

Reef-coral diversity in the Late Oligocene Antigua Formation and temporal variation of local diversity on Caribbean Cenozoic Reefs

Kenneth G. JOHNSON

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Abstract: Biotic responses to regional environmental change can be seen in both the membership and diversity of local coral reef communities. Recent work has documented taxonomic turnover in the regional Cenozoic Caribbean reef-coral fauna in response to changing oceanographic conditions, but it remains unclear how the diversity of local reef-coral communities responded to these changes. To determine whether there was significant change in local ecological diversity during the Late Oligocene to Early Pleistocene, assemblages from the Late Oligocene Antigua Fm. were compared with 45 assemblages obtained from a specimen-based dataset of Neogene zooxanthellate corals. The reef-coral fauna preserved in the Antigua Fm. is one important component of the Oligocene Caribbean regional fauna that has had a long history of study and has been considered typical for Late Oligocene reef biotas of the region. New collections from 12 localities in the Antigua Formation unit yielded 45 species from 26 genera, including abundant *Antiguastrea cellulosa*, *Agathiphyllia tenuis*, *Diploastrea crassolamellata*, and massive forms of *Porites*. Analysis of diversity estimated using species richness, Fisher's α , and Shannon's H revealed no significant differences in diversity between assemblages in the Antigua Fm. and Neogene assemblages. The fact that local diversity was insensitive to the regional environmental changes responsible for the Oligocene/Miocene transition on Caribbean reefs suggests that there was sufficient redundancy in the regional fauna to allow functioning local communities to be built from a reduced species pool.

Key words: Antigua Fm., coral reefs, fossil reefs, biodiversity, Scleractinia, Cenozoic

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Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

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1. INTRODUCTION

The Caribbean region has experienced strong environmental and biotic change during the past 30 million years. Environmental changes include an overall pattern of long term global cooling superimposed on rapid climate fluctuations acting over various time scales, as well as regional oceanographic changes associated with the development of the Central American Isthmus. The regional marine invertebrate fauna responded to these changes through pulsed biotic turnover in corals (BUDD et al., 1996) and mollusks (JACKSON et al., 1993; ALLMON et al., 1996), and changes in the structure and functioning of shallow water benthic communities (JOHNSON et al., 1995; BUDD & JOHNSON 2001; TODD et al., 2002). The goal of this paper is to explore how diversity of local zooxanthellate coral assemblages have changed during this long period of environmental and ecological upheaval. To explore this question, I will compare the ecological diversity of large new collections from the Late Oligocene Antigua Fm. from Antigua with a specimen-based database including collections from Early Miocene to Early Pleistocene stratigraphic units from across the Caribbean region. New collections from the Antigua Fm. allow a rigorous specimen-based comparison of Oligocene with Neogene assemblages for the first time, because similar comparisons in previous studies (for example, BUDD 2000) were based in part on literature records and museum collections that could not be compiled with similar stratigraphic or spatial detail.

Studies of deep sea oxygen and carbon isotopes suggest a general pattern of global cooling since the Late Oligocene (ZACHOS et al., 2001a). In detail, the late Oligocene warm period was terminated by a strong transient (~200 Kyr) glaciation in the earliest Miocene probably caused by an anomalous congruence in orbital cycles (ZACHOS et al., 2001b). This glacial event is associated with a major regression and increasing development of a strong thermocline near the Oligocene/Miocene boundary. Global temperatures rebounded soon after and remained relatively high until the Middle Miocene (~15 Ma). From the Middle Miocene to Recent, the global climates cooled, resulting in the intensification of Antarctic glaciation in the Middle Miocene, and the onset and intensification of glaciation in the Northern Hemisphere after the Late Miocene.

In the Caribbean region, these global changes in climate were confounded by the gradual rise of the Central American Isthmus in the Late Miocene to Late Pliocene (COATES et al., 1992). Changes in oceanographic circulation and regional upwelling (ALLMON, 2001) most likely resulted in a decline in planktonic productivity in the region during the Miocene and Pleistocene. Evidence for this can be found in the apparent increase in carbonate production in the Caribbean (COLLINS et al., 1996), and by changes in the composition and structure of marine communities in the region. There is strong evidence for Plio-Pleistocene faunal turnover in molluscs and zooxanthellate corals (STANLEY, 1986; ALLMON et al., 1996; BUDD et al., 1996; JACKSON & JOHNSON, 2000) and for

reorganization of mollusc food webs with a decrease in the abundance of predatory gastropods and suspension feeding bivalves as planktonic productivity waned resulting in the modern oligotrophic Caribbean (TODD et al., 2002).

The fate of zooxanthellate corals and coral reef building during the Late Oligocene to Recent is closely tied to these regional environmental changes. Extensive development of Caribbean coral reef ecosystems during the Cenozoic was limited to two intervals. These Late Oligocene and Quaternary episodes of large-scale reef construction were interrupted by a long interval without major constructional reef buildups (VAUGHAN, 1919; FROST, 1972, 1977). Surprisingly, the changing regional diversity of reef coral taxa does not seem to mirror this broad pattern (BUDD, 2000; JACKSON & JOHNSON, 2000). Although there are apparently two major extinctions in the reef-coral fauna, the first is associated with the Early Miocene decline of reef building and the second is nearly contemporaneous with the Early Pleistocene renewal of extensive reef development. This paradoxical result illustrates how environmental forcing factors that govern the buildup of reef tracts may be decoupled from factors that control the diversity of the reef building fauna (DONE et al., 1996).

2. STUDY AREA

2.1. The Antigua Formation

The Late Oligocene Antigua Fm. is exposed on the northeast third of the island of Antigua. Antigua is part of the Lesser Antilles, a chain of islands formed near the eastern margin of the Caribbean plate by volcanism and uplift associated with subduction of the Atlantic Plate to the east. The general geological history of Antigua is characterized by a transition from volcanism to open marine island slope deposits during the Oligocene (Weiss, 1994). This history is recorded in a succession of three packages of rock exposed in a simple monocline structure dipping to the northeast (MASCLE & WESTERCAMP, 1983; MULTER et al., 1986). A basal volcanic suite is exposed on the southwest third of the island and includes a mixture of rocks formed in an island arc setting, including both intrusive and extrusive volcanics and thick accumulations of pyroclastic debris. Marine incursions onto the margins of the volcano are recorded by thin limestones interbedded within the volcanoclastic units. The Central Plain Group overlies the basal volcanic suite and is comprised of 600–900 meters of sedimentary rocks including mudstones, tuffs, arenites, conglomerates, and some limestone (MAREK, 1981). These sediments form a complex patchwork of facies deposited in terrestrial to shallow marine settings as volcanism waned. Fully marine conditions were more or less established by the top of the Central Plain Group and carbonate sedimentation became dominant resulting in deposition of the Antigua Fm.

