OLIGOCENE-MIOCENE CARIBBEAN CORAL EXTINCTION

MASS EXTINCTION OF CARIBBEAN CORALS AT THE OLIGOCENE-MIOCENE BOUNDARY: PALEOECOLOGY, PALEOCEANOGRAPHY, PALEOBIOGEOGRAPHY

by

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ABSTRACT

About half the Caribbean hermatypic corals died out at the Oligocene-Miocene boundary, about 25 Ma. Roughly two thirds of those corals which died out in the Caribbean are still extant in the Indo-Pacific. The coral and coral associate faunas of three Upper Oligocene and three Middle Miocene fossil reefs in western Puerto Rico were compared. Corals on these sites suffered 59% generic extinction, and 54% species extinction. Nearly all coral genera which are tolerant of turbidity or turbidity and cold water survived. All corals found exclusively or principally on Oligocene shelf-edge reefs became regionally extinct. There are no shelf-edge reefs documented from the Miocene in the Caribbean.

Coral associates, the endolithic organisms which live in coral skeletons, were almost completely unaffected by this extinction. Likewise, reef and off-reef gastropods, bivalves, and echinoids suffered only insignificant reductions in diversity. Only corals and large benthic foraminifera were strongly affected by the extinction. It is significant that zooxanthellate organisms were the primary victims of this extinction. There is no evidence to suggest effects at higher trophic levels.

Paleontological evidence from corals, coral associates, and gastropods suggests enhanced upwelling in the Caribbean during the Miocene and Early Pliocene. This enhanced upwelling could account for the extinction by cooling Caribbean coastal surface waters and restricting reef development to on-shelf patch reefs, where corals would be subject to more intense sedimentation. Paleoceanographic models indicating West to East deep circulation through the Central American Seaway during the Miocene provide a mechanism for this enhanced upwelling.

Life history characteristics may have influenced survivorship among the corals, but apparently had no effect on coral associates. Corals which brood their larvae survived in greater proportions than corals which broadcast. This pattern is opposite that observed in studies on molluscs and other invertebrates.

This regional extinction was important in the division of a previously cosmopolitan reef fauna into the modern provincial faunas. Explaining this minor mass extinction may contribute to an understanding of the volatile record of reefs in the larger mass extinctions of the Phanerozoic.

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Chapter 1: Introduction

1.1 Reefs and Mass Extinctions

Organic reefs have formed one of the most persistent and most diverse habitat types throughout the Phanerozoic, and many different types of organisms have dominated reefs during the history of life (Newell, 1971; Sheehan, 1985). Reef invertebrates and communities were devastated in each of the five major mass extinctions of the Phanerozoic: Ordovician-Silurian, Late Devonian, Permian-Triassic, Late Triassic, and Cretaceous-Tertiary (Fagerstom, 1987; Raup and Boyajian, 1988). This study examines a regional mass extinction of reef corals in the Caribbean at the Oligocene-Miocene boundary. Roughly half of Caribbean corals became regionally extinct in the Caribbean, but about two thirds of those survived in the Indo-Pacific (Frost, 1977a).

All mass extinctions are selective - some groups of organisms survive, and others do not (Stanley, 1987). The factors controlling this selectivity often remain unclear. Are the factors controlling survivorship in mass extinctions the same factors which normally limit distribution and abundance of organisms, or do mass extinctions operate "by a different set of rules"? (Gould, 1985; Jablonski, 1986a; Bennett, 1990).

Biogeography may be important in many cases (e.g. Valentine, et al., 1978; Jablonski, 1986b; Westrop and Ludvigsen, 1987). Many of the clues about the ecological factors controlling which types of organisms survive mass extinctions - and which do not - may be best examined in minor mass extinctions which did not cause major revolutions in the taxonomic composition and ecological structure of the communities affected (Vermeij, 1989b). In minor and/or regional extinctions, the ecological context of the extinction is more stable, so it is easier to examine individual factors in isolation.

Studies of regional mass extinctions may also help us evaluate our impact on the modern biosphere. The modern, human induced mass extinction, which is biogeographically and ecologically concentrated in tropical moist forests, may equal or surpass the largest mass extinctions of the Phanerozoic in magnitude (Wilson, 1988). An understanding of relatively recent (Cenozoic, and particularly Neogene) regional mass extinctions may be of greater applicability to managing our impact on the biosphere than large statistical compilations of the Phanerozoic record of mass extinctions.

Reefs have harboured a significant portion of the total marine invertebrate fauna for nearly all of the Phanerozoic. Reefs have been dominated by a diverse set of organisms, from stromatolites, stromatoporoids, and bryozoans to rudist bivalves and scleractinian corals (Newell, 1971; Fagerstrom, 1987). Mass extinctions often had their most dramatic effects on reef communities (Stanley, 1984a, 1987). The large scale faunal changes on reefs generally (but not always) followed the pattern of large scale faunal changes in marine invertebrates on the whole (Newell, 1972; Sheehan, 1985; Fagerstrom, 1987; Raup and Boyajian, 1988; see chapter 2).

Since the Latest Triassic, scleractinian corals have been the dominant reef building organisms, except for the brief reign of rudist bivalves in the Middle and Upper Cretaceous (Newell, 1971; Stanley, 1981). Scleractinians suffered heavily in the Cretaceous-Tertiary boundary extinctions, but nonetheless, many of the dominant reef forming families and genera of the Mesozoic survive today (Newell, 1984). Other reef faunas have also changed considerably during this time, in part due to the "Mesozoic Marine Revolution" (Vermeij, 1977). Among the many groups which underwent radiation during the Mesozoic, and which still retain high diversity, are reef-building corals and their bioeroding associates. Most of the modern bioeroding reef invertebrates - endolithic sponges (De Laubenfels, 1955), lithophagid and gastrochaenid bivalves (Cox et al., 1969), and diademid urchins (Wyatt Durham, et al., 1966) - arose in the Jurassic or Cretaceous. Pomacentrid and acanthurid fish, the major vertebrate bioeroders, date from the Eocene (Hutchings, 1986). Internal coral associates are of necessity preserved *in situ*, either as borings or, in some cases, as body fossils in borings (Bromley, 1970; Warme, 1975).

Ecologically and evolutionarily, post-Cretaceous fossil reefs resemble modern reefs much more than older fossil reefs (James, 1983). In many cases, the same genera that dominated mid-Cenozoic reefs are extant today (Frost and Langenheim, 1974), in the Pacific if not the Caribbean (see chapter 3), so extrapolations of the biology of their modern counterparts to the fossil organisms are more easily, and more confidently, made.

Two minor mass extinctions, at the end of the Oligocene and at the end of the Pliocene, severely reduced coral diversity in the Caribbean and Mediterranean, but not in the Indo-Pacific (Frost, 1977a). Although these were regional, rather than global extinctions, they had profound effects on ecology, evolution, and biogeography of Cenozoic reef systems (Frost, 1977a; Jones and Hasson, 1985; Vermeij and Petuch, 1986). This study treats the first of these two extinctions, at the Oligocene-Miocene boundary.

1.2 Global Tectonics, Oceanography, and Extinctions

For the most part, the configuration of the continents has changed little since the Cretaceous (Briggs, 1987). Certain important changes, however, occurred around the time of the Oligocene-Miocene boundary, and these have caused critical differences between Paleogene and Neogene oceanographic conditions. The Eastern Tethys marine connection between the Mediterranean and the Indian Ocean was blocked about 25 Ma ago, around the Oligocene-Miocene boundary, when Africa + Arabia collided with Eurasia in the vicinity of Iran (Adams, et al., 1986). At about the same time, Drake Passage, between Antarctica and Patagonia, opened to deep circulation (Zinsmeister, 1982). The closure of the Eastern Tethys interrupted the pattern of circumtropical circulation which had prevailed since the Cretaceous (Luyendyk, et al., 1972). The opening of Drake Passage allowed circum-Antarctic deep circulation to begin (Kennett, 1982). How these global oceanographic changes relate to the Oligocene-Miocene extinction of Caribbean corals has not been studied previously studied.

These geographic and oceanographic changes, among other effects, divided a Cretaceous and Palaeogene cosmopolitan tropical marine fauna into its modern biogeographic provinces (Kennett, 1982). Numerous studies have pointed to the critical role that changes in biogeographic provinciality play in regulating faunal diversity, both on regional (Erwin, 1989) and global (Valentine, et al., 1978) scales (see chapter 2). The regional extinctions at the Plio-Pleistocene boundary are related to a third crucial change in continental configuration: the rise of the Isthmus of Panama (Jones and Hasson, 1985; Vermeij and Petuch, 1986) and to the onset of Northern hemisphere glaciation (Stanley and Campbell, 1981; Stanley 1986a).

1.3 Approaches to Mass Extinctions

There are three major ways to study mass extinctions. (1) Large database compilations of stratigraphic ranges (e.g. Sepkoski, 1982 and many others) may be used to analyze "the big picture" - long term changes in faunal composition and major fluctuations in evolutionary diversity. These compilations cannot, however, directly address mechanisms of extinction, particularly proximal mechanisms (e.g. Simberloff, 1986). (2) Stratigraphic sections spanning a particular extinction may be sampled to determine what changes in physical environment coincided with the biological extinction (e.g. Zinsmeister, et al., 1989, and many others). (3) Fossil communities on either side of a known extinction can be compared to detect differences in community composition resulting from the extinction (e.g. Raffi, et al., 1985). I refer to (2) and (3) as the stratigraphic and comparative approaches, respectively. Both of these approaches have their merits, and their problems. Ideally, all three approaches complement each other, and should be combined in a comprehensive study.

Both the stratigraphic approach and the comparative approach can give information about the causes of a given mass extinction. One particularly intriguing aspect of mass extinctions is their selectivity. By examining the survivorship of groups which share a community but respond to different ecological factors, we can test hypotheses about the causes of that extinction. The comparative approach is particularly amenable to such a comparison of survivorship patterns. The communities studied on either side of the extinction should be separated by as little time as possible.

One of the chief limitations to any study of mass extinctions, regardless of approach, is the stratigraphic distribution of rocks containing fossils of the community in question. This is a particular problem in reef ecosystems, which do not typically have continuous accretion for long stretches of geological time (Walker and Alberstadt, 1975; James, 1983; Fagerstrom, 1987; Copper, 1988). In the tectonically active Caribbean, there are no complete sections of reefs spanning the Oligocene-Miocene boundary (see section 1.7). This limitation of the data base makes the comparative approach to mass extinctions the most feasible approach available for this study of the Cenozoic evolution of Caribbean reef systems. This study uses the comparative approach.

1.4 Research Questions

I compared the coral faunas and internal coral associate faunas of Oligocene, Miocene, and modern reefs of Puerto Rico to determine, by analyzing patterns of differential survivorship, what could have caused the Oligocene-Miocene mass extinction of Caribbean reef corals. I attempt to answer six specific questions: (1) What were the ecological differences between the coral species which survived and those which did not? (2) How did the survivorship pattern of bioeroding internal coral associates differ from that of the corals? (3) Were differences in trophic level between corals and coral associates responsible for their differential survivorship? (4) What are the unique ecological characteristics of internal coral associates which were responsible for their differential survival from corals? (5) How does the modern biogeography of corals and coral associates relate to the separation of tropical marine biogeographic provinces at the Oligocene-Miocene boundary? (6) How did reproductive and life history characteristics affect survivorship of corals and coral associates during this extinction? This information combined can help to answer the main question: what caused the extinction?

1.5 Basic Ecology of Corals and Coral Associates

Before examining the survivorship patterns in the fossil record, it is important to understand the ecological requirements of corals and coral associates (Table 1.1). All hermatypic reef corals share the following requirements: light, warm water (>18°C), normal oceanic salinity (32-38 ppt.), and low rates of sedimentation. Tolerance to changes in any of these factors varies by genus or species. Nutrient loading may increase the growth rates of individual coral heads (but see Thomascik and Sander, 1985; Davies, 1990), but tends to inhibit reef accretion, due to enhanced rates of bioerosion and competition from fleshy algae (Glynn and Wellington, 1983; Hallock and Schlager, 1986; Birkeland, 1987; Scott, et al., 1988). By examining the tolerance of the modern representatives of the Oligocene and Miocene coral genera seen in this study, it is possible to narrow down the causes of this extinction.

Table 1.1: Habitat tolerances of Corals and Coral Associates "Janus effect" refers to the bifold effect of nutrients on corals: individual corals may grow faster under high nutrient conditions, but coral reef growth is inhibited by competition with non-calcified organisms and bioerosion. Named for Janus, the two-faced god of Greek mythology.

factor	reef corals	coral associates
light	necessary	mostly not necessary
salinity	fully marine	mostly fully marine
temperature	warm (18< <40)	cool to warm
turbidity	low (-moderate)	low to high
nutrients	"janus effect"	beneficial
nutritional mode	mostly autotrophic (zooxanthellate)	mostly heterotrophic

Modern coral associates generally have a much broader range of ecological tolerance than do corals. Nearly all coral associates are heterotrophic and do not require light (Bergquist, 1978). Many coral associates also occur in deep or cold water habitats. Associates are generally more tolerant of sediment loading than corals (Cortes and Risk, 1985), although they mostly cannot withstand heavy sedimentation (Stearley and Ekdale, 1988). The salinity requirements of endolithic organisms are not well known. As heterotrophs, bioeroding coral associates thrive in nutrient-rich waters (Rose and Risk, 1985; Hallock, 1988).

Most coral associates bore into dead coral, and can easily bore into other substrates. Consequently, most coral associates have biogeographic ranges extending well beyond the range of coral reefs themselves, and would be resistant to most environmental changes which would adversely affect corals (see chapter 8). The major exception here are the coral inhabiting organisms which do not bore, but rather, inhibit calcification, causing the coral to grow around them.

Fagerstrom (1988) divided reef organisms into five guilds: constructors, destroyers, baffles, binders, and dwellers. The two guilds which most control rates of reef accretion are constructors and destroyers, here represented by scleractinian corals and the bioeroding coral associates, respectively. Because the associates leave borings, and sometimes skeletal parts, in the corals they inhabit, taphonomic bias between the two guilds is minimized.

1.6 Previous work on this extinction

About half of the reef coral fauna in the Caribbean and Western Tethyan (Mediterranean) provinces became regionally extinct at the end of the Oligocene. Many of the genera which died out in the Caribbean and Western Tethyan provinces survived in the Indo-Pacific. The extinction was fairly sudden in geological time, being confined to the upper part of the _Globorotalia_ _kugleri_ planktonic foram zone of the latest

Oligocene or earliest Miocene (Frost, 1977a) and probably spanning less than 1 Ma (see Kennett, 1985 for updated Miocene biostratigraphy and chronology).

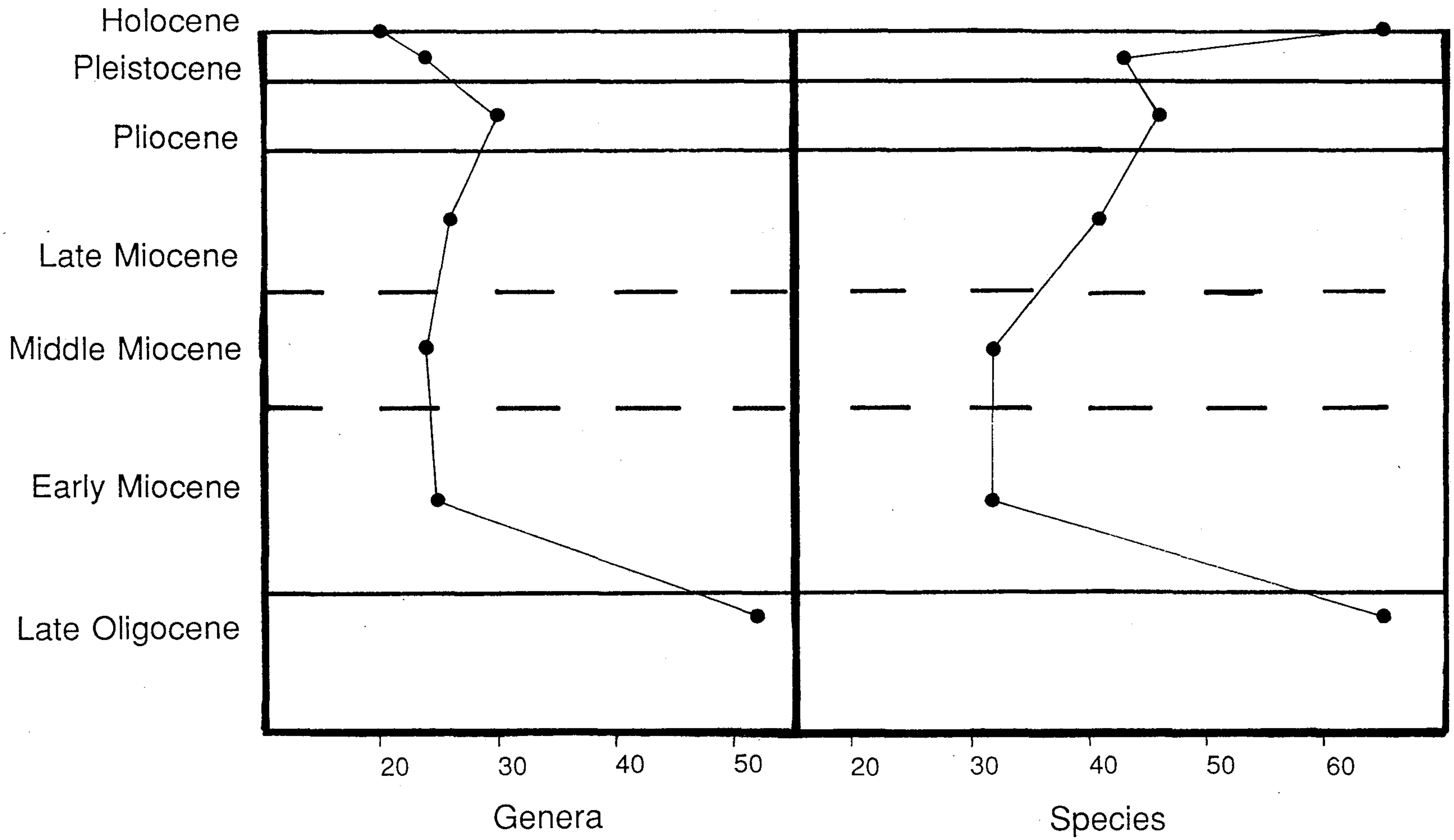
This extinction primarily affected reef corals and large benthic foraminifera, and had little or no effect on molluscs, echinoids, or planktonic foraminifera (Frost and Langenheim, 1974; Frost, personal communication, 1989). Large benthic forams suffered a sharp decline in diversity in the Caribbean during the Late Oligocene - Early Miocene interval (Frost and Langenheim, 1974; Adams, 1983; Brasier, 1988). Most families of reef corals actually increased in global generic diversity between the Oligocene and the Miocene (Newell, 1977), although diversity in the Caribbean remains reduced compared to Oligocene times and is much lower than in the modern Indo-Pacific (table 3.1; figure 3.1; Stehli and Wells, 1971; Frost, 1977a; Veron, 1986). The global impact of this extinction on scleractinian corals thus was negligible, and cannot compare with the huge coral losses at the Cretaceous-Tertiary boundary (Newell, 1982).

Table 1.2: Species Diversity of Oligocene and Modern Reef Corals. Data from Veron, 1986, Rosen, 1984, Frost and Langenheim, 1974, and Frost, 1977a,c.

	Mod. Indo-Pac.	Mod. Carib.	Olig. Cosmop.
Families	23	10	15
Genera	90	21	55-60
Species	ca. 300 (-500)	65	65 (-90)

Figure 1.1. Oligocene to Holocene Diversity of Caribbean Reef Corals. Compiled from Frost and Langenheim (1974), Frost (1977a), Rosen (1984), Foster (1986). Increased species/genus ratio in Holocene probably attributable to "pull of the recent".

Oligocene to Holocene Diversity of Caribbean Reef Corals



Compiled from: Frost and Langenheim, 1974; Frost, 1977a;
Rosen, 1984; Foster, 1986.

The biogeographic impact, however, was immense. It represents the first major division between the cosmopolitan reef fauna of the Paleogene and the provincial reef fauna of the Neogene (Frost, 1977a; Vermeij, 1986). Caribbean corals suffered a second regional extinction at the Plio-Pleistocene boundary (Vaughan, 1921; Frost, 1977a; Budd, 1990), when the Isthmus of Panama separated the Caribbean from the Pacific. This second extinction, however, had much less severe effects than the first.

The Oligocene was the heyday of Cenozoic reefs. Many of the dominant massive corals of modern Indo-Pacific reefs are congeneric, and in some cases, conspecific with the dominant Oligocene massive corals (Frost and Langenheim, 1974; Frost, 1981). Caribbean and Mediterranean fossil reefs, where the extinction had its greatest impact, suffered a drastic reduction in diversity of framework builders (Frost, 1977a). Montastrea and Porites emerged as the dominant constructors of Miocene Caribbean reefs after the Oligocene-Miocene extinction (Frost, 1972). Miocene reefs in the Caribbean are almost exclusively low-relief patch reefs, rather than large shelf-edge buildups such as those of the Oligocene (Frost, 1977a,b; Frost, 1981).

Early and Middle Miocene Caribbean reefs had several Pacific species in addition to the Caribbean survivors of the mass extinction. Most of these Pacific species died out in the Middle Miocene, but some lasted until the Pliocene-Pleistocene boundary (Frost, 1977a).

The modern Caribbean coral fauna can be viewed as a relict fauna which has changed little since its isolation from the Indo-Pacific (Stehli and Wells, 1971; Rosen, 1984; Vermeij, 1986). Furthermore, most of the significant radiation of Indo-West Pacific corals is post-Oligocene, and may be post-Miocene for the highly speciose genera Acropora and Montipora (Veron, 1986; Veron and Kelley, 1988). An explanation of the Oligocene-Miocene mass extinction may be important both to understand the historical development of modern reef communities and to explore the role of biogeography in mass extinctions in general.

Fossil reefs in the Caribbean and the Middle East clearly record the extinction (Frost, pers. comm., 1989), but there are no continuous reef sections across the Oligocene-Miocene boundary in the Caribbean (Frost, 1977a). The exposed fossil record of Cenozoic coral reefs in the Indo-West Pacific is rather poor, so events there have received little attention. Western Puerto Rico has well developed Oligocene and Miocene fossil reef exposures, and a conformable carbonate sequence from the Upper Oligocene to the Upper Miocene (see section 1.7). There are also modern reefs, making it a good study area for a comparison of Oligocene, Miocene, and modern Caribbean reef faunas.

Prior to the Oligocene-Miocene boundary, circumtropical currents connected a cosmopolitan reef fauna. The closure of the Eastern Tethys during the Latest Oligocene and Early Miocene reduced this circumtropical circulation (Luyendyk, 1972; Maier-Reimer, et al., 1990), and the rise of the Isthmus of Panama during the Pliocene eliminated it entirely. The Early Miocene, thus, was the beginning of the modern provincial reef faunas in separate, colder oceans. Although the Caribbean and the Eastern Pacific were fully connected until mid-Pliocene time (Jones and Hasson, 1985), the coral faunas of the Indo-Pacific and the Caribbean have followed largely separate evolutionary paths since the Oligocene-Miocene boundary (Frost and Langenheim, 1974; McCoy and Heck, 1976). Following the closure of the Central American Seaway and Pleistocene extinction of relict Caribbean corals in the Eastern Pacific (Dana, 1975; Glynn, 1982), the coral fauna of the Eastern Pacific has been completely separate from that of the Caribbean. The environmental changes in the Caribean caused by this sequence of oceanographic and tectonic events, and their probable relation to the extinction under study, are discussed in chapter 6.

1.7 Regional Geology and Puerto Rican Stratigraphy,

1.7.1 Origin and Volcanic Core

Puerto Rico is the smallest and farthest east of the Greater Antilles, the string of large islands forming the northern boundary of the Caribbean Sea. Cuba, Hispaniola, Jamaica, and Puerto Rico all formed as a result of island arc volcanism during the Jurassic, Cretaceous, and early Tertiary (Khudoley and Meyerhoff, 1971). The island lies at 19° latitude and has been in the tropics throughout its entire existence. Southwest Puerto Rico contains the oldest rocks on the island, including late Jurassic and Cretaceous sedimentary basins filled with volcaniclastics and carbonates (Kauffman, et al., 1990). There are some rudist buildups, including some on Isla Magueyes, the site of the University of Puerto Rico marine lab (Kauffman, et al., 1990).

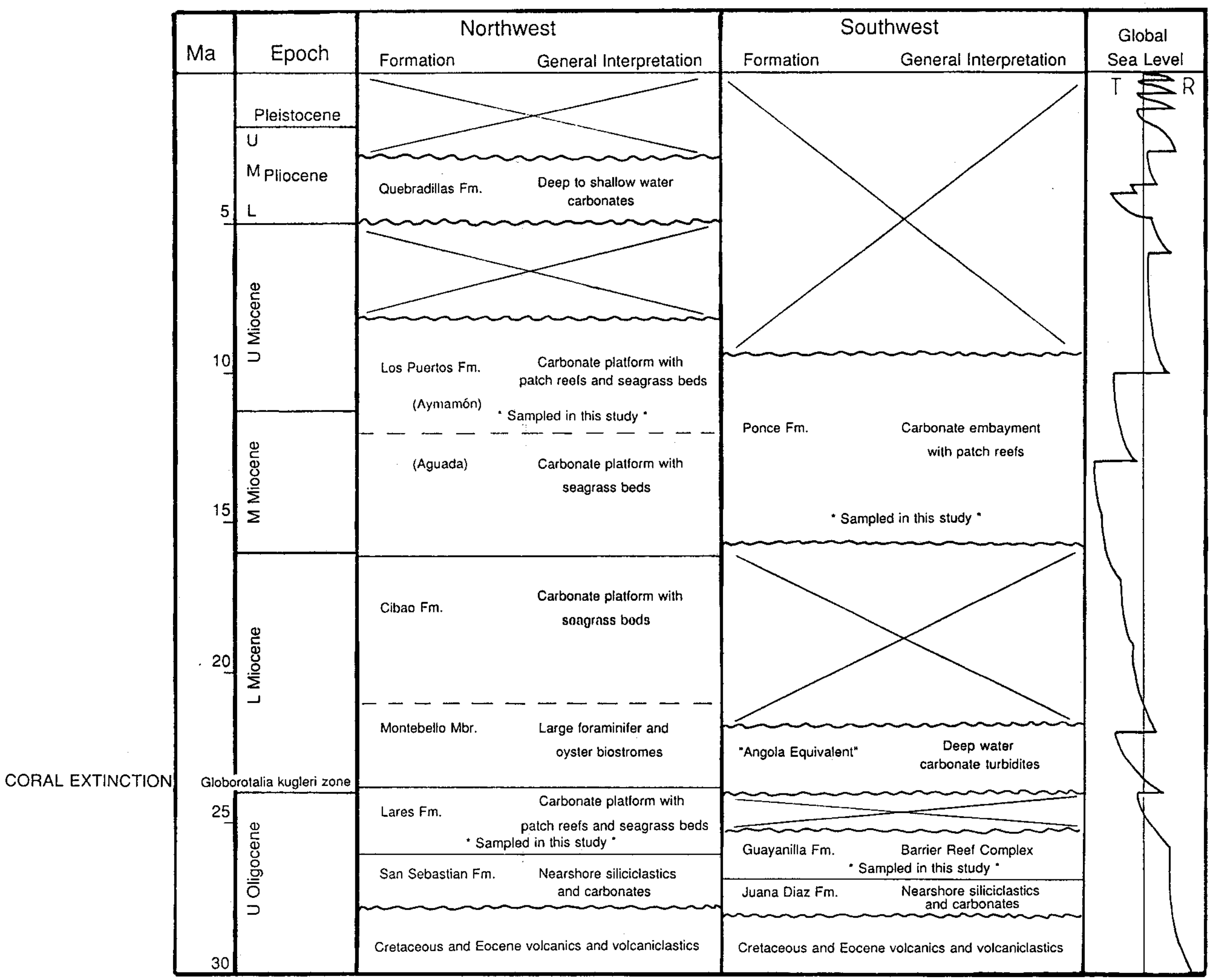
The core of the island is the Cordillera Central, made of Cretaceous and early Tertiary volcanics. This core is flanked by broad (north) and narrow (south) sedimentary blankets, formed mostly of carbonates. The Muertos Trough, which runs along the south coast of the island, was an active subduction zone until Late Miocene (probably Messinian) time, with the Caribbean plate underriding the island. In Pliocene time, the direction of subduction reversed, with the North American plate underriding the island in the Puerto Rico Trench (Khudoley and Meyerhoff, 1971; Birch, 1986). This change in tectonic regime may account for the uplift of the carbonate sequences on both sides of the island (Birch, 1986). Khudoley and Meyerhoff (1971), Bonini, et al., (1984), Durham (1985), and Stehli and Webb (1985) review the geologic history and tectonic development of the Caribbean.

The island arc volcanics which form the core of the island are overlain by Eocene to middle Oligocene volcaniclastic sediments. On the north side of the island, the San Sebastian Fm. (late Oligocene) is composed of conglomerates, nearshore sandstones, and marls near the top (Monroe, 1980). This formation represents the initial transgression after the drastic late Middle Oligocene sea level fall (Moussa and Sieglie, 1984; Haq, et al., 1986). The latest Oligocene Lares limestone conformably overlies the San Sebastian Fm. On the more tectonically active South Coast, the late Oligocene Juana Diaz Fm. grades from nearshore clastics into a carbonate facies with an extensive latest Oligocene reef tract (Monroe, 1980; Frost et al., 1983).

1.7.2 North Coast Carbonates

From late Oligocene to late-Miocene time, the north coast of Puerto Rico was a broad, gently sloping carbonate platform with locally developed patch reefs (Monroe, 1980; Sieglie and Moussa,

Figure 1.2. General Tertiary Stratigraphy of Northwest and Southwest Puerto Rico. Global Sea Level curve from Vail, et al. (1977). Absolute ages of formations are rough estimates based on Kennett, et al. (1985a). Correlations are relatively precise, probably to within 1 Ma; compiled from Monroe (1980), Frost, et al. (1983), Sieglie and Moussa (1984), Moussa, et al. (1987). Coral extinction occurred in *Globorotalia kugleri* planktonic foram zone, roughly at Oligocene-Miocene boundary. * indicates formation sampled in this study.



General Tertiary Stratigraphy of Northwest and Southwest Puerto Rico

Correlations and absolute ages ± 1 Ma
Compiled from Frost, et al., 1983; Moussa and Sieglie, 1984.
Sea Level Curve from Vail, et al., 1977.

1984, Moussa et al., 1987). The limestone formations, in ascending order, are the Lares Fm. (uppermost Oligocene), Montebello Mbr. of the Cibao Fm. (lowest Miocene), Cibao Fm. proper (lower Miocene), Aguada Mbr. of the Los Puertos Fm. (lower middle Miocene), Aymamon Mbr. of the Los Puertos Fm. (upper middle to upper Miocene), and Quebradillas Fm. (Pliocene). The Quebradillas Fm. consists of deep shelf chalks and foraminiferal deposits, and probably marks the origin of the Puerto Rico Trench (Moussa, et al., 1987). An unconformity of unknown duration separates the Los Puertos and the Quebradillas. Figure 1.2 shows the currently accepted stratigraphy of northwestern Puerto Rico in relation to depositional environment. The contact between the Lares and Cibao formations is conformable.

Patch reefs are exposed in the Lares and the Los Puertos (Aymamon) (Monroe, 1980; Frost, et al., 1983; personal observation), and may have been found in cores in the Cibao formation (J. Joyce, personal communication, 1989). My own searches of the Montebello and Cibao yielded only <u>Crassostrea</u> biostromes, <u>Stombus</u> molds, tubes of the enigmatic bivalve <u>Kuphus</u>, which probably burrowed into nearshore firmgrounds (Frost, et al., 1983; Jones and Pemberton, 1988) and rare solitary corals. These are all interpreted as shallow lagoonal or back-reef (near-shore) deposits (Moussa and Sieglie, 1984), likely dominated by seagrass beds. The uplifted carbonate platform of northwestern Puerto Rico has been extensively karstified, both creating and destroying numerous outcrops (Monroe, 1976). Fossils are often extensively leached and preserved as molds, particularly in the middle and upper Miocene rocks.

1.7.3 South Coast Carbonates

Extensive tectonic activity on the South coast of Puerto Rico has lead to the development of carbonate sequences which are far less complete than those of the North coast. The clastic facies of the Late Oligocene Juana Diaz Fm. gives way to a latest Oligocene barrier reef tract which was repeatedly uplifted and submerged during its lifetime (Frost, et al., 1983). The carbonate facies of the Juana Diaz is already mapped separately from the clastic facies (map 3.2, map 3.3), and always occurs above the clastics. Accordingly, it is here proposed as a separate formation, the Guayanilla Formation, and the Guayanilla I and II Sections of Frost et al. (1983) are proposed as the type section (see Appendix 3). All maps and charts in this thesis use the name Guayanilla Fm.

The Guayanilla Fm. (Juana Diaz carbonate facies) is unconformably overlain by Lower Miocene carbonate turbidites of an unnamed formation referred to as the "Angola Equivalent" (figure 4.1; Monroe, 1980; Frost, et al., 1983). Another unconformity, again of unknown duration, separates these deep water deposits from the Middle Miocene Ponce Fm., which was deposited on a narrow carbonate shelf or embayment. Patch reefs are locally developed in the Ponce Fm. The exact age of the Ponce Fm. is unknown, but it is tentatively recognized as the lateral equivalent of the Los Puertos (Aymamon) Fm. (Monroe, 1980). The south coast of Puerto Rico is the dry side of the island, and fossil preservation is generally better on the south than on the north coast.

1.8 Absolute age and timing of extinctions.

The large unconformity between the Guayanilla Fm. and the Ponce Fm. precludes any studies on early Miocene reefs in southern Puerto Rico, and the Montebello, Cibao, and lower Los Puertos (Aguada) contain no reefal facies exposed in outcrop. Although precise ages of the sites are unknown, rough estimates place 10 Ma between the Oligocene and Miocene sites. This is much more than desired for a comparative study of a mass extinction. The actual extinction probably took place 1-2 million years after deposition of the Oligocene reefs studied here. The long time gap between the Oligocene and Miocene reefs studied here is a significant, but not crippling problem. Any greater proximity in time (e.g. patch reefs in the Lower Miocene Newport Fm. of Jamaica; Frost, 1977a; pers. comm., 1989) would have compromised proximity in geography or depositional environment.

Chapter 2: Ecology, Biogeography, and Mass Extinctions

2.1 Introduction

Mass extinctions have been among the most controversial topics in paleobiology during the last 10 years. The literature has been dominated by attempts to delineate ultimate causes of the largest mass extinctions, often through large scale statistical analyses (e.g. Raup and Sepkoski, 1982, 1984; Sepkoski and Raup, 1986, Raup and Boyajian, 1988; and others). Are the causes catastrophic (e.g. McLaren and Goodfellow, 1990) or simply extreme cases of the normal factors which always limit population sizes and species durations (e.g. Teichert, 1987)? What is the time scale over which these mass extinctions occur? How do patterns of extinction vary among major habitat types?

The extinction under study here is somewhat enigmatic, a regional extinction which primarily affected two taxonomic groups: scleractinian corals and large benthic foraminifera (Frost and Langenheim, 1974; Frost, 1977a). Furthermore, among the corals, the majority of genera which became extinct in the Carobbean survive until today in the Indo-Pacific. The extinction among the large foraminifera followed a similar biogeographic pattern. There is no sedimentological or geochemical evidence to support any of the proposed mechanisms for the largest mass extinctions of the Phanerozoic: regression, global cooling, constriction/elimination of biogeographic provinces, or a bolide impact. As always, one of the critical kinds of evidence is the nature of the survivorship patterns across the extinction boundary. These patterns of selective survival provide a robust test of any hypothesis regarding the causes of the extinction.

2.2 Scales of Extinction

Flessa, et al. (1986) suggested two levels of extinction processes: background extinctions and mass extinctions, defining mass extinctions as only those events which (1) were global in extent, (2) profoundly affected a variety of taxa, and (3) occurred rapidly in geological time. On this basis, five truly mass extinctions were identified: end-Ordovician, Late Devonian, Late Permian, Late Triassic, and end-Cretaceous. Donovan (1989), however, suggested that such a definition was too strict, and he separated regional or taxon-specific extinction events from background extinctions on the basis that they likely reflected different processes operating on different spatial and temporal scales (see table 2.1). This study treats a regional extinction which is largely, but not exclusively, taxon-specific.

Table 2.1. Essential features of background, regional, taxon, and mass extinctions. After Donovan, 1989.

	Background	Mass	Regional	Taxon
Occurrence	Continuous	Episodic	Episodic	Episodic
Rate	Gradual	Fast	Fast	Fast
Effect	Local	Global	Broad Area	Global
Species Affected	Few	Numerous	Many	Single Taxon

2.3

Proposed Causes of Mass Extinctions

A variety of mechanisms have been proposed for various mass extinctions: the most "traditional" is regression, which can reduce, or in extreme cases, eliminate, continental shelf areas and may also cause constriction or elimination of biogeographic provinces (Valentine, et al., 1978). For example, global sea level dropped over 250m to its lowest stand of the Phanerozoic during the latest Permian (Schopf, 1974; Erwin, 1990). In particular, major regressions greatly restrict or eliminate epeiric sea habitats, which were of great importance during the Paleozoic and Mesozoic (Hallam, 1981b). Each of the major mass extinctions has been associated with some sort of regression, but the inverse is not true (Stanley, 1987). Some drastic regressions have occurred without the simultaneous occurrance of widespread extinctions, such as the >300m mid-Oligocene sea level drop which preceeded deposition of the sediments observed in this study (Haq, et al., 1986; Frost, et al., 1983). Jablonski (1980) discussed the ecological and evolutionary consequences of regressions, and showed that in today's oceans, a regression alone could not account for the severity or biogeographic pattern, in particular the tropical bias, of major extinction events (Jablonski, 1985).

Today's climate and biogeographic structure, however, are radically different from that of the Permian, or much of the Paleozoic (Cowen, 1990), and the effects of a regression on a shallow marine biota depend heavily on initial conditions (Jablonski, 1985). A 100m regression today, during a period of high continental emergence, would eliminate only a small percentage of shallow marine habitats (e.g. Wise and Schopf, 1981). An equivalent regression during the Late Cretaceous or Mid- to Late Paleozoic, however, when sea levels were high and there were extensive epieric seas, would eliminate large areas of unique habitats, and possible whole biogeographic provinces (Jablonski, 1985).

Continuous deposition of carbonate sediments, though not reefs, in Puerto Rico across the Oligocene-Miocene bondary rule out regression alone as the cause of this extinction (see section 1.7).

2.3.1 Refrigeration

Stanley has been the most vocal proponent of global cooling as a cause of mass extinctions among marine invertebrates (e.g. Stanley, 1984a, 1984b, 1987, 1988). The tropical bias of all five major extinctions suggests that cooling, through contraction of tropical biogeographic regions, may have been linked to all major mass extinctions (Stanley, 1984a). Most global cooling is associated with glaciation, which also tends to reduce eustatic sea levels by locking up water in the polar ice caps, so the effects of cooling and regression are often somewhat confounded, if not self-reinforcing (Stanley, 1987). Major glacial episodes during the last billion years occurred in the Late PreCambrian, Late Ordovician, Carboniferous (and some of the Permian), and Late Pliocene to Recent (Kennett, 1982; Stanley, 1986a). More recently, climate models have suggested that onset of glaciation and attendant climatic cooling may be quite rapid (Crowley and North, 1988), and the same may be true for oceanographic changes (Maier-Reimer, et al., 1990).

There are suggestions, however, of oceanographic cooling without glaciation, e.g. in the Late Devonian extinction (Copper, 1986). Isotopic records of global ocean temperature changes from Atlantic and Pacific planktonic forams do not show any dramatic cooling at the Oligocene-Miocene boundary. On the contrary, global ocean temperatures rose during the early and middle Miocene (Savin, et al., 1975; Haq, 1981; Kennett, et al., 1985). Regional cooling, however, may have been involved in this extinction (see chapter 6).

2.3.2 Ocean Chemistry

Changes in ocean chemistry have been invoked to explain the Late Permian and some of the mid-Mesozoic extinction events. Extensive Permian salt deposits, common around the world, have led some workers to propose hyposaline oceans as a cause of the end-Permian extinctions (Stevens, 1977). Several workers (e.g. Fischer and Arthur, 1977; Wilde and Berry, 1984; Malkowski, et al., 1989) have suggested dramatic changes in both oxygen availability and nutrient dynamics as causes of various Paleozoic extinctions. The widespread presence of black shales at certain times during the Mesozoic prompted several workers (Hallam, 1981b; Wilde and Berry, 1984; Elder, 1989) to suggest that global anoxic events might have caused mid-Mesozoic extinctions. Pederson and Calvert (1990), however, have suggested that black shales record high carbon production and incorporation into the sediment, rather than anoxia. In general, changes in ocean chemistry seem to enjoy little favour as general mechanisms to explain mass extinctions (Cowen, 1990).

Vermeij (1986, 1987, 1989b) has suggested that nutrient depletion may have been important in several of the regional molluscan extinctions of the Cenozoic, as previously implied by Fischer and Arthur (1977) for post-Paleozoic pelagic ecosystems. Coral reefs thrive best in oligotrophic waters (Muscatine and Porter, 1977; Birkeland, 1987), however, and Hallock and Schlager (1986) have argued that eutrophication may be responsible for the collapse of some modern and ancient reef systems. Although a relationship between eutrophication and collapse of global reef ecosystems during mass extinctions has not been documented, such a relationship may relate to the relatively high susceptibility of reefs to mass extinctions (see section 2.6). Nutrients may have played a role in this regional extinction (see chapter 6).

2.3.3 Periodicity and Extraterrestrial Forcing

Since Alvarez, et al. (1980) proposed the impact hypothesis for the Cretaceous-Tertiary extinctions, the variety of proposed extraterrestrial causes of mass extinctions has grown astronomically. Raup and Sepkoski (1982, 1984) have identified a possible 26 Ma periodicity to post-Paleozoic mass extinctions, but others have criticized their statistics (Stigler and Wagner, 1988; Patterson and Smith, 1989). Nonetheless, we now have various astronomical proposals for Nemesis, a proposed dark companion star of our sun or an undiscovered tenth planet loosing a storm of comets or asteroids on the earth every 26 Ma (Rampino and Stothers, 1984; Alvarez and Muller, 1984). See Gould (1984) for a particularly poetic version of these theories, and see Quinn and Signor (1989) for an almost equally poetic rejection of them. A few have voiced words of caution, reminders that we cannot reconfigure the solar system based on a questionable statistical periodicity (e.g. Quinn and Signor, 1989, Cowen, 1990). KcKinney (1989) has shown that this apparent periodicity could be a product of the rate and manner in which biotic diversity grows. Stanley (1990) has developed a similar idea, suggesting that delayed recovery of biotic diversity automatically imposed a minimum spacing on mass extinctions. Lastly, Baksi (1990) has suggested that all analyses of periodicity in extinction are flawed by imprecise and/or inaccurate radiometric data.

There are no proposed impact sites associated with the extinction in this study (McLaren and Goodfellow, 1990), nor does this extinction fit into any proposed periodicity of extinctions.

Fischer and Arthur (1977) proposed an approximate 32 Ma periodicity to short oligotaxic periods separating longer polytaxic periods. They related these periods primarily to patterns of oceanic circulation and nutrient dynamics. Mass extinctions occurred at their oligotaxic times, which were characterized by enhanced upwelling and oceanic circulation and lack of extensive black shales. Pelagic superpredators - large (>6m) vertebrate carnivores - occurred only during polytaxic episodes, characterized by more sluggish circulation, extensive burial of surplus pelagic organic carbon, and an expanded oxygen minimum zone. Fischer and Arthur related their apparent periodicity to internal dynamics of the earth, rather than extraterrestrial forcing, but did not name an explicit mechanism. Rampino and Stothers (1988) and Courtillot (1990) proposed a general correlation of episodes of massive volcanism, specifically, explosive extrusion of massive flood basalts, with mass extinctions, most notably the Deccan Traps of western India, which coincided with the Cretaceous-Tertiary extinction.

The extinction in this study occurred during one of Fischer and Arthur's polytaxic periods, and no major flood basalts were erupted in the Caribbean near the Oligocene-Miocene boundary (Khudoley and Meyerhoff, 1971).

2.3.4 Biotic Innovations

Evolution and/or invasions of novel organisms have played an important role in the modern anthropogenic extinctions (Simberloff, 1986), but their role in the other major extinction events of the Phanerozoic is generally discounted (Stanley, 1987). Tappan (1982) suggested that all major extinctions of marine invertebrates coincided with expansions of terrestrial vegetation, which would have stabilized slopes and reduced runoff and erosion, thereby causing reductions in the amount of terrestrial organic matter and nutrients reaching the seas.

There were a few originations or immigrations of reef organisms in the Caribbean in the early Miocene, such as the corals *Agaricia* and *Coscinaraea* (Frost, 1977a), miosoritid large foraminifera (Frost and Langenheim, 1974), and the gastropod *Strombus*, but there has been no suggestion that these organisms could have caused the extinction.

2.4 Biogeography and Provinciality

The number of biogeographic provinces in the world is a primary controlling factor on global biotic diversity (Valentine and Moores, 1972; Valentine, et al., 1978; Schopf, 1979; Jablonski, et al., 1985). In particular, the end-Permian mass extinction has been attributed to the drastic reduction and/or elimination of biogeographic provinces, as has the near-exponential increase in global biotic diversity since the Jurassic (Valentine et al., 1978). Such changes in provinciality, however, primarily act on a global scale, with much reduced effects on individual regions.

