NMB	
NMB 14599	Gasparillo Quarry	Gasparillo (East)	NMB	
Gasparillo	Gasparillo Quarry	Gasparillo (East)	NMB	Vaughan and Hoffmeister (1926), latitude 10°19'50"N, longitude 62°25'10"W.
USGS 8297	Gasparillo Quarry	Gasparillo (East)	USNM	481° E, 334° N, "Basal Miocene, Mach. 1st reef basal tunnel hill beds, Brasso Formation.
Machapoorie Quarry	Machapoorie Quarry	Machapoorie	BM(NH)	
Matchapoorie Quarry	Matchapoorie Quarry	Machapoorie	BM(NH)	Latitude 10°27'23"N, longitude 61°14'22"W.
KJ9, KJ17	Matchapoorie Quarry	Machapoorie	SIO	
K 10978, K 10981, K10982	Machapure Quarry	Machapoorie	NMB	
Machapure	Machapure Quarry	Machapoorie	NMB	
USGS 8301, USGS 9220	Machapoorie Quarry	Machapoorie	USNM	Vaughan and Hoffmeister (1926), latitude 10°27'25"N, longitude 61°14'35"W.
Wall coll. 6, Wall coll. 10	Savanna Grande	St. Croix	BM(NH)	Duncan (1868)
KJ1, KJ13	Tabaquite Road Quarry	Tabaquite	SIO	Road cut north of Tabaquite-Navet Road, latitude 10°23'23"N, Longitude 61°17'43"W.
TLL 37368	Nariva Quarry RR56	Tabaquite	NMB	
Nariva	Nariva Quarry	Tabaquite	NMB	
TAB	Tabaquite Nariva Quarry	Tabaquite	NMB	
TLL 56026	Tabaquite Quarry	Tabaquite	NMB	
USGS 8298, USGS 9198	Nariva Road Quarry	Tabaquite	USNM	Vaughan and Hoffmeister (1926); latitude 10°23'40"N, longitude 61°17'10"W.
KJ15	Tamana Cave	Tamana Cave	SIO	Latitude 10°28'17"N, longitude 61°11'21"W.
KJ2, KJ10	Gasparillo West Quarry	Gasparillo (West)	SIO	Quarry east of San Fabian Road and west of Gasparillo Road, Latitude 10°20'30"N, longitude 61°25'37"W.
K 12850	Norman Joseph Quarry	Gasparillo (West)	NMB	Equals PJ 24-5-1968, north of Gasparillo
KJ6, KJ8, KJ11, KJ12	Gasparillo West of West Quarry	Gasparillo (West of West)	SIO	Quarry west of San Fabian Road, e of Sir Solomon Hochoy Highway. latitude 10°19'59"N, longitude 61°25'44"W.

APPENDIX II

Regional distribution of early to middle Miocene Caribbean zooanthellate coral species. Oligocene or late Miocene to Recent occurrences are indicated, and the typical growth form for colonies is shown for each species. The number of post-Oligocene occurrences are also included. Data sources are listed in the text.