The Antigua Fm. includes more than 500 m of limestones and minor lime mudstones, marls, tuffs, and rubble. The lower contact of the unit is gradational, and the top of the unit is no longer exposed. Facies geometry has not been fully established, but the lower and middle parts of the Antigua Fm. are predominately composed of micrites and biomicrites with coral algal biostromes and reefs. The upper part of the Antigua Fm. contains island slope facies including rhythmic sequences (THEIS, 1980; WEISS, 1994).

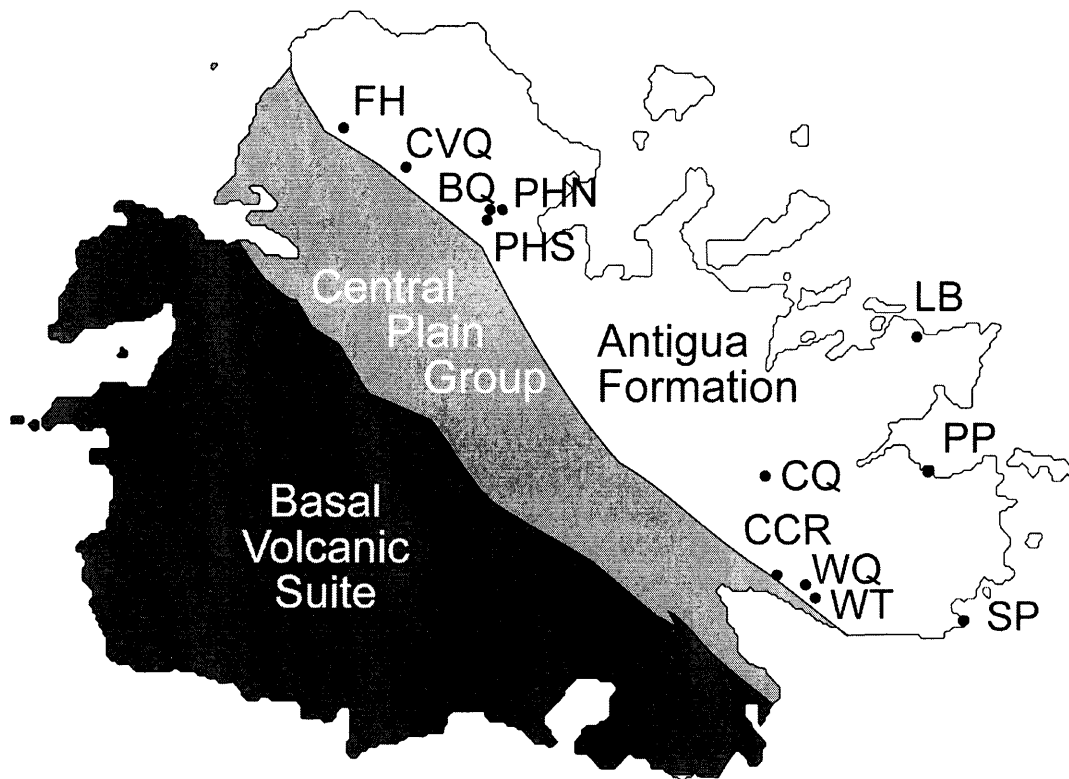


Fig. 1: Map showing general geology of Antigua and collecting localities in the Antigua Fm. The geology follows WEISS (1994). Collection codes are listed in Table 1, and detailed descriptions of localities can be found in JOHNSON & FILKORN (2003).

Sedimentary structures such as soft sediment slumps give evidence for paleoslope in this part of the unit. WEISS (1994) states that the Antigua Fm. was deposited during the Chattian (Late Oligocene) based on the discovery of planktonic foraminifera from the *Globigerina ciperoensis ciperoensis* biozone.

2.2. Coral assemblages in the Antigua Formation

During the spring of 2000, collections were made from 12 localities in the Antigua Formation (Fig. 1). Localities include large active quarries on the north side of Piggotts Hill (PHN, PHS), and a large quarry in Cedar Valley (CVQ). Sections were also exposed in smaller disused quarries including one in Collins to the east of the road between Newfield and Glanvilles (CQ). Sea cliff exposures were also studied at Pig Point (PP) and Soldiers Point (SP). Other exposures were found at fresh road cuts and construction sites. In most cases it was not possible to work on the classic localities of VAUGHAN (1919) and FROST & WEISS (1979), because exposures were no longer adequate for detailed study. At each locality stratigraphic sections were described, but no attempt was made to correlate sections between localities. All collections are housed in the Department of

Invertebrate Paleontology, Natural History Museum of Los Angeles County (LACMIP), and detailed descriptions of the localities and specimen data are available from the LACMIP collections database (JOHNSON & FILKORN, 2003).

The terms 'collection', 'occurrence', 'lot', and 'specimen' are used in this contribution and are defined as follows. A 'specimen' is single fossil or piece of a fossil. Reef-corals are colonial organisms, so it is common to collect multiple pieces of what is presumed to be a single colony. In practice it is often difficult to determine whether pieces found in close proximity to one another actually were parts of a single colony, but in general specimens identified as the same species that were collected within a few tens of centimeters from one are grouped together as a specimen lot. In museum collections these would normally be placed in a single container. A group of lots collected from one locality comprises a collection. Species lists can be compiled for each collection, and each element of a list is an 'occurrence' of a species in a collection. Occurrences represent one or more specimen lots identified as a particular taxon in a collection.

A total of 45 species from 26 genera were recovered from the Antigua Fm. (Tab. 1, Pls. 1, 2). Eleven of the species are kept in open nomenclature pending formal taxonomic revision of the group. VAUGHAN (1919) listed 62 species (and five varieties) in 33 genera from the Antigua Fm. He left 23 of these species in open nomenclature and discussed 34 others. The new collections described here include 25 of the species discussed by VAUGHAN plus 20 others that were either not recorded or left in open nomenclature by VAUGHAN (1919). Of the 34 species discussed by VAUGHAN, 13 were not recovered from these new collections. Genera reported by VAUGHAN but not recovered in these collections include *Pocillopora*, *Stylocoenia*, *Asterosmilia*, *Cladocora*, *Diplothe-castraea* (= ?*Antiguastrea*), *Pavona*, *Dendrophyllia*, *Lamellastrea* (= ?*Goniastrea*), *Lep-toria* (= ?*Meandrina*), and *Favia*. Some of these differences reflect changes in taxonomic practice, and will no doubt be resolved after further taxonomic revision.

The number of species recovered from each locality varied from one to 36, and assemblages characterized by high richness were recovered from localities that produced large collections such as Collins Quarry and the active quarry on Piggotts Hill. The most abundant species recovered from the Antigua Fm. are the typical Late Oligocene Caribbean fauna including species with massive colonies such as *Agathiphyllia tenuis*, *Agath-iphyllia hilli*, *Antiguastrea cellulosa*, *Diploastrea crassolamellata*, *Diploastrea magnifica*, and *Porites regularis* (Pls. 1 and 2). Species that grow as branching and foliaceous colonies are also abundant, including *Acropora saludensis*, *Porites macdonaldi*, *Porites portoricensis*, and *Stylophora imperatoris*. The foliaceous species *Fungophyllia* sp. A is especially common, although it is preserved mainly as small fragments suggesting that true cover was much less than numbers of lots suggests. The common Cenozoic Caribbean dominants *Montastraea* spp. are rare.