While studies of historical biogeography of individual taxa abound (e.g Stehli and Wells, 1971, for reef corals), studies of the historical biogeography of communities (e.g. corals in relation to coral associates, or reefs in general) are far less common. This study will attempt to synthesize some of this information with respect to Cenozoic reef communities.

Biogeographic range of individual taxa has an important influence on species longevity and survivorship in extinctions (e.g. Hansen, 1980; Jablonski, 1986a,b; Erwin, 1989). More widely dispersed taxa are less susceptible to local habitat changes which might drive small populations to extinction. Dispersal range is generally correlated with mode of larval development, and is probably the means by which larval ecology exerts its primary influence on survivorship (see Life History Characteristics, section 6.7).

Throughout the Phanerozoic, regional mass extinctions have decimated individual groups or whole faunas within one or a few a biogeographic provinces (e.g. Raffi, et al., 1985; Stanley, 1986a). Regional extinctions have been particularly important in shaping the composition of Cenozoic reef faunas (e.g. Vermeij, 1987; see Plio-Pleistocene extinctions, below).

2.5 Patterns of Selectivity

Extinctions are selective because various environmental variables interact with the biological characteristics of organisms to influence survival. Differential tolerance to turbidity, substrate type, water temperature, nutrient levels, and other factors which influence distribution and abundance of organisms also influence their survivorship in mass extinctions. For reef organisms in particular, turbidity and temperature are often major controlling factors on survivorship (Fagerstrom, 1987, and many others).

Many of these patterns involve biogeography as well as ecology, for example, the tropical bias observed in all major mass extinctions. The patterns of survivorship can often indicate which environmental changes were most important in causing a given extinction.

2.5.1 Life History Characteristics

In recent years, paleoecologists have begun to look at larval biology as one of the ecological factors which could be important in influencing survivorship during mass extinctions. Dispersal range is generally correlated with mode of larval dispersal, and widely distributed taxa generally survive extinctions in greater proportions than do endemics. Species with planktotrophic larvae ("broadcasters") generally have greater dispersal capabilities thant do species with lecithotrophic larvae ("brooders"), because their larvae spend a longer time in the water column (see Jablonski and Lutz, 1983 for a more complete review of larval development and paleoecology).

Larval biology has been correlated with survivorhsip in Ordovician trilobites (Chatterton and Speyer, 1989), Permian brachiopods, crinoids, and gastropods (Valentine and Jablonski, 1986; but see also Erwin, 1989), Late Cretaceous gastropods (Jablonski, 1986a), Late Cretaceous diatoms (Kitchell, et al., 1986), Eocene gastropods (Hansen, 1980, 1982), and Plio-Pleistocene gastropods (Shuto, 1974). Several of these cases remain somewhat controversial. The best documented cases involve the Cretaceous and Tertiary molluscs, which have skeletonized larvae. Larval life history is recorded in gastropod larval shell morphology, and the larval shell remains attached to the adult throughout life.

Most reef organisms are less amenable to study of life history patterns in fossil material, than the Gulf Coast molluscs which Hansen (1980, 1982) and Jablonski (1986a) studied. The high porosity of reefal carbonates often leads to preservation as molds, eliminating fine scale details such as larval shell morphology (James, 1983). Furthermore, corals, sponges, crinoids, brachiopods, and other organisms which have built fossil or modern reefs do not have skeletonized larvae (Jablonski and Lutz, 1983). For these organisms, we are largely limited to comparisons with the reproductive characteristics of modern representatives.

Reproductive and larval ecology of modern corals remains an active and controversial field (for reviews, see Fadlallah, 1983; Szmant, 1986; Richmond and Hunter, 1990). Dispersal ranges of modern corals are also correlated with larval biology, but the pattern is opposite that observed in molluscs (see chapter 7). Reef corals which are brooders supply their larvae with zooxanthellae, but broadcasting corals mostly do not (Babcock and Heyward, 1984). Zooxanthellae contribute greatly to the energy budgets of brooded coral larvae, which can survive a longer time in the water column than broadcast larvae (Richmond, 1985). Potential larval lifespan, hence potential dispersal distance, is greater in brooded larvae than in broadcast larvae (Richmond, 1990; see section 7.2).

The reproductive ecology and life history characteristics of internal coral associates, an ecologically, rather than phyletically defined group, remains largely a mystery. The role of life history characteristics in this extinction is discussed in detail in chapter 7.

2.5.2 Trophic Status

Trophic status would seem to be an important factor influencing survivorship in mass extinctions, but little convincing evidence has been presented on this question. The Cretaceous-Tertiary extinctions have received some study in this regard. Catastrophist workers in particular have attributed the K/T extinction to collapse of the planktonic food web, with cessastion or great restriction of primarly productivity causing mass starvation, the mass extinction at higher trophic levels. Freshwater ecosystems were not similarly affected, however. All of these hypotheses operate on temporal scales which may be beyond the resolution of the fossil record (Schindel, 1980), and thus may be impossible to document or refute.

In the Oligocene-Miocene extinction, zooxanthellate organisms were the primary victims, and with little turnover among grazers or predators. The possible role of trophic status in Phanerozoic extinctions and in this extinction is discussed in section 7.6

2.6 Reefs and Mass Extinctions

Reefs have existed in one form or another since PreCambrian times, and a number of metazoan groups have built reefs at different times during the Phanerozoic. The history of reefs has been rather volatile. Most of the major and minor mass extinctions which affected marine invertebrates in level-bottom habitats also affected reef organisms (figure 2.1; Raup and Boyajian, 1988). In addition, reefs underwent major transformations in the composition of the primary reef-building organisms, punctuated by mass extinctions (Newell, 1972; Fagerstrom, 1987). Reefs seem to be more susceptible to perturbation and extinction than level bottom communities. This pattern suggests that mass extinctions in reefs are subject to the same factors which control mass extinctions in general, but are either affected more severely or are subject to additional factors. The role of nutrients in reef extinctions may be particularly important (see chapter 6).

Fagerstrom separated mass extinctions into two types with respect to their effects on reefs (table 2.2). First order mass extinctions, characterized by an "annihilation/ collapse/ rebuild scenario" eliminated many higher taxa of reef-builders, and were followed by periods without reef building activity. Subsequent reefs, which generally did not develop for at least 5 Ma, were of dramatically different taxonomic and ecologic structure. Second order mass extinctions, characterized by a "high impact/ crisis/ revival scenario" mostly eliminated lower taxa, and did not cause major shifts in taxonomic or ecologic structure of reefs. Revival times following second order mass extinctions are generally less than 5 Ma.

Figure 2.1. Mass Extinctions in Reefs and Level Bottom Communities through the Phanerozoic. Compiled from Newell (1972), Boucot (1983), Sheehan (1985), and Fagerstrom (1987).

Mass Extinctions in Reefs and Level Bottom Communities through the Phanerozoic

After Boucot, 1983; Sheehan, 1985; Fagerstrom, 1987.

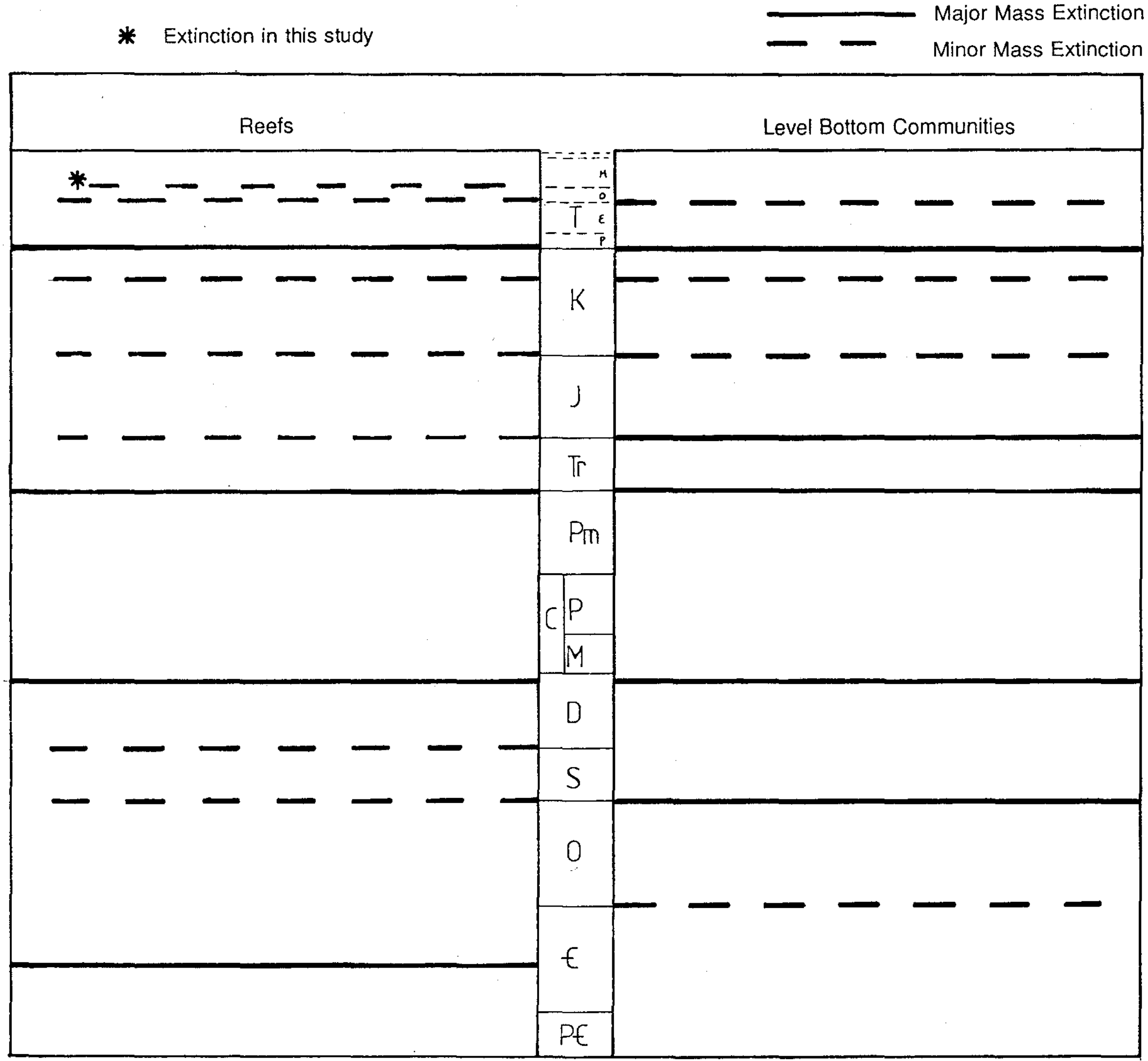


Table 2.2. First- and Second-order Mass Extinctions in Phanerozoic Reefs. Modified from Fagerstrom, 1987.

Scale	Time of Extinction	Higher Taxa Affected	Rebuilding Time
1	Maastrichtian	Rudists, Scleractinian corals, Stromatoporoids	ca. 5 Ma.
1	Tatarian	Calcareous Algae, Various sponges, Bryozoans	ca. 5 Ma.
1	Frasnian-Famennian	Stromatoporoids, Tabulate and Rugose Corals	ca. 8 Ma.
1	Botomian	Archaeocyathids	ca. 10 Ma.
2	Late Eocene	Scleractinian corals, Large forams	2-3 Ma.
2	Late Cenomanian	Rudists	2 Ma.
2	Tithonian	Scleractinian corals, Algae, Silicious sponges	3-5 Ma.
2	Carnian-Norian	Scleractinian corals, Calcareous sponges	ca. 10 Ma.
2	Late Silurian	Stromatoporoids, Colonial Tabulate and Rugose corals	3-5 Ma.
2	Ashgillian	Bryozoans, Crinoids, Solenoporacean algae	5-8 Ma.

Both Newell (1972) and Fagerstrom (1987) identify four first order mass extinctions with respect to reefs: Botomian (MC), Frasnian-Famennian (LD), Tatarian (LPm), and Maastrichtian (LK). Fagerstrom includes the Ashgillian (LO) and Carnian-Norian (LTr) among the second order mass extinctions, although both of these extinctions involved major extinction of higher taxa, collapse, and restructuring of reef communities and were followed by intervals devoid of reef deposition (Brenchley, 1989; Stanley, 1988). Likewise, Fagerstrom lists the recovery time following the Maastrichtian extinction as "virtually none", but there were no-major reef deposits during the Paleocene, rather only poorly developed patch reefs (Newell, 1972; James, 1983; Babic and Zupanic, 1981).

Fagerstrom delineated nine reef Ecologic-Evolutionary units, time periods when reefs were characterized by a particular taxonomic composition and ecological structure (table 2.3). These do not agree with the 12 Phanerozoic Ecologic-Evolutionary units which Boucot (1983) delineated in level-bottom commmunities, and which Sheehan (1985) had applied to reefs. Both schemes, however, have the ecologic-evolutionary units punctuated by mass extinctions, major and minor, such that mass extinctions may have been a driving force in Phanerozoic reef evolution.

By focusing on Cenzoic extinctions which primarily affected reefs, we can illuminate some of the differences in the extinction patterns of reefs and level bottom communities. To that end, I review some of the literature on selectivity in Cenozoic minor mass extinctions, especially regional extinctions.

Table 2.3 Reef Ecologic-Evolutionary Units (based on Fagerstrom, 1987).

Unit	Time Interval	Major Reef Building Taxa
9b	Oligocene-Holocene	Scleractinia; Milleporina; Corallinacea; Codiacea
9a	Paleocene-Eocene	Scleractinia (diff. families)
8	Albian-Maast.	Hippuritacea
7	Norian-Aptian	Scleractinia; Porifera
6	M. Tr. - Carnian	Sphinctozoa; Inozoa;Dasycladacea
5	Famennian- L. Pm.	Sphinctozoa; Inozoa; Chaetitida; Demospongia; Bryozoa; Articulata
4	M. Ord. -Frasnian	Stromatoporoida; Tabulata; Rugosa; Bryozoa; stromatolites
3	M. Ꞓ. - E. Ord.	Demospongia; stromatolites
2	E. Ꞓ.	Archaeocyathida; stromatolites
1	PreCambrian	stromatolites

2.7 Cenozoic Extinctions

The Cenozoic has not seen a mass extinction of the scale of the K/T or Pm/Tr boundary extinctions. The mass extinctions of the Cenozoic are mostly minor in scale and regional in geographic extent, and stand out against a pattern of fluctuating climates, oceanographic changes, and dramatic biotic overturn as the earth spun toward its present glacial mode. Sepkoski and Raup (1986) identified two Cenozoic extinctions which fell into their suggested 26 Ma periodicity: one at the Eocene-Oligocene boundary, and one during the middle Miocene. The mid-Miocene event, however, scarcely stands out above background levels, and was certainly less important for marine macro-invertebrates than the assortment of regional extinctions around the Plio-Pleistocene boundary (see below). These were all clearly related to the onset of Northern Hemisphere glaciation (see Crowley and North, 1988, and references below) and to the closing of the Central American Seaway (rise of the Isthmus of Panama) (see Stehli and Webb, 1985). Reefs were affected by three Cenozoic minor mass extinctions: Eocene-Oligocene, Oligocene-Miocene (this study) and Plio-Pleistocene (Frost, 1977a; Fagerstrom, 1987).

2.8 Late Eocene Extinctions

Paleoceanographically, the late Eocene extinctions are among the best documented of all the major and minor extinctions cited by Sepkoski (1986). Surprisingly, there still remains considerable debate regarding the causal factors responsible for the various extinctions recorded around the Eocene-Oligocene boundary. Proposed mechanisms include regression (Adams, et al., 1986; Dockery, 1986), climatic cooling (Hansen, 1987; Stanley, 1987), drought (Morner, 1984); dramatic oceanographic changes (Kennett, 1982), and extraterrestrial impact (see Sepkoski and Raup, 1966 for summary). This event did not cause major disruption of reef ecosystems (Newell, 1972; Fagerstrom, 1987), although reef faunas were affected and there was some reorganization (see below). I will discuss several groups, concentrating on marine invertebrates

Figure 2.2. Extinctions and Environmental Changes in Deep Sea, Shallow Marine, and Terrestrial Habitats around the Eocene-Oligocene boundary. Compiled from various sources.

			Deep Sea	Shallow Marine	Terrestrial	North Am. Land Mammal Stages	
							Oceanographic / Ecologic Events
OLIGOCENE		Rupelian	•Extinction of many cool water planktonic forams and calcareous nanoplankton. d18-O increase (cooling)	Major unconformiity.		Whitneyan Orellian	•Initiation of major mid-Oligocene regression. •Antarctic sea ice, initiation of Antarctic glaciation.
EOCENE	U	Priabonian	•Increasing domination of cold water planktonic forams, minor extinction; major extinctions of benthic forams, ostracods. d18-O increase (cooling), microtektites.	•Major extinction of Gulf Coast molluscs. •Regression, unconformity. •Extinction of Gulf Coast molluscs. < Decline of Indo-Pacific warm-water taxa in New Zealand; North Sea cooling.	•Major extinction of North American mammals. < Decline of tropical forests, expansion of woodland and savanna habitats. < La Grande Coupure - major extinction of European mammals & reptiles.	Chadronian	•Initiation of deep circulation through Tasman Sea, major oceanic cooling event; initial development of psychrosphere. < Increased seasonality, cooling in terrestrial habitats, especially at high latitudes.
	M	Bartonian	•Major extinction of planktonic and benthic forams, and of calcareous nanoplankton. d18-O increase (cooling), hiatuses.	•Extinction of Gulf Coast molluscs. •Decline of Antarctic molluscs. < Decline of Gulf Coast echinoids.	•High extinction and origination of North American mammals. •High extinction and origination of North American mammals. •Major extinction of North American mammals.	Duchesnian Uintan	Major episodes of deep sea, > island arc, and flood basalt volcanism. •Peak Cenozoic warming.
		Lutetian	•Minor foram extinction. Begining of cooling, hiatuses.			Bridgerian	•Change in direction of Pacific plate motion, as seen in Emperor-Hawaiian seamount chain.

associated with reefs, and will conclude with a brief discussion of paleoceanographic changes around the Eocene-Oligocene boundary. Prothero (1989) emphasizes that the late Eocene extinctions were spread over the latter third of the Eocene, and cannot be attributed to a single extraterrestrial event. Figure 2.2 summarizes the scope and timing of late Eocene deep sea, shallow marine, and terrestrial extinctions and their relationship to oceanographic and tectonic changes.

2.8.1 Marine Extinctions

Both planktonic (Keller, 1986) and benthic foraminifera (Keigwin, 1980; Adams, et al., 1986) suffered major extinctions during the Late Eocene and Early Oligocene. Planktonic and deep-sea benthic forams showed a stepped pattern of extinction, with reduction in diversity occurring in pulses over the last 3 Ma of the Eocene (Keller, 1983, 1986). Deep sea benthic forams underwent considerable turnover during Late Eocene and earliest Oligocene times (Boersma, 1986), again apparently following a stepped extinction pattern (Keller, 1986).

While Adams, et al. (1986) indicate simultaneous extinction of a variety of large benthic forams of tropical carbonate environments, they also discuss the rarity of conformable sections in shallow carbonate environments across the Eocene-Oligocene boundary, due to a regression of 40-50m (Haq, et al., 1986). Frost and Langenheim (1974) did not note a catastrophic extinction of larger forams in Chiapas, Mexico, but rather, more gradual turnover; here again, however, an unconformity of unknown duration in the lowest Oligocene complicates matters. A stepped or gradual pattern of extinction is most likely for larger forams. Large forams had been important constructors of Eocene reefs and carbonate platforms, but lost much of their importance to corals in the Oligocene (Frost, 1972; see below).

Corals underwent significant taxonomic replacement during the Late Eocene, although actual reduction of diversity was limited (Newell, 1984). Four families, the Stylinidae, Calamophylliidae, Cyclolitidae, and Montlivaltiidae, which had their greatest diversity in the Cretaceous, but survived the K/T boundary extinction, finally died out in the late Eocene (Wells, 1956). Significant diversification in the Poritidae and Faviidae made up for these generic losses, such that overall generic diversity changed little. Among the most significant Eocene originations was the genus Porites, which quickly became a ubiquitous and important framework builder, a position it has maintained to this day, particularly in the Caribbean (Frost and Langenheim, 1974). Corals increased their importance as framework builders in the Oligocene (Frost and Langenheim, 1974; Frost, pers. comm., 1990), but there was no major change in the organization of reef communities between the Eocene and Oligocene (Fagerstrom, 1987).

Molluscs, particularly gastropods, underwent a stepped series of minor extinctions in the Gulf Coast clastic sequences during the Late Eocene, which apparently correlate directly with the stepped extinctions of planktonic and deep-sea benthic forams (Hansen, 1987). At the Bartonian-Priabonian boundary, 89% of Gulf Coast gastropod and 84% of bivalve species became extinct. A second pulse of extinction, in the late Priabonian, eliminated 72% of the remaining (and new) gastropod, and 63% of the bivalve species. The third wave of extinctions, at the Priabonian-Rupellian boundary, drove 97% of gastropod and 89% of bivalve species to extinction.

Dockery (1986), using a computer database of first and last appearances in the Gulf Coast sequence, has proposed that gastropod extinctions occurred during regressive intervals, when prograding deltas not only reduced, but eliminated clear-water shelf habitats. Hansen (1987), however, sees a closer correlation between periods of climatic cooling and extinction than between regressions and cooling, and noted that patterns of selective extinction were biased against warm-water taxa. Although gastropods with non-planktotrophic larval development had higher rates of species turnover than planktotrophic members of the same families during the middle and late Eocene, they also had higher rates of origination, and did not suffer greater overall loss of diversity (Hansen, 1980, 1982). Hansen (1987) thus discounts the role of larval ecology in the Eocene-Oligocene molluscan extinctions.

Zinsmeister (1982) documented a similar pulse of molluscan extinction (69% of genera) in New Zealand and Seymour Is. (Antarctic peninsula), in which immigrant taxa from the warmer Indo-Pacific suffered far more heavily than did the endemic Weddellian (paleoaustral) fauna, but he did not discuss the precise (substage) timing of these extinctions. Zinsmeister attributed the molluscan extinctions in the South Pacific to the dramatic cooling in the Southern oceans at that time. DSDP cores from the Tasman sea show a decline of surface temperature to 7°C, and decline of bottom water temperature to 5°C. The paleoceanographic causes of this cooling are discussed below.

Irregular echinoids reached their greatest diversity during the Eocene, and sharply declined into the Oligocene, both worldwide and in the Gulf Coast clastic sequences (McKinney and Oyen, 1989). I do not know of any detailed stratigraphic studies which illuminate the temporal and spatial patterns of this decline, particularly in reefal habitats. Because the changes in Gulf Coast echinoid diversity correlate with paleobotanical evidence for climatic cooling in the Late Eocene (Wolfe, 1978), McKinney and Oyen attribute the Gulf Coast echinoid extinctions primarily to cooling, rather than effects of widespread and repeated regressions (see Hansen, 1987, discussed above, for a more detailed examination). McKinney and Oyen's data were based solely on literature compilations, and they did not collect independent environmental data.

2.8.2 Terrestrial Extinctions

Terrestrial biotas also experienced major changes around the Eocene-Oligocene boundary. European reptiles and amphibians underwent a dramatic Late Eocene diversification, followed by decimation at the Eocene-Oligocene boundary (Rage, 1986). Widespread Arctic and Antarctic forests of the Eocene deteriorated and disappeared by Oligocene times, and temperate vegetation underwent broad changes (Wolfe, 1978).

By far, mammals have the most complete record of terrestrial biotas, and show the most dramatic extinction patterns (Prothero, 1985, 1989). Prothero and Swisher (1989) cite new Ar-Ar dates (both terrestrial and marine) implying new correlations of North American land mammal ages with marine stages (fig. 2.2). These dates place the Eocene-Oligocene boundary at approx. 33 Ma., as opposed to the more traditional date of 38 Ma. (Harland, et al., 1982). According to these new dates, the major extinctions of land mammals in Europe and North America correlate directly with major pulses of extinction in deep sea and shallow marine habitats (fig. 2.2). Major peaks of mammal extinction in North American occurred in the late Uintan, early and late Duchesnian, and at the Chadronian-Orellian boundary. Prothero (1985), using early terrestrial-marine correlations, had called these last the mid-Oligocene extinction event. Peaks of originations immediately followed the early and late Duchesnian extinctions. The Uintan and Duchesnian extinctions in particular coincide with the Grande Coupure, a major extinction and overturn in the nature of European mammal and reptile faunas (Russel and Tobien, 1986).

The Chadronian-Orellian extinction eliminated the multituberculates, titanotheres and other primarily Paleocene and early Eocene groups, and a wide variety of rodent, primate, and ungulate families (Russell and Tobien, 1986; Prothero, 1985, 1989). The general pattern is one of a decline of forest-dwelling (primarily browsing) faunas, which were replaced by woodland- and savanna-dwelling faunas (with more abrasion-resistant teeth. Janis (1989) however, examining the perissodactyls and artiodactyls, argued that the patterns of faunal replacement cannot be reduced to a simple replacement of browsers by grazers, but was also related to preferential survival of ruminants. Regardless, the major extinction and ecological overturn in mammals in late Eocene - early Oligocene times is apparently related to increasing seasonality and major changes in the distribution and importance of terrestrial vegetation zones (Wolfe, 1975, 1978; Hubbard and Boulter, 1983; Niklas, 1986; Savage, 1988; Janis, 1989).

The mammalian extinctions in North America and Europe also had a strong biogeographic component (McKenna, 1975, 1983; Prothero 1985, 1989). In both Europe and North American, many of the new taxa following these extinctions were immigrant taxa, rather than true originations. The Eastern European Obik sea, which had separated Europe from Asia during the Late Cretaceous, Paleocene, and Eocene, drained during Late Eocene time (McKenna, 1975). Futhermore, Scandinavia, whose fauna had been more similar to that of North America than to that of the rest of Europe, mixed its fauna with sub-Baltic Europe (McKenna, 1975, 1983. Alaska and Siberia remained connected by the Bering Sea land bridge. The result was holarctic faunal interchange, accompanied by contraction of warm and wet vegetation zones to the tropics, as high latitude floras became more like those of modern cold temperate vegetation zones (Wolfe, 1975; Hubbard and Boulter, 1983). In this respect, the Eocene-Oligocene mammalian extinctions resemble events the Plio-Pleistocene Great American Interchange (see Marshall, 1981; Stehli and Webb, 1985), which will be discussed below.

2.8.3 Paleoceanography

In addition to a ca. 50m eustatic regression (Haq, et al., 1986), the Late Eocene witnessed a variety of climatic and oceanographic changes. Terrestrial climates became cooler (Wolfe and Poore, 1982), drier (Morner, 1986), and had greater seasonal fluctuations (Wolfe, 1978). Oceanic bottom waters became colder and more aerated, and there was greater deep water current motion, as indicated by hiatuses (Keller, 1983; Boersma, 1986; Miller, et al., 1987). These have all been related to the development of the psychrosphere during Late Eocene- Early Oligocene times (Crowley and North, 1988).

Oxygen isotopes from benthic forams record the episodic nature of this cooling, which is also associated with episodic extinctions of deep-sea benthic forams (Keller, 1983; Boersma, 1986). Cooling apparently affected the whole water column in cold temperate habitats, which decreased in temperature about 5-6°C, but primarily affected bottom waters in tropical habitats (Keigwin, 1980; Keigwin and Corliss, 1986).

During the Eocene, Australia separated from Antarctica enough to allow significant deepening of the Tasman Sea (Kennett and Shackleton, 1976). Deep circulation through the Tasman Sea led to significant cooling of Southern high latitude and polar waters

(Kennett and Shackleton, 1976). There is evidence of sea ice formation by Late Eocene and early Oligocene times (Zinsmeister, 1982), but Antarctica was not inundated by continental glaciers until the early or middle Miocene (Kennett, 1982). Likewise, complete deep water circum-Antarctic circulation, which is today responsible for the Antarctic convergence and extensive production of cold Antarctic bottom water, probably did not begin until latest Oligocene or early Miocene times (ca. 25 Ma.), when shallow-water connections between South America and Antarctica deepened considerably (Kennett, 1982; Zinsmeister, 1982). Kennett and Shackleton (1976), Kennett (1982), Keigwin and Corliss (1985), and other references above discuss the paleoceanographic data in greater detail.

2.8.4 Volcanism and Tectonics

Kennett, et al. (1985b) found evidence for increased deep sea volcanism around New Zealand during the Middle and Late Eocene (42-35 Ma.). This increase in volcanic activity is correlated with incresed island arc volcanism in New Zealand, Japan, and the various arc systems of the Southwest Pacific. Major flood basalts in Ethiopia erupted during the Late Eocene (ca. 35 Ma., Rampino and Stothers, 1988). It was also in this time period that the direction of Pacific plate motion changed, as evidenced by the bend in the Emperor-Hawaiian seamount chain (Kennett, et al., 1985b).

This major tectonic change is apparently correlated with a number of other major orogenic episodes in the Himalayas, Mexico, Spain, and elsewhere (see Kennett, et al., 1985b and references therein). Axelrod (1981) has reviewed the effects on Late Cretaceous and Cenozoic volcanism on terrestrial climates and biotas (see also GSA Special Paper 246, 1990).

2.9 Middle Miocene Events

The Miocene was a time of major, prolonged, climatic and oceanographic change (see Kennett, ed., 1985; Crowley and North, 1988). While there were dramatic changes in deep sea, shallow marine, and terrestrial biotas and habitats, there is little evidence for major rapid extinctions at any one point in the Miocene, especially among marine macroinvertebrates. Sepkoski and Raup (1986) and Sepkoski (1986) provide only scanty documentation of their claim for a mid-Miocene peak of extinctions, and even include the Plio-Pleistocene extinction of sub-tropical Atlantic molluscs (Stanley, 1986) as part of their mid-Miocene extinction peak. In general, mid-Miocene extinctions were concentrated among terrestrial mammals (see Carroll, 1988 for reviews) and pelagic microfossils (see Kennett, ed., 1985). Corals increased their diversity during the Miocene, both globally (Newell, 1984) and in the Caribbean (see fig. 1.1; Frost, 1977a). The Oligocene-Miocene extinction does not appear in Sepkoski and Raup's compilations.

2.10 Plio-Pleistocene Extinctions

During mid-Pliocene to Early Pleistocene times, a variety of marine invertebrates suffered regional extinctions, including molluscs (North Sea, Mediterranean, Western Atlantic, Caribbean), corals (Caribbean, tropical Eastern Pacific), and forams (pelagic, worldwide). These extinctions involved both true species extinctions and range truncations. Three major climatic/ oceanographic changes are associated with these extinctions: (1) the onset of Northern Hemisphere glaciation (and the attendant glacioeustatic sea level fluctuations; Shackleton, et al., 1984); (2) a prolonged regression (Haq, et al., 1986); and (3) the closing of the Central American Seaway (or alternately, the rise of the Isthmus of Panama; Stehli and Webb, 1985). Savin and Douglas (1985) point out that the mid-Pliocene rise of the Isthmus of Panama was primarily the result of a major and prolonged regression (Haq, et al., 1986), combined with slower tectonic uplift (but see also Durham, 1985, for an opposing view). Maier-Reimer, et al. (1990) have suggested that this third event may have caused the first (see chapter 6). I will attempt to discuss the faunal changes, and their presumed causes, by region, treating the Caribbean last.

2.10.1 Biogeography

Petuch (1982) divided Caribbean and tropical Eastern Pacific gastropods into two provinces: Caloosahatchian (Florida, Northern side of Cuba, Atlantic and Gulf Coast) and Gatunian (Caribbean including south side of Cuba, tropical Eastern Pacific from Baja California to Peru). The Isthmus of Panama divided the Gatunian province into Caribbean and Pacific portions after the Middle Pliocene (ca. 3.2 Ma; Keigwin, 1982). This new biogeographic scheme for the Western Atlantic and Eastern Pacific helps to explain the extinction patterns in those regions.

2.10.2 North Atlantic

Bivalves in the North Sea (Raffi, et al., 1985; Vermeij, 1989a), Mediterranean (Raffi, et al., 1985), and subtropical to temperate Western Atlantic (Stanley, 1986a) all suffered extinctions of endemic species and range truncations of cosmopolitan species. These extinctions came in two pulses: mid-Pliocene (ca. 3.2 Ma) and late Pliocene-Early Pleistocene (ca. 2.5-2 Ma). These pulses correspond to initiation (3.2) of Northern Hemisphere glaciation and intensification (2.5-2) to Pliocene levels of glaciation. The first of these also corresponds to the emergence of the Isthmus of Panama (Keigwin, 1982).

In the Western Atlantic, which suffered the most intense regional extinctions (65% species extinction), endemic species had significantly lower survivorship levels than did cosmopolitan species (Stanley and Campbell, 1981; Stanley, 1986a). Stanley (1986) equated endemic species with stenothermic species, and attributed the high extinction rates of endemic species to the inability of stenothermal species to shift their geographic ranges as quickly as climatic zones moved. In particular, in South Florida, he suggested that an upwelling zone in the Florida Strait acted as a thermal barrier, separating northerly Caloosahatchian faunas from those of the southerly Gatunian province. Interestingly, Gatunian province bivalves (mostly in the Caribbean) suffered equally high mortality (Stanley, 1986a). In the temperate to subtopical Eastern Pacific, where biogeographic zones were able to shift more freely, bivalves suffered no mass extinction.

In the Mediterranean and North Sea basins, bivalves again suffered widespread extinctions and range truncations (46% of species; Raffi et al., 1985). Endemic species (restricted to one of the two basins) suffered higher levels of extinction than widespread species (found in both basins), and tropical-subtopical species suffered more than warm to cool temperate species. Many previously pandemic species survive today only in the Mediterranean, which apparently served as a warm-water refuge (Raffi, et al., 1985).

Vermeij (1989a) discussed a trans-Arctic migration of bivalves from the North Pacific to the North Atlantic during the Pliocene and Early Pleistocene, and its relationship to North Sea bivalve extinctions. This migration was highly unequal, with about 125 spp. expanding their ranges from the Pacific to the Atlantic, but only 16 making the opposite migration. The North Pacific apparently served as a refuge for previously Holarctic species (Vermeij, 1989b), and Pacific immigrants suffered less extinction than did North Atlantic endemic species except during the Early Pleistocene (table 2.4). While believing these differences to be biologically real, Vermeij points out that the low sample size makes the statistical validity of these ratios questionable at best. North Atlantic endemics suffered their greatest extinction during the Late Pliocene; Pacific spp. only became important elements of the North Sea fauna after this extinction, and almost certainly did not cause the extinction of endemic species. Transarctic interchange was interrupted no later than mid-Pleistocene time by permanent sea ice cover (Vermeij, 1989a).

Table 2.4. Biogeography and North Sea Bivalve Extinctions. Modified from Vermeij (1989a).

Stage	Tot Spp	Tot Ext	Imm Spp	% Im Spp	New Imm	Imm Ext	%Im Ext
Eemian (Late Pleist.)	70	5.7%	21	30%	5	0	0
Early Pleistocene	63	17%	23	36.5%	16	4	17%
Merksemian (L. Plio)	64	42%	7	11.3%	3	1	14%
Scaldisian (M. Plio.)	116	29%	5	4.3%	5	0	0
Kattendijkian (E.Plio)	115	23%	0	0	0	0	0

2.10.3 North Pacific

Molluscs also suffered extinctions and range truncations in the North Pacific, but on a much smaller scale than in the North Atlantic (Stanley, 1986a; Vermeij, 1989b). Fifteen species of molluscs which had previously occupied shallow water habitats of both the Northeast and Northwest Pacific became restricted to the Northwest Pacific during the Late Pliocene - Early Pleistocene interval; those species comprise 5-16% of modern Northwest Pacific faunas sampled, and, numerically, are thus rather unimportant. In toto, 20-40% of Northeast Pacific molluscan species became extinct or restricted to the Northeast Pacific (Stanley, 1986a; Vermeij, 1989b). Nonetheless, Vermeij suggests that they may provide a model of mechanisms of background extinction. All of these species are large molluscs, and Vermeij attributed their local extinctions to the elimination of wide, shallow, somewhat restricted embayments in the Northeast Pacific during the Late Pliocene regressions. Such embayments today are important sites of high nearshore productivity. Vermeij concluded (tentatively) that productivity crises were the major cause of these range truncations.

2.10.4 Tropical Indo-Pacific

The tropical Indo-Pacific today is the centre of diversity of modern corals, and a variety of reef-associated organisms, including gastropods, echinoids, and reef fish (Stehli and Wells, 1971; Stoddart, 1976; Rosen, 1984; Vermeij, 1987). Potts (1983, 1984) has suggested that continental shelf habitats in the Indo-Pacific were the main sites of coral speciation until Early Pleistocene times, after which high frequency sea level fluctuations did not allow sufficient time for founder effects to develop in corals, which have long, overlapping generation times. In most other reef organisms, however, generation times are generally short (<20 yrs), and sea level changes could have provided many opportunities for local speciation (and extinction) events (e.g. McManus, 1985).

The onset of Pleistocene glaciation, with its attendant large fluctuations in sea level, must have had dramatic consequences for the faunas of mid-Pacific atolls. Paulay (1990) showed that lagoonal habitats of atolls were often completely eliminated during Pleistocene sea level lowstands, and became karst plateaus (Paulay and Spencer, 1988). All modern organisms living solely in atoll lagoons were extirpated and then re-immigrated with the next transgression; only organisms capable of living on the outer slopes of atolls could survive locally by tracking changing sea levels on the sides of the atoll. This pattern implies that the onset of Pleistocene glacioeustatic sea level fluctuations must have driven many occupants of atoll lagoons to extinction.

Unfortunately, most Pliocene and older lagoonal facies of atolls are accessible only in core, rather than outcrop (e.g Wells, 1964, 1982), so documentation of this supposed extinction pattern promises to be quite difficult.

2.10.5 Caribbean and Eastern Pacific

Corals, molluscs, echinoids, forams, and other Caribbean invertebrates suffered widespread extinctions and range truncations in the mid-Pliocene to early Pleistocene interval. These extinctions are all clearly related to the rise of the Isthmus of Panama (Jones and Hasson, 1985; Vermeij and Petuch, 1986) and the onset of Northern Hemisphere glaciation (e.g. Stanley, 1986a). For all groups except corals, extinction of Caribbean vicariant faunas was more intense than that of Eastern Pacific faunas (Jones and Hasson, 1985). The modern coral fauna of the Eastern Pacific is apparently derived from Holocene long-distance migrants from the Central or Western Pacific; the relict Caribbean reef corals of the Eastern Pacific were eliminated during Pleistocene glaciations (Dana, 1975; Glynn, 1982; but see also Heck and McCoy, 1978). Corals of Caribbean affinity persisted in the Northern Sea of Cortez until Late Pliocene time (Vaughan, 1917; Watkins, 1990).

Gastropod subgenera on opposite sides of the Isthmus suffered widely different extinction patterns: 32% in the Caloosahatchian, 32 % in the Atlantic Gatunian, and 15% in the Pacific Gatunian. In all three regions, endemic taxa were particularly extinction-prone, and Vermeij and Petuch (1986) ascribe most of the differential extinction to the relative importance of endemic taxa within each province. Gastropods from hard-bottom habitats had lower degrees of endemism, and lower levels of percent extinction than those from soft-bottom environments.

There was also an apparent selectivity based on predator-resistant shell morphology, but this pattern differed by facies, and by biogeographic province. Vermeij and Petuch suggest that predator resistance was not the actual character under selective pressure, but rather, that correlated demographic patterns were responsible. High productivity upwelling regions, especially the Pacific coast of Panama and two small areas on the Caribbean coast of Venezuela (Petuch, 1981) may have acted as refuges where recruitment rates were higher, thus reducing the demographic costs of heavy armour in gastropods (Vermeij and Petuch, 1986). By contrast, corals were eliminated from such environments, and low productivity environments probably acted as refuges for them (Jones and Hasson, 1985; Vermeij and Petuch, 1986).

The relict Gatunian gastropod faunas of Northern Venezuela, found today in restricted zones of topographic upwelling, were widespread throughout the Caribbean during the Miocene and Early Pliocene (Petuch, 1981, 1982). Their distribution implies that much of the Caribbean was characterized by nutrient-rich upwelling environments during this time period, which would have tended to restrict development of coral reefs (Birkeland, 1977; Jones and Hasson, 1985; Hallock and Schlager, 1986). These changing patterns of productivity, their oceanographic basis, and their effects on the reef biota of the Caribbean will be discussed in Chapter 6.

Caribbean corals suffered the second of two Cenozoic regional mass extinctions at the Plio-Pleistocene boundary (Frost, 1977a). Eight of thirty genera (26%) and 13 of 46 species (28%) became extinct or restricted to the Indo-Pacific (fig. 1.1). Alveopora, Goniopora, Pocillopora, and Stylophora became extinct in the Caribbean, but persist today in the Indo-Pacific (Frost, 1977a; Foster, 1986). Most of the large solitary corals of Caribbean Miocene and Pliocene off-reef and seagrass bed habitats became extinct. On the other side of the isthmus, corals of Caribbean affinity in the Eastern Pacific were also eliminated (Vaughan, 1917; Jones and Hasson, 1985). This extinction affected corals less than the Oligocene-Miocene extinction, in which approximately 50% of Caribbean coral genera became extinct or restricted to the Indo-Pacific (Frost, 1977a; this study).

The continental shelves of SouthEast Asia, then, are both refuge and the centre of diversity for corals and many reef-associated organisms, housing the bulk of the once-cosmopolitan reef fauna of the Eocene and Oligocene (Stoddart, 1976; Frost, 1977c; Heck and McCoy, 1978; Vermeij, 1987). The Indo-Pacific has also witnessed an explosive diversification at the species (and, to a lesser extent, genus) level among tropical invertebrates during the late Neogene (Newell, 1971; Briggs, 1987). The paleoecology and evolutionary patterns of corals and reef-associated faunas of the Indo-Pacific during the mid-Cenozoic remains large unknown (Veron and Kelley, 1988). Exploration of these areas is of prime importance for understanding the biogeographic patterns behind the evolution of modern reef faunas.

2.10.6 Terrestrial Systems

The Great American Interchange of mammals between North America and South America is one of the most important events in the Late Cenozoic evolution of New World mammalian faunas (Carroll, 1988). It is also one of the best documented examples of faunal mixing, and of the influence of biogeographic changes on evolutionary patterns (Simpson, 1953; Marshall, 1981; Stehli and Webb, 1985). Faunal mixing during the Great American Interchange led to extinctions of endemic taxa in both North and South America, as well as adaptive radiation in the new immigrants to each continent (Marshall, 1981).

2.11 Summary of Cenozoic Extinctions

Regional mass extinctions, typical of the Cenozoic, provide smaller and easier studied examples of the same patterns and processes responsible for major mass extinctions. In the Neogene, they generally have the advantage of greater taxonomic, spatial, and temporal resolution than older extinction events, and can be documented in greater detail. In some cases, both "victims" and "survivors" are extant, allowing easier comparison of ecological attributes of each group.

The common denominator in the Cenozoic regional extinctions is the opening and closing of oceanic passages, with attendant changes in oceanic circulation patterns and terrestrial climates. These changes increased latitudinal and depth-related marine temperature gradients, causing faunal mixing and/or increased division of biotic provinces, with consequent speciation and extinction. Some regions, such as the Mediterranean and Caribbean, became biogeographic traps, in which marine communities experienced relatively high extinction rates, and which eventually came to harbour relict faunas. All of these changes can be related to paleoceanographic events.

Viewed in this context, the Oligocene-Miocene extinction in this study is not an anomaly, but was simply early. Why were Caribbean reef corals affected 20 Ma earlier than gastropods, echinoids, and most other members of Caribbean reef communities? How did changing patterns of oceanic circulation affect the oceanography of the Caribean at the Oligocene-Miocene boundary? These questions are discussed in chapter 6.

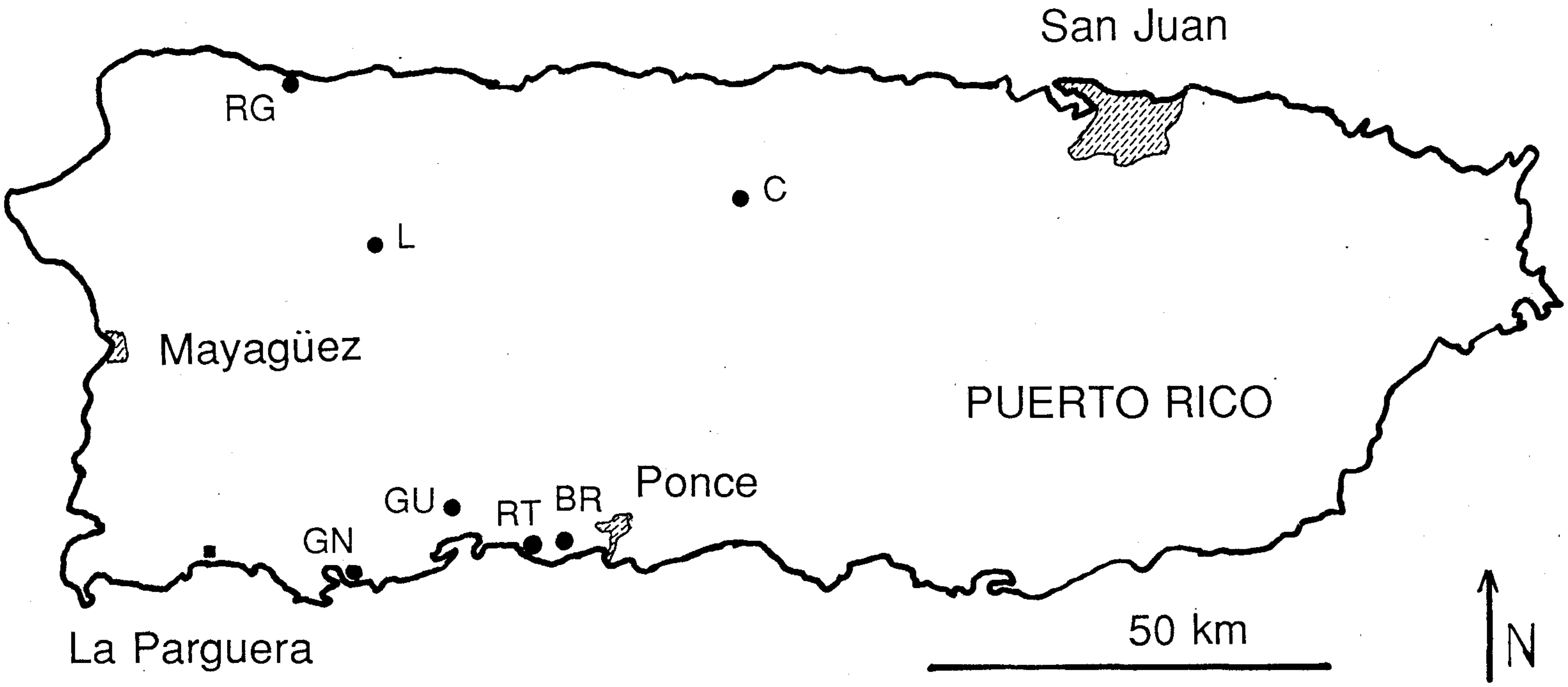
Chapter 3: Study Site Descriptions, Sampling and Analytical Methods.