Species	Colony form	Oligocene	Early Miocene			Early to middle Miocene			Middle Miocene		Late Miocene to Recent	Total
			Anguilla	Emperador	Tampa	Baitoa	Chipola	Tamana	Seroe domi	Valiente		
<i>Astrocoenia incrustans</i>	M	1		1								1
<i>Stephanocoenia intersepta</i>	M							1			1	1
<i>Stephanocoenia duncani</i>	M	1	1						1	1	1	3
<i>Stephanocoenia spongiformis</i>	M								1		1	1
<i>Stephanocoenia</i> sp. A	M								1			1
<i>Stylophora affinis</i>	B			1		1		1	1		1	4
<i>Stylophora canalis</i>	B			1	1		1					3
<i>Stylophora granulata</i>	B	1		1				1	1	1	1	4
<i>Stylophora imperatoris</i>	B		1	1			1	1	1		1	5
<i>Stylophora minor</i>	B	1		1	1	1		1	1	1	1	6
<i>Stylophora monticulosa</i>	B					1			1		1	2
<i>Stylophora panamensis</i>	B								1		1	1
<i>Stylophora undata</i>	M						1	1	1	1		4
<i>Pocillopora arnoldi</i>	B			1				1			1	2
<i>Pocillopora crassoramosa</i>	B	1				1					1	1
<i>Pocillopora portoricensis</i>	B								1			1
<i>Madracis decaseptata</i>	B						1				1	1
<i>Madracis</i> sp. Z	B								1		1	1
<i>Acropora panamensis</i>	B	1		1					1	1	1	3
<i>Acropora saludensis</i>	B	1	1	1	1				1		1	4
<i>Astreopora goethalsi</i>	B	1		1								1
<i>Agaricia lamarcki</i>	P								1		1	1
<i>Agaricia undata</i>	P							1	1			2
<i>Undaria crassa</i>	P							1			1	1
<i>Pavona machapooriensis</i>	P							1				1
<i>Pavona panamensis</i>	M			1								1
<i>Pavona pennyi</i>	P							1				1
<i>Pavona trinitatis</i>	P	1						1	1			2
<i>Pavona</i> sp. X	B								1			1
<i>Leptoseris anguillensis</i>	B		1									1
<i>Leptoseris gardineri</i>	B							1	1		1	2
<i>Leptoseris glabra</i>	B								1		1	1
<i>Leptoseris walli</i>	P			1				1				2
<i>Psammocora gasparillensis</i>	M							1				1
<i>Psammocora trinitatis</i>	M					1		1	1	1	1	4
<i>Psammocora</i> sp. A.	M								1			1
<i>Siderastrea conferta</i>	M	1	1									1
<i>Siderastrea mendenhalli</i>	M					1					1	1
<i>Siderastrea siderea</i>	M					1		1		1	1	3
<i>Siderastrea</i> aff. <i>siderea</i>	M							1				1
<i>Siderastrea silecensis</i>	M				1	1						2
<i>Pironastrea anguillensis</i>	M		1						1	1	1	3
<i>Porites-I anguillensis</i>	P	1	1	1								2
<i>Porites-I astreoides</i>	M							1			1	1
<i>Porites-I</i> aff. <i>astreoides</i>	M							1	1		1	2
<i>Porites-I macdonaldi</i>	M	1	1	1							1	2
<i>Porites-I portoricensis</i>	B	1	1	1	1				1	1	1	5
<i>Porites-I trinitatis</i>	P							1				1
<i>Porites-I waylandi</i>	M	1	1	1	1	1		1	1	1	1	7
<i>Porites-II baracoensis</i>	B	1	1	1				1	1	1	1	5
<i>Porites-II chipolanum</i>	M						1					1
<i>Goniopora calhounensis</i>	M						1				1	1
<i>Goniopora hilli</i>	M	1	1	1	1	1		1			1	5
<i>Goniopora imperatoris</i>	M	1	1	1	1	1			1	1	1	6
<i>Goniopora panamensis</i>	M			1								1
<i>Alveopora tampae</i>	M	1			1							1
<i>Alveopora</i> sp. A	M								1		1	1
<i>Caulastrea portoricensis</i>	B							1			1	1
<i>Favia dominicensis</i>	M					1		1			1	3
<i>Favia</i> aff. <i>dominicensis</i>	M					1				1		1
<i>Goniastrea trinitatis</i>	M							1				1
<i>Goniastrea canalis</i>	M	1		1	1							2
<i>Diploria zambensis</i>	M							1			1	1
<i>Thysanus corbicula</i>	F						1				1	1
<i>Antiguastrea cellulosa</i>	M	1	1		1		1					3
<i>Montastrea-I brevis</i>	M							1			1	1
<i>Montastrea-I imperatoris</i>	M	1	1	1	1				1	1		5
<i>Montastrea-I limbata-1</i>	M								1		1	1
<i>Montastrea-I limbata-2</i>	M							1	1		1	2
<i>Montastrea-I limbata-3</i>	M								1		1	1
<i>Montastrea-I</i> sp. A	M							1			1	1

APPENDIX II

Continued.

Species	Colony form	Oligocene	Early Miocene			Early to middle Miocene			Middle Miocene		Late Miocene to Recent	Total
			Anguilla	Emperador	Tampa	Baitoa	Chipola	Tamana	Seroe domi	Valiente		
<i>Montastraea-I trinitatis</i>	M					1		1	1	1	1	4
<i>Montastraea-II canalis</i>	M	1	1	1	1	1	1	1	1	1	1	8
<i>Montastraea-II cavernosa-2</i>	M	1				1			1	1	1	3
<i>Montastraea-II cylindrica</i>	M							1	1		1	2
<i>Montastraea-II endothecata</i>	M	1	1				1	1	1	1	1	5
<i>Montastraea-II tampaensis</i>	M		1		1						1	2
<i>Solenastrea bournoni</i>	M	1			1	1		1			1	3
<i>Solenastrea hyades</i>	M				1	1					1	2
<i>Agathiophyllia hilli</i>	M	1	1							1		2
<i>Trachyphyllia bilobata</i>	F	1			1		1	1			1	3
<i>Antillophyllia sawkinsi</i>	F		1					1		1	1	3
<i>Placocyathus trinitatis</i>	F							1			1	1
<i>Placocyathus variabilis</i>	F					1					1	1
<i>Dichocoenia tuberosa</i>	M								1		1	1
<i>Galaxea excelsa</i>	M				1						1	1
<i>Antillia gregorii</i>	F				1						1	1
<i>Isophyllia</i> sp. A	M		1								1	1
<i>Isophyllastrea</i> sp. A	M									1		1
<i>Mycetophyllia bullbrooki</i>	M	1						1	1		1	2
Number of species		28	21	23	19	19	11	40	40	21		