2.3. Caribbean reef-coral diversity – Oligocene to Pleistocene


A specimen-based dataset was compiled to explore patterns of diversity change in the Caribbean reef-coral fauna during the Late Oligocene to Pleistocene. Abundance data from the Antigua Fm. were combined with data from Neogene localities from the Brasso and Tamana Fms. in Trinidad (JOHNSON, 2001), the Emperador Limestone of the La Boca

Fm. in Panama (JOHNSON & KIRBY, 2006), The Seroe Domi Fm. from Curacao (BUDD et al., 1998), the Moin and Quebrada Chocolate Fm. of Costa Rico (BUDD et al., 1999), the Old Pera Beds and Bowden Shell Beds of Jamaica (BUDD & McNEILL, 1998), and the Cercado, Gurabo, and Mao Fm. of the Dominican Republic (BUDD et al., 1994). In all cases, records are based on specimens that were identified in the lab after suitable preparation including analysis of petrographic thin sections. These units span a wide geographic range and represent collections from a range of reef and non-reef environments, and include both zooxanthellate scleractinians and hydrozoans (*Millepora*, *Heliopora*). The resulting data set includes 210 species in 54 genera from 419 collections including 6305 lots and 2576 occurrences.

Comparison of local diversity using individual collections is problematic because the data come from a wide range of localities characterized by differences in exposure, fossil preservation, paleoenvironment, and collecting effort. Direct comparisons of collections is problematic because of small sample sizes. Therefore, individual collections were grouped into faunules and diversity was estimated for the faunule assemblages. Combining collections in this way could average out local variation and will reduced the power of tests so that small differences in local diversity might not be detected. However, this is preferable to interpreting local sampling noise as real pattern. Faunules are groups of collections from geographically (<100 m) and stratigraphically (< 5 m) limited areas (JACKSON et al., 1999). No attempt was made to place uniform numbers of collections or specimen lots in each faunule. Faunules with less than 10 species and 20 lots were not considered in the study of diversity because they most likely represent undercollected units. Note that five of the Antigua Fm. faunules failed to meet these criteria. A total of 52 faunules were defined for this analysis (Appendix 1). This reduced dataset included 207 species in 54 genera from 397 collections and 6004 lots and 2460 occurrence records. The midpoint of the maximum stratigraphic range of constituent collections was used to estimate stratigraphic range for each faunule (Fig. 2). All data sets used in this study can be obtained at the LACMIP data repository (<http://ip.nhm.org/datasets>).

2.4. Measuring diversity

Estimating abundance of colonial organisms is difficult because a single genetic individual can be preserved in the record as multiple fragments. In this study, the number of specimen lots in each collection was used as a proxy for abundance. A specimen lot is one or more specimens collected from a very restricted area (one bedding plane or at

Tab. 1: Distribution of coral species in the Antigua Fm. For each locality the number of specimen lots recovered from each locality are shown. Summary statistics including the number of specimens per taxon and number of taxa per locality are also indicated. Locality codes are BQ=Burma Quarry, CVQ=Cedar Valley Quarry, CCR=Crossroads Clinic Roadcut, LB=Long's Bay, PHN=Piggott's Hill (North), PHS=Piggott's Hill (South), SP=Soldier's Point, WQ=Willoughby Quarry, WT=Willoughby Track, CQ=Collins Quarry, FH=Friar's Hill, PP=Pig Point. 

	BQ	CVQ	CCR	LB	PHN	PHS	SP	WQ	WT	CQ	FH	PP	Specimens	Localities
<i>Astrocoenia portoricensis</i>		3	7						1	2			13	4
<i>Astrocoenia guantana- mensis</i>		1				4	1		4	3	1	3	17	7
<i>Astrocoenia sp B</i>							1						1	1
<i>Stephanocoenia duncani</i>										1		1	2	2
<i>Stylophora imperatoris</i>		4	1			3				5		8	21	5
<i>Stylophora minor</i>										1		1	2	2
<i>Stylophora sp C</i>		1								2	1		4	3
<i>Acropora saludensis</i>		1	2			1			2	13	2	1	22	7
<i>Astreopora antiguensis</i>		1				1						3	5	3
<i>Montipora sp A</i>								4					4	1
<i>Fungophyllia sp A</i>		2	1					1		25			29	4
<i>Leptoseris sp C</i>						1					1		2	2
<i>Leptoseris portoricensis</i>										1			1	1
<i>Siderastrea conferta</i>		2										2	4	2
<i>Pironastrea antiguensis</i>						3							3	1
<i>Actinacis sp A</i>		1							1	1			3	3
<i>Porites macdonaldi</i>		1								1			2	2
<i>Porites portoricensis</i>		2	3			2				5		14	26	5
<i>Porites microscopica</i>		1		2		4				15	3	2	27	6
<i>Porites regularis</i>		7	1			3			2	10	1	5	29	7
<i>Porites baracoensis</i>										4		3	7	2
<i>Goniopora imperatoris</i>			1									1	2	2
<i>Alveopora tampae</i>	1	3	1			3				3		5	16	6
<i>Alveopora sp A</i>						1				1	3	1	6	4
<i>Agathiphyllia browni</i>		1						1				1	3	3
<i>Agathiphyllia tenuis</i>		9	2	5	1	8				17	2	8	52	8
<i>Agathiphyllia hilli</i>		8	1		1	10			3	2		1	26	7
<i>Agathiphyllia antiguensis</i>		1				1					1		3	3
<i>Caulastrea portoricensis</i>		1				1						1	3	3
<i>Favites polygonalis</i>		8				4			1		1		14	4
<i>Goniastrea canalis</i>		1				2					1	1	5	4
<i>Diploria antiguensis</i>				1					2	1			4	3
<i>Colpophyllia willough- biensis</i>		2				3			1			2	8	4
<i>Antiguastrea cellulosa</i>		13	4			15			6	6	4	18	66	7
<i>Hydnophora sp A</i>				1		4							5	2
<i>Montastrea canalis</i>			3			2				1			6	3
<i>Montastrea cavernosa</i>												1	1	1
<i>Montastrea endothecata</i>			2						1			3	6	3
<i>Agathiphyllia splendens</i>		1				1							2	2
<i>Agathiphyllia sp 3</i>											2	1	3	2
<i>Diploastrea crassola- mellata</i>		3		2		8			3	11	1	4	32	7
<i>Diploastrea magnifica</i>		1	2			10				4	1		18	5
<i>Diploastrea nugenti</i>		1							2				3	2
<i>Diploastrea sp T</i>						3			1	2	1		7	4
<i>Heliopora sp A</i>												1	1	1
Total lots	1	81	30	11	2	98	2	5	31	137	26	92	516	--
Total species	1	28	13	5	2	25	2	2	15	25	16	26	45	--