I selected three Oligocene and three Miocene sites for detailed description and sampling (map 3.1) on the basis of stratigraphic proximity to the Oligocene-Miocene boundary, accessibility, and the abundance and exposure of fossil material. The study sites are: the Guayanilla II and Guanica sites described by Frost et al. (1983) (Guayanilla Fm., uppermost Oligocene.), the Lares Quarry site (Lares Fm., uppermost Oligocene.), the Brizas del Caribe and Rio Tallaboa sites (Ponce Fm., middle Mio.), and the Rio Guajataca site (Los Puertos (Aymamon) Fm., middle to upper Miocene). I also briefly examined the Ciales Roadcut section (Lares Fm., uppermost Oligocene; Frost, unpublished). At the Ciales, Guanica and Rio Tallaboa sites, I did not collect complete samples due to constraints on field time (see methods, below). Stratigraphic sections of the sites are presented in figures 3.2 through 3.9.

3.1 Sampling Design

The coral fauna of each site was qualitatively described as part of the stratigraphic section. Some of the corals collected as part of this initial description were later analyzed for bioeroders. They are indicated by dashed numbers, indicating the unit in which each was collected (e.g. L-2-3 is the third coral collected in describing unit 2 at the Lares Quarry site; see appendix 1). In

Map 3.1. Location of Study Sites in Puerto Rico. Circles indicate fossil outcrops; square indicates site of modern sampling.



Study Sites

Oligocene		Miocene	
C	Ciales	BR	Brizas del Caribe
GN	Guánica	RG	Rio Guajataca
GU	Guayanilla	RT	Rio Tallaboa
L	Lares		

addition, 20-30 corals were systematically collected for analysis of the bioeroding fauna.

Systematic samples were collected from the Guayanilla II, Lares, Brizas del Caribe and Rio Guajataca sites. At each of these sites, a 10-15m long, 2m high grid was erected at one horizon within the framestone unit and corals were mapped within this grid (plate 3.5b). At average reef accretion rates of 1m/1000 yrs. (James, 1983), this 2m slice probably represents about 2-3000 years of reef growth. The upper contact of the framestone unit was used as a datum plane from which to hang the sample grid, except at the Rio Guajataca site, where the upper contact is gradational. At the latter, the grid was hung level, close to the regional dip (4°). All massive and branching coral colonies within the sampling grid were numbered. At least one sample of every distinguishable coral species was collected, and part or all of 20 massive and up to 10 branching colonies were collected in ascending order. The colonies collected are not a random sample, but are a representative sample of the coral fauna of each site. At the Rio Tallaboa and Guanica sites, no sample grid was erected, but corals were still collected from a 2m thick horizon, parallel to bedding, within the framestone unit.

After collection, corals were cleaned and cut in the laboratory at the University of Puerto Rico, Mayaguez, for identification. Large coral heads were subsampled for shipment back to McMaster. 195 corals were slabbed parallel to the corallites to examine boring trace fossils of internal associates. About 40 thin sections and 30 acetate peels were made from transverse sections of corals to positively identify corals and to highlight boreholes within the corals. Data from the Ciales section are derived from incidental observation and from those species listed in units 4 and 6 of Frost's unpublished section (fig. 3.5).

3.2 Oligocene Sites

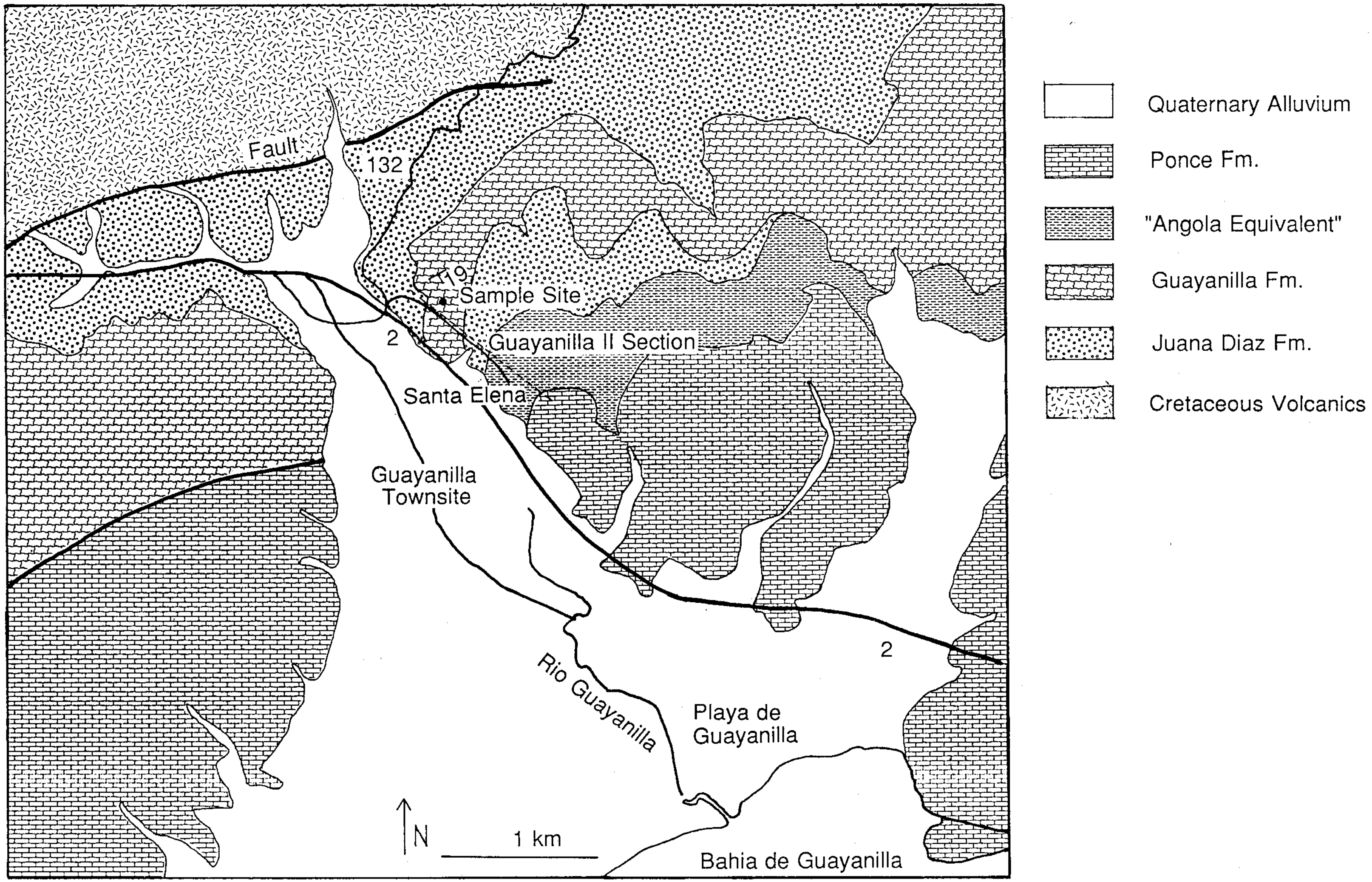
Guayanilla Fm.

Frost et al. (1983) studied both of the Oligocene sites which were sampled from the Guayanilla Fm, the latest Oligocene barrier reef tract on the South coast. Their stratigraphic sections are reproduced in figure 3.2. Frost et al. published detailed descriptions and depositional histories for each of these sections. Here, I describe in detail only the units sampled for this study.

3.2.1 Guayanilla II

This is the main south coast Oligocene section described by Frost, et al (1983). The outcrop is located on the entry road into the Santa Elena housing development just north of Hwy. 2, near the

Map 3.2. Geologic Map, Guayanilla Section. Punta Cuchara Quadrangle, Puerto Rico. Redrafted from USGS maps and Frost et al (1983).



Geologic Map, Guayanilla Section
Punta Cuchara Quadrangle

Figure 3.1. Legend for Stratigraphic Sections, figs. 3.4-3.9.

LEGEND

Lithologic Features

- Framestone
- Rudstone
- Bioclastic Wackestone-Packstone
- Chalky Bioclastic Wackestone
- Marl

——— sharp contact

- - - - gradational contact

〜〜 unconformity

Other Fossils

- upright massive coral
- overturned massive coral
- horizontal burrow
- vertical burrow
- *Clypeaster*
- oyster
- gastropod
- infaunal bivalve
    - veneroid
    - myoid
    - disarticulated
- *Pecten*
- *Kuphus* tube
- large foram
    - *Lepidocyclina* (Olig.)
    - *Sorites* (Mio.)
- platy bryozoan

Oligocene Corals

Massive species

- *Montastrea costata*
- *Montastrea tampaensis*
- *Antiguastrea cellulosa*
- *Diploastrea crassolamellata*
- *Colpophyllia willoughbiensis*
- *Porites panamensis*
- *Goniopora hilli*
- *Alveopora chiapaneca*
- *Pironastrea sp.*
- *Agathiphyllia roxboroughi*
- *Favites polygonalis*
- *Siderastrea conferta*
- *Siderastrea siderea*
- *Hydnophora* species unnamed

Branching and foliose species

- fine branching coral
    - *Porites douvillei*
    - *Stylophora imperatoris*
    - *Caulastrea portoricoensis*
- stout branching *Porites panamensis*
- *Stylocoeniella lobatorotundata*
- *Acropora saludensis*
- *Leptoseris portoricoensis*

Miocene Corals

Massive species

- *Montastrea limbata*
- *Solenastrea hyades*
- *Coscinaraea colei*
- *Favia mexicana*
- *Colpophyllia mexicana*
- *Porites trinitatis*
- *Goniopora jacobiana*

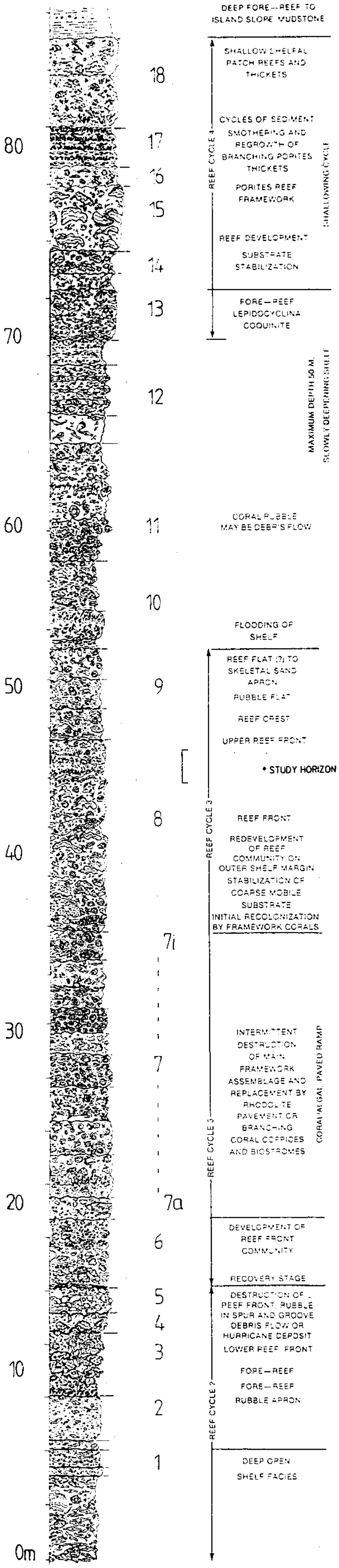
Branching, foliose, and solitary species

- fine branching coral
    - *Porites baracoaensis*
    - *Stylophora* sp.
- stout branching *Porites trinitatis*
- *Astrocoenia portoricoensis*
- *Agaricia* sp.
- solitary coral
    - *Placocyathus barretti*
    - *Placocyathus moorei*
    - *Thysanus* sp.
    - *Antillophyllia* sp.

Figure 3.2. Stratigraphic Sections of Guayanilla II and Guanica Sections. Compiled and modified from Frost, et al. (1983). For unit descriptions, see Frost et al. (1983).

Guayanilla II Section

Modified from Frost, et al., 1983.



Guanica Section

Modified from Frost, et al., 1983.

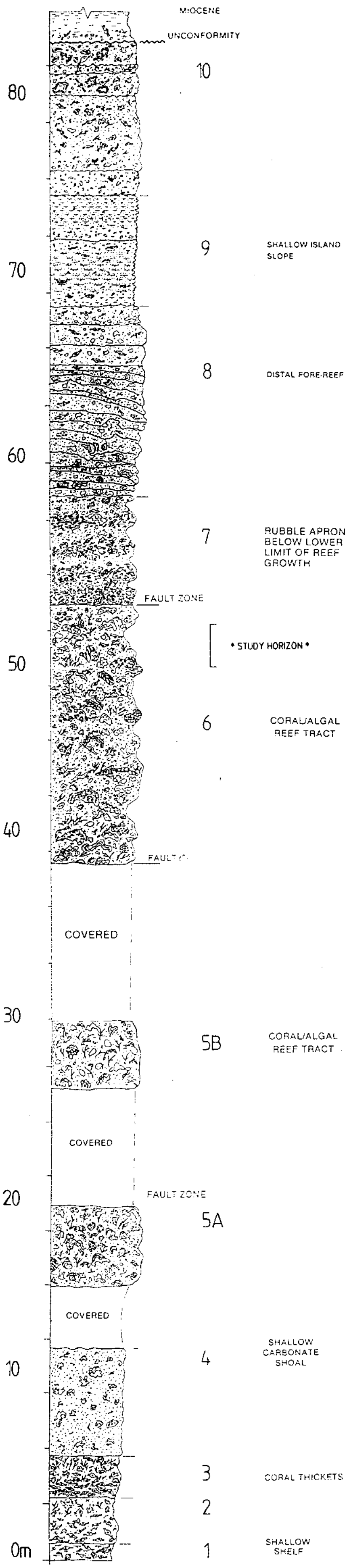
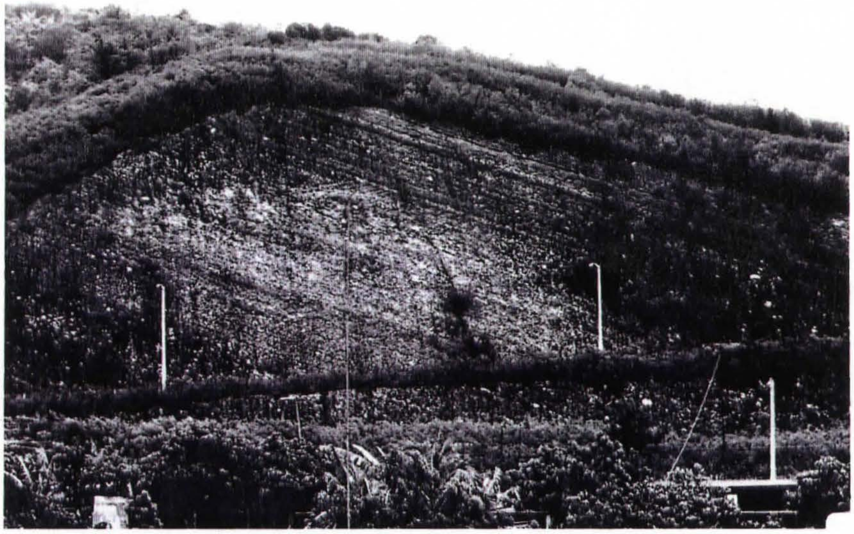
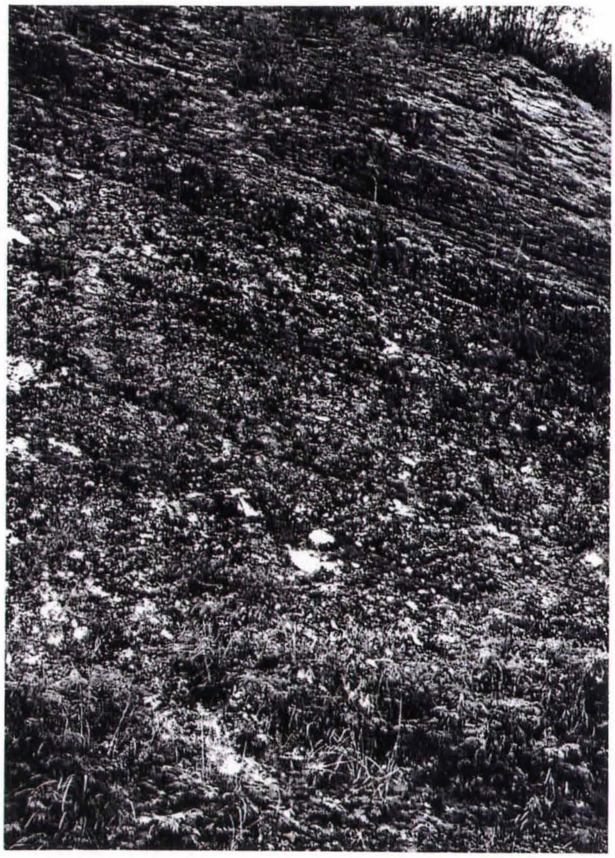


Plate 3.1a. Long distance outcrop view of Guayanilla II section. Beds dip 19° to southwest. Light poles for scale are about 15m high.

Plate 3.1b. Outcrop view of Guayanilla II site. Horizon sampled, at top of unit 8, running diagonally from upper left to centre right, where view is partly obscured by bushes. Large white objects are heavily recrystallized massive corals. Large coral in lower centre is about 50 cm diameter.





town of Guayanilla (map 3.2; plate 3.1a). The whole section dips 19° to the southeast and is a fairly steep roadcut. Since Frost, et al.'s study, the section, composed of well indurated rocks, has been overgrown with black lichen, obscuring fossils in gross outcrop view. These features make excavation of samples difficult.

For this study, the uppermost (closest to the Oligocene-Miocene boundary) framestone unit (#8) in the section was sampled (plate 3.1b). This unit, 18m thick, is conformably underlain by a rhodolite pavement, interpreted as a fore-reef coral-algal rampart (Unit 7I, fig. 3.2) and conformably overlain by a *Lepidocyclina*-rich packstone, interpreted as a reef flat or back reef environment (Unit 9, fig. 3.2). It records a long period of reef accretion with framestone dominated by the massive corals *Porites waylandi*, *Goniopora hilli*, *Antiquastrea cellulosa*, *Siderastrea conferta*, *Diploastrea crassolamellata*, and the pseudomassive branching coral *Stylocoeniella lobatorotunda*. Near the top, there is an apparent spur and groove system, with both channel walls and channel fill present. Corals were collected from the uppermost 3m of unit 8 (the youngest Oligocene framestone at the site). In the two meter horizon sampled for this study, the most abundant corals were *Porites panamensis* and *Goniopora hilli*, with lesser amounts of *Siderastrea conferta*, *Antiquastrea cellulosa*, *Diploastrea crassolamellata*, and *Stylocoeniella lobatorotundata*.

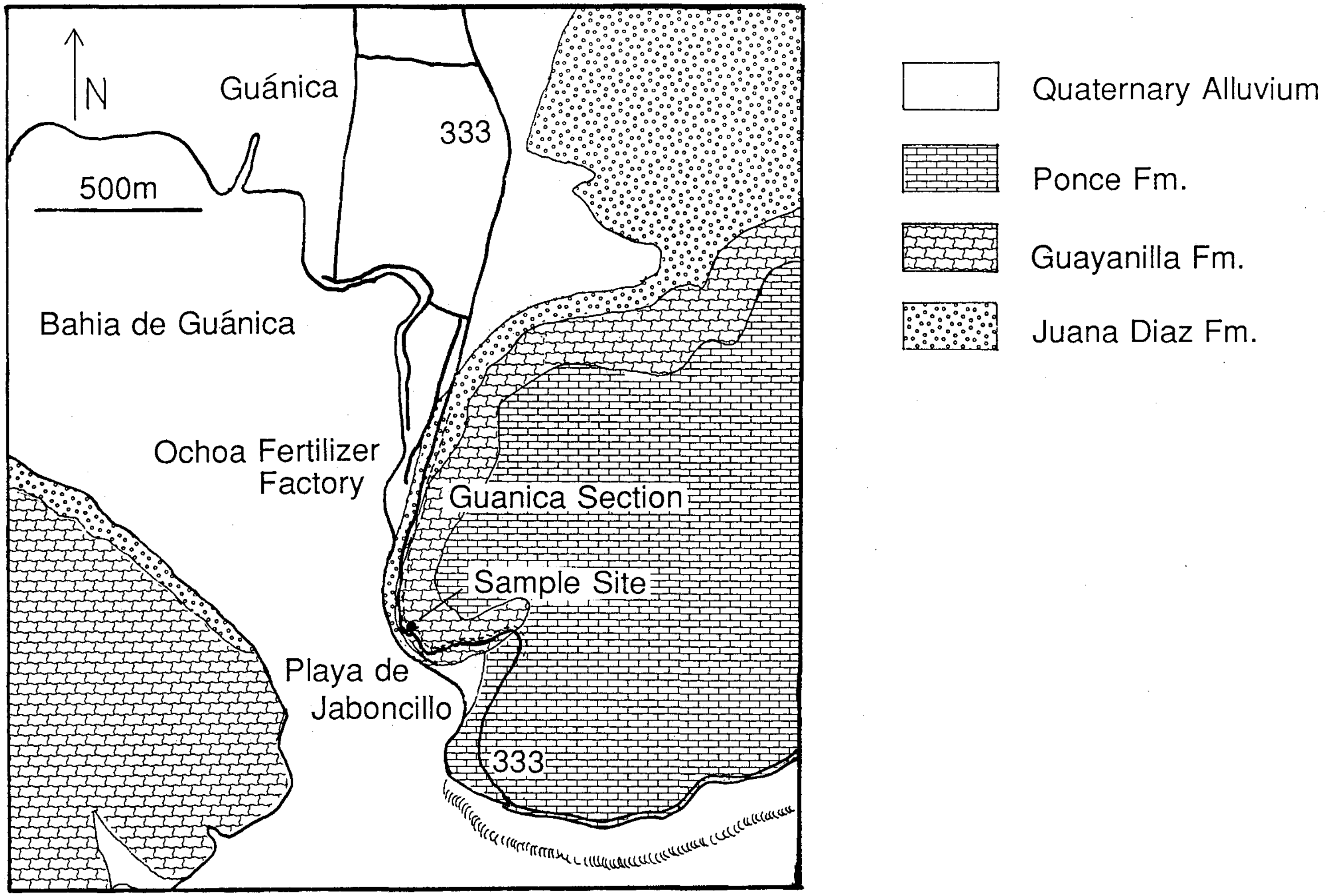
Material: Forty corals were collected from the Guayanilla II site for analysis of the bioeroding fauna. These are: 8 *Porites waylandi*, 6 *Goniopora*, 7 *Siderastrea conferta*, 4 *Stylocoeniella*, 4 *Antiquastrea*, 4 *Stylophora imperatoris*, 2 *Porites baracoaensis*, and one each of *Montastrea tampaensis*, *Astreopora*, *Acropora*, *Caulastrea*, and *Hydnophora*. Most of these samples are fragments of moderately large (20-40 cm) colonies which appear relatively complete in outcrop view, but could not be extracted whole. Most are recrystallized and are quite well preserved. These samples are listed in Appendix 1.

Age: The Guayanilla II section is of latest Oligocene age (Frost, et al., 1983). Puerto Rican foraminiferan biostratigraphy developed by Sieglie and Moussa (1984, 1987, unpublished) and the latest global compilation of planktonic and benthic foraminiferan biostratigraphy (Kennett, et al.,1985a) suggest an absolute age of about 26 Ma. All of the absolute ages reported here are based on these biostratigraphic works, and are only rough estimates.

3.2.2 Guanica

The Guanica harbor outcrops are also part of the latest Oligocene reef tract of the Guayanilla Fm. (map 3.3; fig. 3.2; Frost, et al., 1983). Frost et al. describe the stratigraphy and paleoecology of this section in detail. The section grades upwards

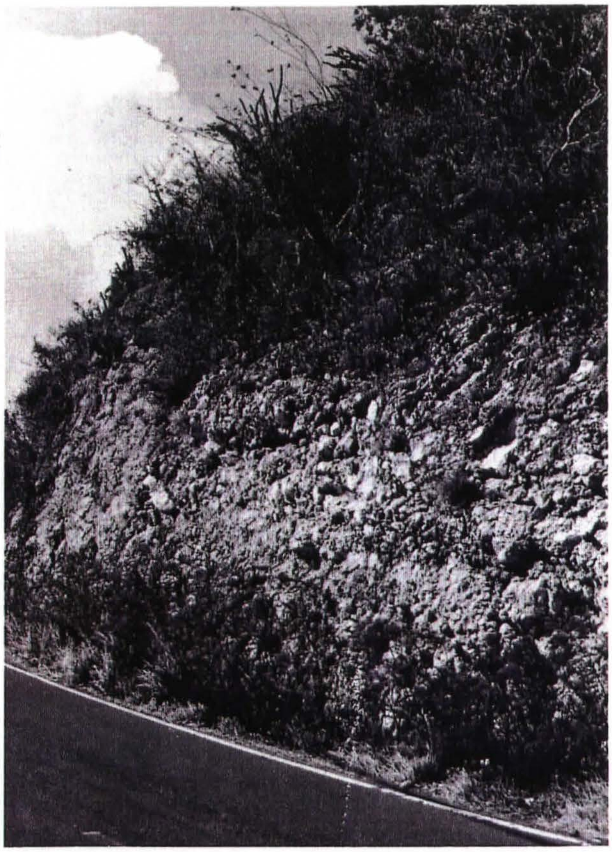
Map 3.3. Geologic Map, Guanica Section. Guanica Quadrangle, Puerto Rico. Redrafted from USGS topographic map and Frost, et al. (1983). There is no published USGS geologic map of the Guanica quadrangle.



Geologic Map, Guánica Section
Guánica Quadrangle

Plate 3.2a. Outcrop view of Guanica section, sample site in Unit 6. Face is about 3.5m high. Large partly shaded coral head at centre right, <u>Hydnophora</u> sp. unnamed, is about 60 cm high.

Plate 3.2b. Outcrop view of Guanica section, unit 7, exposed behind Ochoa Fertilizer factory. Field book for scale.



from a lagoonal/back reef setting through at least 20m of reef core into proximal, and then distal fore reef sediments (plate 3.2b). The framestone unit (Unit 6), which was sampled in this study has a highly diverse coral fauna which includes more presumed deep water species than the fauna of the Guayanilla II sample unit. The dominant framework builders are Hydnophora (sp. unnamed), Favites polygonalis, Antiquastrea cellulosa, and Porites waylandi, with lesser amounts of Stylocoeniella lobatorotundata, Goniopora hilli, and Acropora sp. (probably A. saludensis), and others. Many of these corals are heavily bioeroded. Corals were sampled from a 2m horizon in the uppermost 5m of Unit 6 (plate 3.2a). This horizon represents the latest episode of reef growth at the Guanica site.

Material: Only eight coral colonies were collected from the Guanica site and analyzed for bioeroders. These are: 3 Stylocoeniella, 2 Favites, and one colony each of Hydnophora, Colpophyllia, and Montastrea tampaensis. All are fairly complete, moderate sized heads (20-40 cm) with the exception for the Colpophyllia and M. tampaensis. All are recrystallized and quite well preserved. See Appendix 1 for a list of specimens.

Age: The Guanica section is probably of roughly equivalent age to the Guayanilla section, although a precise correlation between the two is not possible due to extensive faulting (Frost, et al., 1983). Again, absolute age is probably about 26 Ma.

Lares Fm.

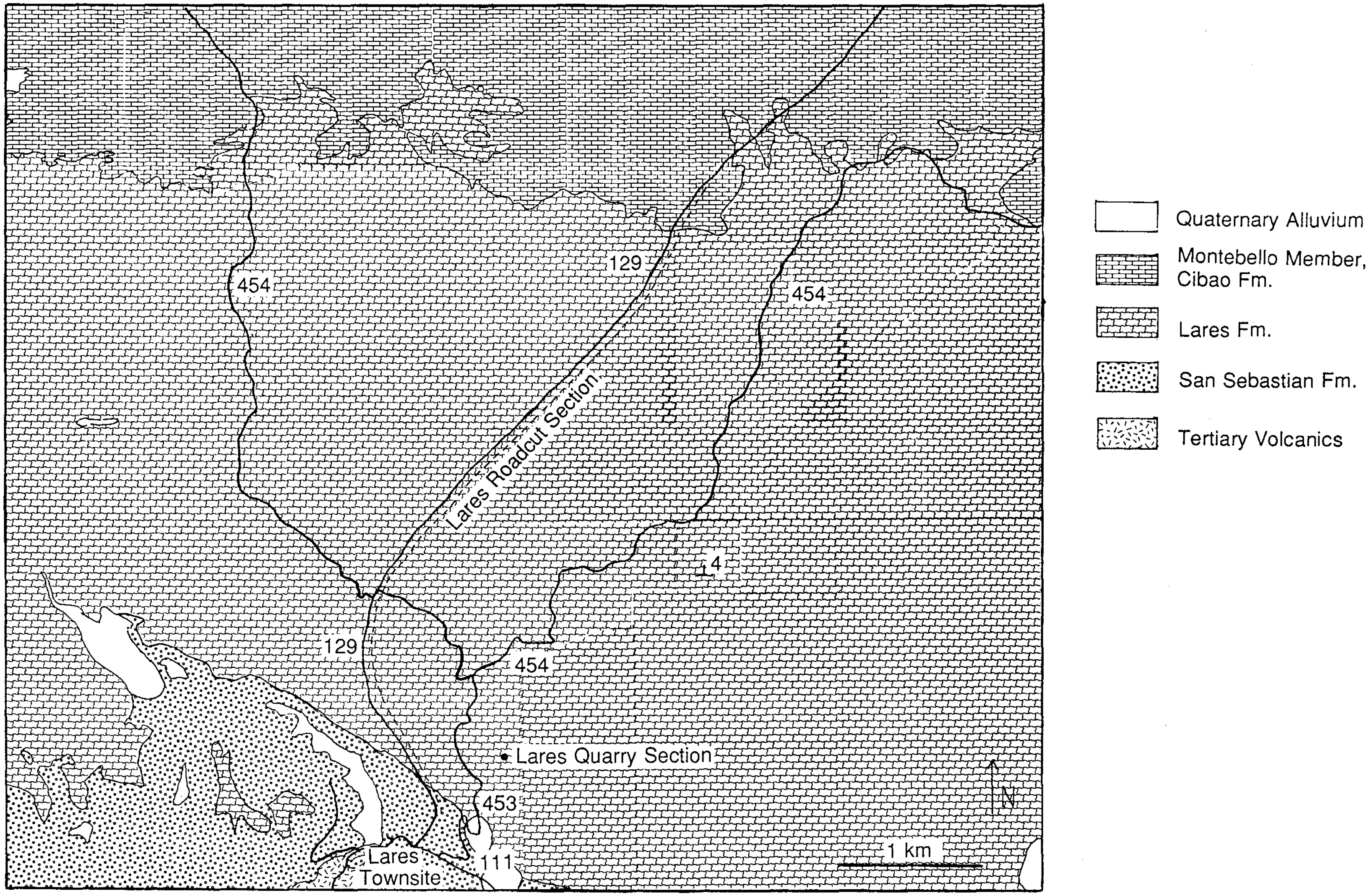
3.2.3 Lares Quarry

The Lares Quarry site is located in the abandoned part of a quarry immediately southwest of the intersection of SR 453 with SR 454, about 1.5km NE of the town of Lares (Bayaney quadrangle, map 3.4). Figure 3.4 shows a stratigraphic section of the site. This section correlates to units 28 to 42 of Frost's Lares Highway 129 Roadcut section (fig. 3.3; Frost et al., 1983), and sits in the middle third of the Lares Fm. Frost et al., interpret the Lares Fm. as a broad carbonate platform with scattered patch reefs.

The entire section dips slightly (4°) to the North, and has been subjected to extensve karstification and minor faulting. Units 0 to 4 are exposed in the Southwest wall of the quarry (plate 3.3a); units 5 to 8, in the Northeast wall. The Southeast wall has some exposures of units 5 and 6. The section consists of carbonate platform sediments, which may have included seagrass banks, with occasional patch reefs and branching coral thickets. Units 2, 4, and 6 are all framestones, representing the cores of patch reefs; only unit 2, the most easily (and safely) accessible, was systematically sampled.

This unit varies in thickness from 3 to 4m, and is exposed laterally for at least 50m. It is dominated by Montastrea costata

Map 3.4. Geologic Map, Lares Sections. San Sebastian and Bayaney Quadrangles, Puerto Rico. Redrafted from USGS maps and Frost, et al (1983).



Geologic Map, Lares Section

Figure 3.3. Stratigraphic Section, Lares Roadcut Section. Compiled and modified from Frost, et al. (1983).

Lares Roadcut Section

Modified from Frost, et al., 1983.

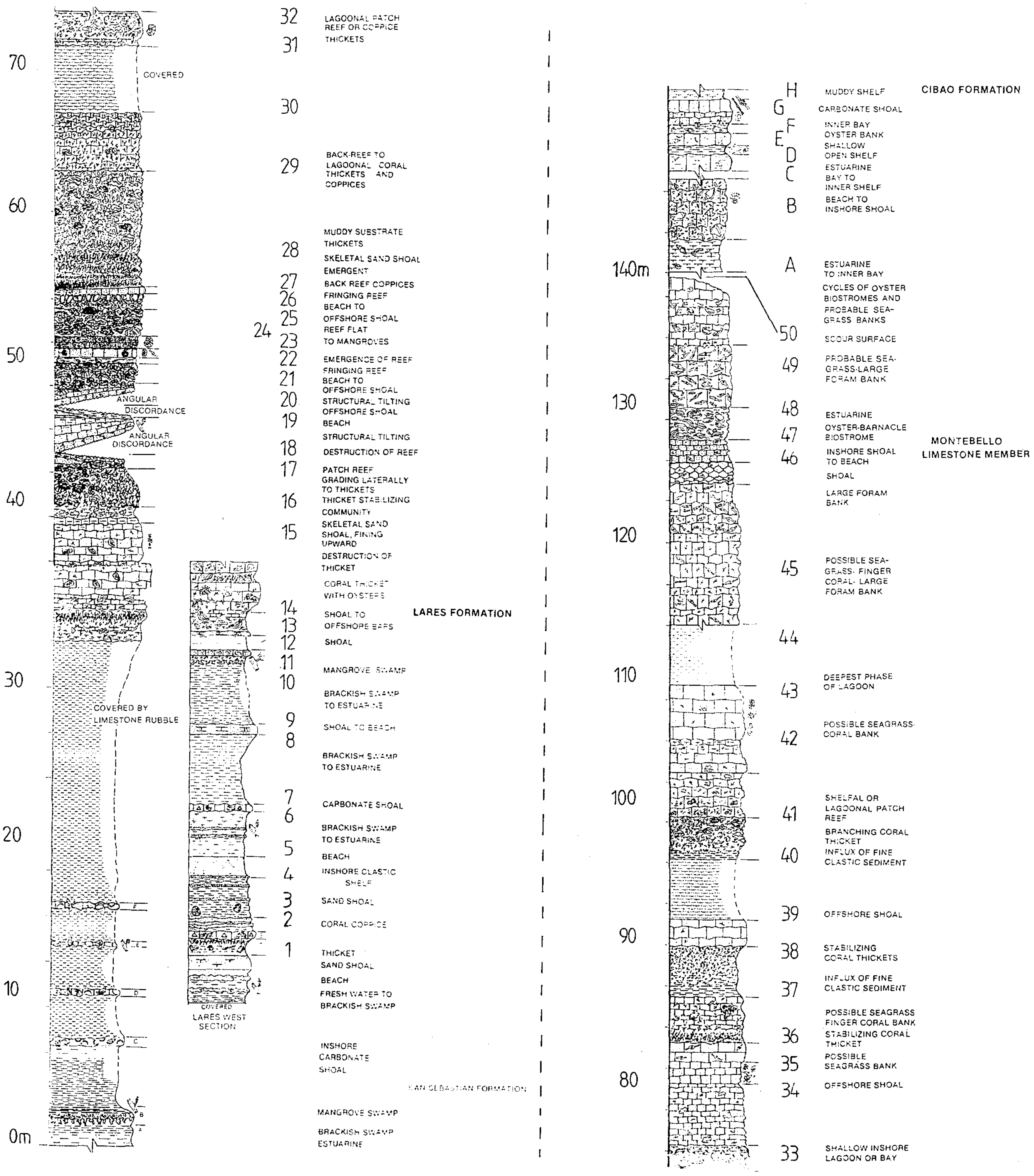
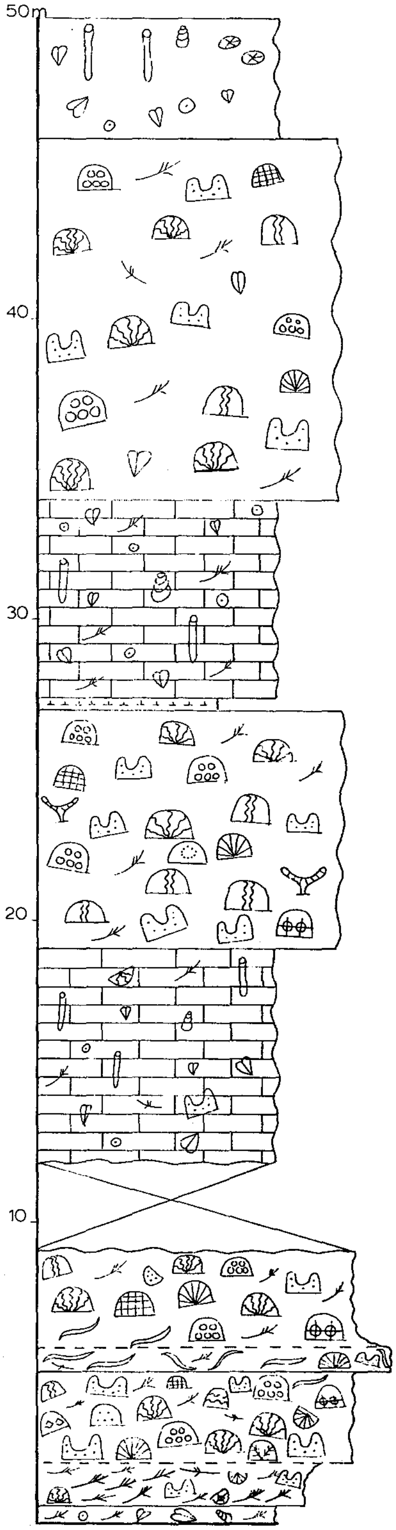


Figure 3.4. Stratigraphic Sections, Lares Quarry Section. Units 1-4 exposed in Southwest wall, Unit 5-6 in Southeast wall, and Units 5-8 in Northeast wall.

Stratigraphic Section Lares Quarry Site Lares Fm.

Rock Column



Unit	Description	Interpretation
9	Bioclastic wackestone–packstone with *Kuphus* tubes, *Clypeaster*, *Lepidocyclina*, infaunal bivalves and gastropods.	SEAGRASS BEDS ON CARBONATE PLATFORM
8	Framestone composed mostly of *Antiguastrea*, *Diploastrea*, *Porites panamensis*, and *Colpophyllia*.	PATCH REEF
	poorly exposed	
	FAULT CONTACT	
7	Massive chalky bioclastic wackestone with infaunal bivalves, gastropods, *Kuphus* tubes, and *Lepidocyclina*.	OPEN CARBONATE PLATFORM
	Heavily leached marl.	KARSTIFIED LAYER
6	Framestone composed mainly of *Colpophyllia*, *Antiguastrea*, and *Diploastrea*, with some massive and stout branching *Porites panamensis*; rare *Siderastrea siderea*, *Leptoseris portoricoensis* and *Alveopora chiapaneca*.	PATCH REEF
5	Massive chalky bioclastic wackestone with infaunal bivalves, gastropods, *Kuphus* tubes, *Lepidocyclina*, and rare branching and massive coral fragments.	OPEN CARBONATE PLATFORM WITH NEARBY PATCH REEF.
	COVERED	
4	Framestone composed of same species as in Unit 2, in approximately the same relative abundance.	PATCH REEF
3	Oyster biostrome with uncommon, mostly fragmented, branching and massive corals as in unit 2, also including *Caulastrea portoricoensis*.	OYSTER BIOSTROME
2	Framestone composed mainly of massive and stout branching corals. Dominant species are *Montastrea costata*, *Porites panamensis*, *Antiguastrea cellulosa*, *Diploastrea crassolamellata*. Rare corals include *Colpophyllia willoughbiensis*, *Montastrea tampaensis*, *Alveopora chiapaneca*, *Cyathoseris* sp., *Stylophora imperatoris*, and *Acropora saludensis*.	PATCH REEF • STUDY UNIT •
1b	Rudstone, composed mostly of fragmented and imbricated *Porites douvillei*, with some stout branching *Porites panamensis* and massive coral fragments.	BRANCHING PORITES THICKET
1a	Bioclastic wackestone with infaunal bivalves, gastropods, *Lepidocyclina*, and *Porites douvillei* fragments.	OPEN CARBONATE PLATFORM

Plate 3.3a. Outcrop view of Lares Quarry site, southwest face, units 1-4. Unit 2 lies below dark recessed horizon. Person at top of ladder for scale.

Plate 3.3b. Clustered domal corals in ouctrop view of Lares Quarry site. Two large heads at left are *Montastrea costata*; head at right is *Diploastrea crassolamellata*. Hammer for scale.

and *Porites waylandi*, with lesser amounts of *Diploastrea crassolamellata*, *Antiquastrea cellulosa* (plate 3.4), *Goniopora hilli*, *Stylophora* spp., rare branching *Porites*, and others. Corals are mostly clustered (plate 3.3b).

Unit 2 is sharply underlain by a rudstone (unit 1b) composed primarily of horizontally oriented fragments of stout branching *Porites waylandi* and *P. baracoaensis*. Unit 1b is thus interpreted as a branching *Porites* thicket, although some size sorting and imbrication of fossils may suggest storm deposition. Unit 2 is sharply overlain by an oyster biostrome 80 cm thick, which then grades back into framestone (unit 4) of similar species composition to Unit 2. A 2m horizon of Unit 2, extending upward to .5m from the contact with unit 3, was sampled.

Other corals found in the Lares Quarry section (either in float or in units 4 or 6), include *Acropora saludensis*, *Alveopora tampae*, *Agathiphyllia roxboroughi*, *Astreopora* (sp.?), *Colpophyllia willoughbiensis*, *Montastrea tampaensis*, *Siderastrea siderea*, and *Leptoseris portoricoensis*. Incidental samples of these species were collected and analyzed for coral associates, but this sampling was not systematic, as in unit 2.