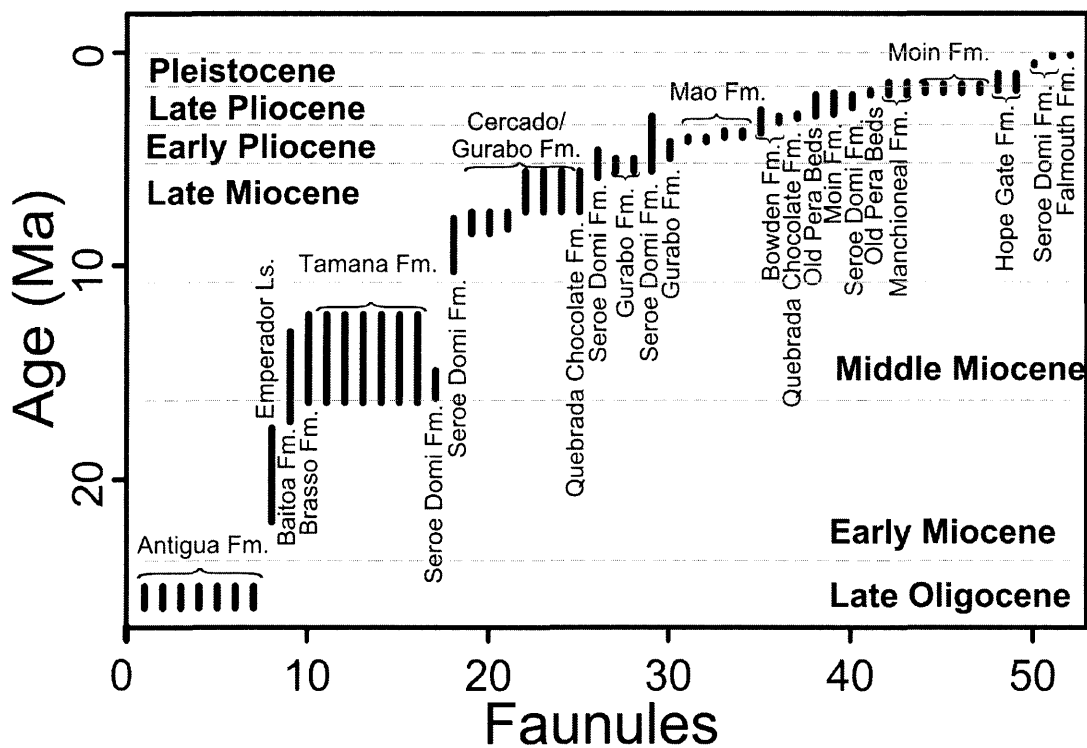


Fig. 2: Stratigraphic range of faunules included in the Cenozoic reef-coral diversity database. Each vertical line represents the inferred stratigraphic range of one faunule. Age data are included in Appendix 1 and age boundaries are defined in BERGGREN et al. (1995).

most within a meter of section within the same facies). Strictly speaking, this proxy is more closely related to the time-averaged cover of each taxon, but the term abundance will be used to maintain consistency with the ecological literature.

Taxonomic richness (S), Fisher's alpha (α), and Shannon's H were used to describe the species diversity of coral faunules. MAGURRAN (1988) distinguishes between three general classes of diversity indices including: taxon richness indices, parameters from taxon abundance models, and indices that incorporate proportional abundances of taxa. Each approach has strengths and weaknesses, and here we have selected one widely used index from each class. Taxonomic richness (S) is the number of species in each assemblage. Although richness is easy to interpret, it is highly sensitive to sample size. Fisher's α is one of the many diversity indices derived from fitting the observed data to a theoretical abundance distribution (HAYEK & BUZAS, 1997). If the taxon abundance follows a log-series distribution then α should be independent of sample size (N). A simple interpretation of α is that it approximates the number of taxa represented by one specimen in each assemblage.

Shannon's index (H) is one of the most commonly used diversity indices that includes information on proportional abundances of taxa in an assemblage. However, H is moderately sensitive to sample size, because it is strongly influenced by the number and abundance of rare taxa (MAGURRAN, 1988). To better understand variation in H we also

calculated evenness (E) as e^H/S . Besides estimating these commonly used measures of diversity, actual species abundance distributions were examined using rank abundance plots. These are created by calculating the proportional abundance of each taxon in an assemblage as the number of lots of each species divided by the total number lots in the assemblage. The proportional abundances are then plotted in decreasing order to illustrate the abundance distribution of taxa in the assemblage. The R statistical programming language was used for all analyses (IHAKA & GENTLEMAN, 1996).

3. RESULTS

Numbers of lots recorded within each faunule (N) range from 16 to 927 with a median of 55 (Appendix 1). Three faunules include significantly larger numbers of lots than the others (Fig. 3), including Lomas del Mar – East (Plio/Pleistocene Moin Fm.), Rio Gurabo