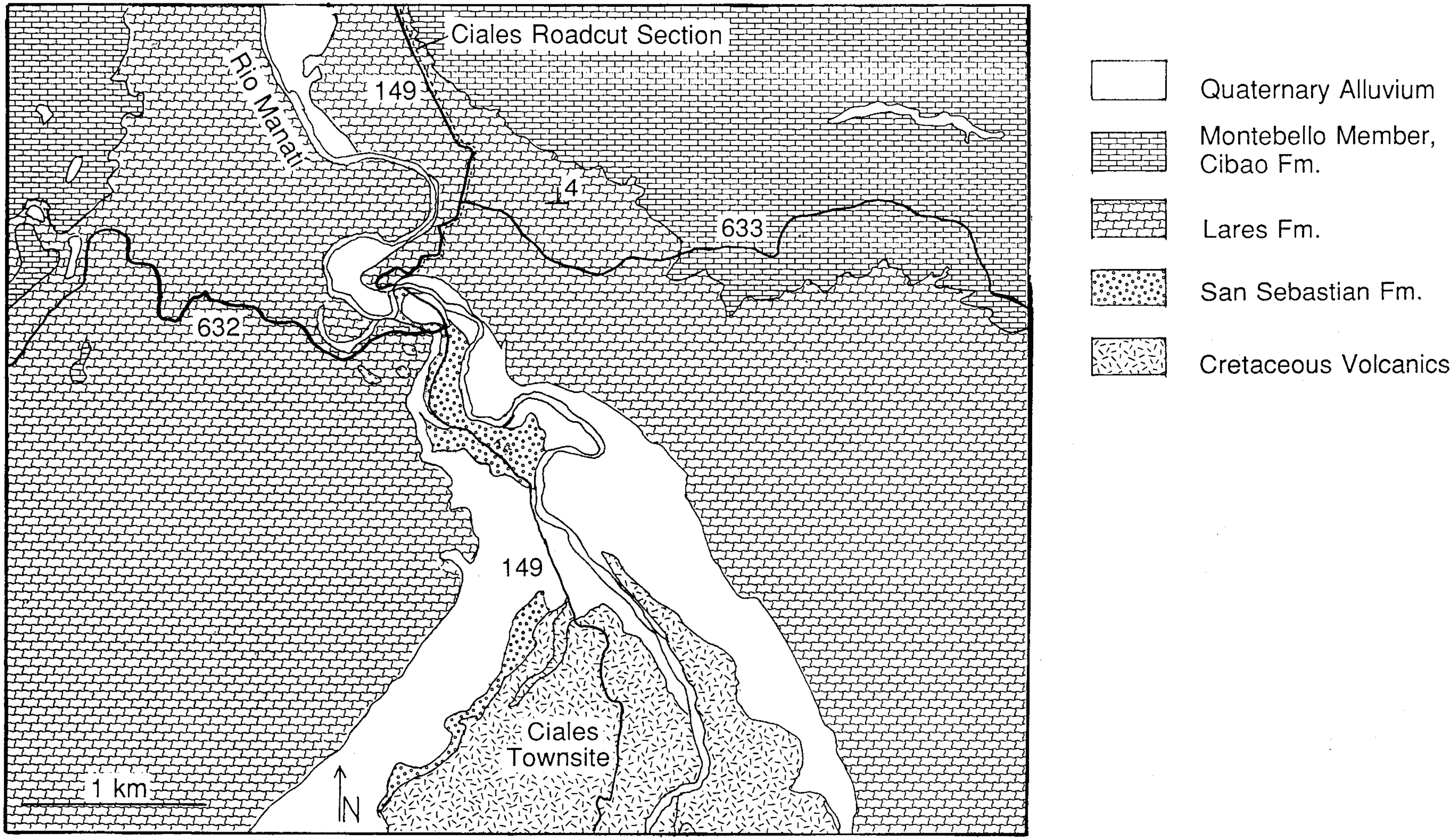
Material: Forty-two corals were collected from the lower part of the Lares Quarry section (see Appendix 1). Thsese are: 12 *Porites waylandi*, 4 *Montastrea costata*, 5 *Diploastrea*, 3 *Antiguastrea*, 3 *Porites baracoaensis*, 2 each of *Montastrea tampaensis*, *Stylophora*, *Alveopora*, *Cladocora*, and *Acropora*, and 1 each of *Colpophyllia* and *Pironastrea*. Most of these are fairly complete, and many are very large colonies (50-100 cm) from which only fragments could be collected. Nearly all are recrystallized and are quite well preserved; a few are internal molds. Corals sampled from the Lares section are listed in Appendix 1.

Age: The Lares Quarry section correlates to the approximate middle of the Lares Fm. (Frost, pers. comm., 1990). Frost (pers. comm., 1990) places the Oligocene-Miocene boundary (24 Ma) at the base of the Montebello, making the age of the Lares Quarry section approximately 25 Ma.

3.2.4 Ciales Roadcut Section

Frost (unpublished) has measured a second section through the Lares Fm. at the prominent roadcut along SR 149 about 3 km north of Ciales (map 3.5; fig. 3.5). As at the Lares Roadcut (SR 129) site, the Lares Fm. here represents a broad carbonate platform with occasional patch reefs. The patch reefs in this section have a similar species composition to those studied at the Lares Quarry

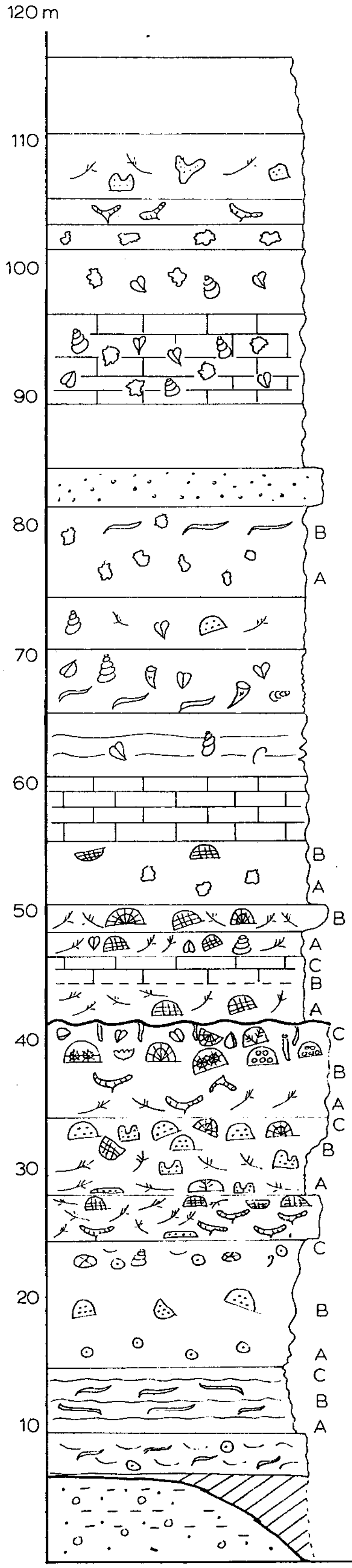
Map 3.5. Geologic Map, Ciales Roadcut Section, Ciales Quadrangle, Puerto Rico. Redrafted from USGS map.



Geologic Map, Ciales Section
Ciales Quadrangle

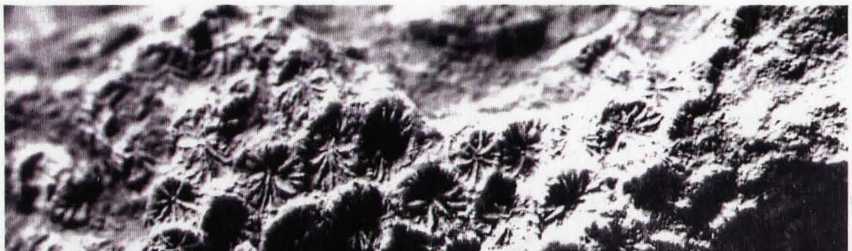
Figure 3.5. Stratigraphic Section, Ciales Roadcut Section. Redrafted from field section of Frost, et al. (unpublished).

Rock Column



Unit	Description	Interpretation
22	Uppermost beds inaccessible, weather with medium bedded character as in wackestone (below).	
21	*Porites*, branching, knobby, and encrusting.	
20	*Leptoseris* juveniles in wackestone.	
19	Coralline algae.	
18	Coralline algal – mollusc shell packstone.	
17	Scattered rhodolite – coralline algal fine grained wackestone–packstone with many molluscs.	
16	Nodular–weathering wackestone–packstone.	
15	Fine packstone.	
14	Coralline algal coarse packstones with large oysters near top.	
13	Mollusc – coral packstone.	
12	Mollusc–algal packstone with *Spondylus*, *Cricocyathus* solitary corals.	
11	Fine to medium bedded mollusc wackestone–packstone, slightly alternating degrees of induration.	
10	Moderately well–exposed fine wackestone–packstone. (SWITCH TO EAST SIDE OF ROAD)	
9	Wackestone with *Alveopora*. Rhodolite algal wackestone–packstone.	
8	Branching *Porites* framestone with *Montastrea* and *Alveopora*. Fine skeletal packstone with molluscs; *Porites* and *Alveopora* thicket on other side of road.	
7	Coralline algal packstone. Hardground, encrusted by coralline algae. Coralline algal/*Porites* packstone, *Alveopora tampae*.	
6	*Kuphus* and reef flat assemblage, cowry shells, *Conus*, large bivalves, *Leptomussa*, *Acropora saludensis*, *Diploastrea crassolamellata*, *Montastrea antiguensis*. Scattered juvenile *Leptoseris* wackestone. Branching *Porites* and *Leptoseris* (juvenile stage only).	* PATCH REEF
5	*Porites* and mixed reef framestone. *Porites* grainy wackestone–packstone. Frondose and branching *Porites*, nodular *Porites* and *Stylocoenia* wackestone.	
4	*Porites* and *Alveopora* thickets. *Leptoseris* bafflestone with rare foliose *Porites*.	* LAGOONAL CORAL THICKETS
3	Coralline algal/*Lepidocyclina* wackestone, echinoid and gastropod debris. Very hard *Porites* wackestone. More resistant weathering *Lepidocyclina* wackestone.	
2	Rubbly weathering packstone as below, becomes finer grained upwards. Two oyster layers.	
1	Massive to thick–bedded mollusc fragment – algal skeletal packstone with large *Crassostrea* oysters, sorted and rounded. Some *Lepidocyclina*, *Miogypsina*, and *Operculinoides*.	
	Covered by talus from Lares Cuesta.	
	San Sebastian Formation.	

Plate 3.4. *Antiquastrea cellulosa*, major framework builder on Oligocene reefs, became extinct at Oligocene-Miocene boundary. Lares Quarry site. Scale bar 1 cm.



site. A few species observed by Frost (unpublished) at the Ciales section, but not seen in any of the other study sites, were not included in these analyses. Corals were collected incidentally from units 4 and 6.

Material

Only five corals were collected from the Ciales section. These are: 4 samples of Leptoseris bafflestone from unit 4, all moldic, and a small part of one large, fairly complete colony of Agathiphyllia from unit 6, recrystallized but well preserved. Each of the Leptoseris samples contains parts of several colonies, including a few fairly complete "leaves" of this fan-like coral. These corals are quite well preserved internal molds. Coral samples from the Ciales section are listed in Appendix 1.

Age: Direct correlation with Frost et al.'s (1983) Lares section is not possible, but the units sampled here lie about one third of the way up through the Lares formation as seen in the Ciales section (figure 3.6). They are roughly correlative with the patch reef described from the Lares Quarry site.

3.3 Miocene Sites

Ponce Fm.

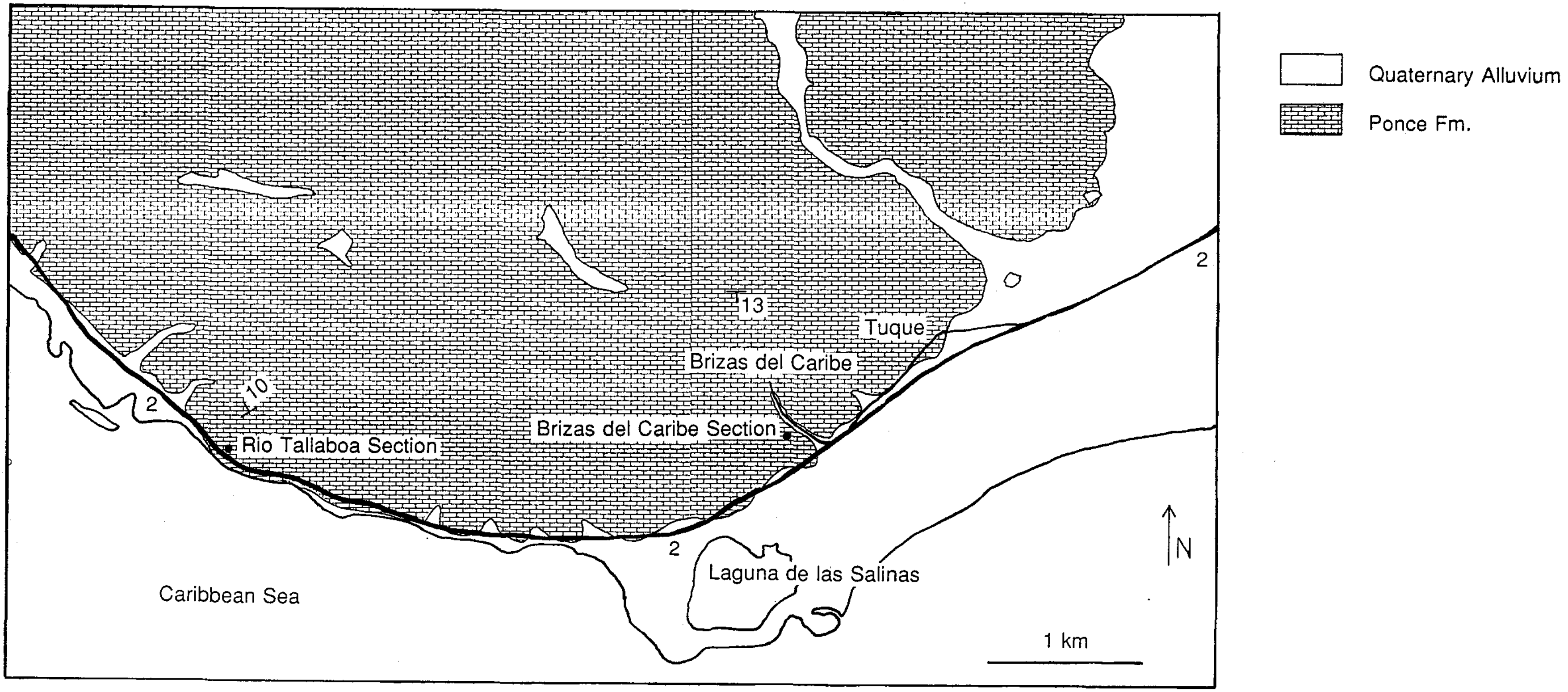
The Brizas del Caribe and Rio Tallaboa sites are fairly close together (map. 3.6), but precise correlation of the two is not possible due to extensive faulting.

Brizas del Caribe

The Brizas del Caribe outcrop is located west of Ponce, in a quarry behind the Cementerio del Camposanto de Jesucristo, immediately west of the road to the Brizas del Caribe neighborhood (map 3.6). All beds dip approximately 13° to the Southwest and the section is somewhat faulted in a horst-graben system (fig. 3.6). The section is about 60m thick, and is covered below and eroded above (fig. 3.7). The strata were deposited in a carbonate embayment or platform with seagrass beds and occasional patch reefs. Unit 2, the patch reef sampled for this study, can be traced horizontally for at least 100m, but is best exposed in a 30m face on the West wall of the quarry (plates 3.5a,b).

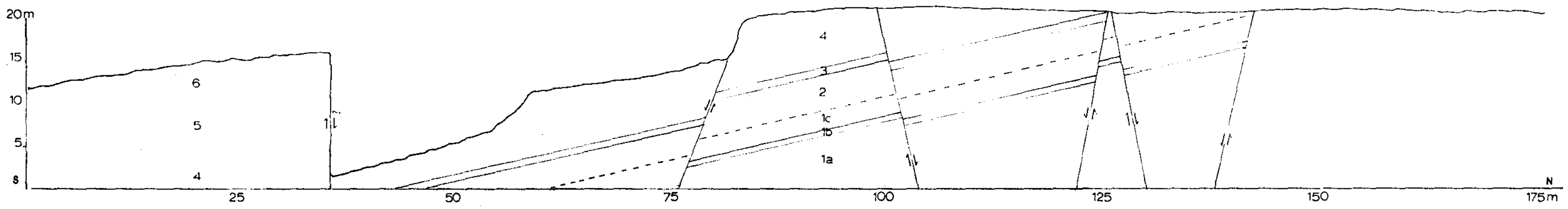
Unit 2 consists of a framestone bounded sharply below by platformal sediments and sharply above by a *Porites baracoaensis* - *P. trinitatis* rudstone, which is interpreted as either a branching *Porites* thicket or a storm lag. The lower part of the patch reef is dominated by the massive corals *Coscinaraea colei* and *Montastrea*

Map 3.6. Geologic Map, Brizas del Caribe and Rio Tallaboa Sections, Yauco and Punta Verraco Quadrangles, Puerto Rico. Redrafted from USGS map.



Geologic Map, Brizas del Caribe and Rio Tallaboa Sections
Yauco and Punta Verraco Quadrangles

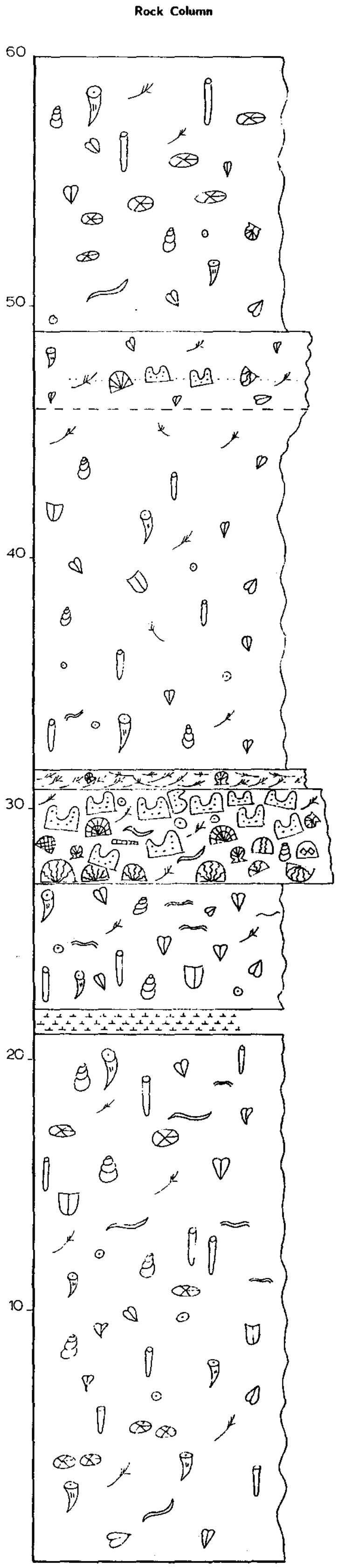
Figure 3.6. Structural cross-section, Brizas del Caribe Site.



Structural Cross Section Brizas del Caribe Site Ponce Fm. VE=1

Figure 3.7. Stratigraphic Section, Brizas del Caribe Section.

Stratigraphic Section Brizas del Caribe Site Ponce Fm.



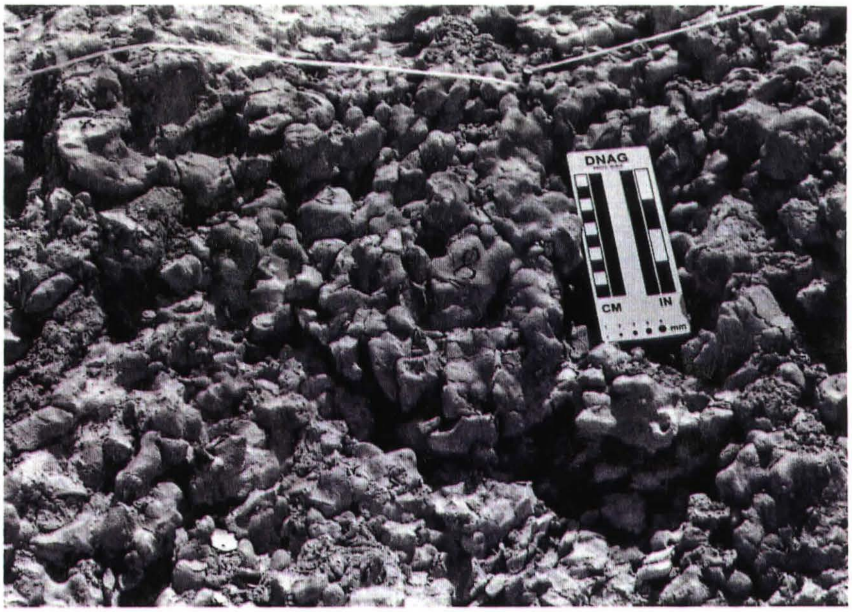
Unit	Description	Interpretation
6	Bioclastic wackestone–packstone with abundant infaunal bivalves, Clypeaster cubaensis, Kuphus tubes, Strombus and Sorites. Rare branching Porites baracoaensis and solitary corals.	SEAGRASS BEDS ON OPEN CARBONATE EMBAYMENT
5	Bioclastic wackestone–packstone with rare horizons of abraded branching and massive corals. Most skeletal components are bivalves, with some Strombus.	OPEN CARBONATE EMBAYMENT WITH NEARBY PATCH REEF
4	Bioclastic wackestone with infaunal bivalves, Kuphus tubes, and Strombus. Rare solitary corals, heavily bioturbated.	OPEN CARBONATE EMBAYMENT
3	Rudstone, composed primarily of Porites baracoaensis with common Pecten and uncommon Porites trinitatis.	STORM DEPOSIT OR PORITES THICKET
2	Framestone, composed primarily of Coscinaraea colei at base, superceded by encrusting to stout branching Porites trinitatis above. Uncommon Montastrea limbata, Pecten, Spondylus, Chama, Strombus, and Sorites. Rare Colpophyllia mexicana, Goniopora jacobiana, Arca, Pinna, and Astrocoenia portoricoensis.	PATCH REEF * STUDY UNIT *
1c	Bioclastic wackestone with common infaunal bivalves Strombus, and prominent subhorizontal burrows, and uncommon Kuphus tubes and solitary corals.	OPEN CARBONATE EMBAYMENT
1b	Heavily leached marl. Fossil content unknown.	KARSTIC ALTERATION
1a	Bioclastic wackestone with abundant infaunal bivalves, Kuphus tubes, Spondylus and Strombus, common Clypeaster cubaensis, solitary corals, and Sorites. Rare naticid gastropods and subhorizontal burrows.	SEAGRASS BEDS IN OPEN CARBONATE EMBAYMENT

Plate 3.5a. Outcrop view of Brizas del Caribe site. Framestone (Unit 2) is dark band in lower third of outcrop. Automobile for scale is approx 1.3m high.

Plate 3.5b. Brizas del Caribe outcrop, with 2m high sampling grid. Framestone (Unit 2) runs diagonally from lower left to centre right. Person for scale.

Plate 3.6a. <u>Porites</u> <u>trinitatis</u> thickets, Brizas del Caribe site, Unit 2.

Plate 3.6b. Solitary coral <u>Placocyathus</u> <u>barretti</u>, internal molds. These are frequently bored by sponges and bivalves. Brizas del Caribe site. Scale bar 1 cm.


DNAG
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limbata, which then grade upward into foliose and stout branching *Porites trinitatis*, which dominates the remainder of the patch reef (plate 5.6a). Other, less important, corals in unit 2 include *Agaricia* sp., ?*Astrocoenia* (portoricoensis), *Colpophyllia mexicana*, *Goniopora hilli*, *Stylophora (imperatoris?)*, and the solitary coral *Placocyathus barretti* (plate 5.6b). *P. barretti* was much more common in the other (non-reefal) units. *Colpophyllia* and *Goniopora* were found in float associated with Unit 2, while the remainder of the minor coral species were mainly found among the stout branches of *P. trinitatis*. Cheilostome bryozoans and *Pecten* are moderately abundant, and there are rare *Spondylus*, *Pinna*, *Arca*, and *Strombus*.

The branching corals in unit 3 are neither size sorted nor imbricated. Hence Frost (pers. comm., 1990) considers them an *in situ Porites* thicket which grew in quite shallow agitated water. Risk (pers. comm., 1989), however, noted that they are not heavily bioeroded, which suggests to him a storm lag. For this study, the exact interpretation of unit 3 is not important; it certainly was deposited in shallow water, and it brought the growth of the patch reef in unit 2 to an end.

The platform sediments above and below the patch reef are rich in *Strombus*, *Polynisces*, *Conus*, *Spondylus*, *Clypeaster cubaensis*, miosoritid large forams, infaunal bivalves, *Kuphus* tubes, and several species of hermatypic (Frost and Langenheim, 1974) solitary corals. These corals include *Placocyathus barretti* (most abundant), *Thysanus* sp., and *Antillophyllia* sp. All of these sediments are heavily bioturbated and contain both large diameter (5-8mm) and small diameter (2-3mm) subhorizontal burrows. The *Clypeaster* and the large forams in particular suggest that seagrass beds dominated this carbonate embayment during its deposition (Ivany, et al., 1990). The solitary corals, *Strombus*, and *Spondylus* are all heavily bioeroded (e.g. plate 6.4).

Material: Forty-five corals, and an assortment of molluscs, echinoids, and forams, were collected from the Brizas outcrop. Most of the colonial corals are from unit 2, but solitary corals and associated fauna were more abundant in units above and below the patch reef. These corals collected are: 13 *Coscinaraea*, 13 *Porites trinitatis*, 5 *Montastrea*, 4 *Porites baracoaensis*, 3 *Agaricia*, 5 *Placocyathus*, and one each of *Colpophyllia* and *Goniopora*, Most of the *Coscinaraea* and *P. trinitatis* are fairly complete and well-preserved; the *Montastrea* are usually heavily leached, and are generally incomplete, although they do not show signs of physical abrasion. *Agaricia*, *Placocyathus*, and *Colpophyllia* are preserved exclusively as molds. The single specimen of *Goniopora* is a poorly preserved fragment of a colony. These samples are listed in Appendix 1.

Age: The Brizas Del Caribe site is probably in the middle to upper part of the Ponce Fm., which is considered middle Miocene in age. Estimated absolute age is approximately 15 Ma.

3.3.2 Rio Tallaboa

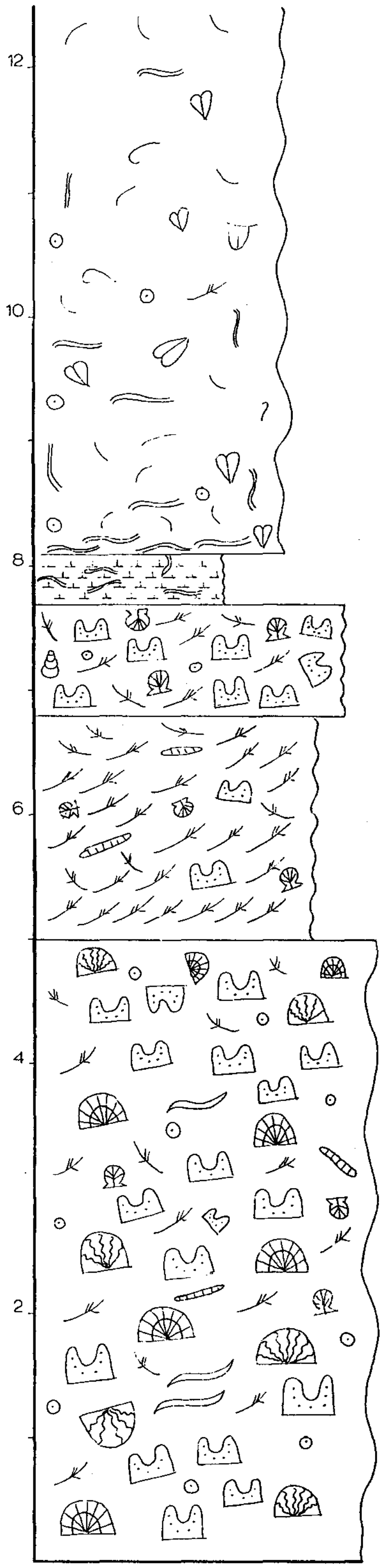
The Rio Tallaboa outcrop is located along Hwy 2 at km 217, immediately east of the highway crossing with the Rio Tallaboa (map 3.6). The beds here dip 10° to the West, and the outcrop is surrounded by minor faults and zones of karstic collapse (plate 3.7).

Like the patch reef at Brizas del Caribe, the framestone unit at Rio Talloboa is dominated by, in order of decreasing abundance, <u>Porites trinitatis</u>, <u>Montastrea limbata</u>, and <u>Coscinaraea colei</u>. The framestone (unit 1) is at least 5m thick, and is sharply overlain by fine and stout branching <u>Porites</u> rudstone with some <u>Pecten</u>, <u>Spondylus</u>, and platy cheilostome bryozoans. These 3m of rudstones are overlain by a recessed marly layer and then by more platform sediments (figure 3.8). The section is interpreted as a patch reef and branching <u>Porites</u> thicket on a carbonate embayment, quite similar to the Brizas del Caribe site (which is better exposed). The Rio Tallaboa site was only incidentally sampled.

Figure 3.8. Stratigraphic Section, Rio Tallaboa Section.

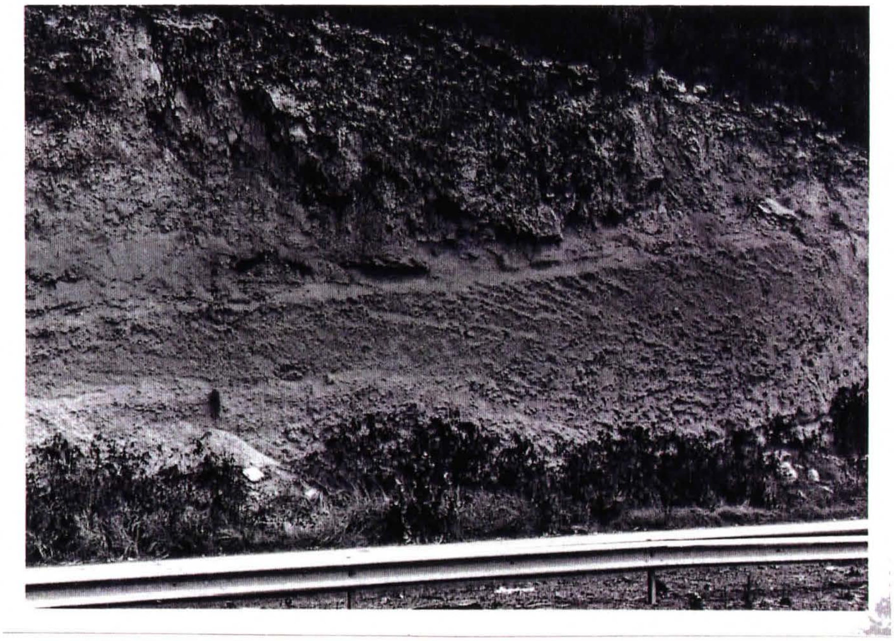
Stratigraphic Section Rio Tallaboa Site Ponce Fm.

Rock Column



Unit	Description	Interpretation
5	Heavily leached wackestone with large horizontal and vertical burrows, rare branching *Porites* fragments, disarticulated and articulated infaunal bivalves, rare *Sorites*.	OPEN CARBONATE EMBAYMENT
4	Heavily leached marl with prominent thick sub-horizontal burrows and rare, thinner, vertical burrows. No macrofossils.	NEARSHORE PLATFORM MUDS
3	*Porites trinitatis* and *P. baracoaensis* rudstone with *Pecten*, platy bryozoans, *Sorites*, and rare *Strombus*.	MIXED (EXPOSED) PORITES THICKET
2	*Porites baracoaensis* rudstone with uncommon *Porites trinitatis*, platy bryozoans, and *Pecten*.	FINE (PROTECTED) PORITES THICKET
1	Framestone dominated by stout branching and semi-platy *Porites trinitatis* with common *Montastrea limbata*, *Coscinaraea colei* and *Porites baracoaensis*. Uncommon *Spondylus*, *Pecten*, platy bryozoans, and *Sorites*.	PATCH REEF

Plate 3.7. Outcrop view of Rio Tallaboa site. Framestone (unit 1) is at lower right. Dark area at top centre is zone of Karstic collapse. Face is 8-9m high. Bushes at base of outcrop mostly 2-3m high.



Material: Only two massive corals, one Coscinaraea and one Montastrea, were collected and slabbed from this site. These corals are each about 15 cm in diameter and are fairly complete. As at the Brizas site, the Coscinaraea is recrystallized, and the Montastrea is moldic. They are described in detail in Appendix 1, along with the coral and oyster collected from the Guayanilla Dump site (basal Ponce Fm.).

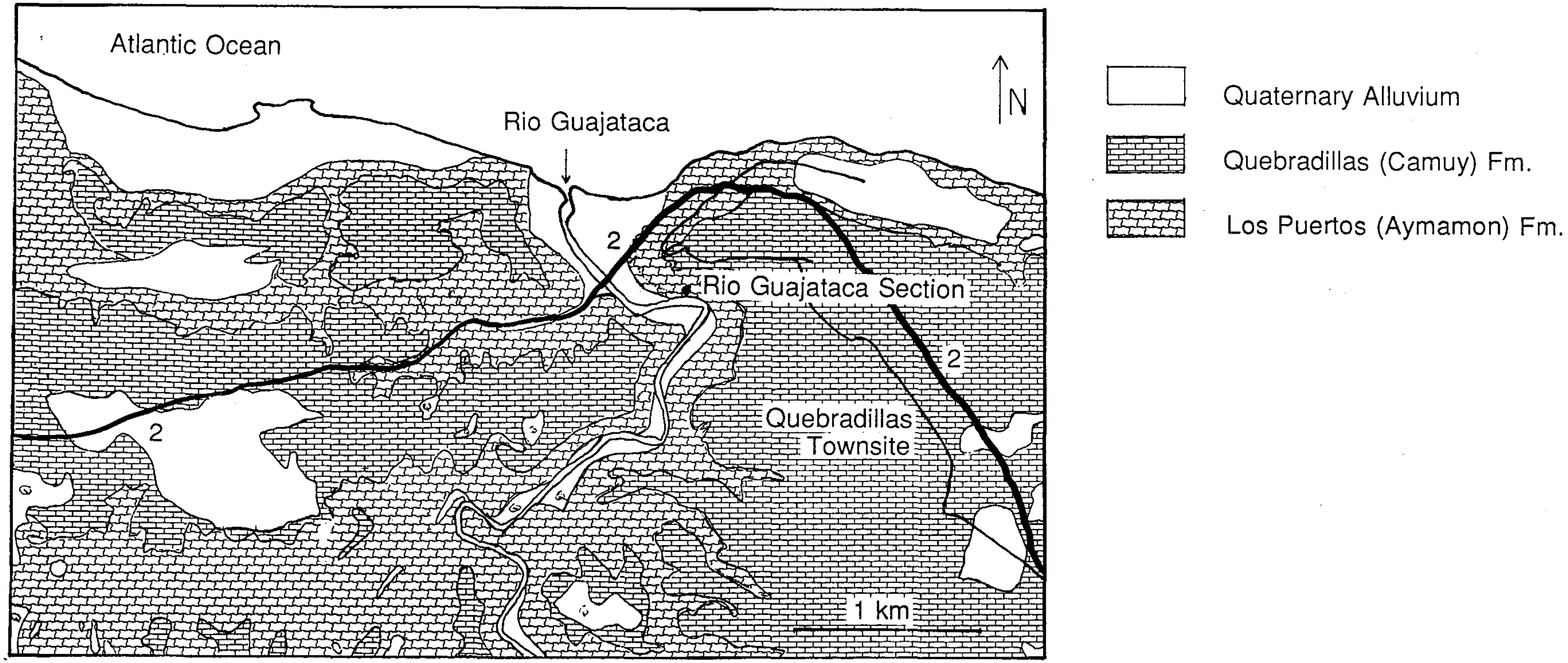
Age: the Rio Tallaboa site is probably of equivalent age to the Brizas del Caribe site, estimated at about 15 Ma.

Los Puertos Fm. (Aymamon Mbr.)

3.3.3 Rio Guajataca Section

This outcrop is located in a small quarry at the bend in the Rio Guajataca about 200m south of the crossing with Hwy 2 between Quebradillas and Isabella. Quarrying operations have exposed about 15m of dirty yellow-brown limestone along the east wall of the river canyon (plate 3.8); only the lower 4-5m are safely accessible. Hubbard (1920) collected fossil molluscs from this site (Monroe, 1980).

The site has been extensively karstified, making it unstable and nearly uniform in aspect. Only two units can be distinguished: a patch reef 4m thick and carbonate platform sediments 11-12m thick, Map 3.7. Geologic Map, Rio Guajataca Section, Quebradillas Quadrangle, Puerto Rico. Redrafted from USGS map.

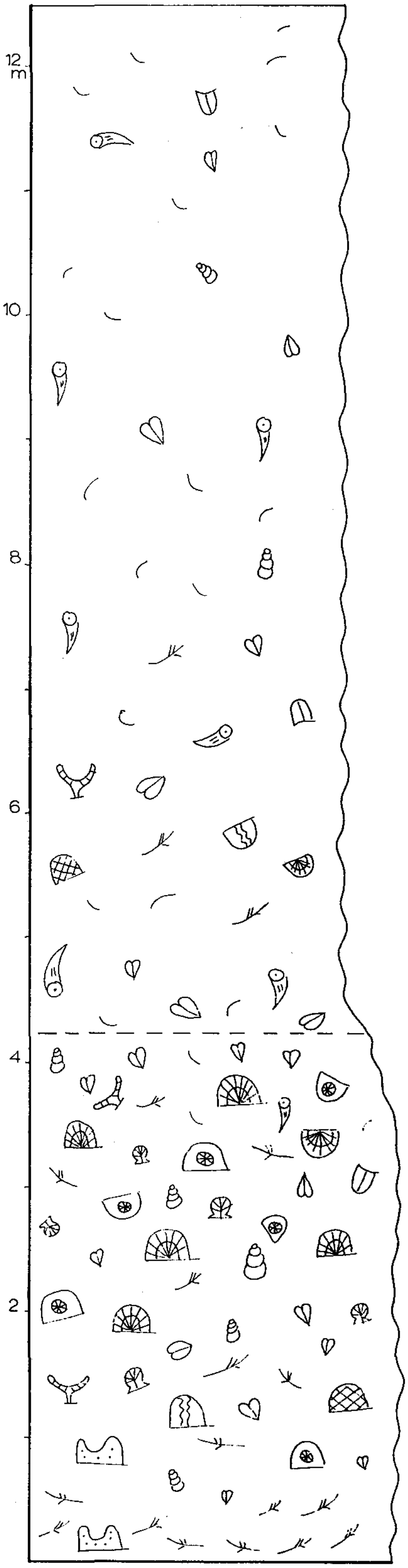


Geologic Map, Rio Guajataca Section
Quebradillas Quadrangle

Figure 3.9. Stratigraphic Section, Rio Guajataca Section.

Stratigraphic Section Rio Guajataca Site Los Puertos (Aymamon) Fm.

Rock Column



Unit	Description	Interpretation
	Exposed to approx. 15m, inaccessible.	
2	Skeletal wackestone composed primarily of molds of disarticulated and articulated infaunal bivalves with molds of solitary corals, *Strombus*, *Stylophora*, and rare colonial corals, mostly near base.	OPEN CARBONATE PLATFORM
1	Framestone, with massive corals far more abundant than either stout or fine branching species. Dominant species are *Montastrea limbata* and *Solenastrea hyades*, with uncommon *Porites trinitatis*, *P. baracoaensis* and *Stylophora*. Rare *Favia mexicana*, *Colpophyllia mexicana* and *Agaricia* sp. Uncommon articulated infaunal bivalves, *Strombus*, *Pecten*, and solitary corals.	SEDIMENT STRESSED PATCH REEF

Plate 3.8. Outcrop view of Rio Guajataca site. Note horizon of massive coral heads in lower third of outcrop. Darker material higher on rock face is Unit 2, interpreted as carbonate platform sediments. Seated person for scale.

of which only the lower third is accessible (by ladder). The patch reef consists of a *Montastrea limbata/altissima* - *Solenastrea* framework with rarer *Agaricia* sp., *Colpophyllia mexicana*, *Favia mexicana*, *Goniopora hilli*, *Porites trinitatis*, *Stephanocoenia duncani*, and *Stylophora* sp. Solitary corals include *Placocyathus barretti* and *P. moorei*. The rarity of *Porites* is unusual for reefs of this age (Frost, pers. comm., 1990). There are abundant *Strombus* and infaunal bivalves, suggesting a fair amount of loose sediment between coral heads. Many of the corals, and all of the molluscs, are preserved as molds. Both the corals and the molluscs are heavily bioeroded, suggesting a high productivity environment (e.g. Rose and Risk, 1985), possibly a mixed coral-seagrass bank.

The overlying platform sediments are poorly exposed and consist mainly of molds of gastropods and disarticulated bivalves together with a few solitary corals.

Material: Forty-three corals were collected for bioeroder samples from this site. These are: 17 *Montastrea limbata*, 4 *Solenastrea*, 6 *Stylophora*, 3 *Porites trinitatis*, 2 each of *Goniopora*, *Agaricia*, *Favia*, and *Colpophyllia*, and one each of *Porites baracoaensis*, *Siderastrea siderea*, *Placocyathus moorei*, and

Placocyathus barretti. Nearly all of these corals are moldic, and nearly all are incomplete. They do not, however, show signs of mechanical abrasion. Specimens are listed in Appendix 1.

Age: The exact age of the Los Puertos (Aymamon) Fm. is not known. Moussa, et al., (1987) placed the Aymamon in the late Middle Miocene, and the Rio Guajataca site is quite close to the upper contact with the Quebradillas Fm. Frost (pers. comm., 1990) considers the Rio Guajataca site to be Tortonian (early Late Miocene). Absolute age is probably about 8-10 Ma.

3.4 Data analysis

Abundance of fossils at each outcrop was qualitatively described, but not quantitatively measured. Therefore, facies distribution patterns are based primarily on presence/absence data. and the number of sites studied is too small for statistical tests to be meaningful.

Morphometric analysis of modern and fossil sponge borings was performed using Lotus 1-2-3. The following variables were measured on approximately 200 boreholes: maximum diameter, minimum diameter, irregularity (a scale of 1 to 5, in which 1 is a smooth circular hole, and 5 is a jagged complicated polygon), separation distance from next chamber, aperture (or connecting filament) diameter and length, and number of chambers. In borings which had multiple chambers, each of the first 5 variables was repeated on up to six chambers per colony. All measurements were made with calipers under a hand lens or binocular microscope, and recorded to a precision of .1mm. Results of this morphometric analysis are discussed in chapter 4.

3.5 Nomenclature

Coral systematic nomenclature for this study follows Wells (1957), Frost and Langenheim (1974), Foster (1986, 1987) and Veron (1986). Budd (1990) is continuing with morphometric analysis and species level reclassification of Neogene corals of the Caribbean. To date, only the Poritidae (Foster, 1986; see table 3.1), the genus Stephanocoenia (Foster, 1987), and solitary corals in the Caryophylliina and Dendrophylliina (Cairns and Wells, 1987) have been revised. Budd (1990) indicates up to seven Miocene species of Montastrea and Siderastrea, but she provides no key or figures for identification of these different species. Continuing taxonomic work in this regard will not seriously affect the results of the present study, since the majority of coral genera which became extinct were represented by only one species (see chapter 4, fig. 4.1).

Coral associates are mostly preserved as trace fossils, and ichnospecies names are mostly used instead of organism names. Hence, boring sponges are mostly Entobia (Bromley, 1970). Bromley and D'Alessandro (1989) caution that actual diversity of boring organisms cannot be inferred directly from trace fossil diversity. Rather, sponge borings can best be attributed to groups of species within the same genus. Bivalves were often preserved with their shells inside their borings, so the zoological names (Lithophaga, Gastrochaena) are used, rather than the ichnological name (Gastrochaenolites; Kelly and Bromley, 1984). Worms generally lack hard parts and can only preserved as the boring Trypanites (Bromley, 1970). Documentation of taxonomic turnover at the genus level in corals and the ichnospecies level in coral associates is roughly comparable.

Table 3.1. List of all poritid species described from the Miocene through Lower Pliocene of the Caribbean region, showing current taxonomic status (modified from Foster, 1986).

Alveropora fenestrata = P. portoricensis
A. tampae*/** (= A. chiapaneca of Frost and Langenheim, 1974)

Goniopora aucillana = G. hilli
G. ballistensis = P. portoricensis
G. calhounensis
G. canalis = G. hilli
G. cascadensis = P. portoricensis
G. clevei = P. portoricoensis
G. decaturensis = ?G. imperatoris
G. hilli*/**
G. imperatoris*
G. jacobiana = G. hilli/**
G. matsoni = P. portoricensis
G. panamensis
G. tampaensis = G. hilli

Porites anguillensis*
P. astreoides (fossil) = P. waylandi
P. baracoaensis*/**
P. carrizensis*
P. chipolanum*
P. collegniana = P. waylandi
P. conviviatoris n sp.* (Foster, 1986)
P. douvillei = ?P. baracoaensis/**
P. howei = ?P. portoricensis
P. macdonaldi*
P. portoricensis*
P. toulai = P. baracaoensis
P. trinitatis*/**
P. waylandi* nom. nov. (=P. panamensis of Frost and Langenheim)./**

* indicates valid species.
** indicates species found in this study.

Chapter 4: Species Composition and Species Turnover of corals and coral associates on fossil reefs.

4.1 Coral Distribution and Survivorship

Tables 4.1 and 4.2 list the coral species found on the Oligocene and Miocene reefs studied, and indicate whether, and where, each genus lives today. Figure 4.1 summarizes this information in the form of a range chart. My one record of *Astrocoenia* from the Miocene, observed in the field at the Brizas del Caribe site, but not collected, is questionable, and is disregarded in calculations of percent survival. *Astrocoenia* has not been reported from the Miocene elsewhere. *Alveopora* has been reported from the Middle Pliocene of the Dominican Republic (Foster, 1986). *Agathiphyllia* and *Siderastrea conferta* have been reported from the Middle Miocene of Anguilla, BWI (Budd, et al., 1989). None of these taxa were observed in the Miocene in this study. As indicated in table 4.1, *Alveopora* is extant, but restricted to the Indo-Pacific, and *Agathiphyllia* is extinct. *S. conferta* is morphologically closest to the Indo-Pacific *Pseudosiderastrea*, and is considered extinct in the Caribbean.

Although *Favia*, *Solenastrea*, and *Stephanocoenia* have been reported from the Oligocene of the Caribbean and Mediterranean, (Vaughan, 1921; Wells, 1957; Frost and Weiss, 1979), they were not observed on these sites, and will not be included in calculations of survivorship. Frost (pers. comm., 1991) questions the reported occurrence of Oligocene *Solenastrea*.

Table 4.1: Diversity and Survivorship of Oligocene Corals

	Study Sites				Mod. Distrib.		
Coral Species	Gu	Gn	Ls	Cl	Ext.	IP	Car.
Actinacis sp. cf. alabamiensis			x		X		
Acropora saludensis		x	x	x		X	X
Agathiphyllia roxboroughi	x		x	x	X		
Alveopora tampae			x	x		X	
Antiguastrea cellulosa	x	x	x		X		
Astreopora sp.	x	x	x			X	
Astrocoenia		x			X		
Caulastrea portoricoensis	x	x				X	
Cladocora bosquensis			x				X
Colpophyllia willoughbiensis	x		x				X
Diploastrea crassolamellata	x	x	x	x		X	
Favites polygonalis	x	x				X	
Goniopora hilli	x	x	x			X	
Hydnophora sp. (unnamed)		x				X	
Leptoseris portoricoensis		x	x	x		X	X
Montastrea costata	x		x			X	X
Montastrea tampaensis			x			X	X
Pironastrea sp. (?) (Siderastreidae)			x		X		
Portes baracoaensis	x		x	x		X	X
Porites waylandi	x	x	x	x		X	X
Siderastrea conferta	x					X	
Siderastrea siderea			x			X	X
Stylocoeniella lobatorotundata	x	x				X	
Stlyophora imperatoris	x	x	x			X	
Totals: 24	14	13	18	7	4	18	8

Gu: Guayanilla II section. Gn: Guanica section.
Ls: Lares section. Cl: Ciales section.

Ext.: Genus extinct globally.
IP. : Genus extant in Indo-Pacific.
Car.: Genus extant in Caribbean.

Sources of Modern Distributions: Wells, 1956; Wood, 1983; Veron, 1986. Ciales list includes only units 4 and 6 of Frost, 1985, unpub. Only species observed elsewhere are reported from the Ciales site in order to maintain balance with Miocene sampling.

Notes: (1) Budd, et al. (1989) reported *Siderastrea conferta* and *Agathiphyllia anquillensis* from the Middle Miocene of Anguilla, BWI. (2) Foster (1986) reported *Alveopora tampae* from the Pliocene of the Dominican Republic. (3) *S. conferta* is morphologically closer to *Pseuodsiderastrea* than to *S. siderea*, which only survives in the Indo-Pacific (Wood, 1983; Veron, 1986). For this reason, it is classified as extant only in the Indo-Pacific.

Table 4.2: Diversity and Survivorship of Miocene corals

Coral Species	Study Sites Br	RT	RG	Mod. Distrib. Ext.	IP	Car.
Agaricia sp.	x		x			X
Astrocoenia portoricoensis(?)	x			X		
Colpophyllia mexicana (fl)	x		x			X
Coscinaraea colei	x	x			X	
Favia sp. cf. mexicana (fl)			x		X	X
Goniopora hilli (fl)	x		x		X	
Montastrea altissima			x		X	X
Montastrea limbata	x	x	x		X	X
Porites baracoaensis	x	x	x		X	X
Porites trinitatis	x	x	x		X	X
Solenastrea hyades			x			X
Stephanocoenia duncani			x			X
Stylophora sp.	x		x		X	
Total: 12(13)	9	4	11	1	8	9

In addition, the following solitary hermatypic corals (Frost and Langenheim, 1974) were found. Of these, only *P. barretti* occurred in reefal facies. All three genera became extinct at the Plio-Pleistocene boundary (Frost, 1977).

	Br	RG	Ext.
(Placocyathus barretti)	x	x	X
(Placocyathus moorei) (fl)		x	X
(Thysanus sp.) (fl)	x		X
(Antillophyllia sp.) (fl)	x		X

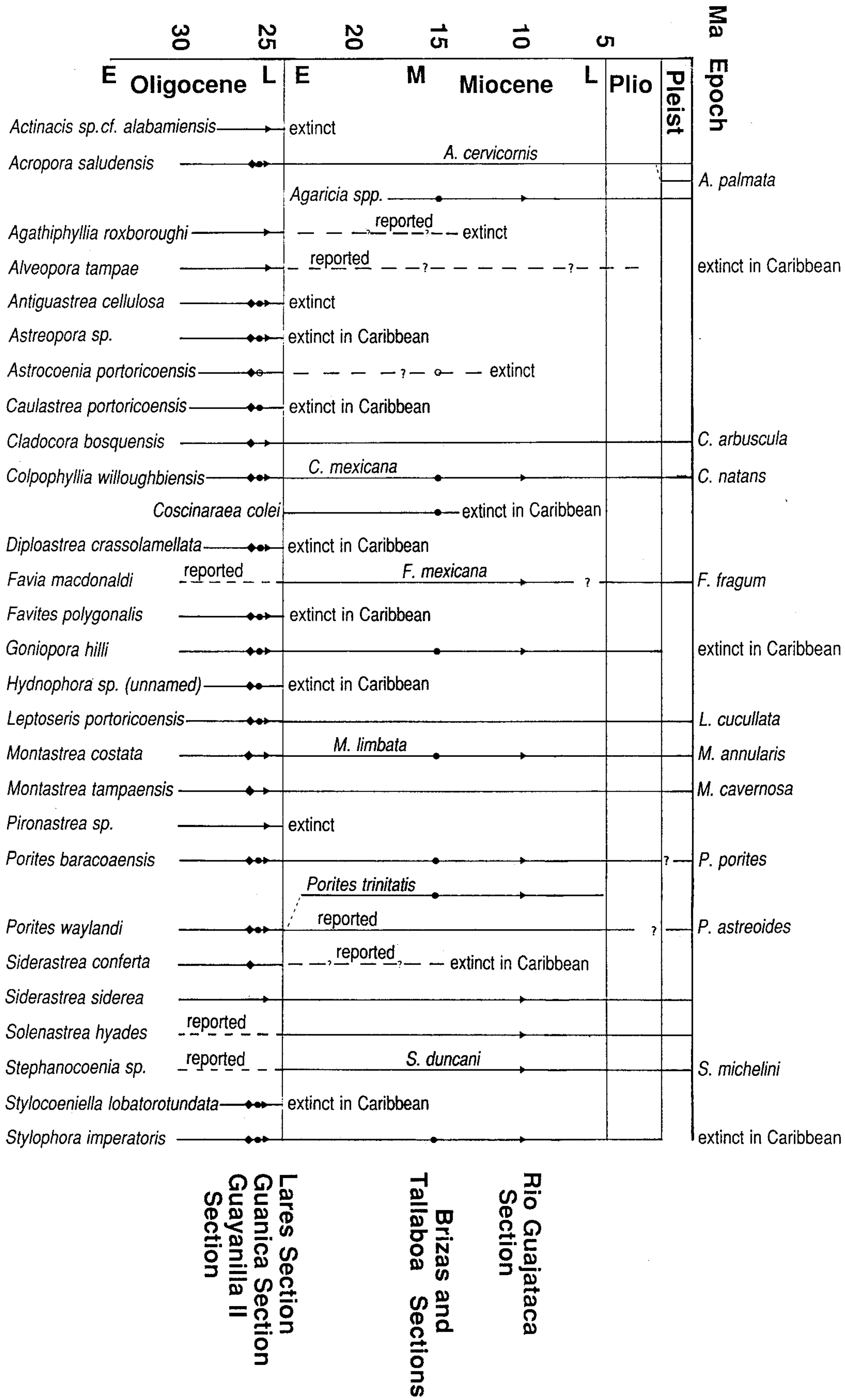
Br :Brizas del Caribe Section.
RT :Rio Tallaboa Section   RG :Rio Guajataca Section

Ext. : Genus extinct globally.
IP : Genus extant in Indo-Pacific.
Car. : Genus extant in Caribbean.

Source of Modern Distributions: Wells, 1957; Wood, 1983; Veron, 1986.

Note: (1) Low species count at RT is probably erroneous. (2) *Montastrea altissima* and *M. limbata* may be synonyms. (3) Occurrence of *Astrocoenia* is questionable.
(fl) denotes species found only in float.

Figure 4.1. Range Chart for Corals. Triangles, circles, and diamonds in the Oligocene represent occurrence at the Lares/Ciales, Guanica, and Guayanilla sites, respectively. Triangles and circles in the Miocene represent occurrence at the Rio Guajataca and Brizas del Caribe/Rio Tallaboa sites, respectively. Unfilled symbols represent questionable records. Time scale as in fig. 1.2. Diagrams are meant to imply neither gradual nor punctuated evolution of coral species, but rather the apparent pattern of ecological and phyletic replacement within lineages.


Ma
30
25
20
15
10
5
Epoch
E Oligocene L
E M Miocene L
Plio
Pleist
Actinacis sp.cf. alabamiensis
extinct
Acropora saludensis
A. cervicornis
A. palmata
Agaricia spp.
Agathiphyllia roxboroughi
reported
?
extinct
Alveopora tampae
reported
?
?
extinct in Caribbean
Antiguastrea cellulosa
extinct
Astreopora sp.
extinct in Caribbean
Astrocoenia portoricoensis
?
extinct
Caulastrea portoricoensis
extinct in Caribbean
Cladocora bosquensis
C. arbuscula
Colpophyllia willoughbiensis
C. mexicana
C. natans
Coscinaraea colei
extinct in Caribbean
Diploastrea crassolamellata
extinct in Caribbean
Favia macdonaldi
reported
F. mexicana
?
F. fragum
Favites polygonalis
extinct in Caribbean
Goniopora hilli
extinct in Caribbean
Hydnophora sp. (unnamed)
extinct in Caribbean
Leptoseris portoricoensis
L. cucullata
Montastrea costata
M. limbata
M. annularis
Montastrea tampaensis
M. cavernosa
Pironastrea sp.
extinct
Porites baracoaensis
?
P. porites
Porites trinitatis
Porites waylandi
reported
?
P. astreoides
Siderastrea conferta
reported
?
?
extinct in Caribbean
Siderastrea siderea
Solenastrea hyades
reported
Stephanocoenia sp.
reported
S. duncani
S. michelini
Stylocoeniella lobatorotundata
extinct in Caribbean
Stylophora imperatoris
extinct in Caribbean
Lares Section
Guanica Section
Guayanilla II Section
Brizas and Tallaboa Sections
Rio Guajataca Section

Counting Agathiphyllia, Alveopora, and Astrocoenia as extinct or regionally extinct, generic extinction among corals at the Oligocene-Miocene boundary was 59%; species extinction, 54% (see summary, table 4.7). Counting these three questionable genera as surviving, generic extinction was 48%; species extinction, 44%. Each of these figures roughly agrees with Frost's (1977a) estimate of 50% generic extinction; some increased variation should be expected from the small number of sites in this study.

All corals found primarily or exclusively at shelf-edge barrier reef complex sites became regionally extinct, although not all corals found at those sites became extinct (table 4.3). This pattern is statically significant (χ^2=12.093, p<.005, d.f.=2).

Table 4.3. Summary chart of Oligocene coral distribution and survivorship. (χ^2=12.093, p<.005, d.f.=2).

	Shelf Edge Only	Patch Reef only	Both
Survived	0	4	8
Extinct	6	2	4

Frost and Langenheim (1974) found about 65 coral species in the Oligocene of Chiapas, and Frost (pers. comm., 1990) estimates that there may be 90-100 species in the Caribbean Oligocene coral fauna. Frost (1977a) reported 43 Miocene hermatypic coral species, of which 7 were solitary corals (usually found in off-reef facies). Clearly, there were many more corals than those seen in the sections studied here. For each age, about 1/3 of the total reported coral fauna was found in this study (see table 4.7).

The similar proportions of the species found in this study to the total reported fauna for each age shows that these samples are representative, and do not over-represent either the Oligocene or the Miocene. Thus the high species turnover between the Oligocene and the Miocene seen in these sites is probably real, and not a sampling artifact. The stratigraphic distribution of the study sites does not allow documentation of the abruptness of the extinction as reported by Frost (1977a, unpublished) in Caribbean and Middle Eastern compilations.

4.2 Coral Associate Description, Distribution, and Survivorship

Table 4.4 lists the coral associates found in the Oligocene and Miocene reefs studied. Figure 4.2 summarizes this information as a range chart. Figure 4.3 illustrates the morphology of the sponge borings; their similarity with modern borings is discussed in chapter 5. Table 4.5 lists the results of a morphometric analysis of the sponge borings. Table 4.6 lists the occurrence of each coral associate in each coral species examined.

Table 4.4: Coral Associates Occurrence Oligocene and Miocene Study Sites.

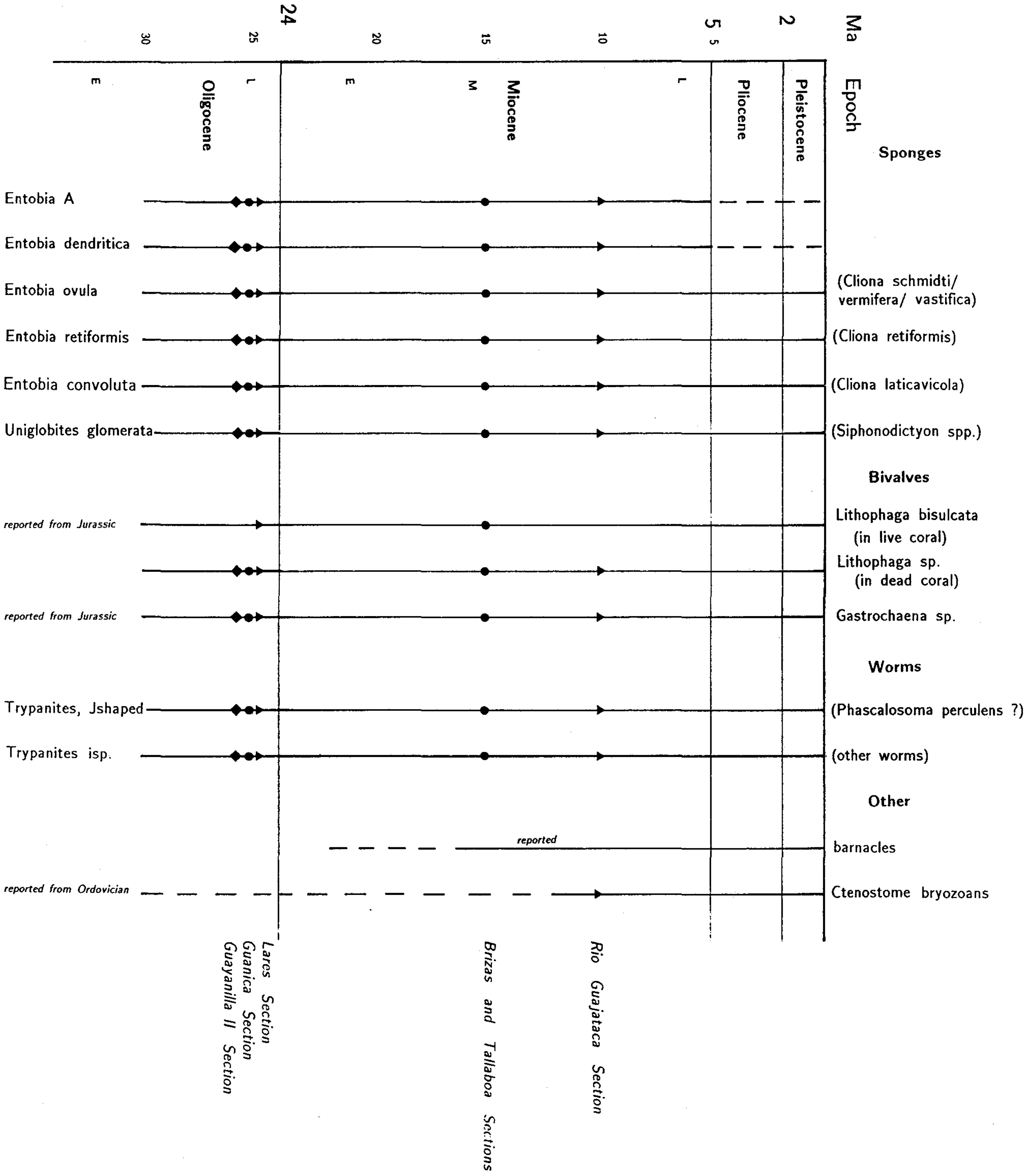
	Oligocene Sites				Miocene Sites		
Coral Associate Species	Gu	Gn	Ls	Cl	Br*	Rg	(*& RT)
Sponges							
(*Cliona*)							
Entobia A (cf. geometrica)	x	x	x	x	x		
Entobia B (cf. dendritica)	x	x	x	x	x	x	
Entobia ovula	x	x	x	x	x	x	
Entobia retiformis	x	x	x	x	x	x	
(*Cliona laticavicola*)							
E. convoluta n. isp., "Ct."	x	x	x	x	x	x	
(*Siphonodictyon*)							
Uniglobites glomerata	x	x	x	x	x	x	
Bivalves							
Lithophaga bisulcata			x		x		
Lithophaga sp.	x	x	x	x	x	x	
Gastrochaena sp.	x	x	x	x	x	x	
Worms							
(*Phascalosoma* spp.)							
Trypanites, J-shaped	x	x	x	x	x	x	
(other worms)							
Trypanites ispp.	x	x	x	x	x	x	
Crustaceans							
(Balanidae)	x						
Bryozoans							
(*Harmoria* sp.?)						x	

Site Abbreviations:

Gu	Guayanilla II	Br	Brizas del Caribe
Gn	Guanica	RT	Rio Tallaboa
Ls	Lares Quarry	RG	Rio Guajataca
Cl	Ciales Roadcut		

Notes: *Lithophaga* makes the boring *Gastrochaenolites torpedo*, but there is as yet no trace name for *Lithophaga* borings with false floors (as made by *L. bisulcata* boring into live coral). *Gastrochaena* makes the boring *Gastrochaenolites turbinatus*. Endolithic barnalces were not found in this study, but they are reported from the Early Miocene. Only epilithic barnalces were found on the Oligocene site.

Figure 4.2. Range Chart for Coral Associates. Symbols as in fig 4.1.


Ma
2
5
24
30
25
20
15
10
5
Epoch
Pleistocene
Pliocene
Miocene
Oligocene
E
L
E
M
L
Sponges
Entobia A
Entobia dendritica
Entobia ovula
(Cliona schmidti/ vermifera/ vastifica)
Entobia retiformis
(Cliona retiformis)
Entobia convoluta
(Cliona laticavicola)
Uniglobites glomerata
(Siphonodictyon spp.)
Bivalves
reported from Jurassic
Lithophaga bisulcata (in live coral)
Lithophaga sp. (in dead coral)
reported from Jurassic
Gastrochaena sp.
Worms
Trypanites, Jshaped
(Phascalosoma perculens ?)
Trypanites isp.
(other worms)
Other
reported
barnacles
reported from Ordovician
Ctenostome bryozoans
Lares Section
Guanica Section
Guayanilla II Section
Brizas and Tallaboa Sections
Rio Guajataca Section

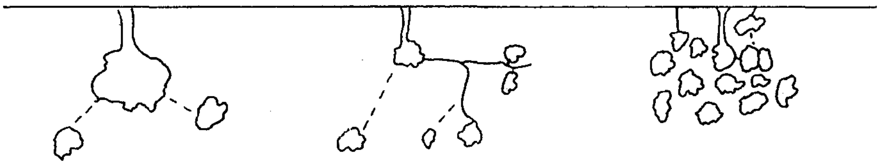
Four groups of internal coral associates were found in the Oligocene and Miocene corals: sponges, bivalves, worms, and bryozoans. Newman et al. (1976) report endolithic (but not truly boring) balanid barnacles from Early and Middle Miocene corals in the Caribbean.

Sponges include the ichnogenera Entobia, unnamed, and Uniglobites, made by the genera Cliona, Cliona laticavicola, and Siphonodictyon, respectively. Bivalves include the ichnospecies Gastrochaenolites torpedo and G. lapidicus, and body fossils of Lithophaga, and Gastrochaena. Worm borings mostly follow the corallites, but some are J-shaped, and others are convoluted. Stearley and Ekdale (1988) report J-shaped worm burrows made by Phascalosoma; worms in similar shaped burrows of modern Diploria were found at Caracoles reef, La Parguera (see chapter 5).

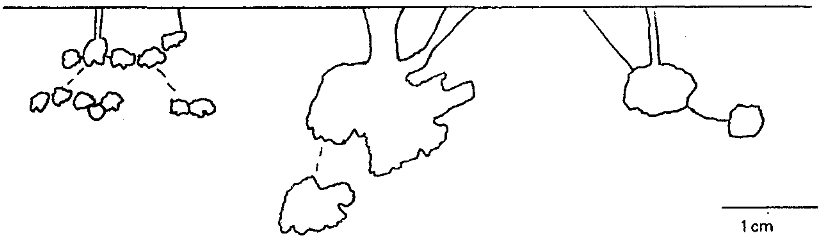
4.2.1 Sponges

Sponge borings are preserved in two ways: as sediment infilled holes within the coral skeleton in recrystallized corals, or as internal molds of the galleries in internal molds of corals or other substrates. Among the Entobia molds, three different morphologies of borings can be distinguished: (1) thin connecting filaments between widely spaced small (<2mm) chambers, cf. Entobia dentritica (Pleydell and Jones, 1988; fig. 4.3; plate 4.2) (2) strings of small (<2mm) chambers immediately adjacent,

Figure 4.3. Shapes and Average dimensions of fossil sponge borings as seen in cross section. For more complete summary of morphometric analysis data, see table 4.5.



	Entobia A	Entobia B (cf. E. dendritica)	Entobia D (E. ovula)
Number of chambers	1-2(-3) $\bar{x}$=1.5	several to many, $\bar{x}$=4.7	Several to many, $\bar{x}$=31
Avg. dimensions	6.2mm x 3.8mm	2.4mm x 1.5mm	1.7mm x 1.25mm
Avg. irregularity (scale of 1-5)	irreg. 2.1	irreg. 2.1	irreg. 1.4
Avg. aperature dimensions	1.0mm diam/ 3.3mm long	-----	-----
Avg. separation/diameter	-----	sep by 0.94 diam.	sep. by 0.16 diam.
arrangement	-----	loose cluster	tight cluster
	(N=36)	(N=14)	(N=10)



	Entobia E (E. retiformis)	Entobia convoluta n. isp. (Cliona laticavicola)	Uniglobites glomerata (Siphonodictyon spp.)
Number of chambers	several to many, $\bar{x}$=18	1 (rarely 2-3) x=1.3	1 (rarely 2-3) x=1.3
Avg. dimensions	2.1mm x 1.4mm	18.3mm x 10.2mm	10.5mm x 8.3mm
Avg. irregularity (scale of 1-5)	irreg. 1.5	irreg. 3.2	irreg. 1.3
Avg. aperture dimensions	0.4mm diam/ 1.4mm long	3.2mm diam./ 6.0mm long.	1.7mm diam./ 7.5mm long
Avg. separation/diameter	sep. by 0.14 diam.	----	----
arrangement	linear "string of beads"	----	----
	(N=11)	(N=66)	(N=35)

Entobia retiformis (Bromley and D'Alessandro, 1987; fig. 4.3; plates 4.3, 4.4a,b, 4.5), and (3) masses of small (<2mm) chambers with no linear orientation and few or no connecting filaments *Entobia ovula* (Bromley and D'Alessandro, 1984; fig. 4.3; plates 4.6a,b). Molds are mostly found in the Miocene rocks, but molds of *Entobia* cf. *dendritica* and *E*. *retiformis* were found in the Oligocene coral *Leptoseris* (fig. 4.3; plate 4.3).

When preserved as sediment-infilled holes, sponge borings were seen only in cross-section. These cross-sections were classified as Entobians A through F (fig. 4.3). Entobian A consists of single or several clustered sub-rounded to slightly convolute chambers ranging in size from 3x5mm to 5x7mm (fig 4.3; plate 4.1); in some cases, it was difficult to distinguish from Entobian F (*Uniglobites* = *Siphonodictyon*), but was usually smaller and more irregular.

Entobian B consists of multiple, loosely clustered small chambers (generally <2x3mm) which are sometimes connected by narrow connecting filaments. The chambers are usually separated by about one diameter. Entobian B is assigned to *E*. cf. *dendritica* (Pleydell and Jones, 1988).

Entobian D consists of small (generally <2x3mm) tightly

Plate 4.1. Miocene Porites trinitatis branch with Entobia A and Entobia ovula. Brizas del Caribe site. Scale bar 1 cm.

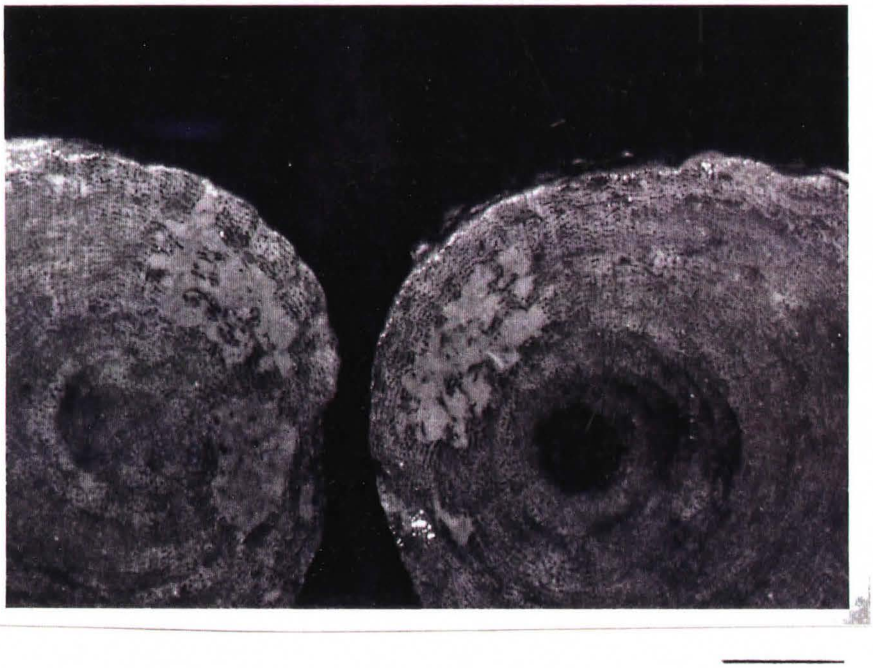


Plate 4.2. Miocene Agaricia sp. with Entobia dendritica, internal mold. Brizas del Caribe site. Penny for scale.

Plate 4.3. Oligocene Leptoseris with Entobia retiformis, internal mold. Ciales site. Penny for scale.


ELIZABETH II

Plate 4.4a. Miocene gastropod *Strombus* bored by *Entobia retiformis*. Brizas del Caribe site. Scale bar 1 cm.

Plate 4.4b. Miocene gastropod *Strombus* bored by *Entobia retiformis*. Brizas del Caribe site. Scale bar 1 cm.

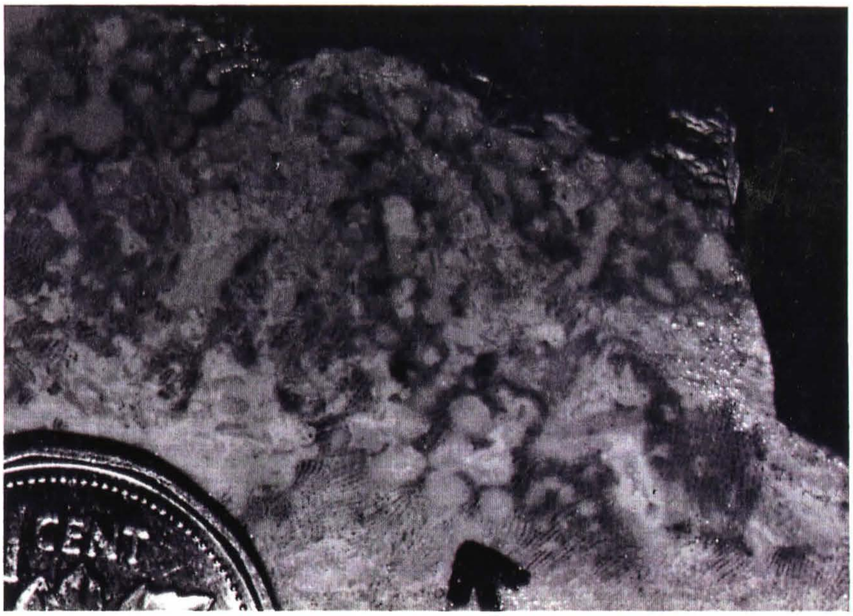
Plate 4.5a. *Entobia retiformis* borings in Miocene reef rock. Brizas del Caribe site.

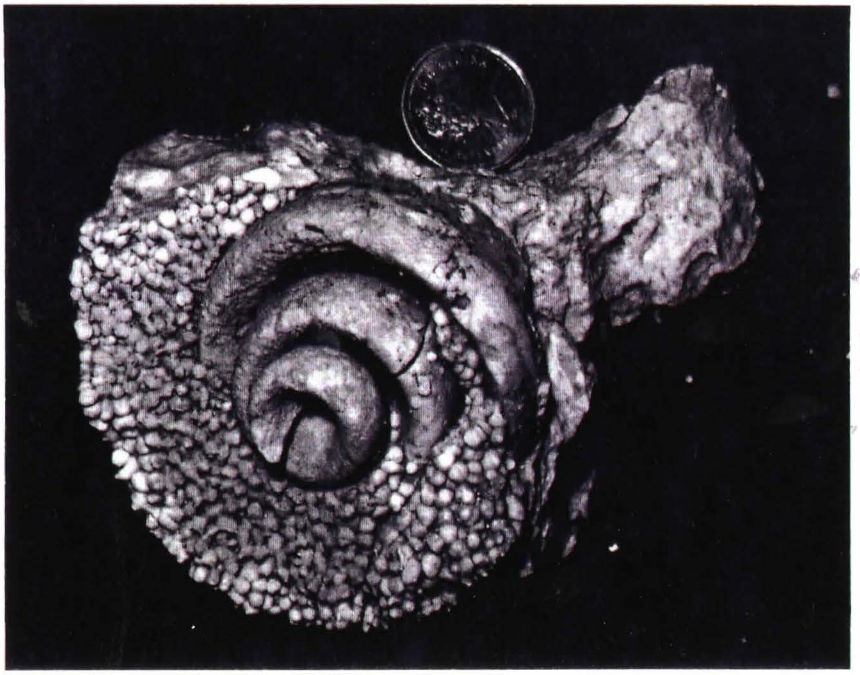
Plate 4.5b. *Entobia convoluta* n. isp. in Miocene coral *Porites trinitatis*, Brizas del Caribe site. Penny for scale.


30
40
mm

Plate 4.6a. Oligocene *Pironastrea* sp. with *Entobia ovula* (arrow). Lares Quarry site. Penny for scale.

Plate 4.6b. Miocene gastropod *Strombus* with *Entobia ovula* borings. Internal molds. Rio Guajataca site. Penny for scale.


CENT



clustered chambers which are sometimes connected by thin connecting filaments. Chambers in the clusters are generally separated by less than half a diameter, and clusters may occupy a space of 10x10mm or more. Entobian D is assigned to E. ovula (Bromley and D'Alessandro, 1984).

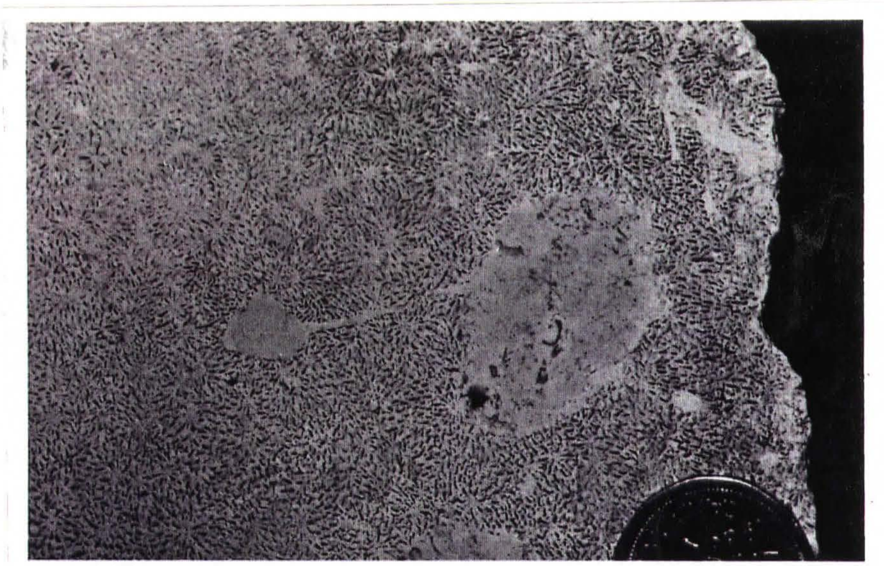
Entobian E consists of linear or (usually) branched borings, generally less than 2mm in diameter, and often with annulations along the branches. Entobian E is assigned to E. retiformis (Stephenson) (see Bromley and D'Alessandro, 1987), although it also closely approximates the form of E. cateniformis (Bromley and D'Alessandro, 1984).

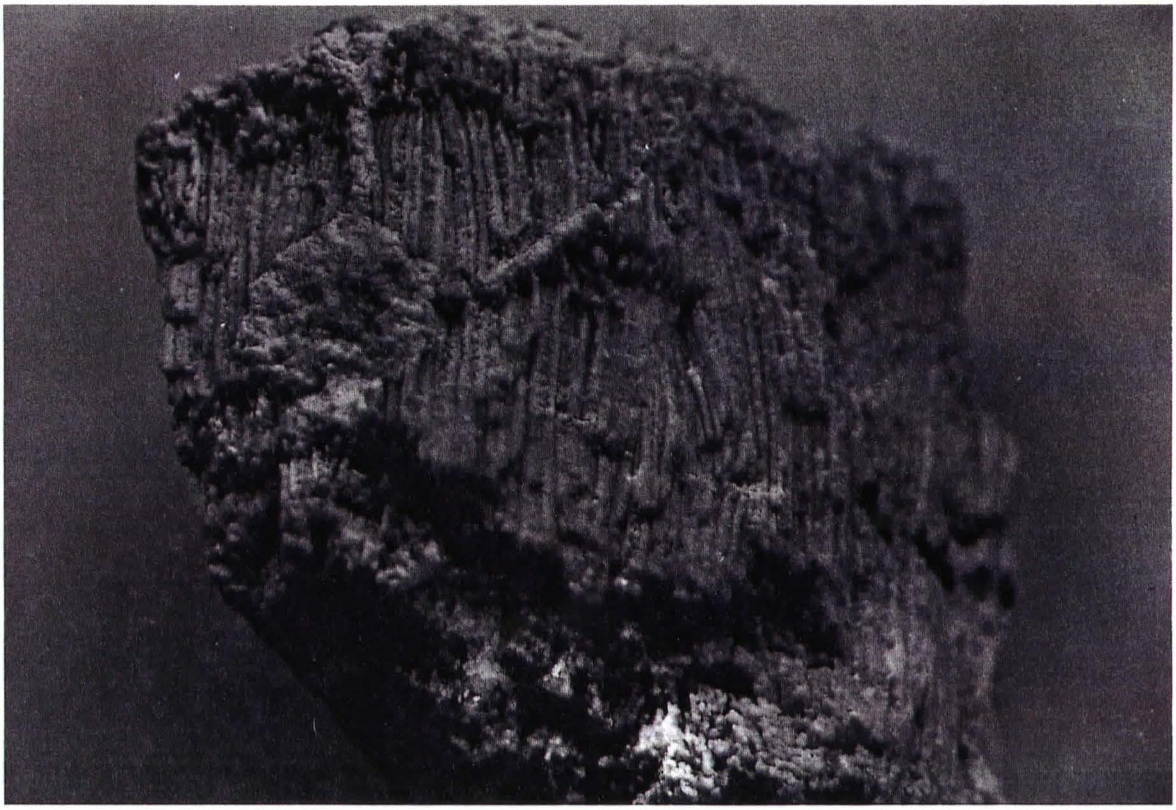
Entobia convoluta n. isp. (Entobian C; see Appendix 4 for formal description) consists of large (>5mm, usually >10mm), highly convoluted galleries with broad (2-3mm) papillae (fig. 4.3; plate 4.5b). These are clearly recognizable in both Oligocene and Miocene corals. These borings are attributed to Cliona laticavicola, on the basis of the morphometric analysis data (see section 4.3)

Siphonodictyon galleries (fig. 4.3; plates 4.7a,b), recognized by large (5-10mm) roughly circular galleries with long narrow (<2mm) papillae, occur in both Oligocene and Miocene corals. Pleydell and Jones (1988) designated the ichnogenus Uniglobites

Plate 4.7a. *Uniglobites glomerata* borings in Miocene *Coscinaraea colei*. Polished slab, Brizas del Caribe site. Penny for scale.

Plate 4.7b. *Uniglobites glomerata* boring in Miocene *Coscinaraea colei*. Brizas del Caribe site. Scale bar 1 cm.





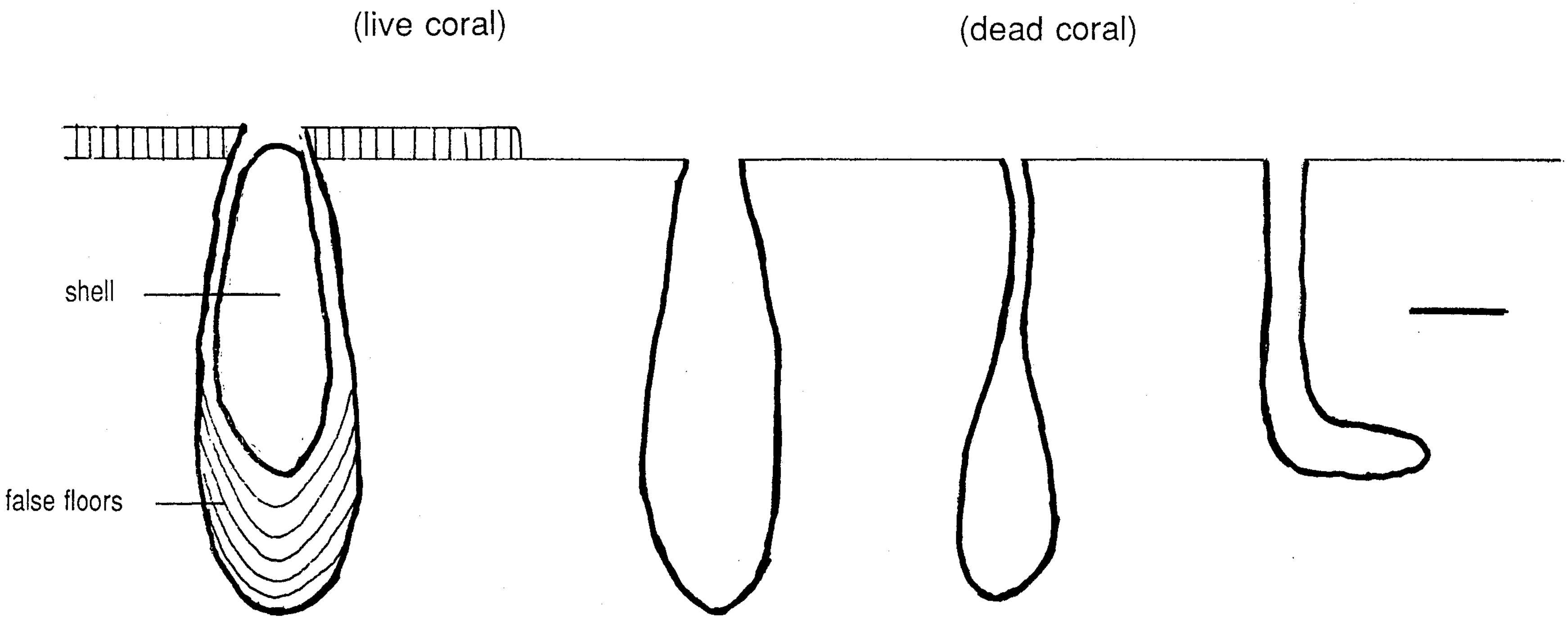
for borings of *Siphonodictyon*, but Bromley and D'Alessandro (1984) assign these to *Entobia gigantea*. In this study, *Uniglobites* will be used in order to emphasize the taxonomic distinctness of the known trace-maker. These borings were primarily distinguished on the basis of shape, rather than size.

Bromley and D'Alessandro (1989) caution that, due to the extreme variability in the form of sponge borings, (1) identification of Entobian species based on cross sections are tentative at best, and (2) correlations of Entobian diversity with biological diversity of boring sponges are unreliable. With those caveats in mind, this study identifies at least five morphospecies of *Cliona* (four of which conform to *Entobia*, sensu stricto; the fifth is *E. convoluta* n. isp.), and *Siphonodictyon* (*Uniglobites*), all of which persisted from the Oligocene into the Miocene.

4.2.2 Bivalves

Bivalve borings can readily be recognized as those of *Lithophaga* (fig. 4.4; plate 4.8a,b, 4.9a,b, 4.10b) or *Gastrochaena* (fig. 4.4; plates 4.8b, 4.9b). These traces are classified as *Gastrochaenolites torpedo*, and *G. turbinatus*, respectively (Kelly and Bromley, 1984). *G. lapidicus* can be formed by either *Lithophaga* or *Gastrochaena* (Kelly and Bromley,

Figure 4.4. Fossil bivalve and worm borings as seen in cross section.



Gastrochaenolites vivus n. isp. — made by *Lithophaga bisulcata*

G. torpedo — made by *Lithophaga* spp.

G. lapidicus — made by *Gastrochaena* spp.

J-shape *Trypanites* — made by *Phascalosoma* sp.

Plate 4.8a. Lithophaga boring in Oligocene Montastrea costata; sediment infill in borehole includes fragment of branching coral Stylophora. Lares Quarry site. Scale bar 1 cm.

Plate 4.8b. Oligocene Montastrea costata with Lithophaga and Gastrochaena borings. Coral growth bands and geopetals in borings indicate that coral was overturned before being bored. Lares Quarry site. Scale bar 1 cm.

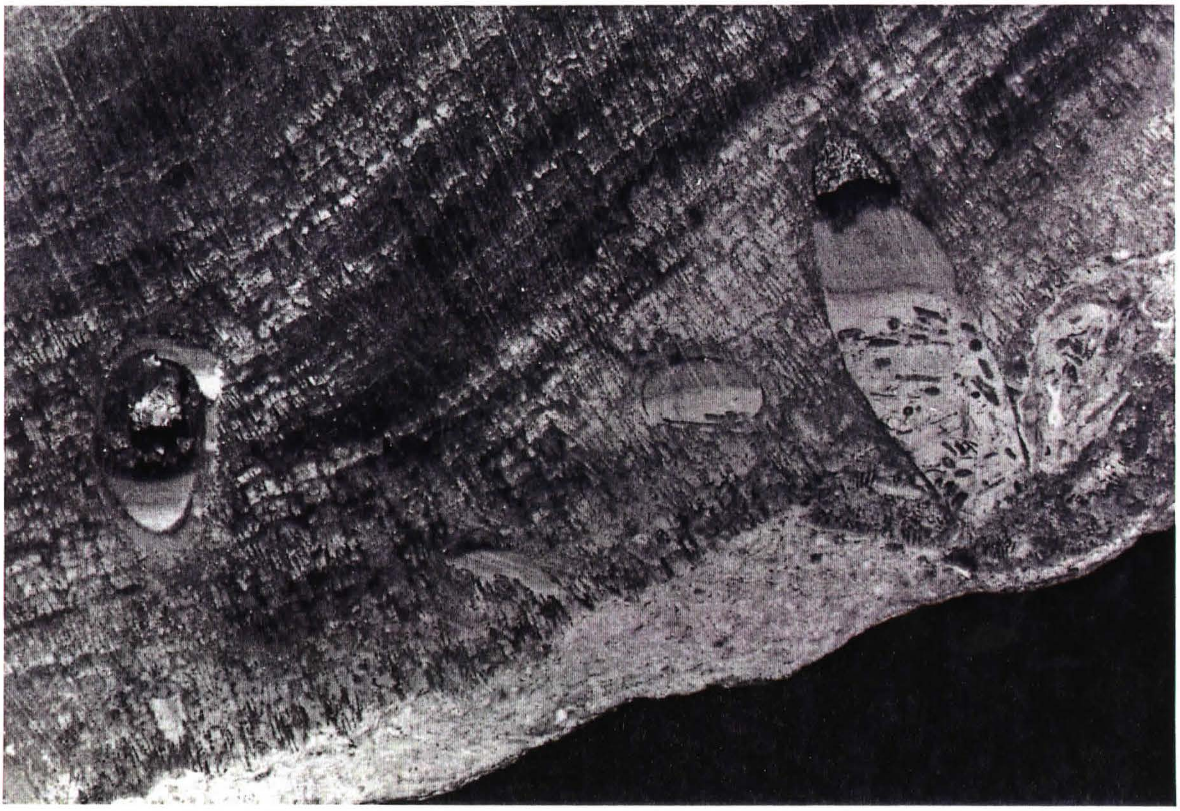


Plate 4.8c. Oligocene Gastrochaenolites vivus n. isp. in Diploastrea crassolamellata. Bivalve boring follows coral growth to left and into plane of page. Note shell remains and false floors.

Plate 4.8d. Close-up of false floors in plate 4.8c. Shell and two false floors are clearly visible, other "ghosts" are present, but difficult to see.

Plate 4.9a. Oligocene *Montastrea tampaensis* with *Lithophaga* boring and shell. Bivalve bored parallel to corallites. Lares Quarry site. Scale bar 1 cm.

Plate 4.9b. *Lithophaga* and *Gastrochaena* borings and shells in the Miocene coral *Coscinaraea colei*. Brizas del Caribe site. Scale bar 1 cm.