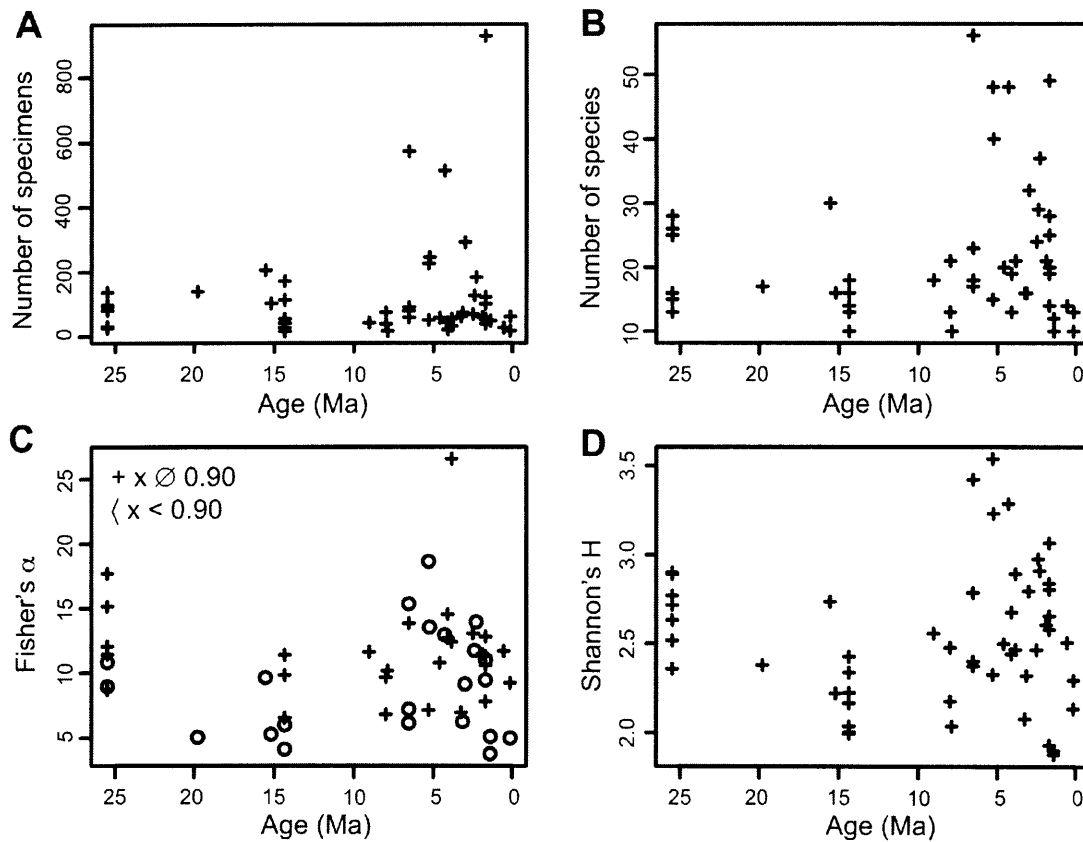


Fig. 3: Scatter plots showing variation in numbers of lots included in each faunule and local diversity plotted against the midpoint of the stratigraphic interval associated with each faunule. Sampling and diversity measures include: A, the number of lots recorded in each assemblage; B, the number of species recorded in each faunule; C, values of Fisher's alpha estimated for each faunule, + symbols indicate assemblages with estimates of the constant $x < 0.90$ and round symbols indicate assemblages with $x \geq 0.90$; and D, estimates of Shannon's H for each faunule.

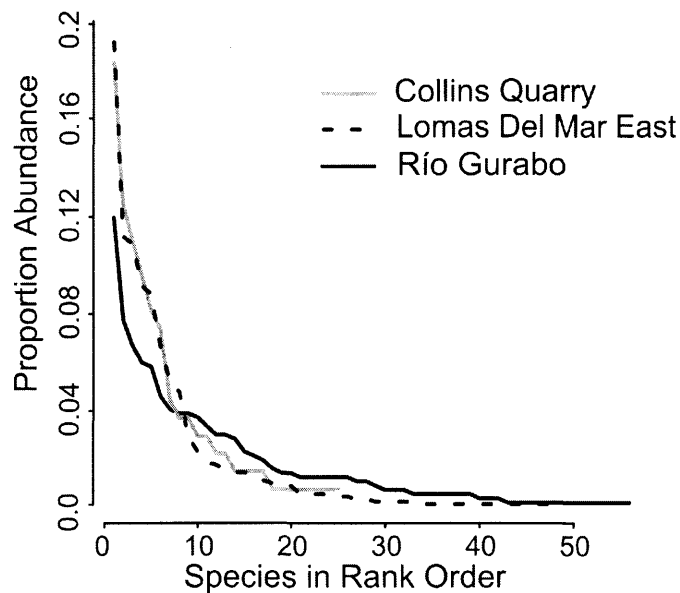
NN11U (Late Miocene Gurabo Fm.), and Ridges (Early Pliocene Seroe Domi Fm.). These three faunules were all collected from late Neogene units, but there is still no significant correlation between N and the median age for each faunule ($r = -0.139$, $p = 0.33$, 50 df). Species richness (S) within faunules ranged from 5 to 56 with a median richness of 17 species per faunule. Faunules characterized by high species richness include those with extremely large collections plus Rio Cana NN12 (Late Miocene Gurabo Fm.) that is comprised of 226 lots. This confirms the result that S and N are strongly correlated ($r = 0.815$, $p \ll 0.0001$, 50 df). However, richness is not correlated with faunule age ($r = -0.109$, $p = 0.436$, 50 df).

Estimates of Fisher's alpha (α) for each faunule range from 26.5 to 3.80 with a median of 10.02. Faunules with high values of α include Rio Gurabo NN15 (Early Pliocene Mao Fm.). However, this estimate is likely to be unreliable because of low values of the constant x (Appendix 1). Fitting an observed abundance distribution to the log-series distribution requires estimation of both the parameter α and a constant x , and the utility of α as a diversity measure results from the fact that the number of expected number of species represented by one specimen can be estimated as αx . HAYEK & BUZAS (1997) report that values of x are usually close to 1 in natural populations, but values for x calculated for Cenozoic coral faunules range from 0.546 to 0.989. Therefore, values of α cannot directly be compared as measures of diversity for all of these assemblages. Values of the constant x less than 0.9 have been calculated for 28 of the 52 assemblages studied here, and the correlation between α and age for the remaining 24 faunules is not significantly different from zero ($r = -0.028$, $p = 0.897$, 22 df). However, α is correlated with N ($r = 0.521$, $p = 0.009$, 22 df), suggesting that differences in sampling may be obscuring any real change in local diversity with time. Fisher's α is known to be more closely related to richness than to dominance (MAGURRAN, 1986), and this is supported by the strong correlation between α and S ($r = 0.914$, $p \ll 0.001$, 22 df) and the lack of significant correlation between α and evenness ($r = -0.068$, $p = 0.753$, 22 df).

Shannon's H ranges from 1.88 to 3.54 with a median value of 2.49. Faunules with high estimates of H include some of the assemblages characterized from large collections with high species richness, including Rio Cana NN12 (Late Miocene Gurabo Fm.), Rio Gurabo NN11U (Late Miocene Gurabo Fm.), Ridges (Early Pliocene Seroe Domi Fm.), and Salina (Late Miocene Seroe Domi Fm.). All four of these assemblages include more than 200 specimens, but there are other assemblages including large collections with lower values of H . For example the assemblage from Lomas Del Mar East faunule includes over 4 times as many specimens as the Rio Cana NN12 faunule but a lower value of H . Regardless, there is a strong positive correlation between N and H ($r = 0.859$, $p \ll 0.001$, 50 df), but there is no correlation between H and age ($r = -0.126$, $p = 0.373$, 50 df).

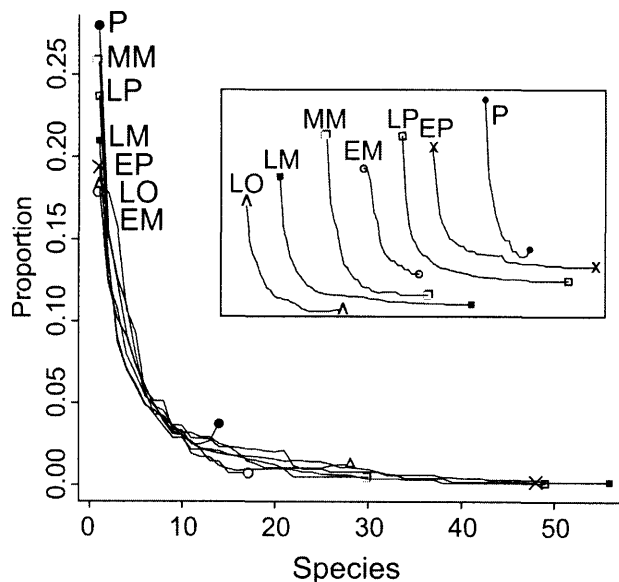
Analysis of all three measures of diversity suggest no change in local diversity with time, but S , α , and H are all correlated with N suggesting that uneven sampling may be obscuring any pattern. Rarefaction analysis is one approach to removing the effects of sampling artifacts from diversity estimates (HURLBERT, 1971), but this precludes the study of relative abundances in the faunules. However, examination of the actual species abundance distribution can provide insight into diversity of assemblages. Examination of rank abundance curves for Collins Quarry and Lomas del Mar East (Fig. 4) suggest

Fig. 4:
Rank abundance curves for Lomas del Mar East, Collins Quarry and Rio Gurabo NN11U faunules. Note that the shapes of the curves for Lomas del Mar East and Collins Quarry are similar except that more species were recovered from the larger collections at Lomas del Mar East. The curve for Rio Gurabo NN11U is less convex indicating lower dominance and therefore higher diversity for this assemblage than for the other two assemblages.



that diversity of the two assemblages are equal even though more species were recovered from Lomas del Mar East than from Collins Quarry. The short tail on the right side of the curve for Collins Quarry suggests that significant numbers of rare species remain to be discovered from this faunule. Assemblages from Lomas del Mar East are clearly sampled more adequately than those from Collins Quarry, because collections from Lomas del Mar East are nearly seven times larger than collections from Collins Quarry. The rank abundance curve for the Rio Gurabo NN11U faunule suggests that coral di-

Fig. 5:
Median rank abundance curves for faunules classified into stratigraphic intervals. Each curve represents the median of curves calculated for each faunule recovered from each stratigraphic interval. Different numbers of species were collected in each faunule, so the number of values used to calculate the median generally decreases as more species were added to the analysis. This may result in slight increase in median abundance observed in the medians of Pleistocene faunules. The inset box shows the same curves at slightly smaller scale. They have been separated to illustrate the shapes of individual curves.



versity recorded in this assemblage is higher than diversity of the other two assemblages. The peak on the left side of the curve for Rio Gurabo NN11U suggests that the most abundant species in this faunule includes 12 percent of the total number of lots recovered, nearly half as abundant as the most abundant species from either Collins Quarry or Lomas del Mar East. The shape of the curve for Rio Gurabo 11U is less convex indicating lower dominance of common species. Values of α and H estimated for the three faunules confirm this result (Appendix 1).

Median rank abundance curves calculated for a series of broad stratigraphic intervals (Fig. 5) suggests that species abundance distributions did not change significantly since the Late Oligocene. The most abundant species range between 17 and 27 percent of the total abundance in each faunule. Differences in the length of the right tail of the median species abundance curves indicates variation in the median number of rare species varies among the stratigraphic units. However, these differences most likely result from sampling variation.

4. DISCUSSION

There is no evidence that local diversity of coral assemblages has changed between the Late Oligocene and the Early Pleistocene. This apparent stability persisted in spite of the major regional environmental and biotic changes that occurred during this long interval, including two regional extinctions and the ecological reorganization of benthic communities in response to regional oceanographic changes caused by development of the Central American Isthmus. The current data set is characterized by variation in sampling effort, exposure style, preservation, depositional environment, and taphonomy, and this noise might be obscuring the real signal of change in local diversity. However, these data were compiled by a few teams working with roughly comparable field and laboratory methods. Even though these data represent very large collections relative to the usual standards, the numbers of specimens remains much too small to fully enumerate local species lists because a large number of locally rare or cryptic taxa are likely to be missed. But additional discoveries are only likely to increase the length of the right tail of rank abundance plots, and should not greatly alter the shape of the curve. This highlights the oft-repeated warning against using raw counts of taxa as a measure of diversity. Furthermore, any real signal of diversity change might be swamped by the noise created by merging local microenvironments (or even broader environmental types) into the faunules and comparing all environmental types in a single analysis. A more detailed analysis of a larger data set might allow more faint signals to be detected, although sample sizes required for such a study would be enormous (tens of thousands of occurrences).

These results suggest that reef-corals are living in shallow marine ecosystems that are apparently buffered from long-term directional change (JACKSON, 1994). In this view, most reef-coral species might be ecological generalists able to persist within a shared set of environmental conditions that were maintained for short periods in limited patches throughout regional environmental change. Processes acting at a metapopulation level forced change in the regional species pool from which local communities were assembled (JACKSON et al., 1996). The key is a high level of ecological redundancy in the

regional species pool so that the ecological role of locally extinct species is readily taken over by other members of the regional taxonomic pool.

It is also possible that only a subset of coral species are ecologically important (BUDD & JOHNSON, 2001). In this case, significant change in ecosystem composition and function could occur by replacing only a minor subset of local communities without significant change in local diversity. Using the terminology of HANSKI (1982), core species tend to be abundant on both local and regional scales, while satellite species are usually rare with patchy geographic distributions. Core species are strong ecological interactors and maintain the structure of local systems. VERMEIJ (2001) distinguished between species of large effect that could either be structural species that maintain the three-dimensional architecture of a community or keystone species that have a large effect on communities because of high rates of consumption and generalized diet. BUDD & JOHNSON (2001) demonstrated that rates of taxic turnover in Neogene reef-corals are higher for satellite than for core species in general, but both core and satellite species were affected during the Plio-Pleistocene biotic transition.

Data from only a few Late Pleistocene coastal terraces have been included in this analysis, and it is likely that more information would reveal significant restructuring of shallow water communities during the Pleistocene. Although *Acropora* spp. were locally dominant since at least the Late Miocene (McNEILL et al., 1997), fast growing *Acropora* communities are especially widespread after 1 Ma (ROSEN, 1993). Dense nearly monospecific biofacies are common in late Pleistocene (JACKSON, 1992; PANDOLFI & JACKSON, 2001), Holocene (STEMANN & JOHNSON, 1992), and Recent (GEISTER, 1977) Caribbean reefs. Additional Late Pleistocene to Recent abundance data are required to determine whether there was significant change in the diversity of local reef-coral assemblages during the past million years.