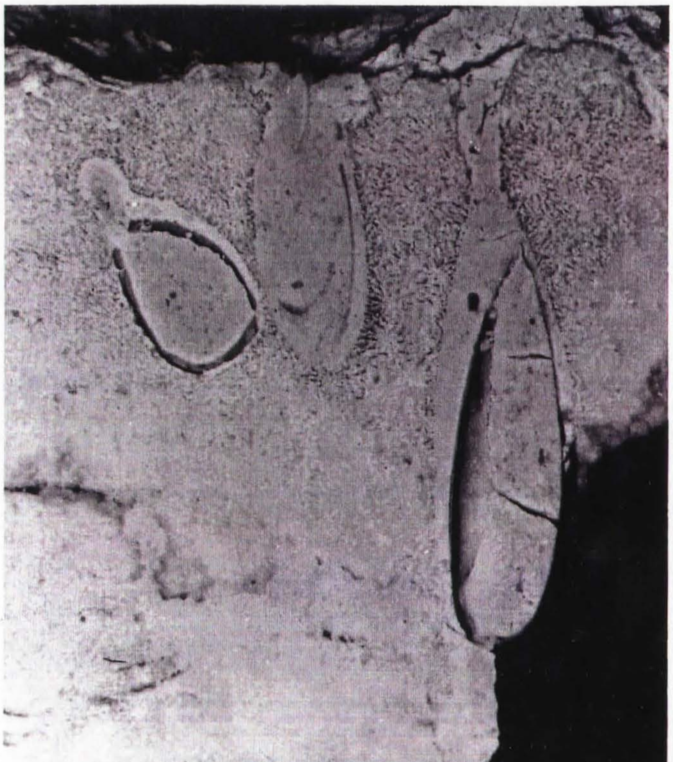


Plate 4.10a. Miocene _Coscinaraea_ _colei_. Note death and regrowth surface with borings extending both up and down. J-shaped _Trypanites_ extends down into dead coral. _Entobia_ _convoluta_ extends up into new coral skeleton above death/regrowth surface. Scale bar 1 cm.

Plate 4.10b. Close-up view of death/regrowth surface in plate 4.10a. This _Lithophaga_ bored upward into new coral skeleton above death/regrowth surface. Scale bar 1 cm.

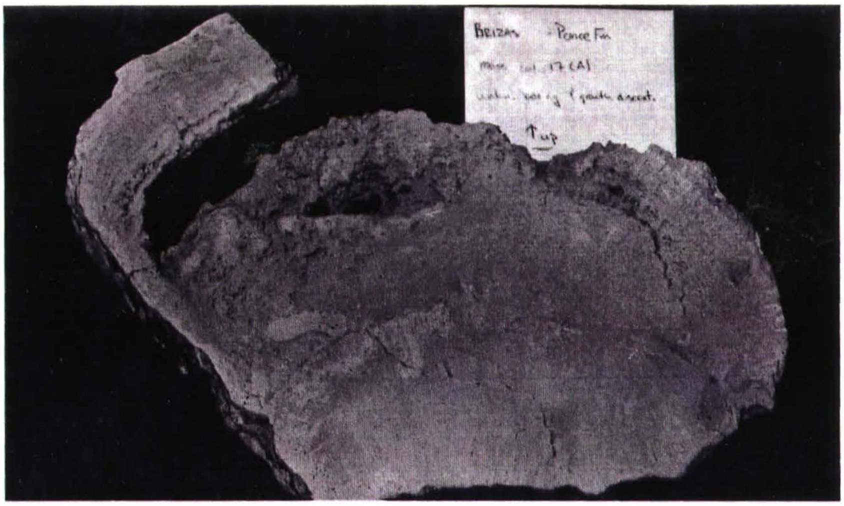
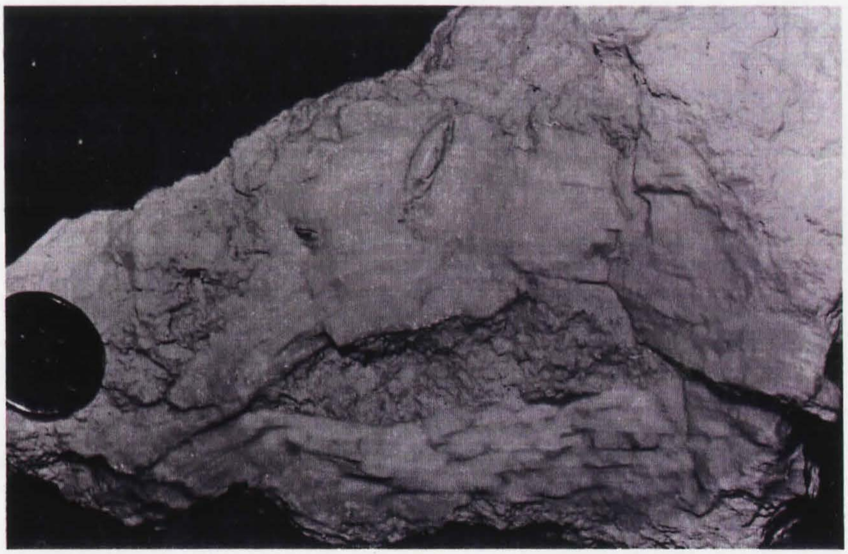

BRIZAS - Ponce Fm
Mon. col. 17 (A)
[illegible] pos. of growth ascent.
↑up

Plate 4.11. Miocene oyster _Spondylus_ with _Lithophaga_ boring into upper valve. Brizas del Caribe site. Penny for scale.

Plate 4.12. J-shaped _Trypanites_ borings in Oligocene _Favites polygonalis_. Guanica site. From polished thin section. Scale bar 1 cm.



1984), but in this study, there was no difficulty distinguishing *Lithophaga* boreholes from those of *Gastrochaena*, particularly because the shells were frequently preserved inside the borehole (plate 4.9a,b, 4.10b).

Modern Caribbean *Lithophaga* are mostly obligate borers of dead coral (2 spp.) or live coral (1 sp.), although a few species are facultative live coral borers (1 sp.) (see table 7.4). In this study, *Lithophaga* shells were found in borings both with and without false floors (fig. 4.4). False floors indicate boring into live coral, and only *L. bisulcata* is known to produce them (Scott, 1988). On this basis, two species of *Lithophaga* are distinguished in this study: *L. bisulcata* in live corals and *L.* sp. in dead corals.

Many of the *Gastrochaena* borings still held shell material or had external molds. No *Gastrochaena* were found boring into the live surfaces of corals, and this habit is not reported in modern *Gastrochaena*. Thus a total of three endolithic bivalve species were found, all of which were found in both the Oligocene and the Miocene.

6.2.3 Other

J-shaped worm borings were found in both Oligocene and Miocene corals (fig. 4.4; plate 4.10a, 4.12). These were probably made by *Phascalosoma* or a similar sipunculan (Williams and Margolis, 1974; Stearley and Ekdale, 1988; see chapter 5). Other worm borings can only be divided into lined or unlined, horizontal or vertical, straight or convoluted borings. Since there are no soft parts, preservation is exclusively as trace fossils, and all are simply classified as *Trypanites* (Bromley, 1970). Except in the case of the J-shaped borings, no inferences can be made about the organism responsible for any of the *Trypanites*. Thus a total of two worm borings were identified, but this in no way adequately reflects the true biological diversity of endolithic worms which probably inhabited these reefs.

Endolithic barnacles are reported from the Early to Middle Miocene (Newman, et al., 1976), but none were found in this study. For purposes of generic counts, one genus will be credited to endolithic barnacles, as is reported from the Miocene. Balanomorph barnacles were found on the external surface of one Oligocene *Goniopora* *hilli* from the Guayanilla II section (plate 4.13), but there is no evidence that they also occurred within the coral skeleton, or that they colonized the surface of a live coral.

Internal molds of ctenostome bryozoans, probably similar to *Harmeria* (Borg, 1940) were found in a few branching *Stylophora* at the Rio Guajataca site (plate 4.14). Due to their rarity, these

Plate 4.13. Epilithic balanid barnacle tests on Oligocene *Goniopora hilli*. Guayanilla II site. Scale bar 1 cm.

Plate 4.14. Ctenostome bryozoan borings in Miocene *Stylophora* sp., internal molds. Rio Guajataca site. Penny for scale.

organisms can be treated as no more than a curiosity. Boring Ctenostomes date from the Ordovician (Cheetham, 1987), and most certainly did not originate in the Miocene.

6.3 Morphometric Analysis of Sponge Boreholes

Approximately 200 individual sponge borings were measured for a statistical description of the size and shape of each ichnospecies (see chapter 3 for methods). The results of these analyses are shown in table 4.5. Figures 4.5 and 4.6 show the relative size of Oligocene vs. Miocene Entobia convoluta, Uniglobites glomerata, and Entobia A, and the number of chambers in Oligocene vs. Miocene Entobia ovula. Miocene E. convoluta and U. glomerata were significantly larger than their Oligocene ancestors (E. convoluta: $t=2.305$, $p<.025$, d.f=52; U. glomerata: $t=2.086$, $p<.025$, d.f=39). Miocene E. ovula had significantly more chambers (analogous to greater size) than did Oligocene E. ovula ($t=2.266$, $p<.05$, d.f.=8). There was no significant size difference between Oligocene and Miocene Entobia A ($t=0.907$, NS, d.f.=34). That Miocene sponge borings are larger or more extensive than their Oligocene counterparts suggests that bioerosion was more intense on the Miocene reefs than on the Oligocene reefs.

Similar analyses were not performed on bivalve shell length and width because oblique cuts would cause too much distortion

Table 4.5. Average dimensions of Oligocene, Miocene, and Recent sponge borings. All measurements in mm.

Ct.	*Entobia convoluta*/ *Cliona laticavicola*.
Si.	*Uniglobites glomerata*/ *Siphonodictyon* sp.
EnA	*Entobia A*
EnB	*Entobia dendritica*
EnD	*Entobia ovula*
EnE	*Entobia retiformis*
C. lampa	*Cliona lampa*

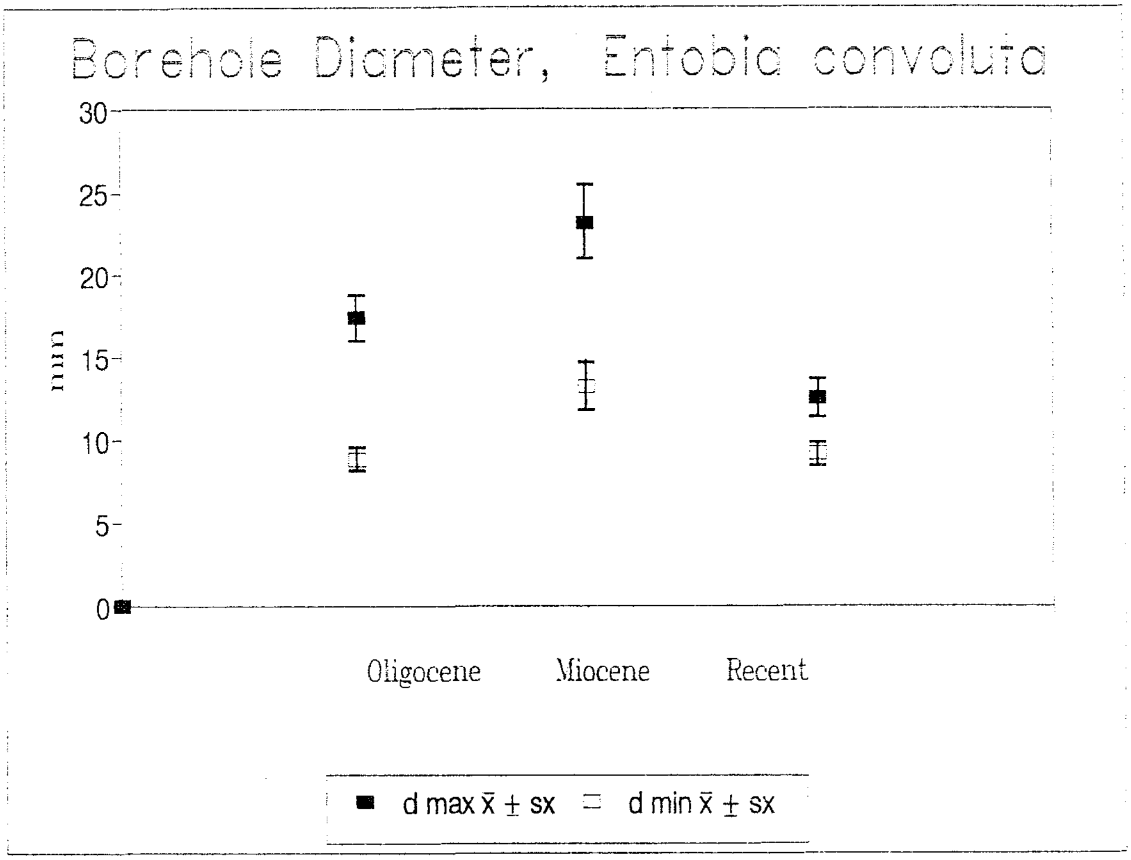
N chmb	Number of Chambers
x max	Mean maximum diameter
x min	Mean minimum diamter
Avg Ap Dim	Avg. Aperture Dimensions
x diam	mean aperture diameter
x length	mean aperture length
Avg Sep/Diam	Average ratio, chamber separation/ chamber diameter

	Ct.-Olig	Ct.-Mio	Ct.-Rec	Si.-Olig	Si.-Mio	Si.-Rec	EnA-Olig	EnA-Mio
N chmb								
x	1.280	1.320	1.100	1.300	1.190	1.600	1.450	1.600
s	0.670	0.700	0.370	0.460	0.500	0.800	0.580	0.610
n	32.000	22.000	10.000	20.000	21.000	5.000	22.000	14.000
Avg Dim.								
x max	17.400	23.200	12.500	10.000	12.700	6.900	6.200	6.800
s max	7.900	10.600	3.800	3.600	4.600	3.700	1.700	1.600
x min	8.800	13.200	9.100	7.400	10.600	4.400	3.800	4.200
s min	3.800	6.800	2.100	2.500	4.300	2.600	1.000	0.670
n	32.000	22.000	10.000	20.000	21.000	5.000	22.000	14.000
Avg Irreg.								
x	3.090	3.450	2.700	1.350	1.330	2.200	2.230	2.200
s	0.840	1.120	0.640	0.480	0.640	0.400	0.670	0.650
n	32.000	22.000	10.000	20.000	21.000	5.000	22.000	14.000
Avg Ap Dim								
x diam	3.200	4.100	2.400	1.400	1.350	3.700	0.900	ND
s diam	0.900	1.400	0.900	0.700	0.500	3.100	0.400	ND
x length	6.400	7.600	4.000	7.300	9.000	3.800	2.900	4.700
s length	3.100	4.000	1.100	4.200	3.600	0.590	1.100	0.650
n	32.000	22.000	10.000	20.000	21.000	5.000	22.000	14.000
Avg Sep/Diam								
x	ND	ND	ND	ND	ND	ND	ND	ND
s	ND	ND	ND	ND	ND	ND	ND	ND
n	ND	ND	ND	ND	ND	ND	ND	ND

	EnB-Olig	EnB-Mio	EnD-Olig	EnD-Mio	EnE-Olig	EnE-Mio	C. lampa
N chmb							
x	3.900	6.750	12.330	60.500	14.600	21.000	7.200
s	2.210	2.590	5.820	53.240	10.070	21.210	4.350
n	10.000	4.000	6.000	4.000	5.000	6.000	5.000
Avg Dim.							
x max	2.400	2.400	2.000	1.800	2.500	2.100	3.100
s max	0.500	0.500	0.300	0.400	1.300	0.800	1.600
x min	1.600	1.300	1.400	1.400	1.500	1.600	2.100
s min	0.400	0.200	0.200	0.400	0.500	0.700	1.200
n	39.000	27.000	36.000	24.000	30.000	36.000	30.000
Avg Irreg.							
x	2.100	2.130	1.830	1.250	1.800	1.670	1.400
s	0.400	0.580	0.690	0.430	0.400	1.110	0.490
n	39.000	27.000	36.000	24.000	30.000	36.000	30.000
Avg Ap Dim							
x diam	ND	ND	ND	ND	ND	ND	ND
s diam	ND	ND	ND	ND	ND	ND	ND
x length	ND	ND	ND	ND	ND	ND	ND
s length	ND	ND	ND	ND	ND	ND	ND
n	ND	ND	ND	ND	ND	ND	ND
Avg Sep/Diam							
x	1.730	1.460	0.230	0.060	0.080	0.180	0.400
s	0.310	0.400	0.120	0.010	0.060	0.190	0.410
n	39.000	27.000	36.000	24.000	30.000	36.000	30.000

Figure 4.5a. Borehole diameters of Oligocene, Miocene, and Recent Entobia convoluta, maximum and minimum diameters, means + standard error. Miocene boreholes are significantly larger than Oligocene boreholes (t=2.305, p<.025, d.f.=52).

Figure 4.5b. Borehole diameters of Oligocene, Miocene, and Recent Uniglobites glomerata, maximum and minimum diameters, means + standard error. Miocene boreholes are significantly larger than Oligocene boreholes (t=2.086, p<.025, d.f.=39).


Borehole Diameter, Entobia convoluta
30
25
20
15
10
5
0
mm
Oligocene
Miocene
Recent
■ d max x̄ ± sx
□ d min x̄ ± sx

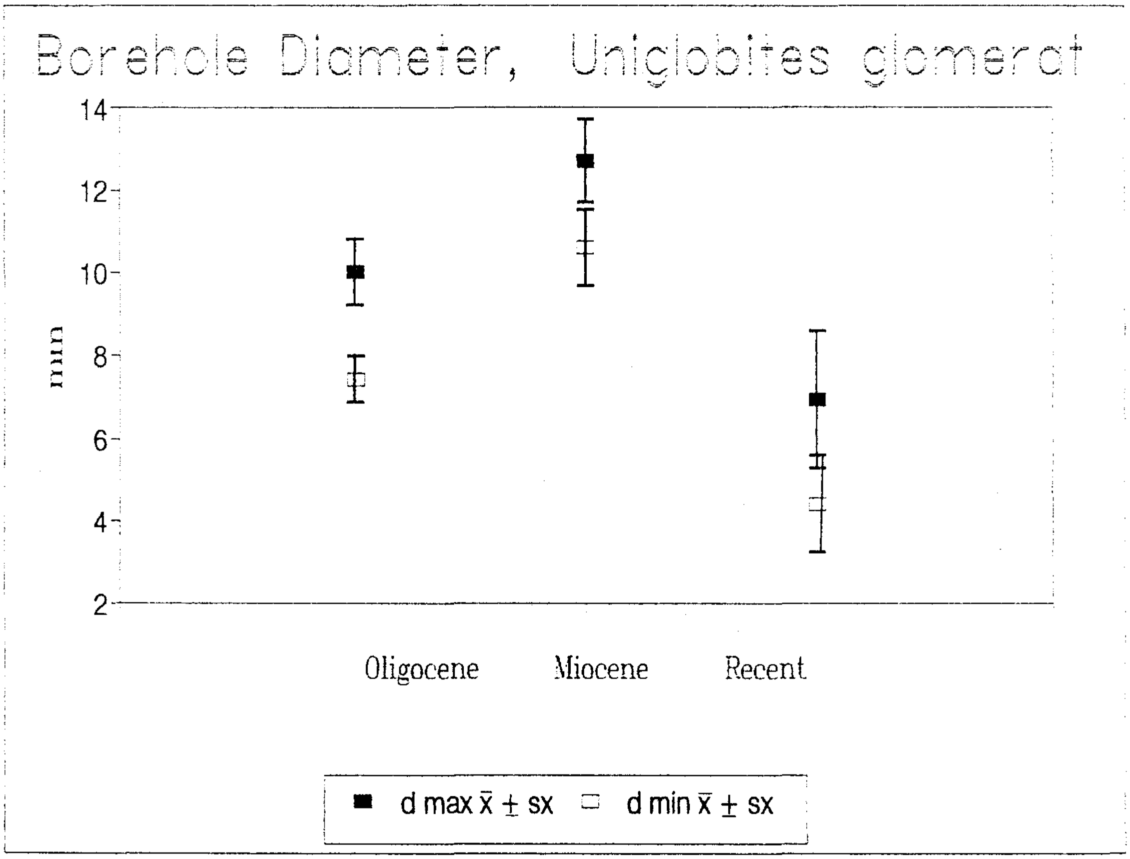
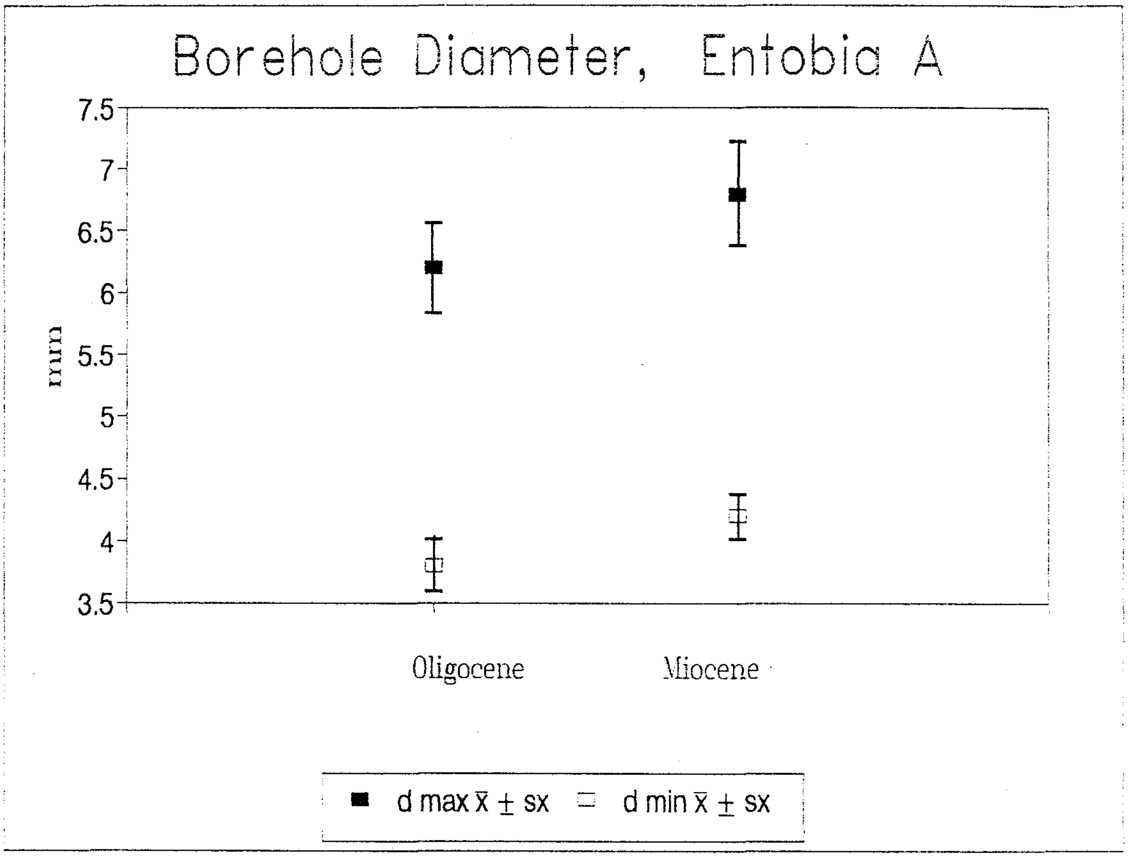
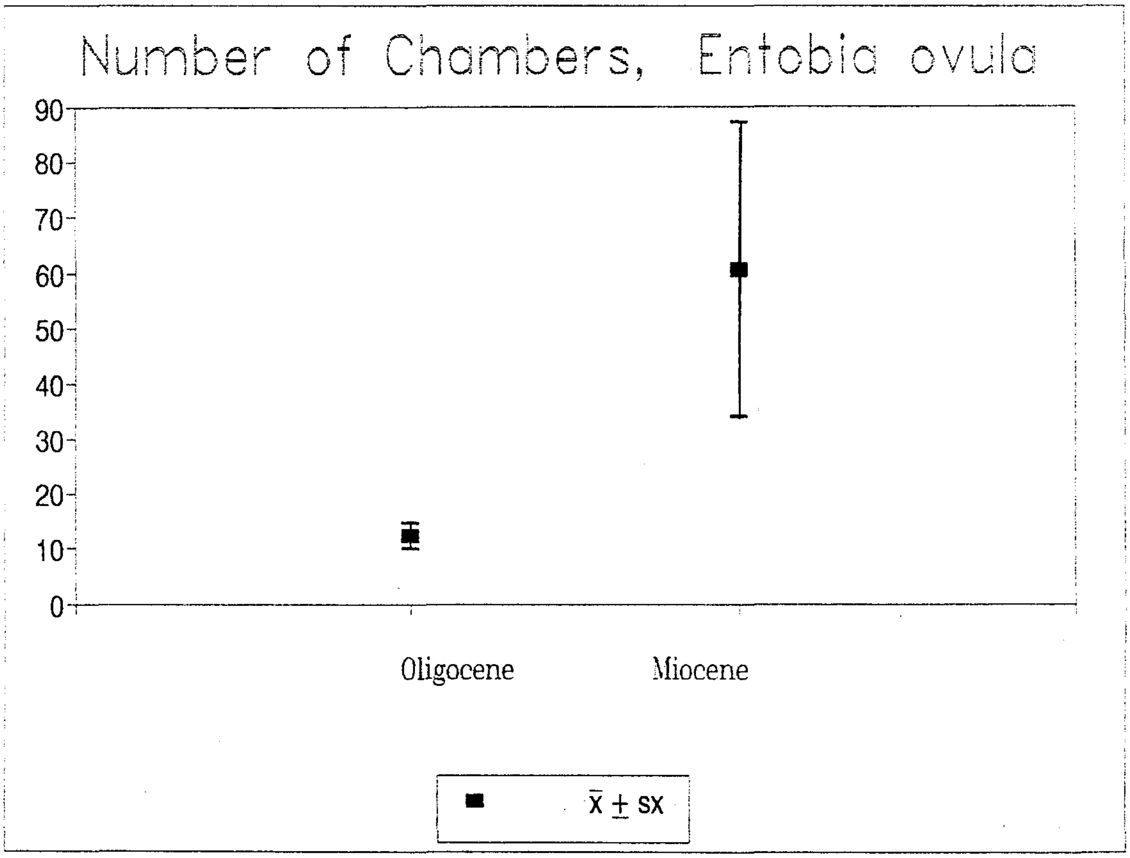

Borehole Diameter, Uniglobites glomerat
14
12
10
8
6
4
2
mm
Oligocene
Miocene
Recent
■ d max x̄ ± sx
□ d min x̄ ± sx

Figure 4.6a. Borehole diameters of Oligocene and Miocene *Entobia* A, maximum and minimum diameters, means + standard error. Miocene boreholes are not significantly larger than Oligocene boreholes (t=0.907, NS, d.f.=34).

Figure 4.6b. Number of Chambers in Oligocene and Miocene *Entobia ovula*, mean + standard error. Miocene boreholes have significantly more chambers than do Oligocene boreholes (t=2.266, p<.05, d.f.=8).


Borehole Diameter, Entobia A
mm
7.5
7
6.5
6
5.5
5
4.5
4
3.5
Oligocene
Miocene
■ d max x̄ ± sx
□ d min x̄ ± sx


Number of Chambers, Entobia ovula
90
80
70
60
50
40
30
20
10
0
Oligocene
Miocene
■ x̄ ± sx

(presumably accounted for in sponges by the large number of borings and their more random orientation within the skeleton). Small *Lithophaga* and *Gastrochaena* are assumed to be juveniles of the same species, rather than adults of separate species.

4.4 Species Specificity of Coral Associates

Table 4.6 shows the occurrence of coral associates by coral host species. No evidence for host specificity was found. The only exceptions are *Lithophaga bisulcata* which bored into live coral, leaving behind false floors. This bivalve was found boring into the live corals of Oligocene coral species *Diploastrea crassolamellata* (genus now restricted to the Indo-Pacific) and *Montastrea tampaensis*, (genus survived, closest relative is *M. cavernosa*), and the Miocene species *Coscinaraea colei* (genus now restricted to the Indo-Pacific). Modern *L. bisulcata* in the Caribbean bore into many dead corals, but only bore into the live surfaces of *Siderastrea siderea* and *Stephanocoenia michelini* (Scott, 1988). Scott suggested that *L. bisulcata* bored primarily into *Siderastrea* and *Stephanocoenia* because in these densely calcified corals, it is better protected from triggerfish predation. It is probably for the same reasons that *L. bisulcata* was observed boring into only two species of live Oligocene corals, and only one genus of Miocene coral. *Coscinaraea colei*, like *Siderastrea*, probably had a denser skeleton than *Porites trinitatis* and *Montastrea limbata*, the other massive corals with which *C. colei* occurred in this study.

Table 4.6. Occurrence of Coral Associates in Oligocene and Miocene corals and other substrates.

Corals	**Associates**																	
Oligocene	Sponges	Entobia A	Entobia dendritica	Entobia ovula	Entobia retiformis	Entobia convoluta	Uniglobites glomerata	Bivalves	Lithophaga bisulcata (in live coral)	Lithophaga sp. (in dead coral)	Gastrochaena sp.	Worms	Trypanites, J-shaped	Trypanites isp.	Other	barnacles	Ctenostome bryozoans		**Number Sampled**
Actinacis			?																1
Acropora		X			X	X	X			X			X	?					2
Agathiphyllia														?					1
Alveopora		X				X				X	X								1
Antiguastrea		X	X	X	X	X	X			X	X		X	X					5
Astreopora																			P
Caulastrea																			P
Cladocora		?																	2
Colpophyllia		X		?	X	X	X			X	?		X						3
Diploastrea		X				X			X	X	X								2
Favites		X				X	X			X			X	X					2
Goniopora						X				X						X			1
Hydnophora		X	X	X	?	X	X			X			X	X					2
Leptoseris			X		X								?						2
Montastrea costata		X	X	X		X	X			X	X			X					3
M. tampaensis		?		X		X			X	X	X			X					3
Pironastrea		X	X	X	X	X				X			X	X					1
Porites baracoaensis		X	X		X	X	X						X						4
P. waylandi		X	X	X	X	X	X			X	X		X	X					12
Siderastrea conferta		X	X			X	X			X	X			X					4
S. siderea					X		X						?						2
Stylocoeniella		X	X			X				X				X					4
Stylophora			X		X														1
Miocene																			
Agaricia			X	X	X														5
Astrocoenia																			P
Colpophyllia														X					3
Coscinaraea		X	X		X	X	X		X	X	X		X	X					9
Favia			?		X														1
Goniopora																			P
Montastrea		?	X	X	X	X	X			X	X			X			?		11
Porites baracoaensis														X					1
P. trinitatis		X	X	X	X	X	X			X	X		X	X					6
Siderastrea										X									1
Solenastrea						X				X	X								3
Stephanocoenia														?					P
Stylophora			X		X												X		4
Other																			
Placocyathus			X	X	X					X	X								6
Clypeaster			?	X															3
Strombus			X	X	X														5
Spondylus			?		X	X				X	X								3
infaunal bivalves			X	X	X														10
calcareous algae							?												1

4.5 Survivorship Patterns

Tables 4.7 and 4.8 summarize survivorship among the corals and coral associates seen in this study. Several patterns are evident:

(1) Corals suffered 59% generic extinction, and 54% specific extinction, between the Oligocene and Miocene sites.

(2) No ichnogenera or ichnospecies became extinct across the Oligocene-Miocene boundary, and no extinction was observed among the boring bivalves. Two groups of associates are newly represented in the Miocene, but only the coral-inhabiting barnacles represent a true origination. All of the trace-makers represented in the Oligocene are extant (see chapter 5), and all are cosmopolitan at the genus level (see chapter 7).

(3) Oligocene reefs (including the patch reefs of the Lares Fm.) studied had more diverse coral faunas than did Miocene reefs, but the small number of sites precludes statistical testing of this pattern.

(4) All coral species which were found only at the shelf-edge sites (Guayanilla-II and Guanica) became extinct, but not all of the corals which became extinct were restricted to these sites.

(5) Of the coral genera which became extinct in the Caribbean, about 2/3 are extant in the Indo-Pacific, and the remaining third are globally extinct.

Table 4.7: Summary Table of Coral Diversity

	Oligocene	Miocene
Total species	23	11
Genera extinct in Caribbean	13 (59%)*	N/A
Species extinct in Carib.	13 (54%)*	N/A
New genera	N/A	5 (42%)
Genera extinct (global)	4 (19%)	1 (9%)
Genera restricted to Indo-Pacific	10 (48%)	3 (27%)
Genera restricted to Caribbean	2 (9%)	4 (36%)
Cosmopolitan genera	4 (15%)	3 (27%)
Total species reported in Caribbean coral fauna	65**	43***
	Frost & Langenheim 1974	Frost, 1977a

* If reported Miocene and Pliocene occurrences of *Agathiphyllia*, *Alveopora*, and *Astrocoenia* are included, then only 10 genera (10 spp.) became extinct, and generic and specific extinction are 48 and 44, respectively. See text.

**Frost (pers. comm., 1990) estimates the total Oligocene Caribbean coral fauna at 90 spp.

***includes 7 solitary hermatypic corals, omitted in above species count (see discussion above).

New genera, rather than new species, are counted in order to view true originations/immigrations rather than direct descendant spp. of Oligocene survivors. Furthermore, species-level taxonomy is under revision (Foster, 1986, 1987; Budd, 1990; Budd, in progress).

Table 4.8: Summary Table of Coral Associate Diversity

	Oligocene	Miocene
Total species	12	14
Total genera	8	10
Genera extinct	0*	0
New genera	N/A	2 (20%)**
Genera extinct (global)	0	0
Genera restricted to Indo-Pacific	0	0
Genera restricted to Caribbean	0	0
Cosmopolitan genera	8 (100%)	10 (100%)

---

*Pleydell (1987) reported Entobia volzi, the boring made by Cliothosa hancocki, from the Oligocene of Grand Cayman Island, BWI. Cliothosa today is found in the Mediterranean and Indo-Pacific, but not the Caribbean (see table 8.6).

**Barnacles and bryozoans are assigned one genus each for purposes of this count, to reflect their scarcity and low diversity in the study area. See table 7.6 on diversity and biogeography of coral-inhabiting barnacles.

Chapter 5: Coral Associates in Selected Corals from a Near-shore Patch Reef, La Parguera.

5.1 Sampling

In order to compare the Miocene coral associate fauna with the modern fauna, a small sample of modern corals was collected from Caracoles Reef, a near-shore patch reef at La Parguera (map 5.1; plate 5.1). At both collection times (July 1989 and Feb. 1990), turbidity was moderate (visibility < 10m) and there was a considerable load of carbonate sediment (although this was not measured). Recent construction activities in the vicinity of La Parguera have probably increased the contribution of terrigeous sediments. Large multilobate heads of Montastrea annularis were very common; other common massive corals were Siderastre siderea, Diploria strigosa, D. labyrinthiformis, Montastrea cavernosa, and Porites astreoides. Porites porites and Acropora cervicornis were uncommon, and A. palmata was rare. This species assemblage is typical of that found in sediment-stressed habitats in the Caribbean (Cortes and Risk, 1985), except for the lack of abundant vertical plates of Agaricia.

Small portions of three heads each of Montastrea annularis, Siderastrea radians, Diploria strigosa, and Porites astreoides, three sticks of Porites porites, and two sticks of Acropora cervicornis were collected, all from between 3m and 8m depth on the

Map 5.1. Map of La Parguera Region, showing Caracoles Reef and Study Site for modern sampling. Redrafted from Frost, et al. (1983).

Map of La Parguera Region

Parguera Quadrangle

Redrawn from Frost, et al., 1983.

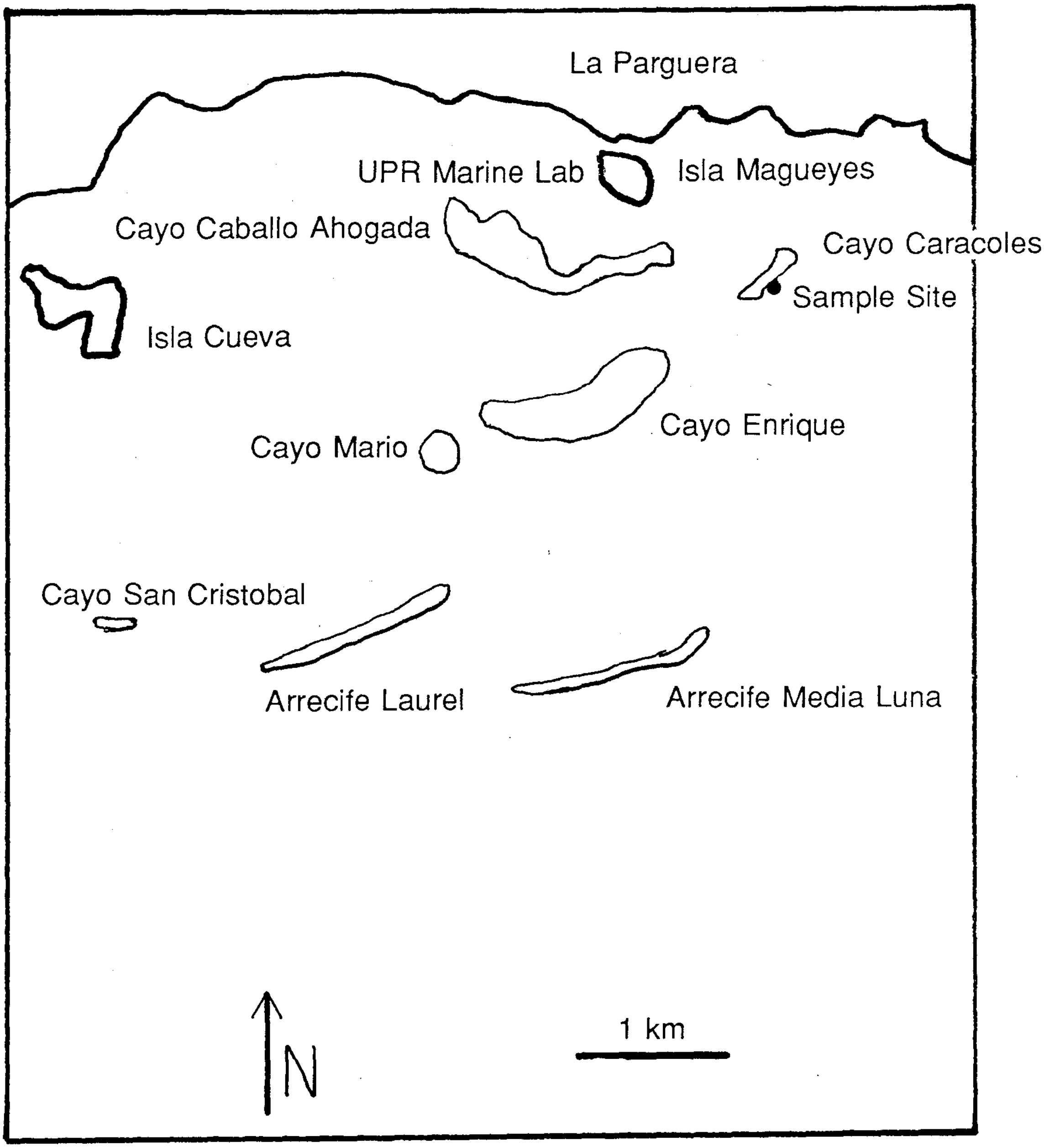
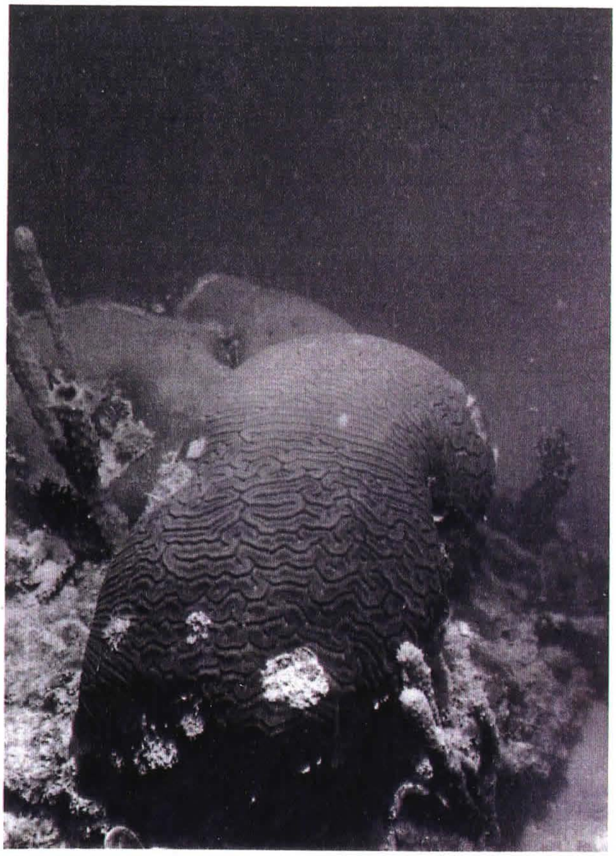
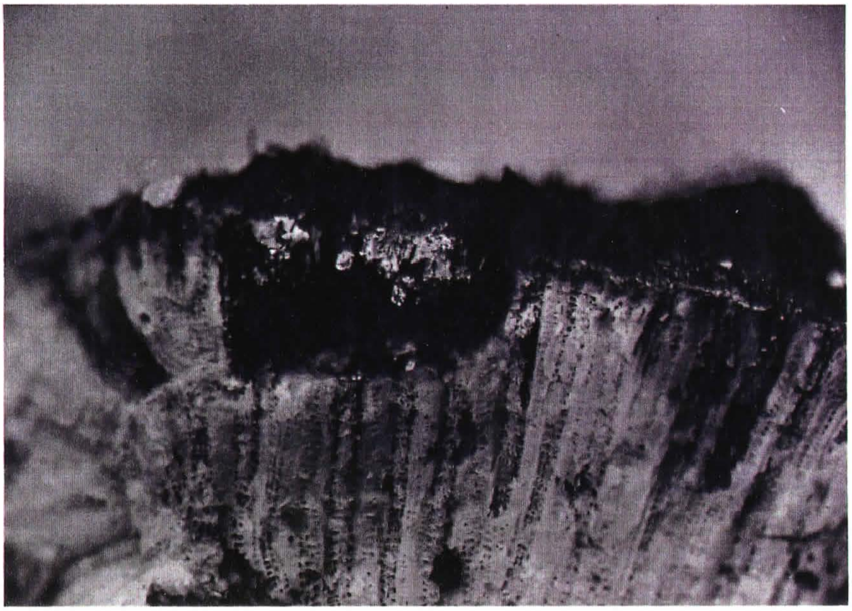


Plate 5.1. Modern *Diploria labyrinthiformis* head, Caracoles Reef, La Parguera. Large dead spots in coral surround papillae of boring sponge *Cliona laticavicola*. Coral head diameter about 60 cm.

Plate 5.2. *Cliona laticavicola* boring in modern *Montastrea annularis*. Caracoles Reef, La Parguera. Scale bar 1 cm.





windward side of the reef. The shoreward/leeward side is predominantly a seagrass bank. Corals were slabbed and photographed in the lab (plate 5.2), and tissues of coral associate were preserved in 5% formalin and then 10% ethanol. The piece of coral from which each bioeroder was removed was bleached, dried, and saved for comparison with fossil material.

Preserved sponge tissue was boiled for 48-72 hours in concentrated nitric acid. The spicules remaining were concentrated in a centrifuge and washed in ethanol, then mounted on glass slides with Permmount. For description of this method, see Rutzler (1971). The small sample collected at Parguera is not intended to be a complete sample of the internal associate fauna of Puerto Rico. Rather, it was collected primarily (1) to assess the taphonomic limits on taxonomic resolution of associates, and (2) to assess the degree of change between middle Miocene boring sponge galleries and modern galleries found in a similar ecological setting.

5.2 Occurrence

Table 5.1 shows the occurrence of internal coral associates in each of five coral species collected at Caracoles Reef, a shallow inshore patch reef at La Parguera, Puerto Rico. Boreholes were measured for each sponge species; these are compared to fossil

Table 5.1. Occurrence of Coral Associates in selected Recent corals, Caracoles Reef, La Parguera, Puerto Rico.

Corals

Associates	Porites porites	Porites astreoides	Diploria strigosa	Siderastrea siderea	Montastrea annularis	
Sponges						
Cliona caribbea		X	X	X		
Cliona lampa		X	X	X	X	
Cliona laticavicola	X	X	X	X	X	
Cliona sp.	X				X	
Anthosigmella varians		X				
Alectona jamaicensis	X					
Siphonodictyon brevitabulatum			X	X		
Siphonodictyon coralliphagum			X	X	X	
Bivalves						
Lithophaga bisulcata (in live coral)				X		
Lithophaga bisulcata (in dead coral)			X		X	
Gastrochaena ovata		X	X	X	X	
Anadara baughmani	X				X	
(nestling) Spondylus sp.				X		
Polychaetes						
Spirobranchus giganteus		X				
unidentified polychaetes	X	X		X	X	
Sipunculans						
Phascalosoma perculens			X			
unidentified sipunculans		X			X	
Crustaceans						
Ceratoconchia (endolithic barnacle)	X				X	
(nestling crab)					X	
(nestling ophiuroid)					X	

borings in a morphometric analysis (see chapter 4). Sponge species were identified on the basis of spiculation, according to Rutzler (1971) and Pang (1973)

Montastrea harboured the following associates:
Sponges: *Cliona lampa*, *C*. *laticavicola*, *Siphonodictyon coralliphagum*, *S*. sp.; bivalves: *Lithophaga bisulcata*, *Gastrochaena ovata*, *Anadara baughmani* (nestling); worms: unidentified small polychaetes and sipunculans in small unlined tubes; crustaceans: *Ceratoconchia* (endolithic barnacle); a nestling crab, and a nestling ophiuroid.