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Faunule Name	Species	Collections	Occurrences	Lots	Stratigraphic Unit	Country	Age Start	Age End	α	x	H	E
Crossroads Clinic Road	13	2	14	30	Antigua Fm.	Antigua	26	25	8.72	0.77	2.36	0.81
Willoughby Track	15	2	18	31	Antigua Fm.	Antigua	26	25	11.44	0.73	2.52	0.83
Friars Hill	16	2	17	26	Antigua Fm.	Antigua	26	25	17.71	0.59	2.63	0.87
Collins Quarry	25	9	68	137	Antigua Fm.	Antigua	26	25	8.96	0.94	2.72	0.60
Pig Point	26	7	48	92	Antigua Fm.	Antigua	26	25	10.84	0.9	2.77	0.61
Piggotts Hill (S)	25	1	25	98	Antigua Fm.	Antigua	26	25	7.96	0.78	2.89	0.72
Cedar Valley Quarry	28	5	30	81	Antigua Fm.	Antigua	26	25	15.15	0.84	2.90	0.65
Portete	14	4	18	39	Moin Fm.	¹ C. R.	1.9	1.5	11.31	0.83	1.93	0.49
Lomas del Mar-West	19	4	32	53	Moin Fm.	C. R.	1.9	1.5	10.61	0.83	2.58	0.69
Lomas del Mar- East	49	10	170	927	Moin Fm.	C. R.	1.9	1.5	11.03	0.99	2.84	0.35
Apt. Complex	28	1	28	101	Moin Fm.	C. R.	1.9	1.5	12.83	0.89	3.07	0.77
Empalme	29	9	65	127	Moin Fm.	C. R.	2.9	1.9	11.74	0.92	2.98	0.68
Buenos Aires C	32	10	91	292	Quebrada	C. R.	3.1	2.9	9.16	0.97	2.80	0.51
Buenos Aires A	23	1	23	59	Chocolate Fm. Quebrada	C. R.	7.5	5.6	13.86	0.81	2.79	0.71
Terraces – Lower	10	1	10	18	Chocolate Fm. Curacao Terraces	Curacao	0.2	0.1	9.26	0.66	2.14	0.85
Terraces – Middle	14	1	14	27	Curacao Terraces	Curacao	0.6	0.5	11.71	0.7	2.51	0.88
Sea Cliff	37	12	83	184	Seroe Domi Fm.	Curacao	2.6	2	11.64	0.79	2.91	0.50
Ridges	48	21	228	513	Seroe Domi Fm.	Curacao	5.6	3	5.14	0.9	3.29	0.56
Salina	40	8	113	246	Seroe Domi Fm.	Curacao	5.9	4.6	12.96	0.98	3.23	0.63
Salina-East	18	5	21	43	Seroe Domi Fm.	Curacao	10.3	7.8	13.55	0.95	2.56	0.72
Flatiron	30	21	105	206	Seroe Domi Fm.	Curacao	16.2	14.9	9.66	0.96	2.74	0.51
Rio Cana NN15	21	3	22	55	Mao Fm.	¹ D.R.	4	3.7	12.41	0.82	2.47	0.56
Rio Gurabo NN15	21	6	27	32	Mao Fm.	D. R.	4	3.7	26.56	0.55	2.89	0.86
Rio Cana NN14	13	6	17	21	Mao Fm.	D. R.	4.2	4	14.56	0.59	2.44	0.88
Rio Gurabo NN14	19	10	31	44	Mao Fm.	D. R.	4.2	4	12.7	0.78	2.68	0.77
Rio Cana NN13	20	10	30	58	Gurabo Fm.	D. R.	5	4.2	10.8	0.84	2.50	0.61
Rio Gurabo NN12	15	13	35	51	Gurabo Fm.	D. R.	5.6	5	7.16	0.88	2.33	0.68
Rio Cana NN12	48	19	117	226	Gurabo Fm.	D. R.	5.6	5	18.65	0.92	3.54	0.72
Rio Cana NN11U	17	20	60	91	Gurabo Fm.	D. R.	7.5	5.6	6.16	0.94	2.37	0.63

Faunule Name	Species	Collections	Occurrences	Lots	Stratigraphic Unit	Country	Age Start	Age End	α	x	H	E
Rio Mao	18	11	29	80	Gurabo ? Fm.	D. R.	7.5	5.6	7.23	0.92	2.40	0.61
Rio Gurabo NN11U	56	51	312	573	Gurabo Fm.	D. R.	7.5	5.6	15.36	0.97	3.42	0.55
Arroyo Lopez	10	5	13	17	Cercado ? Fm.	D. R.	8.3	7.5	10.19	0.63	2.04	0.77
Rio Cana NN11L	13	5	19	39	Cercado Fm.	D. R.	8.5	7.5	6.83	0.85	2.18	0.68
Rio Gurabo NN11L	21	21	50	75	Gurabo Fm.	D. R.	8.5	7.5	9.68	0.89	2.48	0.57
Baitoa	16	19	57	103	Baitoa Fm.	D. R.	17.3	13.1	5.3	0.95	2.22	0.58
Rio Bueno Terrace 1	13	1	13	62	Falmouth Fm.	Jamaica	0.15	0.12	7.67	0.79	2.30	0.76
Rest Sop	12	3	12	48	Hope Gate Fm.	Jamaica	1.8	1	5.01	0.93	1.88	0.55
Discovery Bay	10	3	19	49	Hope Gate Fm.	Jamaica	1.8	1	3.8	0.93	1.90	0.67
Folly Point	25	7	46	123	Manchioneal Fm.	Jamaica	2	1.4	9.48	0.93	2.66	0.57
Port Antonio	20	4	37	55	Manchioneal Fm.	Jamaica	2	1.4	12.07	0.88	2.81	0.83
Old Pera(GH)	21	7	40	60	Old Pera Beds	Jamaica	2	1.8	11.49	0.84	2.61	0.65
Old Pera(DEF)	24	8	40	69	Old Pera Beds	Jamaica	3	2	13.06	0.84	2.47	0.49
Bowden(C)	16	2	24	74	Bowden Fm.	Jamaica	3.3	3	6.28	0.92	2.32	0.64
Bowden(AB)	16	5	29	62	Bowden Fm.	Jamaica	3.8	2.7	6.99	0.9	2.08	0.50
Galliard Cut W	17	15	66	140	Emperador Ls.	Panama	22	17.6	5.07	0.97	2.38	0.63
West Quarry	16	1	16	172	Tamana Fm.	Trinidad	16.4	12.3	4.31	0.98	1.99	0.46
West of West Quarry	10	1	10	42	Tamana Fm.	Trinidad	16.4	12.3	4.15	0.91	2.00	0.74
Gasparillo	14	1	14	55	Tamana Fm.	Trinidad	16.4	12.3	6.06	0.9	2.04	0.55
Cumuto	10	1	10	16	Tamana Fm.	Trinidad	16.4	12.3	11.41	0.58	2.17	0.87
Tabaquite	18	1	18	114	Tamana Fm.	Trinidad	16.4	12.3	6.01	0.95	2.22	0.51
Concord	13	1	13	41	Tamana Fm.	Trinidad	16.4	12.3	6.56	0.86	2.34	0.80
Brasso	13	1	13	27	Brasso Fm.	Trinidad	16.4	12.3	9.86	0.73	2.43	0.87
Total	207	397	2460	6004	--	--	--	--	41.56	0.99	4.56	0.46

¹ C. R. = Costa Rica, D. R. = Dominican Republic.

Appendix 1

Summary characteristics of the 52 Oligocene to Pleistocene faunules included in this study. For each faunule, the number of collections, occurrences and lots are shown. Stratigraphic units, country, and stratigraphic endpoints of each faunule are also included. Diversity measures include number of species, Fisher's α and x, Shannon's H, and Buzas and Gibson's E.

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Plate 1

Selected common coral species recovered from the Late Oligocene Antigua Fm., Antigua. All scale bars are 1cm in length except where indicated.