Siderastrea contained the following associates.
Sponges: *Cliona lampa*, *C*. *laticavicola*, *C*. *caribbea*, *Siphonodictyon coralliphagum*, *S*. *brevitabulatum*, 1 unidentified sponge; bivalves: *Crassostrea* (nestling oyster), *Lithophaga bisulcata*, *Gastrochaena ovata*; worms: 1 empty green worm tube.

Diploria contained the following associates.
Sponges: *Cliona lampa*, *C*. *laticavicola*, *C*. *caribbea*, *Siphonodictyon brevitabulatum*; bivalves: *Lithophaga bisulcata*, *Gastrochaena ovata*; worms: *Phascalosoma perculens*.

Porites astroides contained the following associates. Sponges: *Cliona lampa*, *C. laticavicola*, *Anthosigmella varians*; bivalves: *Anadara sp.* (nestling); worms: large worm tubes with thick calcareous lining, probably of *Spirobranchus giganteus*, unidentified small polychaete and sipunculan in small unlined tubes; crustaceans: *Boscia* (endolithic barnacle).

Porites porites contained the following associates. Sponges: *Cliona laticavicola*, *C.* sp. cf. *lampa*, *C.* sp., *Alectona jamaicensis*; bivalves: *Petricola lapicida*; worms: unidentified small polychaete in small unlined tube; crustaceans: *Ceratoconchia* (endolithic barnacle).

5.3 Species specificity

Of the sponges found in this study, only *Anthosigmella varians* and *Alectona jamaicensis* occurred in fewer than two genera. Pang (1973) describes each of these species in other species of coral which were not sampled here, so the apparent species specificity here is probably a sampling artifact. Furthermore, the one colony of *Alectona* observed may be a secondary occupant of a *Siphonodictyon* gallery.

Among the bivalves, no species specificity was observed. The only live coral into which *Lithophaga bisulcata* bored was

Siderastrea siderea, but this species was also found boring into lower or dead surfaces of other corals. Its absence in *Porites porites* is probably simply a function of space limitations in the smaller branching coral. Scott (1988) found *L. bisulcata* boring into the live surfaces of only *S. siderea* and *Stephanocoenia michelini* and a variety of dead corals. *L. bisulcata* was more abundant in live than in dead corals (Scott, 1988).

The polychaete *Spirobranchus gigantea* was observed only in one specimen of *Porites astreoides*. This restricted distribution is almost certainly a function of small sample size, as Hunte, et al. (1990a) found it in all of the coral species sampled here. They found that distributions were highly clustered, and that *Diploria strigosa* and *Porites astreoides* were the most preferred corals of those studied here. *S. gigantea* also occurred in low numbers on *Montastrea annularis*, *Siderastrea*, and *P. porites*. *Spirobranchus* does not bore into coral, but rather is overgrown and eventually overtopped by the coral (Hunte, et al., 1990b). No *S. gigantea* tubes were observed in the fossil material (see chapter 4).

The sipunculid *Phascalosoma perculens* was observed only in *Diploria*, but it has been reported in other corals (Rice, 1969) and from beachrock (Stearley and Ekdale, 1988).

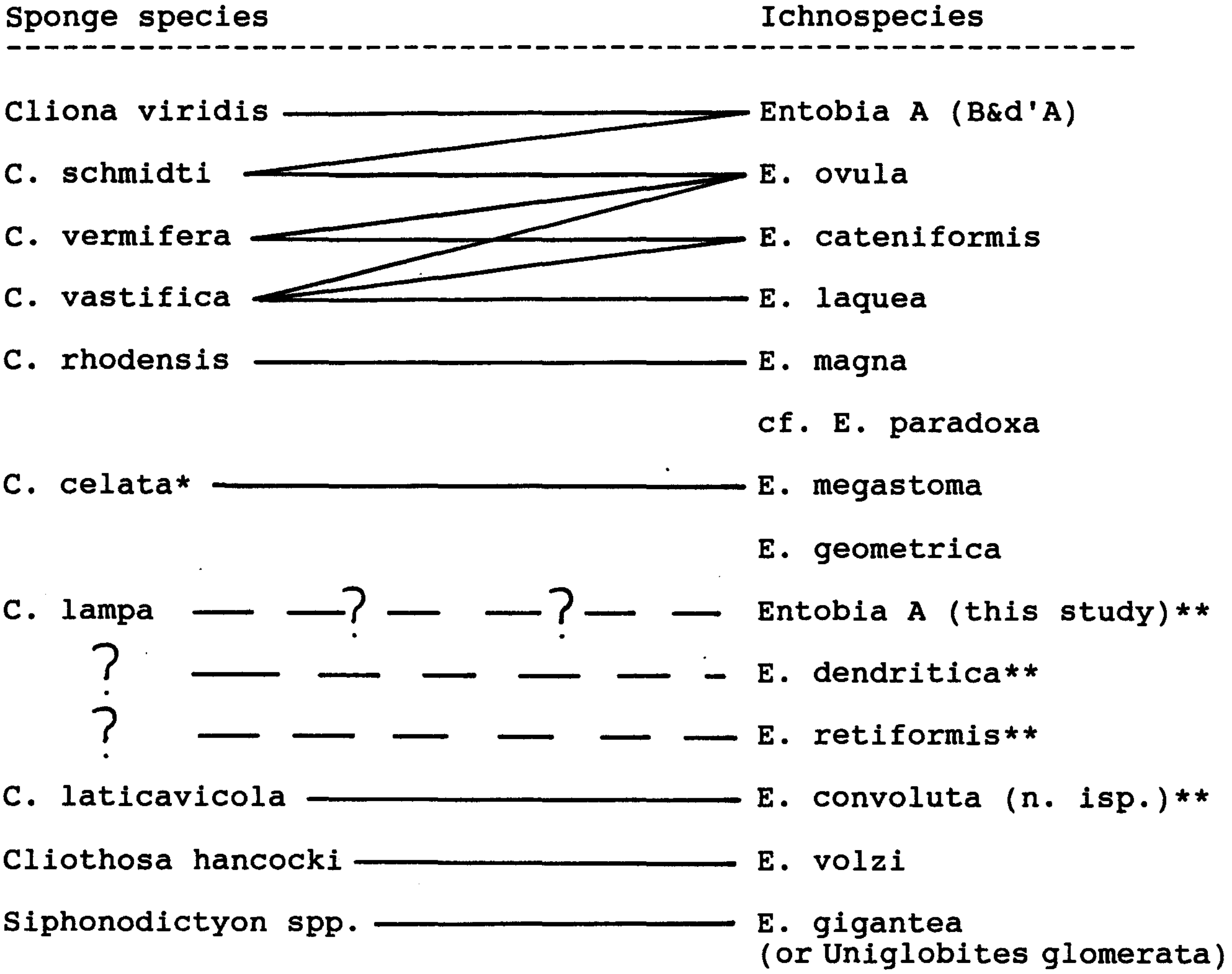
In conclusion, all of the patterns of apparent species specificity observed in this limited sample must be attributed to the small sample size of modern specimens.

5.4 Correspondence with fossil material

Entobia convoluta matches the borings of *Cliona laticavicola*, and *Uniglobites glomerata* (*Entobia gigantea*) matches the borings of *Siphonodictyon* spp. No specific assignments of *Entobia A*, *E. dendritica*, *E. ovula*, or *E. retiformis* can be made on the basis of the modern sampling in this study. Some borings of *Cliona lampa* resemble *Entobia A*. Bivalve borings are all attributable to generic level, and in some cases, to species level (see chapter 4). Of the fossil worm borings, only the J-shaped *Trypanites* can be attributed to a single modern genus, *Phascalosoma*.

Bromley and D'Alessandro (1989) studied the correspondence of modern sponge borings with fossil and modern *Entobia* in the Mediterranean (fig. 5.1). *Entobia ovula* is made by *Cliona schmidti*, *C. vastifica*, and *C. vermifera*, all of which occur in the Caribbean as well as the Mediterranean (Pang, 1973). *Entobia retiformis* is made by *C. retiformis* in the Mediterranean (Stephenson, reported in Bromley and D'Alessandro, 1987). Pleydell and Jones (1988) did not attribute *Entobia dendritica* to any specific sponge. In summary, only *E. convoluta* and *Uniglobites* can be attributed to any single modern sponge species; the remaining be attributed to any single modern sponge species; the remaining entobians were probably made by at least 4 species of Cliona, but species level diversity cannot be more precisely defined.

Figure 5.1. Correspondence of modern sponge species and Entobia ichnospecies in the Mediterranean (from Bromley and D'Alessandro, 1989) and Caribbean (this study).



* Bromley and D'Alessandro (1989) suggest that C. celata may be a species complex.

** Results of this study.

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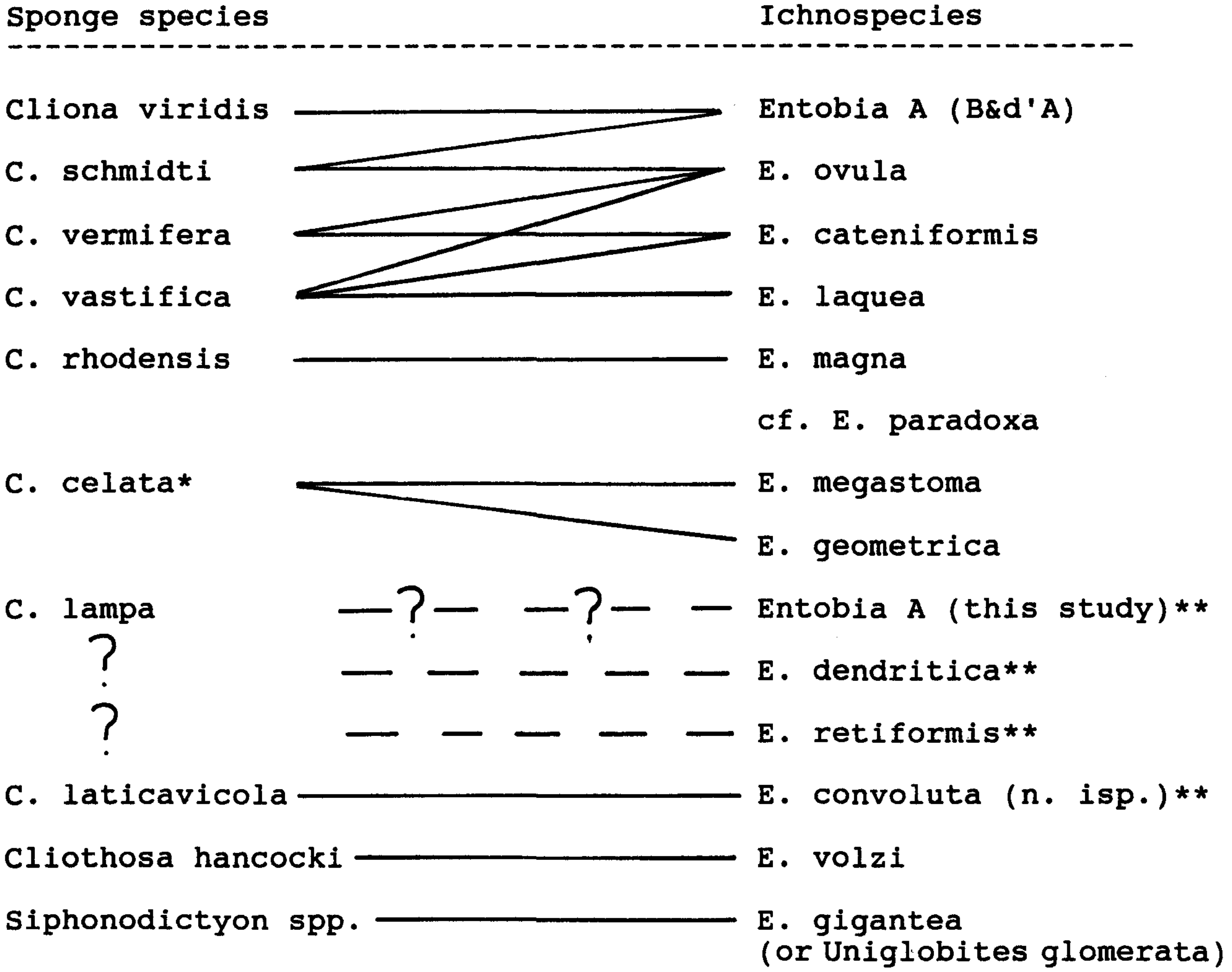
Figure 5.1. Correspondence of modern sponge species and <u>Entobia</u> ichnospecies in the Mediterranean (from Bromley and D'Alessandro, 1989) and Caribbean (this study).



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* Bromley and D'Alessandro (1989) suggest that <u>C</u>. <u>celata</u> may be a species complex.

** Results of this study.

Chapter 6: Ecological Tolerance and Selectivity: What Caused the Extinction?

There are modern representatives of both the "victims" and the survivors of this extinction, but they are now biogeographically separated. This allows a more direct comparison of habitat characteristics, life history patterns, and biogeography of those taxa which survived these extinctions and those which did not. Facies distributions are included in inferences about sediment tolerance, but information on cold tolerance is drawn almost exclusively from modern information. Such an examination can suggest possible environmental changes responsible for this extinction.

6.1 Corals Tolerances and Selective Survivorship

The coral genera which survived this extinction are _Acropora_, _Cladocora_, _Colpophyllia_, _Goniopora_, _Leptoseris_, _Montastrea_, _Porites_, _Siderastrea_, and _Stylophora_. Those which did not survive are _Actinacis_, _Agathiphyllia_, _Antiquastrea_, _Astreopora_, _Astrocoenia_, _Caulastrea_, _Diploastrea_, _Favites_, _Hydnophora_, _Pironastrea_, (Pseudo)_Siderastrea_ (conferta), and _Stylocoeniella_. Tables 6.1 and 6.2 list this information and indicate those genera whose modern representatives are tolerant of either cold water or sediment stress.

Table 6.1 Inferred Ecological Tolerances of Oligocene Corals

Coral Species	Survivorship	Cold	Seds
Actinacis sp. cf. alabamiensis	ext.	?	
Acropora saludensis	surv.		?
Agathiphyllia roxboroughi	ext.		?
Alveopora tampae	surv. to Pl-Pt.	x	
Antiguastrea cellulosa	ext.	?	
Astreopora sp.	ext. in Carib	1sp.	
Astrocoenia portoricoensis	ext.		
Caulastrea portoricoensis	ext. in Carib		1sp.
Cladocora bosquensis	surv.	?	x
Colpophyllia willoughbiensis	surv.		x
Diploastrea crassolamellata	ext. in Carib		x
Favites polygonalis	ext. in Carib	x	x
Goniopora hilli	surv. to Pl-Pt.	?	x
Hydnophora sp. unnamed	ext. in Carib		
Leptoseris portoricoensis	surv.	?	x
Montastrea costata	surv.	x	x
Montastrea tampaensis	surv.	x	x
Pironastrea sp. (?)	ext.		
Porites baracoaensis	surv.	x	x
Porites waylandi	surv.	x	x
Siderastrea conferta	ext. in Carib		
Siderastrea siderea	surv.	x	x
Stylocoeniella lobatorotundata	ext. in Carib	x	x
Stylophora imperatoris	surv. to Pl-Pt.	?	x

Surv.	survived until Holocene in Caribbean.
Ext. in Carib.	extinct in Caribbean at Olig-Mio boundary.
Surv. to Pl-Pt.	survived in Caribbean until Plio-Pleistocene extinction.
Ext.	extinct.
Cold	cold tolerant
Seds	sediment tolerant.

Sources: Hubbard and Pocock (1972), Frost and Schafersman (1978), Frost and Weiss (1979), Frost (1981), Hudson, et al. (1981, 1982), Done (1982), Wood (1983), Cortes and Risk (1985), Brown and Howard (1985), Veron (1986). See text for discussion.

6.1.1 Survivors

Among the survivors, four genera stand out as particularly tolerant of stressful environments: *Montastrea*, *Porites*, *Siderastrea*, and *Colpophyllia*. These four genera are all tolerant of high sediment loading (Hubbard, 1972; Cortes and Risk, 1985). *Agaricia* can also be resistant to sediment stress in its vertical growth form (Cortes and Risk, 1985); this genus first appeared in the Caribbean during the Miocene. Furthermore, *Montastrea*, *Porites*, *Siderastrea* and *Solenastrea* are all tolerant of cold water (MacIntyre and Pilkey 1969; Roberts, et al., 1982).

Acropora today tends to live in high energy reef crest environments, but for much of the Neogene was restricted to patch reef and lagoonal environments (Frost, 1977b,c, 1981). In the Ryuku Islands, it is noted as a genus sensitive to sediment stress - it does not even have cilia capable of rejecting sediment - (Kuhlmann, 1985), but its habit of growing in areas of high wave exposure probably allows it to survive in some reefs with a high level of suspended sediment (Frost, 1981; Cortes and Risk, 1985).

Leptoseris species today live in both deep and shallow reef habitats of both the Pacific and Caribbean (Wood, 1983, Veron, 1986). Kuhlmann (1985) identified *Leptoseris* as a sediment sensitive genus in Japan, although it is common in lagoonal environments in the Maldives and on the Great Barrier Reef (pers. obs.; MJ Risk, pers. comm., 1991). Furthermore, Oligocene *Leptoseris* may have occupied a niche similar to that of *Agaricia* or *Pavona*, its descendent genera in the Caribbean and Indo-Pacific, respectively. These genera are both able to tolerate sediment stress by their habit of growing in vertical plates (Cortes and Risk, 1985; Veron, 1986). In this study, *Leptoseris* was observed mostly in bafflestones or in muddy limestones with a fairly high clastic mud component, e.g. the lowest portions of the Lares Roadcut section (fig. 3.3) and the Ciales section (fig 3.5).

6.1.2 Survivors Extinct at Plio-Pleistocene Boundary

Alveopora, *Goniopora*, and *Stylophora* all survived the extinction in the Caribbean but were restricted to the Indo-Pacific at the Plio-Pleistocene boundary (Frost, 1977; Foster, 1986). *Alveopora* and *Goniopora*, both poritids, are both fairly tolerant of sedimentation stress in their modern reef habitats (Kuhlmann, 1985; Veron, 1986). This is also reflected in their presence in Late Miocene reefs of the Dominican Republic which were characterized by high sediment loading (Foster, 1986, Saunders, et al., 1985). In this study, *Stylophora* typically lived in both reefal and off-reef habitats, such as seagrass beds. Its distribution is similar in the Bluff Fm. of Grand Cayman Is.(Pleydell and Jones, 1988; B. Jones, pers. comm., 1990).

6.1.2 Non-Survivors

The habitat tolerances of the coral genera which did not survive are less clear. For the extinct genera, *Actinacis*, *Agathiphyllia*, *Antiquastrea*, *Astrocoenia* and *Pironastrea*, habitat tolerances can only be inferred from fossil data. All of these species except *Astrocoenia* were found at the Lares site, a patch reef on a carbonate platform, probably characterized by significant loads of resuspended carbonate sediment. The sites on the Lares Carbonate Platform may have also been subject to terrigenous sediment, particularly lower in the Lares Formation (Frost, et al., 1983). *Antiquastrea* also occurred at the Guayanilla and Guanica sites, which were shelf-edge reefs probably less affected by siliciclastic sedimentation. *Actinacis* spp. and *Antiquastrea* *cellulosa* (a cosmopolitan species) both occurred on reefs at the northern limits of the Oligocene tropics (Texas and Italy, Frost and Schafersman, 1978; Frost, 1981) and may have been somewhat tolerant of cool waters.

The habitat tolerances of the genera which became extinct in the Caribbean but survived in the Indo-Pacific are more readily defined. *Caulastrea*, *Favites*, *Hydnophora*, *Siderastrea* *conferta*, and *Stylocoeniella* were found only at the Guayanillia and Guanica sites, in shelf-edge habitats. Other "victims", such as *Astreopora*, *Antiquastrea*, and *Diploastrea*, were found in all reef habitats. Today, *Astreopora*, *Caulastrea*, and *Diploastrea* on the Great Barrier Reef occur mainly in back-reef habitats of middle- and inner-shelf reefs, where water is warmer and more turbid (Done, 1983).

6.1.3 Miocene Corals

The main constructors of the Miocene reefs in this study were *Coscinaraea*, *Porites*, and *Montastrea* at the Brizas del Caribe and Rio Tallaboa sites, and *Montastrea* and *Solenastrea* at the Rio Guajataca Site. According to Frost (pers. comm., 1990), *Montastrea* and *Porites* were the main framework builders of Miocene reefs in the Caribbean. Among the Miocene colonial corals seen in this study, only *Agaricia* and *Coscinaraea* were additions to the Caribbean fauna (Frost, 1977a). *Coscinaraea* is believed to have a Pacific origin (Frost, 1977a), although the fossil record of this species in the Indo-Pacific beyond the Late Pliocene is quite poor (Wells, 1957; Veron, 1986; Veron and Kelley, 1988). Today, it has among the broadest temperature tolerances of any hermatypic coral genus, occurring on subtropical and temperate reefs of Southern Australia and elsewhere (Veron, 1986). It occurs on modern reefs of Hawaii (Veron, 1986), but has not been observed in cores or dredge hauls of submerged Oligocene and Miocene reefs of Hawaii (Grigg, 1988; Grigg, pers. comm., 1990). *Coscinaraea* is found in

Table 6.2: Inferred Ecological Tolerances of Miocene Corals

Coral Species	Survivorship	Cold	Seds
Agaricia sp.	surv.	x	x
Astrocoenia portoricoensis (?)	ext.		
Colpophyllia mexicana (fl)	surv.		x
Coscinaraea colei	ext. in Carib.	x	
Favia sp. cf. mexicana (fl)	surv.	x	
Goniopora hilli (fl)	surv. to Pl-Pt.	x	x
Montastrea altissima	surv.	x	x
Montastrea limbata	surv.	x	x
Porites baracoaensis	surv.	x	x
Porites trinitatis	surv.	x	x
Solenastrea hyades	surv.	x	x
Stephanocoenia duncani	surv.		?
Stylophora sp.	surv. to Pl-Pt.		x

Headings as in table 6.1, except that
ext. in Carib. = extinct in Caribbean after M. Miocene.

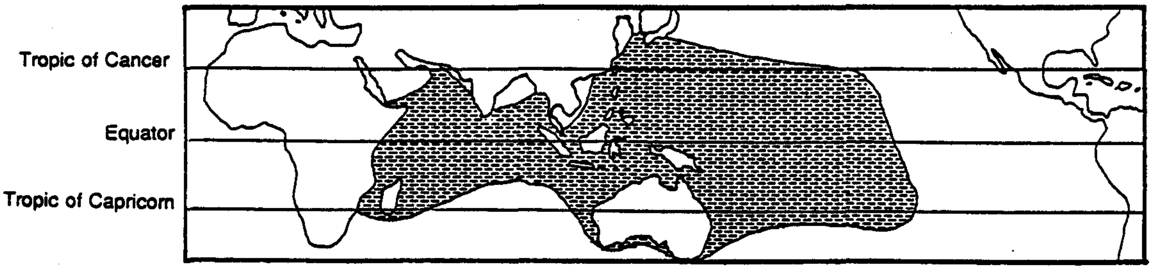
Sources as in table 6.1.

Table 6.3. Habitat Tolerance and Survivorship of Oligocene Corals.

	Cold	Turbidity	Cold+Turbid	Neither
Survived	0	5	7	0
Extinct	2	3	2	4

Data compiled from table 8.1. Two factors appear to have been important to coral survivorship: tolerance of cold water and tolerance of turbidity. Corals whose modern representatives are tolerant of both of these stresses survived in greater proportion (7/9) than those tolerant of only cold (0/2), only turbidity (5/8), or neither (0/4); $\chi^2=8.97$, $p<.05$, d.f.=3).

Fig. 6.1 Range of Modern <u>Coscinaraea</u>; after Veron, 1986.



Range of Modern *Coscinaraea*

Modified from Veron, 1986.

the Caribbean only from the Early and Middle Miocene (Frost, 1977a; this study).

6.1.4 Summary of Coral Tolerance and Survivorship

Tolerance of turbidity and/or cold water are common demoninators of all the corals which survived the extinction. (table 6.3). The distribution of the fossils suggests that elimination of shelf-edge reef habitats was a contributing factor in causing the extinction. (see table 4.3). As discussed below (see paleoceanography), colder and nutrient rich water, such as the conditions in the present Eastern Pacific, could eliminate shelf-edge reef habitats, confining corals to on-shelf patch reefs with higher suspended sediment loads. Stable isotope studies from the Great Barrier Reef show that tidal pumping without Ekman spiral type upwelling brings nutrients as far showeward as mid-shelf patch reefs more than 50 km from the shelf edge (Risk, et al., 1989). Enhanced upwelling in the Miocene could have easily affected the entire shelf of the island arc systems of the Caribbean.

6.2 Coral Associate Tolerance and Survivorship

Modern coral associates generally have a much broader range of ecological tolerance than do corals. Nearly all coral associates are heterotrophic and do not require light (Bergquist, 1978). Many coral associates also occur in deep or cold water habitats. Most associates are fairly tolerant of turbidity. The salinity requirements of endolithic organisms are not well known. As heterotrophs, bioeroding coral associates thrive in nutrient-rich waters (e.g Hallock, 1988).

Most coral associates bore into dead coral, and can easily bore into other substrates. Consequently, most coral associates have biogeographic ranges extending well beyond the range of coral reefs themselves, and would be resistant to most environmental changes which would adversely affect corals. The major exception here are the coral inhabiting organisms which do not bore, but rather, inhibit calcification, causing the coral to grow around them. These include principally the coral inhabiting barnacles (Newman and Ross, 1973) and the Leiosolenus subgenus of the bivalve Lithophaga (Wilson and Tait, 1984; Morton, 1983). These groups will be discussed below.

6.2.1 Sponges

Clionid sponges are found in a wide variety of marine habitats in tropical (e.g. Pang, 1973), temperate (e.g. Evans, 1969), and deep sea waters (e.g. Stanley, 1988b); see table 8.6. Siphonodictyon, however, is reported only from the tropics (Rutzler, 1974). Boring sponges are more tolerant of suspended sediment loading than most corals (e.g. Cortes and Risk, 1985), but are unable to withstand heavy sedimentation (e.g. Stearley and Ekdale, 1988). Endolithic sponges are mostly euhaline, but some species are tolerant of reduced or variable salinity. For example, the diversity of clionid sponges in Louisiana estuaries decreases along a salinity gradient, but there are still some species present in brackish water conditions (Hopkins, 1956).

Some endolithic sponges harbour cyanobacteria in their papillae, which may contribute photosyntetic carbon to the sponge's diet (Bergquist, 1978). Wilkinson (1987) proposed that Caribbean (epilithic) sponges rely more on heterotrophy than do their counterparts on the Great Barrier Reef, which are more dependent on photosymbionts. Organic pollution and natural nutrient enrichment are both known to increase rates of boring sponge growth and bioerosion (e.g. Rose and Risk, 1985; Hallock, 1988; Sammarco and Risk, 1990).

Cliothosa hancocki is present in the Mediterranean and Indo-Pacific, but not in the Caribbean (Volz, 1939); the reasons for this disjunct distribution are unknown, although Risk, et al., MS, suggested that it could be related to predation pressure or differences in autotrophy vs. heterotrophy (see also Wilkinson, 1987). Pleydell (1987) reported _Entobia volzi_, the trace made by _Cliothosa hancocki_ (Bromley and D'Alessandro, 1989) in the

Oligocene-Miocene of the Bluff Fm. of Grand Cayman Is., BWI. Jones (pers. comm., 1990) stated that these borings were in the Oligocene portion of the formation, separated from the Miocene by a previously unrecognized intraformational unconformity. Thus *Entobia volzi* (*Cliothosa*) may represent the only victim of the Oligocene-Miocene extinction among the coral associates. The environmental implications of this possible extinction are unclear.

6.2.2 Bivalves

Lithophaga occurs in subtropical and temperate waters as well as in the tropics (Ricketts and Calvin, 1985). *Gastrochaena* is known only from the tropics, although it is capable of boring other substrates than corals (Carter, 1978). Both *Lithophaga* and *Gastrochaena* occurred in Pliocene corals and carbonate rocks at the North end of the Gulf of California (Watkins, 1990). Endolithic bivalves which are restricted to the tropics today are mostly those which are obligate associates of live corals (Morton, 1983; Scott, 1988; see table 7.3). Likewise, coral-inhabiting (not truly boring) barnalces are restricted to shallow tropical habitats, but boring acrothoracican barnacles (e.g. *Lithotrya*, Ahr and Stanton, 1973) are known from extratropical habitats as well (e.g. Seilacher, 1969).

6.2.3 Other

Boring sipunculan worms are found in temperate waters (Evans, 1969), and <u>Phascalosoma</u> in particular was found boring into rock in the intertidal of the Gulf of California, where it again makes characteristic J-shaped boreholes (Stearley and Ekdale, 1988). With the exception of the J-shaped <u>Trypanites</u>, the fossil worm borings provide little information on the environmental conditions in which their host corals lived.

6.2.4 Associates, Nutrients, and Bioerosion

Numerous studies have demonstrated a positive correlation between nutrient availability and bioerosion by endolithic sponges and other organisms. These include both field (e.g. Rose and Risk, 1985) and museum (e.g. Highsmith 1980) studies. High rates of bioerosion do not apparently limit species diversity of bioeroders (Sammarco and Risk, 1990; Risk et al., submitted).

Although coral associates are generally more eurytopic than reef corals, the most striking differential tolerances are with respect to (1) temperature, (2) light, and (3) nutrients. Sedimentation and salinity both affect associates in a similar manner as they do corals, although associates are less sensitive to these stresses than are corals. Shallow water carbonate sedimentation continued across the Oligocene-Miocene boundary on the North coast of Puerto

Rico (Montebello Member, Cibao Fm.), and often includes *Lepidocyclina* packstones. *Lepidocyclina*, like many large forams, was probably photosymbiotic, hence light dependent, so light (or depth) was almost certainly not a causal factor of the extinction, nor was habitat elimination through a regression. The larger size of Miocene than Oligocene borings (figs. 4.5a,b 4.6b) suggest more intense bioerosion, possibly indicating greater nutrient availability.

6.3 Species Specificity Revisited

The apparent patterns of coral associate host specificity seen in the modern material in this study (see chapter 5) are probably an artifact of small sample size. Every species of associate seen in the fossil material occurs in at least several species of corals, if not from other substrates as well, and the same patterns are documented in the literature on distributions of most modern coral associates. For example, *Lithophaga bisulcata* is reported from live *Siderastrea siderea* and *Stephanocoenia michelini*, but also occurs, in lower numbers, in a wide variety of dead corals (Scott, 1988). *Gastrochaena* has been observed in modern and fossil corals, oysters, other bivalves (Carter, 1978, Morton, 1983), and the Pleistocene echinoid *Clypeaster* (personal observation at Smithsonian Institute; 1990).

Similar absence of host specificity has been documented in the bioeroding associates of Indo-Pacific gastropods. Smyth (1990) discusses the occurrence of various borers in gastropod shells from Guam, including acrothoracican barnacles, Ctenostome bryozoans, polychaetes, clionid sponges, and a foraminifer. She found no evidence of species specificity, with the exception that only truly filter-feeding organisms could bore from the inner side of gastropod shells, while suspension feeders which sweep their feeding organs through the water always occupied outer surfaces. She identified 7 species of boring sponges in the gastropod shells: Cliona vastifica, C. ensifera, C. viridis, Cliona sp., Thoosa bulbosa, Alectona sp., and Amorphinopsis sp.. The absence of Cliothosa and Siphonodictyon in these gastropod shells may be a simple function of their larger gallery size.

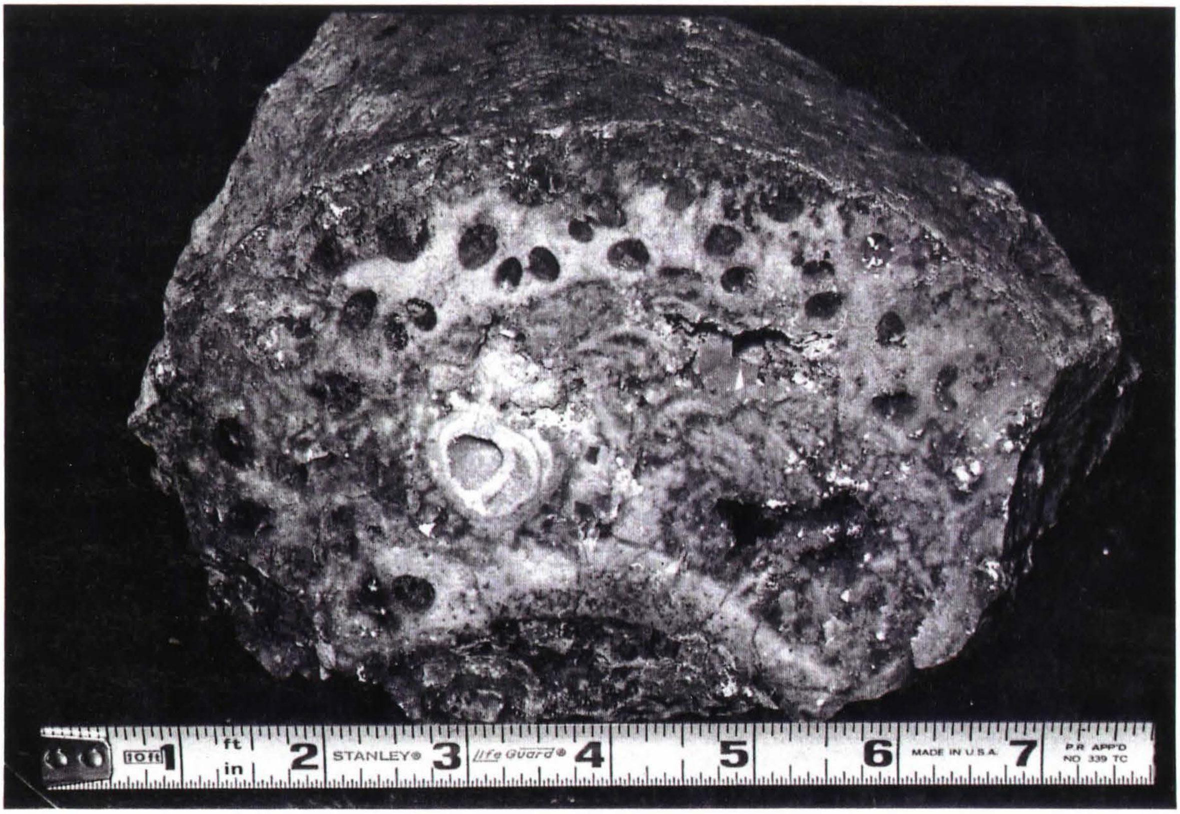
With respect to the coral-inhabiting bivalves, there is only one species of Lithophaga in the Caribbean which exclusively inhabits live corals. This is L. dixonae, which occurs only in the small branching corals Madracis spp. (Scott, 1986). There are eight Indo-Pacific Lithophaga species which are obligate live coral associates (table 7.4). Morton and Scott (1980) suggest that these bivalves all have reduced shell length/width ratios, reflecting their need to inhibit coral calcification at the posterior end as well as bore at the anterior end. No such bivalves have been reported from the fossil record, and none were recognized in this study. This may corroborate Scott's (pers. comm., 1990) suggestion that this group of bivalves is of relatively recent, perhaps only Pleistocene, origin. Most of these species occur exclusively in species of *Acropora*, *Montipora*, *Stylophora*, or branching *Porites*. The first three of these genera apparently underwent dramatic radiation during Plio-Pleistocene times, and those *Lithophaga* which are obligate live coral associates may have radiated in response (see section 7.9).

6.4 Coral Associates in Previous Mass Extinctions

The lack of species turnover among the coral associates is less surprising in light of their almost universal survivorship across the K/T boundary (at the genus level). *Entobia cretacea* occurs in Caribbean rudists (plate 6.1a,b; Kauffman and Sohl, 1974), oysters from the Western Interior Basin (e.g. Birchard, 1987), and a variety of other substrates. Clionid sponge borings have been reported from Jurassic corals (e.g. Fagerstrom, 1987; Oschmann, 1989) and Early Cretaceous corals and rudists (e.g. Scott, 1981), and elsewhere. Likewise, *Lithophaga* and *Gastrochaena* both occurred in Jurassic corals (e.g. Oshmann, 1989) and Cretaceous corals and rudists (Kauffman and Sohl, 1974; Scott, 1981). Pojeta and Palmer (1976) report other (presumably modiomorphoid) endolithic bivalves from the Ordovician; these borers may have perished in the Permo-Triassic extinctions. Seilacher (1969) discusses borings of

Plate 6.1a. *Titanosarcolites* sp., Cretaceous rudist bivalve, with *Entobia cretacea* borings at upper right. Large dark holes are skeletal pores.

Plate 6.1b. *Entobia cretacea* borings in Cretaceous rudist *Titanosarcolites* sp. Rio Minho site, Jamaica. See Kauffman and Sohl, 1974. Scale bar 1 cm.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acrothoracican barnacles in Cretaceous belemnites. Boring ctenostome bryozoans are known from the Ordovician (Cheetham, 1987), and Trypanites borings are known from the Cambrian (James and Kobluk, 1977). Clearly, bioeroding coral associates are an old, extinction-resistant guild, the "Lingulas" of the coral reef ecosystem.

Coral associates are probably extinction resistant because of their non-obligate association with corals. All of the associates observed in this study occurred in at least two genera of corals, and many were found in bivalves, echinoids, even rhodolites (see table 4.6). For their study on modern sponge borings, Bromley and D'Alessandro (1989) collected only sponges growing in rocks (rather than animal skeletons). Goldring and Kazmierczak (1976) discuss the paleoecology of boring organisms in hardgrounds, which include many of the genera treated in this study. In the absence of skeletal substrates to bore, as during times when there was no reef accretion, endolithic associates simply bored into other calcareous substrates. The endolithic habit apparently serves as a refuge from environmental changes and habitat destruction, as well as from predation. In this sense, endolithic coral associates may be a poor group to examine with respect to survivorship in mass extinctions because they are too resistant to extinctions.

6.5 Other Reef Organisms

The other reef organisms found in this study showed little or no generic turnover. *Clypeaster* occurred on both Oligocene and Miocene reefs, as did *Pecten*, oysters and infaunal bivalves. There is no evidence for an extinction of gastropods, although at least one new genus (*Strombus*) appears in the Miocene (Frost, pers. comm., 1990). While there was some turnover among large benthic forams, the extinction was less severe and more protracted than that among (Frost and Langenheim, 1974). Lepidocyclinids, the main Oligocene group found on Caribbean reefs, persisted in the Caribbean until the early Middle Miocene (Adams, 1983).

Evolutionary patterns among gastropods, bivalves, and echinoids from the Late Miocene to the Recent are much better documented. This interval includes the second event which divided Caribbean reef faunas from Indo-Pacific faunas, the various extinctions at the Plio-Pleistocene boundary (see chapter 2). Gastropod species diversity in the Caribbean reached its apex during the Middle Miocene, and was reduced 32% during the Pliocene, when the Isthmus of Panama finally cut off exchange between the Caribbean and the Eastern Pacific (Petuch, 1982; Vermeij and Petuch, 1986). Extinction among Eastern Pacific gastropods was much less, and many gastropods which had had trans-isthmian distributions (Gatunian province, see chapter 2) became restricted to the Eastern Pacific

(Vermeij and Petuch, 1986). Petuch (1981) described a relict modern gastropod fauna in an upwelling zone off Venezuela with a species assemblage essentially unchanged from the typical Late Miocene Gatunian fauna, and with many more species in common with the Eastern Pacific than is true of the modern Caribbean gastropod fauna. Thus cool, nutrient rich waters, as exemplified by the Eastern Pacific, or off northern South America, may have characterized the Caribbean during much of the Miocene. Such conditions could explain the apparent lack of Miocene shelf-edge reefs in the Caribbean. Jones and Hasson (1985) repeatedly stress that the extinction pattern among molluscs associated with the final emergence of the Isthmus of Panama is exactly opposite that observed in corals. More Gatunian molluscs survived in the Eastern Pacific than in the Caribbean (Vermeij and Petuch, 1986), while Gatunian corals in the Eastern Pacific were eventually wiped out completely (Dana, 1975; Jones and Hasson, 1985).

6.6 Nutrients, Upwelling, and Reefs

In upwelling regions, coral reef development tends to be restricted to on-shelf patch reefs, such as are found in the Eastern tropical Pacific (Glynn, 1982; Glynn, 1988; Glynn and Wellington, 1983). More intense competition with benthic heterotrophs and increased bioerosion caused by nutrient loading, such as in upwelling regions, tend to retard rates of reef accretion (Birkeland, 1987). Under these conditions, shelf-edge barrier reef systems develop with difficulty or not at all (Hallock and Schlager, 1986). Hallock, et al. (1988) suggest that nutrient loading, caused partly by local topographic upwelling, prevents development of reefs along most of the Nicaraguan rise.

Viewing the longer term pattern, it appears as though the Miocene in the Caribbean was an anomalous period characterized by cooler, and possibly more nutrient-rich waters, than either the Oligocene or the Pleistocene-Holocene. The change to these conditions can explain the coral extinction at the Oligocene-Miocene boundary. Colder, nutrient-rich water in the Caribbean could in itself exceed the temperature tolerance of some Oligocene corals, and could have eliminated shelf-edge reef habitats. Corals tolerant of cold water, and corals capable of surviving on shallow water patch reefs, where suspended sediment loads are generally higher, would be favoured, while those intolerant of these conditions would be driven to extinction. In this light, the lack of extinction among gastropods, bivalves, and echinoids can be more readily interpreted - these organisms mostly lived in seagrass beds and around patch reefs, rather than on shelf-edge reefs. Likewise, the mostly eurythermal, somewhat sediment tolerant, and primarily heterotrophic bioeroding coral associates would thrive in these conditions.

The survivorship pattern of the corals (see above) and the lack of turnover in associates suggest turbidity, cooling, and possibly eutrophication as causes of the coral extinction. There is no evidence, however, of either a regression or a decrease in global ocean temperatures to account for the increased turbidity or colder water. Enhanced upwelling in the Miocene Caribbean could account for all three of these environmental changes. The lack of turnover in most other reef invertebrates, including gastropods, bivalves, and echinoids is consistent with such a pattern. Paleoceanographic reconstructions suggest that such a regime would be quite possible given the paleogeography of the Miocene.

6.7 Paleoceanography

What oceanographic changes could have brought about cooling, nutrient loading, and sediment loading in the Caribbean at the Oligocene-Miocene boundary? The Oligocene-Miocene boundary marked the first of two turning points in the transition from a longitudinal (E-W) circulation system to a meridional (N-S) circulation system in the world's oceans. The second point, the close of the Central American Seaway, also coincides with a regional extinction of Caribbean reef organisms (see chapter 2). These oceanographic changes have been extensively investigated in the temperate and polar oceans (Kennett, 1982), and in the tropical central Pacific (van Andel et al., 1975; Kennett, 1985), but much less so in the Caribbean.

Two tectonic-geographic changes occurred at about the Oligocene-Miocene boundary. First, Africa + Arabia collided with Eurasia and closed the Eastern end of the Tethys seaway (Crowley and North, 1988). This collision may have begun as early as the Eocene-Oligocene boundary (Ricou, et al., 1986), but was apparently not complete until about 25 Ma (Oligocene-Miocene boundary). Second, Drake Passage (between Patagonia and Antarctica) opened to deep circulation, allowing full circum-Antarctic deep circulation and a major increase in production of Antarctic bottom water (Kennett, 1982). These were later followed by the Messinian eustatic lowstand (which drained the Mediterranean about 6 Ma.; Hsu, et al., 1973), and the Pliocene closing of the Central American Seaway. These events (primarily the first and last) have been incorporated into several paleoceanographic models which are applicable to the Oligocene-Miocene extinction event.