- Fig. 1: *Astrocoenia guantanamoensis* VAUGHAN, 1919, figured specimen, LACMIP 13131, thin section.
- Fig. 2: *Astrocoenia* sp. B, figured specimen, LACMIP 13132, specimen surface.
- Fig. 3: *Stephanocoenia duncani* FOSTER, 1987, figured specimen, LACMIP 13133, polished surface.
- Fig. 4: *Stylophora imperatoris*, VAUGHAN, 1919, figured specimen, LACMIP 13134, specimen surface.
- Fig. 5: *Acropora saludensis* VAUGHAN, 1919, figured specimen, LACMIP 13135, branch tip, scale bar has a length of 5 mm.
- Fig. 6: *Astreopora antiguensis*, VAUGHAN, 1919, figured specimen, LACMIP 13136, polished surface.
- Fig. 7: *Leptoseris* sp. C, figured specimen, LACMIP 13137, polished surface.
- Fig. 8: *Siderastrea conferta* (DUNCAN, 1863), figured specimen, LACMIP 12199, thin section.
- Fig. 9: *Pironastraea antiguensis* VAUGHAN, 1919, figured specimen, LACMIP 13138, thin section.
- Fig. 10: *Porites portoricensis* (VAUGHAN, 1919), figured specimen, LACMIP 13139, specimen surface.
- Fig. 11: *Porites regularis*, (DUNCAN, 1863), figured specimen, LACMIP 13140, specimen surface.
- Fig. 12: *Goniopora imperatoris* VAUGHAN, 1919, figured specimen, LACMIP 13141, specimen surface.

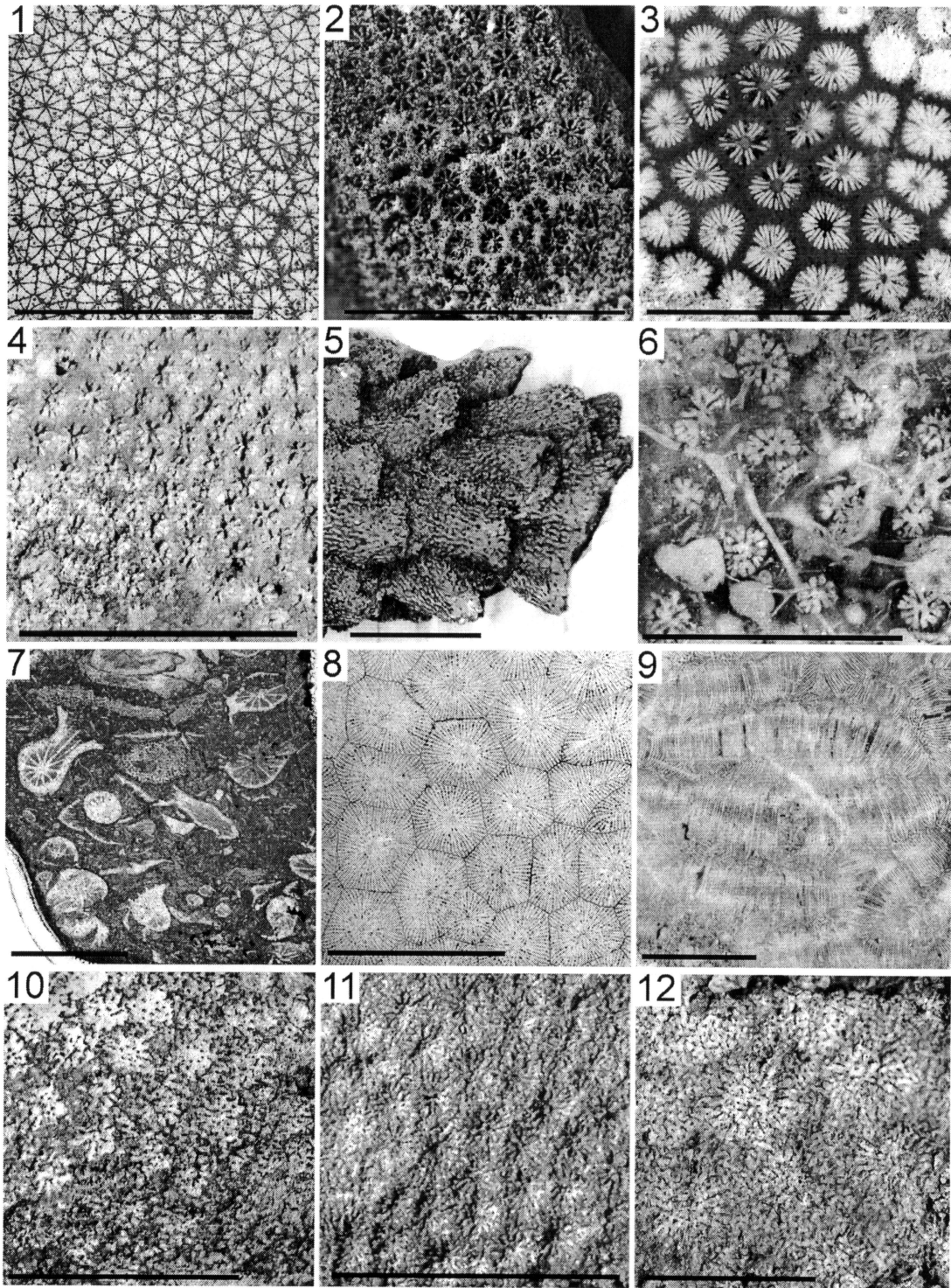


Plate 2

Selected common coral species recovered from the Late Oligocene Antigua Fm., Antigua. All scale bars are 1cm in length.

- Fig. 1: *Agathiphyllia tenuis* (DUNCAN, 1863), figured specimen, LACMIP 13142, specimen surface.
- Fig. 2: *Agathiphyllia hilli* (VAUGHAN, 1919), figured specimen, LACMIP 13143, thin section.
- Fig. 3: *Agathiphyllia* sp. 3, figured specimen, LACMIP 13144, thin section.
- Fig. 4: *Favites polygonalis* (DUNCAN, 1863), figured specimen, LACMIP 13145, thin section.
- Fig. 5: *Colpophyllia willoughbiensis* (VAUGHAN, 1919), figured specimen, LACMIP 13146, thin section.
- Fig. 6: *Antiguastrea cellulosa* (DUNCAN, 1863), figured specimen, LACMIP 13147, specimen surface.
- Fig. 7: *Hydnophora* sp. A, figured specimen, LACMIP 13148, thin section.
- Fig. 8: *Montastraea canalis* (VAUGHAN, 1919), figured specimen, LACMIP 13149, thin section.
- Fig. 9: *Montastraea endothecata* (DUNCAN, 1863), figured specimen, LACMIP 13150, thin section.
- Fig. 10: *Diploastrea crassolamellata* (DUNCAN, 1863), figured specimen, LACMIP 13151, thin section.
- Fig. 11: *Diploastrea* sp. T, figured specimen, LACMIP 13152, thin section.
- Fig. 12: *Heliopora* sp. A, figured specimen, LACMIP 13153, specimen surface.