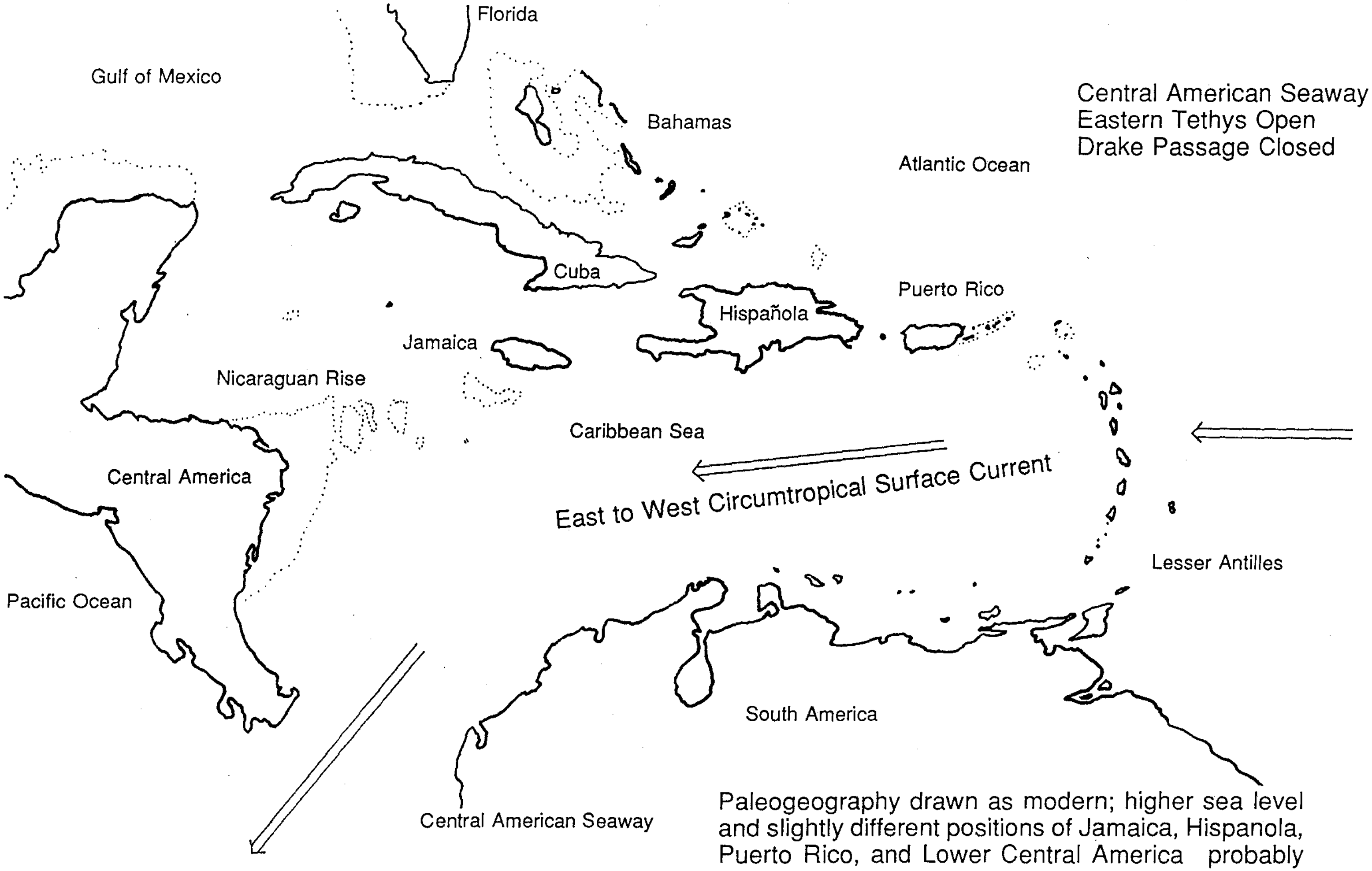
8.7.1 Paleoceanographic Models

Luyendyk, et al., (1972) constructed a physical model of global paleocurrents for the Cretaceous and Tertiary. This consisted of a rotating table with plywood continents and fixed air jets to simulate wind systems. This model simulated only the northern hemisphere. They reached two major conclusions: (1) With an open Tethys seaway all around the globe, circumtropical circulation flowing East to West connected all parts of the tropics (fig. 6.2).

Figure 6.2. Proposed Cretaceous-Oligocene surface and near-surface circulation pattern, Caribbean region. Based on Luyendyk et al. (1972), Haq (1981), and Maier-Reimer, et al. (1990). Islands and continents were mostly in modern positions, with two exceptions: (1) the lesser Antilles were younger, with fewer islands, and (2) the Central American Seaway was open to deep circulation.

Proposed Cretaceous-Oligocene Surface and Near-Surface Circulation Pattern, Caribbean Region.

Central American Seaway Open
Eastern Tethys Open
Drake Passage Closed



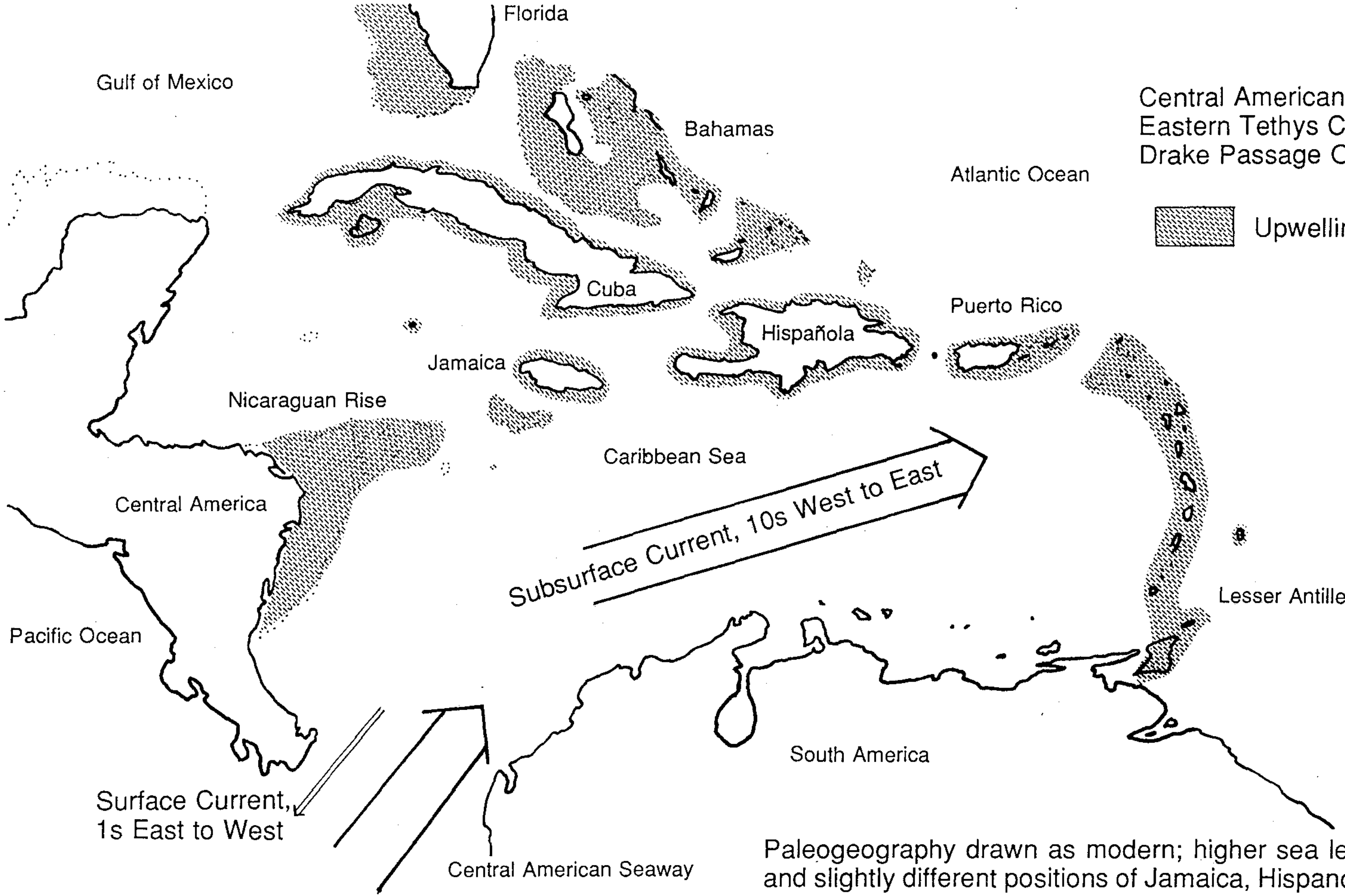
Paleogeography drawn as modern; higher sea level and slightly different positions of Jamaica, Hispanola, Puerto Rico, and Lower Central America probably had no major influence on circulation patterns. See Stehli and Webb (1985) for review of Caribbean tectonics.

This pattern characterized the Cretaceous and Paleogene. (2) With the Eastern Tethys closed and Central American Seaway still open, this circumtropical circulation was interrupted, and flowed West to East through the Straits of Panama (fig 6.3). This pattern would have characterized the Miocene and Early Pliocene, until the Isthmus of Panama was fully emergent.

Maier-Reimer, et al. (1990) refined this model with a computer simulation extending to the Southern Hemisphere and including velocities, mass balances, and vertical circulation. Their results with respect to the closed Eastern Tethys and open Central American seaway agreed with those of Luyendyk, et al., but added several points. (1) When currents through the Strait of Panama changed to West to East flow, they also increased in mass transport from 1 Sv Easterly to 10 Sv Westerly (1 Sv = Sverdrup = $10^6 m^3/sec$). (2) This circulation included deep circulation, at least through Middle Miocene time; shallow wind-driven circulation may have continued to flow East to West through the Straits. (3) Upwelling along the West coast of the Americas was not affected by this change in current direction. (4) This West to East current joined the Gulf Stream and flowed into the North Atlantic, possibly warming it and preventing the onset of Nothern Hemisphere glaciation until after this current was interrupted by the emergence of Panama in the Pliocene.

Figure 6.3. Proposed Miocene surface and near-surface circulation pattern, Caribbean region. Based on Luyendyk et al. (1972) and Maier-Reimer, et al. (1990). Islands and continents were mostly in modern positions, with two exceptions: (1) the lesser Antilles were younger, with fewer islands, and (2) the Central American Seaway was open to deep circulation.

Proposed Miocene Surface and Near-Surface Circulation Pattern, Caribbean Region



Central American Seaway Open
Eastern Tethys Closed
Drake Passage Open

Paleogeography drawn as modern; higher sea level and slightly different positions of Jamaica, Hispanola, Puerto Rico, and Lower Central America probably had no major influence on circulation patterns. See Stehli and Webb (1985) for review of Caribbean tectonics.

The influence of the opening of Drake Passage on these changes is unclear. The beginning of circum-Antarctic deep circulation allowed by the opening of Drake Passage did, however, dramatically increase production of Antarctic bottom water, leading to greater temperature stratification in all oceans. (Kennett, 1982). This also coincides with the beginning of extensive Antarctic continental glaciation (Kennett and Shackleton, 1975; Kennett, 1982).

This reversed tropical current system would have brought large amounts of deep, cold, nutrient-rich water into the Caribbean from the Eastern Pacific. Deep circulation through the Strait of Panama could have transported nutrients into the Caribbean. Local topographic upwelling at the margins of the Caribbean could have brought these nutrients to the surface, thus impeding coral reef development (fig. 6.3). Hallock, et al. (1988) describe such a process along the Nicaraguan Rise today, where there are no reefs, despite the presence of abundant shallow water carbonates. This current regime could explain the lack of shelf-edge reefs in the Caribbean during the Miocene. This scenario is also consistent with the immigration of Coscinaraea and other Pacific corals into the Caribbean during the Early and Middle Miocene (Frost, 1977a). As deep circulation diminished with the progressive rise of a Panamanian Sill during the Middle and Late Miocene (Kennett, et al., 1985), these conditions might have gradually ameliorated. This series of oceanographic changes could also explain the diversity and extinction patterns observed among Caribbean and Eastern Pacific gastropods (Petuch, 1981; Vermeij and Petuch, 1986).

6.7.2 Deep Sea Drilling Project Data

There is no ^{18}O or ^{13}C record across the Oligocene-Miocene boundary in the Caribbean. Cadmium levels in Quaternary foraminiferan shells have been used to infer paleoproductivity (Boyle, 1985; Shen and Boyle, 1988), but no such data are available from the mid-Tertiary. There was a substantial shallowing of the Carbonate Compensation Depth in the Caribbean in the Early Miocene (Bolli and Silva, 1973). Since temperature exerts a primary control over the depth of the CCD (Kennett, 1982), the shallowing of the CCD in the Caribbean could indicate regional oceanographic cooling.

Jones and Hasson (1985) reviewed benthic and planktonic foraminiferan data along with macrofossil data and suggested gradual restriction of deep water communication between the Eastern Pacific and the Caribbean beginning as early as the middle Miocene (ca. 15 Ma.), and certainly by the late Miocene. Keigwin (1978, 1982) and Kennett, et al. (1985) reach similar conclusions, using

DSDP data from the Caribbean, Gulf of Panama, and Central Pacific. Accompanying this diminution of deep circulation was a rise in Caribbean marine temperatures (Jones and Hasson, 1985). Eustatic sea level changes probably exerted a greater influence on the timing of the emergence of the isthmus of Panama than did tectonic uplift (Savin and Douglas, 1985).

To sum up the DSDP data, it is equivocal at best for the Oligocene-Miocene boundary, but appears to show a progressive differentiation of faunas from Middle Miocene time onward, with deep water fauna being affected before shallow water fauna. There is no sedimentological evidence on the direction of currents through the Central American Seaway during this time.

6.7.3 Intensity of Bioerosion

Intense bioerosion and drowned reefs are often associated with upwelling systems (Glynn, 1982; Hallock and Schlager, 1986). Intense bioerosion on Miocene reefs of the Caribbean, and perhaps, a large number of drowned reefs of Miocene age in the Caribbean, might indicate greater nutrient stress on those reefs.

While bioerosion <u>appears</u> to be more intense on the Miocene reefs than on the Oligocene reefs studied here (see chapter 6), the method of sampling in this study does not allow a direct statistical test of this hypothesis. Miocene Entobia convoluta and Uniglobites glomerata are both significantly larger than their Oligocene counterparts (fig 4.5a,b). Likewise, Miocene Entobia ovula had far more chambers than did their Oligocene counterparts (fig. 4.6b). These facts suggest, but do not prove, that bioerosion was more intense on the Miocene reefs than on the Oligocene reefs in this study. The vagaries of preservation, combined with the inherent high variability in intensity of bioerosion on a local scale (Risk, et al., submitted) would necessitate an immense sample size.

There is not enough data on the frequency and stratigraphic distribution of drowned reefs to make any reliable comparisons between the Caribbean and the Indo-Pacific.

6.8 Summary of Paleoceanography: What Caused the Extinction?

The most important factors responsible for the mass extinction among the corals appear to be (1) the decrease in water temperature in the Caribbean, probably associated with eutrophication, and (2) turbidity on nearhsore patch reefs. Increased upwelling of cold and nutrient-rich water could have restricted coral reef development to nearshore fringing, patch, and platform reefs, which are typicaly characterized by higher levels of suspended carbonate and terrigenous sediment than are shelf-edge reefs.

The paleontological evidence in this and other studies suggests a radical change in Caribbean oceanography during the Miocene. Paleoceanographic models provide a mechanism which could account for these changes. A reversal of currents through the Strait (Isthmus) of Panama during the Miocene, accompanied by deep circulation during the Early and Middle Miocene, would have brought cold, nutrient-rich water into the Caribbean, drastically altering conditions for reef growth, and causing the extinction among the corals.

Chapter 7: Life History Effects, Trophic Level Effects, and Biogeographic Consequences of the Extinction.

How did strictly biological factors influence selective survivorship in this extinction? How have such factors affected survivorship of other organisms in other extinctions? Two recent approaches to such questions have been to examine life history characteristics and trophic level as selective factors in mass extinctions. The most commonly investigated division in life history characteristics is between brooders and broadcasters, and the influence that these different modes of larval nutrition may have on dispersal and geographic range.

Table 7.1 Modes of Larval Development and Dispersal in Marine Invertebrates, average and potential larval drift time in coral larvae. Compiled from Jablonski and Lutz (1983), Babcock and Heyward (1985), Richmond (1990).

Larval Mode	Details of Larval Biology	Larval Drift Time in Corals
planktotrophs (broadcasters) BC	larvae feed and develop entirely within the water column; large number of small gametes; long larval drift time	average: longer potential: shorter
lecithotrophs (brooders) BR	larvae feed from yolk sac, develop in water column; small number of large gametes; short larval drift time	average: shorter potential: longer
direct developers (brooders) BR	larvae feed from yolk sac, develop within brood pouch, emerge as juveniles; small number of large gametes; no larval drift time.	NOT POSSIBLE IN CORALS

Table 7.1 describes the general modes of larval nutrition and dispersal in marine invertebrates. Planktotrophic larvae usually require a longer time to develop than do lecithotrophic larvae, and therefore have a longer larval drift time. Their longer larval drift time confers a greater dispersal capability, and in most marine invertebrates, broadcasters have greater geographic ranges than do brooders (Jablonski and Lutz, 1983; Scheltema, 1979; Scheltema, 1986). In scleractinian corals, however, the biogeographic pattern is reversed (see section 7.2). The relationship between larval mode and geographic dispersal may have profound evolutionary consequences, particularly in mass extinctions.

7.1 Life History Characteristics in Phanerozoic Extinctions

Arthropods and molluscs are the organisms most amenable to study of life history characteristics in the fossil record, because they generally leave skeletonized evidence of their larval biology. There is a small body of literature on the influence of larval mode on survivorship in mass extinctions.

7.1.1 Trilobites

Trilobites were devastated in the Ordovician-Silurian extinctions, but mortality was not random (Chatterton and Speyer, 1989). All pelagic trilobites died out, and all but one genus of benthic trilobites with planktonic larvae died out by the end of Ashgillian time. By contrast, trilobites with benthic larvae or a mixed planktonic-benthic larval life suffered considerably less. Chatterton and Speyer interpret this pattern as indicating a productivity crisis as one of the causes of the Ordovician-Silurian extinctions. They also stress that the strong tropical and shallow water biases in trilobite extinctions (Briggs, et al., 1988) indicate (1) elimination of tropical epeiric seas and (2) global oceanic cooling as important causal factors of the extinction.

7.1.2 Permo-Triassic Brachiopods, Crinoids, and Molluscs

Valentine (1986) suggested that the Permo-Triassic extinctions may have selectively eliminated organisms with planktotrophic larval development. This is based on the absence of planktotrophic larvae in modern articulate brachiopods and crinoids. These groups, in the Paleozoic, occupied predominantly tropical habitats, the main region in which planktotrophic larval development is most prominent today (Jablonski and Lutz, 1983). As neither of these groups have skeletonized larvae, no direct evidence can be brought to bear on the issue. Erwin (1989), however, questioned this apparent pattern based on survivorship of gastropods, but again, his assertion was based primarily on comparison with modern representatives, rather than on fossil larval shell morphology. For the time being, the role of larval ecology in the Pm/Tr extinctions remains uncertain.

7.1.3 Mesozoic and Cenozoic Molluscs

In the Western Interior Basin, ammonites and epifaunal bivalves suffered significantly higher turnover than infaunal bivalves and gastropods in a minor extinction at the Cenomanian-Turonian boundary (Upper Cretaceous; Elder, 1989) Molluscs occupying outer shelf clastic habitats were more affected than those of more near-shore environments. Strangely, cosmopolitan groups had lower survivorship than endemic groups, contrary to the usual bias against endemics (Jablonski, et al., 1986c). Elder attributes this bias to extremely high mortality of planktotrophic larvae in the water column, but there is no direct evidence which can be brought to bear on this question.

Most of the work involving life history strategies and surviorship during minor extinctions and across the K/T boundary deals with larval mode of gastropods in the thick Gulf States clastic sequences of the Upper Cretaceous and Lower Tertiary (e.g. Hansen, 1980, 1982; Jablonski, 1986a). Hansen (1980, 1982) showed that Eocene neogastropods with lecithotrophic (short-term planktic or brooded) larvae had significantly higher species turnover rates than did members of the same families with planktotrophic larvae. Furthermore, suites of species with lecithotrophic larvae came in discrete sets, punctuated by regional extinctions throughout the Gulf States. He attributed this difference to restricted ranges and greater endemism among non-planktotrophic species, with greater possibilities for local extinction as clastic facies migrated with prograding deltas or eustatic sea level changes.

Jablonski (1986a) showed the same trend in Upper Cretaceous gastropods, but also showed that larval mode did not significantly correlate with survivorship across the K/T boundary. Furthermore, the number of species within a genus did not affect generic survivorship, and the only apparent determinant of survivorship was geographic distribution of the clade (genus, subfamily, or family). On this basis, he proposed an alternation of macroevolutionary modes between times of background processes and times of mass extinctions (Jablonski, 1986a).

7.1.4 Other organisms

The planktonic ecosystem was particularly devastated in the Cretaceous-Tertiary extinctions, but the extinctions were not uniform. Coccolithophores suffered 73% extinction; radiolarians, 85%; planktonic foraminifera, 92%; but diatoms, only 23% (Thierstein, 1982). Interestingly, among the planktonic forams, all deep water planktonic forams became extinct while some surficial forms survived and others did not. Deep sea benthic forams, however, were relatively unaffected (Brasier, 1988). This pattern bears some similarity to that among the Ordovician-Silurian trilobites discussed above.

Kitchell, et al. (1986) proposed that the relatively high survivorship of centric diatoms across the K/T boundary (77%) was a consequence of their having resting stages with which to escape the plankton during periods of low nutrient availability following biological depletion in upwelling zones. How long these resting stages remain viable is unknown. Dinoflagellates, which also encyst, also suffered relatively low rates of extinction (33%), and actually diversified across the K/T boundary (Thierstein, 1982). This selective pattern of extinction is consistent with the collapse of planktonic productivity sugested by isotopic studies (Magaritz, 1989) and selective survival among the macrofauna (see trophic level effects, section 7.5).

This apparent life history effect is also connected with biogeography: most diatoms lived in polar seas and were presumably adapted to wide seasonal fluctuations in temperature, light, and nutrient availability (Kitchell, et al., 1986). In general, Late Cretaceous polar and cold temperate marine faunas suffered much less extinction than their tropical counterparts (Kauffman, 1984; Stanley, 1984, 1987).

7.2 Reproductive Ecology of Corals

All corals produce planula larvae for sexual reproduction, although asexual reproduction by colony fragmentation may be more important in some cases (Tunnicliffe, 1981; Highsmith, 1982). Some corals (broadcasters) release eggs and sperm, and fertilization takes place in the water column. Although the eggs sometimes contain zooxanthellae (e.g. Willis, et al., 1985), the larvae produced by these corals are usually azooxanthellate and must acquire algal symbionts directly from the water column (Babcock and Heyward, 1984). Other corals (brooders) retain eggs until after fertilization and release fully developed zooxanthellate planula larvae. Brooded, zooxanthellate larvae have a longer lifespan in the water column and have greater capabilities of long distance dispersal (Richmond, 1990). Thus the relative dispersal capabilities of planktotrophic vs. nonplanktotrophic coral larvae are opposite from those of molluscs or other non-zooxanthellate organisms. Reproductive mode (both broadcasting vs. brooding and hermaphrodism vs. gonochory) in corals is generally consistent within families or genera (Fadlallah, 1983; Richmond and Hunter, 1990), although in Acropora and a few other large genera, there appears to be interspecific variation (Fadlallah, 1983). It is probably a reasonable assumption that the reproductive mode of fossil corals was the same as their modern congeners.

The same size constraints which apply to mode of larval dispersal in solitary marine invertebrates (Menge, 1975; Jablonski and Lutz, 1983) apply to coral colonies (Szmant, 1986). For example, Siderastrea siderea broadcasts its larvae, but its smaller relative, S. radians, broods its larvae. Below a certain size, coral colonies are unable to reproduce, even if these small colonies are fragments of a once larger colony which was reproductive (Szmant, 1986).

7.3 Coral Reproductive Modes and Survivorship

Table 7.2 lists two reproductive modes of the modern representatives of all coral genera seen in this study: whether the genus broods its larvae (BR) or broadcasts gametes (BC), and whether it is hermaphroditic (h) or gonochoric (g; separate sexes). The survivorship data are summarized in table 7.3.

Table 7.2: Inferred Reproductive Characteristics of Oligocene Corals

Abbreviations: Ext: Extinct. I-P: restricted to the Indo-Pacific at the O-M boundary. Surv: Survived O-M extinction. Genera marked with ++ died out in the Caribbean in the Plio-Pleistocene extinction. BR: brooder. BC: broadcaster. gon: gonochoric. herm: hermaphroditic. Five genera are globally extinct. Agaricia and Coscinaraea are not present in the Caribbean until the Miocene, and are not listed here. Pseudosiderastrea is the probable descendent of Siderastrea conferta, and is confined to the Indo-Pacific; its reproductive biology is unknown.

* All known Indo-Pacific Favia are broadcasters; only the Caribbean species F. fragum broods (Richmond and Hunter 1990).

** All known Goniopora are broadcasters, except the Central Pacific G. queenslandiae (Richmond and Hunter 1990). Affinities of the Mio-Pliocene Goniopora of the Caribbean are unknown.

*** Reproductive biology of Leptoseris is unknown, but is probably a brooder in the Caribbean, like its descendant Agaricia (Van Moorsel 1983). Szmant (pers. com., 1990) suspects that Leptoseris and Stephanocoenia are brooders, based on their size, general ecology, and recruitment characteristics, but there are no published reports on the reproductive ecology of these genera.

Coral Genus	Survival	Larval Type	Sex	Source
Actinacis	Ext	UNK	unk	-----
Acropora	Surv	BC	herm	Szmant, 1986
Agathiphyllia	Ext	UNK	unk	-----
Alveopora ++	Surv	BR	herm	Schlesinger and Loya, 1985
Antiguastrea	Ext	UNK	unk	-----
Astreopora	I-P	BC	herm	Veron, 1986
Astrocoenia	Ext	UNK	unk	-----
Caulastrea	I-P	BC	herm	Willis, et al., 1986
Cladocora	Surv	BC	herm	Fadlallah, 1983
Colpophyllia	Surv	BC	herm	Fadlallah, 1983
Diploastrea	I-P	BC	gon	Harrison, 1985
Favia	Surv	BR*	herm	Szmant, 1986

Favites	I-P	BC	herm	Richmond and Hunter, 1990
Goniopora ++	Surv	BC**	gon	Yamazato, 1975
Hydnophora	I-P	BC	herm	Veron, 1986
Leptoseris	Surv	UNK***	unk	Richmond and Hunter, 1986
Montastrea	Surv	BC	herm	Szmant, 1986
Pironastrea	Ext	UNK	unk	-----
Porites	Surv	BR	gon	Szmant, 1986
Pseudosiderastrea	I-P	UNK	gon	Veron, 1986
Siderastrea	Surv	BC	gon	Szmant, 1986
Solenastrea	Surv	BC	gon	Wood, 1983
Stephanocoenia	Surv	UNK***	unk	Richmond and Hunter, 1990
Stylocoeniella	I-P	UNK	unk	Richmond and Hunter, 1990
Stylophora ++	Surv	BR	herm	Schlesinger and Loya, 1985

Table 7.3: Summary Table of Coral Survivorship and Reproductive Modes. Abrreviations as in Table 7.2.

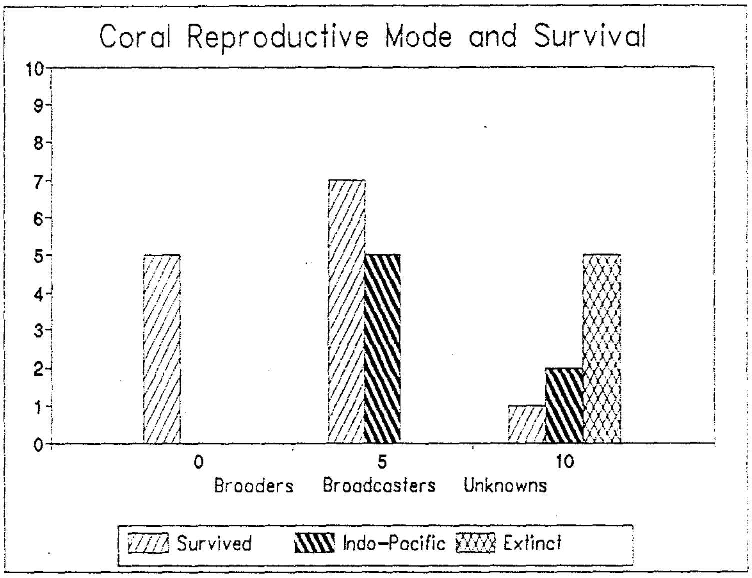
	BR	BC	UNK	TOTAL	gon	herm	unk	total
Surv	5	7	1	13	4	7	2	13
IP	0	5	2	7	1	5	1	7
Ext	0	0	5	5	0	0	5	5
Total	5	12	8	25	5	12	8	25

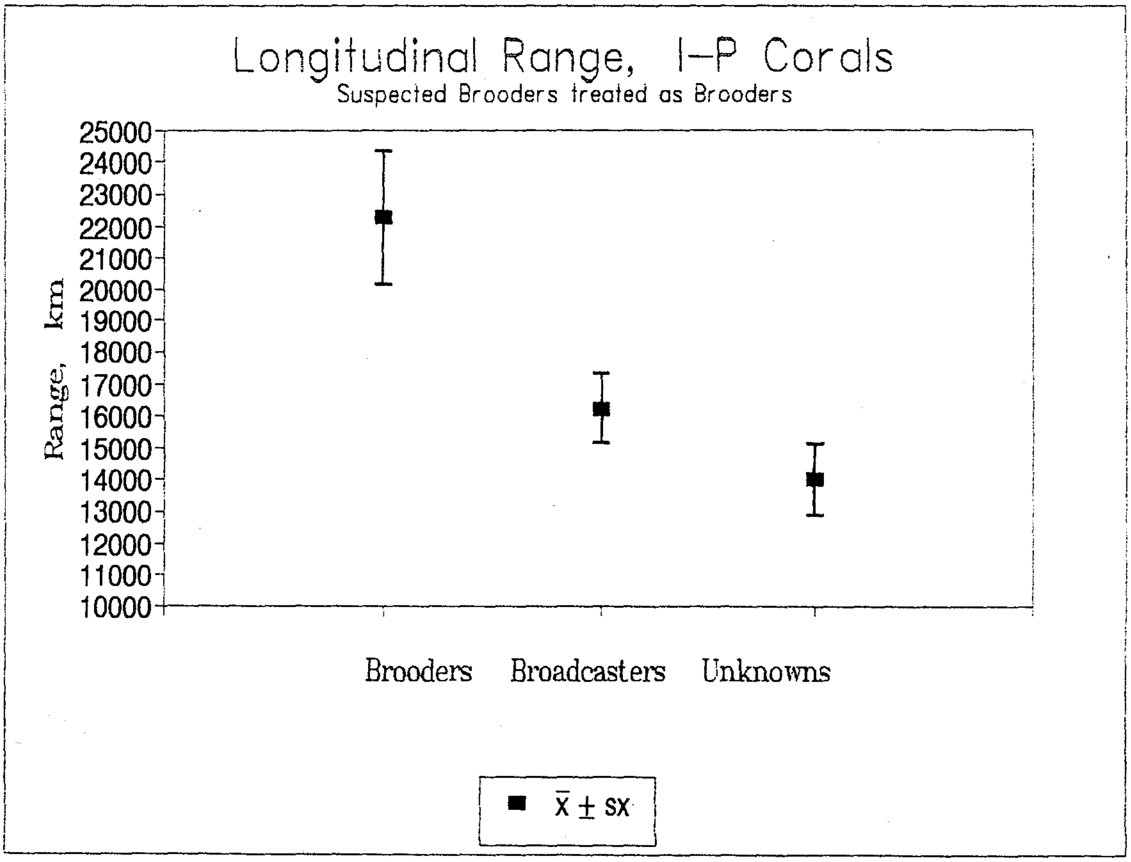
Among corals of known reproductive mode, all of the brooders survived the extinction, but only 55% of the broadcasters survived (χ^2=3.86, p<.05). About half of the genera which became extinct or restricted to the Indo-Pacific are broadcasters or have unknown reproductive characters (fig. 7.1; χ^2=7.02, p<.05). Gonochoric and hermaphroditic corals survived in equal proportions (χ^2=0.158, NS). Likewise, the reproductive characteristics of the Oligocene and Miocene coral faunas are not significantly different (χ^2=1.20, NS). Agaricia, one of the two genera which occurred only in the Miocene, broods its larvae, while the reproductive characteristics of Coscinaraea are unknown. If the reproductive characteristics of the eight unknown genera followed colony size to a first order approximation (an uncertain assumption at best), then the unknowns would include five brooders and three broadcasters. Following this assumption, 77% of brooders survived, while 47% of broadcasters survived; these ratios are not significantly different (χ^2=0.915, NS, d.f.=1).

In this study, corals which brood their larvae survived the extinction in significantly higher proportions than broadcasting corals. This difference is probably a result of the greater disperal abilities of brooded zooxanthellate coral planulae than planulae derived from broadcast gametes, which generally must capture zooxanthellae while in the water column (e.g. Willis, et

Figure 7.1. Coral Reproductive Modes and Survivorship. Known brooders survived in greater proportions than did known broadcasters.

Figure 7.2. Longitudinal Ranges of Brooding and Broadcasting Indo-Pacific Coral Genera. Measured from Mercator projection maps in Veron (1986). Assumes that suspected brooders are brooders, rather than unknowns.


Coral Reproductive Mode and Survival
0
1
2
3
4
5
6
7
8
9
10
0
5
10
Brooders
Broadcasters
Unknowns
Survived
Indo-Pacific
Extinct


Longitudinal Range, I-P Corals
Suspected Brooders treated as Brooders
Range, km
10000
11000
12000
13000
14000
15000
16000
17000
18000
19000
20000
21000
22000
23000
24000
25000
Brooders
Broadcasters
Unknowns
$\bar{x} \pm sx$

al., 1985; Richmond, 1990). The correlation between reproductive mode and survivorship does not prove causation, but suggests that life history characteristics, or other ecological traits with which they are associated, had some influence on survivorship. It is expecially significant that the bias is opposite from that observed in molluscs and other strictly heterotrophic organisms.

7.4 Biogeographic Patterns of Coral Reproductive Modes.

Indo-Pacific coral genera which include brooders have larger geographic ranges than those which are exclusively broadcasters (figure 7.2; t=2.845, p<.01). Ranges were measured from Mercator projection maps in Veron (1986); range data are listed in Appendix 2. For this analysis, it was assumed that Psammocora, Pavona, Gardineroseris, Leptoseris, Cycloseris, and Diaseris, six suspected brooding genera whose larval biology is not definitely known (Richmond and Hunter, 1990) are brooders (see Appendix 2). Brooding is the general pattern among agariciids and is common among smaller fungiids (Van Moorsel, 1983; Fadlallah, 1983), the families to which these corals belong, although there are exceptions (Veron, 1986; Richmond and Hunter, 1990). Members of all of these genera are present on Eastern Pacific reefs, where most corals whose reproductive ecology is known either brood or reproduce exclusively by asexual means (Highsmith, 1982; Richmond, 1985).

There is a great deal of geographic variation in the reproductive patterns of some corals. For example, all known Indo-Pacific *Favia* are broadcasters, but the Caribbean species, *F. fragum* is a brooder. *F. fragum* is one of the most widely distributed Caribbean corals, occurring as far east as West Africa, and north and south to Bermuda and Brazil, respectively (Veron, 1986, Jackson, 1986). Likewise, the brooding *Siderastrea radians* is much more widely distributed than its larger broadcasting relative *S. siderea*. All Caribbean *Porites* are brooders (Szmant, 1986), but several species in the Indo-Pacific are broadcasters (Kojis and Quinn, 1982). *Goniopora*, which survived in the Caribbean until the Plio-Pleistocene boundary, is a broadcaster through most of its range, but broods in the Central Pacific (Yamazato, 1975; Richmond and Hunter, 1990). Given this variation, it is difficult to surmise the reproductive modes of some Miocene corals in the Caribbean, particularly genera like *Favia* and *Goniopora*. Richmond and Hunter noted that within widely distributed and speciose Indo-Pacific genera, species living in more seasonal environments were more likely to be broadcasters than those living in more constant environments.

Pocillopora is another coral which survived in the Caribbean until the Plio-Pleistocene boundary (Frost, 1977a). Modern *Pocillopora damicornis* is one of the most widely distributed corals in the Indo-Pacific, occurring from the Red Sea to the Eastern Pacific. Although it has been thought to be a brooder thorughout its entire range (Richmond and Hunter, 1990), Glynn et al. (1991) report histological evidence suggesting that Eastern Pacific populations are broadcast spawners. Coral colonies growing in intense upwelling regions, however, had extremely low rates of gamete production. In such regions, fragmentation appears to be the dominant, if not the sole, mode of reproduction (Highsmith, 1982; Richmond, 1985).

The modern Caribbean has a much higher proportion of brooders to broadcasters that that of the Indo-Pacific and the Red Sea, among those species which have been studied (Richmond and Hunter, 1990). Is this a historical accident, a consequence of differential survivorship, or do brooding corals enjoy some selective advantage over broadcasting corals in the Caribbean?

7.5 Ecological Correlates of Coral Reproductive Modes

Szmant (1986) has suggested that in such unfavourable conditions, characterized by low recruitment and high mortality of adult coral colonies, year-round brooding may be the optimal reproductive strategy for local recruitment. In-shore patch reefs might be expected to have a higher proportion of brooders than shelf-edge barrier reefs, but such a pattern has not been documented in the literature. If, indeed, the Caribbean became a region of enhanced upwelling in the Miocene with conditions similar to those in the modern Eastern Pacific (see paleoceanography, above), Miocene corals in the Caribbean might have encountered selection for brooding and/or fragmentation as the primary modes of reproduction. This could explain the higher incidence of brooding in modern Caribbean corals than in the Indo-Pacific and the Red Sea. It might also help to account for the survival of several brooding or possibly brooding corals in the Caribbean through the Miocene, such as Alveopora, Pocillopora, Goniopora, Pavona, Psammocora, and Stylophora.

7.6 Average and Potential Dispersal of Coral Larvae

Recent evidence suggests that most coral larvae on the Great Barrier Reef are transported only limited distances from their home reefs (e.g. Sammarco and Andrews, 1988, 1989). Furthermore, brooded planulae seem to have much shorter average larval drift times and distances than broadcast planulae (Willis, et al., 1985). While the capability for long distance transport may be unimportant in local ecology, it is of great importance in biogeographic and evolutionary patterns operating on greater temporal and spatial scales. For example, all corals presently occurring on Eastern Pacific reefs appear to be Holocene immigrants from the Western and Central Pacific (Dana, 1975; Glynn, 1982; but see also Heck and

McCoy, 1978). This long distance dispersal, and its evolutionary consequences, are an example of sweepstakes dispersal (sensu Simpson, 1953), improbable in ecological time, but inevitable in evolutionary time. With respect to survivorship in the Oligocene-Miocene extinction, long term processes are of much greater importance than those operating in ecological time.

Modern corals in the Eastern Pacific undergo episodic productivity crises, and suffer massive mortality, during El Nino-Southern Oscillation (ENSO) events (Glynn, 1988; Carriquiry, et al., 1988). Recruitment following these events depends on fragmentation and long-distance larval transport, and is extremely slow (Glynn, 1988; Scott, et al., 1988). ENSO events may represent an apposite microcosm of the fate of Caribbean reefs during two Cenozoic regional extinctions at the Oligocene-Miocene and Plio-Pleistocene boundaries (Vermeij, 1989). Changing currents in ENSO's bring about drastic, but short-term, changes in temperature and nutrient regimes which have disastrous consequences for Eastern Pacific coral reefs. ENSO's, however, cause local warming and collapse of upwelling systems, as opposed to the local cooling and enhanced upwelling proposed for the Caribbean around the Oligocene-Miocene boundary. If Caribbean corals suffered massive mortality during these regional extinctions, long distance dispersal capability may have had a significant influence on which corals could recolonize the afflicted areas.

There are still too many gaps in our knowledge of modern coral reproduction to confidently surmise the reproductive characteristics of some Oligocene and Miocene Caribbean corals. The apparent survivorship bias seen here presents hypotheses to be tested when more information is available.

7.7 Reproductive Ecology and Survivorship of Coral Associates.

The reproductive ecology of coral associates is poorly understood at best. All demosponges, including boring sponges, have lecithotrophic larve with very short or nonexistent planktonic stages (Bergquist, 1978). Larval drift time has been measure in only one species of <u>Cliona</u> (<u>C</u>. <u>celata</u>), and is generally less than 30 hrs. Clionid sponges are capable of forming gemmules which can become dormant resting stages or potentially serve in long distance dispersal (Bergquist, 1978).

Both lithophagids and gastrochaenids are hermaphroditic and spawn their gametes (Carter, 1978; Morton, 1983). The reproductive characteristic of <u>Phascalosoma</u> are unknown. Like all balanids, endolithic barnacles must copulate, but they mostly have planktotrophic larvae, with the exception of a few species which are wholly parasitic, and spend the entire life cycle in a single coral head (Newman and Ladd, 1974).

In short, there is too little information on this aspect of the biology of the coral associates to draw any conclusions with respect to the any relation between life history characteristics and survival during this mass extinction. The lack of turnover in both sponges (BR) and bivalves (BC) does suggest, however, that any differences in life history characteristics had little or no influence on survivorship patterns among the coral associates.

7.8 Trophic Level Effects

Productivity crises have been advanced as causes of several major and minor extinctions (Ordovian-Silurian, Brenchley, 1988; Cretaceous-Tertiary, Sheehan and Hansen, 1986 and others; North Pacific Pleistocene range truncations, Vermeij, 1989b). While none of these suggestions relate directly to reef communities, they raise important issues. How well integrated are marine communites? Are extinctions generally more severe at higher trophic levels? These questions have been most thoroughly investigated with respect to the Cretaceous-Tertiary mass extinction.

7.8.1 Trophic Level Effects in the Cretaceous-Tertiary Extinction

The Cretaceous-Tertiary extinctions were strikingly selective with respect to habitat; pelagic and shallow benthic marine organisms were devastated, but deep sea, terrestrial, and aquatic ecosystems were relatively unaffected (Russell, 1979; Thierstein, 1982), despite the loss of dinosaurs and considerable (but longer term) morhological and distributional changes among terrestrial plants (e.g. Hickey, 1984; Wolfe, 1987; Stanley, 1987; Traverse, 1988). These patterns of differential extinction are presumably related to differences in trophic structure of communities in these habitat types (Sheehan and Hansen, 1986).

The K/T boundary itself is usually defined by the dramatic and abrupt overturn of microfossils between uppermost Maastrichtian and lowermost Danian sediments (e.g. Hansen, et al., 1987), although sections with a conformable K/T contact are exceedingly rare (e.g. Perch-Nielsen, 1982). Furthermore, recent studies (e.g. Keller, 1989) have shown that even the planktonic extinctions were more protracted than originally thought. Likewise, extinction of most marine invertebrate macrofauna was not instantaneous, but rather, protracted over the latter half of the Maastrichtian (summarized in Kauffman, 1984 and Stanley, 1987).

Nonetheless, the planktonic record does show a dramatic collapse, with most phytoplankton and all zooplankton groups suffering severe losses (Thierstein, 1982). Isotopic studies (Perch-Nielsen, et al., 1982; Hsu, et al., 1982; Magaritz, 1989) showed a negative excursion of 1-3 per mil in $\delta^{13}C$ values, usually interpreted as indicating a collapse of marine planktonic primary production. Fischer and Arthur (1977) had earlier proposed that diminution of pelagic primary production at the K/T boundary (and at other times during the Mesozoic and Cenozoic, including the present) and other oceanographic changes were associated with the K/T boundary extinctions (see discussion of periodicity, above; see also Perch-Nielsen, et al., 1982). Studies in which abundance of individuals was quantified also show a dramatic decrease in planktonic biomass across the K/T boundary (Hansen, et al.,1987; McLaren and Goodfellow, 1990). This collapse of the calcareous plankton ecosystem is responsible for presence of "boundary clay" at most deep sea K/T boundary sections (Perch-Nielsen, et al., 1982; Keller, 1989).

The collapse of the calcareous planktonic ecosystem, combined with a large and sudden regression (Haq, et al., 1986) also meant the elimination of the epieric chalk sea habitats (Jablonski and Bottjer, 1983), which in turn caused massive extinctions among European brachiopods (Johansen, 1989) and North American soft-sediment dwelling bivalves and gastropods (Jablonski and Bottjer, 1983). Hansen, et al. (1987) showed that benthic suspension feeders and swimming macrofauna were almost entirely elimnated in an East Texas section, but deposit feeders and (to a lessr extent) benthic carnivores fared much better. In the immediate aftermath of the extinction (time scale as yet unclear), survivors among the suspension feeders and carnivores again radiated, re-filling the ecological spaces vacated during the extinctions (Hansen, 1988).

On this basis, Sheehan and Hansen (1986) proposed that detritus-feeding acted as a buffer to extinction in both marine and terrestrial habitats across the K/T boundary. While this model may appear to work for marine invertebrates (if extinctions occurred relatively rapidly in geological time), the extrapolation to terrestrial and aquatic habitats would require extinction and recovery in ecological time, i.e. quickly enough for significant primary production to resume before soil- and water-borne organic matter supplies were exhausted. Currently available evidence on the timing of the terrestrial and marine extinctions does not support such a scenario (e.g Kauffman, 1984; Hickey, 1984; Wolfe, 1987; Keller, 1989), but as Schindel (1980) points out, ecological time (i.e. $<10^3$ yrs) is probably beyond the resolution of the sedimentary record in all but the most extraordinary circumstances). It is of interest here to note that most marine invertebrate macrofaunal groups which became extinct at the K/T boundary underwent a period of decline during most of the middle and late Maastrichtian prior to their complete disappearance at or below the K/T boundary (summarized in Kauffman, 1984, and Stanley, 1987).

Suspension feeding bivalves suffered more severe extinction than did deposit-feeding forms in the Cretaceous-Tertiary extinction (Rhodes and Thayer, 1991). The percent extinction among suspension feeding bivalves was about equal to that among articulate brachiopods, although the brachiopods had had a much higher background extinction rate than suspension feeding bivalves during the Jurassic. Rhodes and Thayer suggest that the low energy requirements of brachiopods would have given them an advantage during a possible productivity crisis at the K/T boundary.

Birkelund and Hankasson (1982), however, noted that soft sediment dwelling bryozoans were the immediate re-colonizers after the elimination of Maastrichtian communities in the Danish chalk seas, such that tolerance of turbidity was a more important factor in survivorship than was trophic status. These bryozoans, however, were immigrants, rather than survivors. Likewise, Johansen (1989) noted that morphologically unspecialized brachiopods were the survivors and recolonizers among brachiopods of the Danish chalks, again pointing to the importance of turbidity as a factor in survivorship. Fagerstrom (1987) suggested that most of the corals which survived the extinction lived in cold water or clastic environments (see below), rather than on reefs.

Ultimately, it is difficult to establish a firm role of trophic status in influencing survivorship in the K/T or other mass extinctions. In this study, the role of trophic status is briefly examined as a factor in survivorship.

7.8.2 Trophic Level Effects in this Extinction

There is no evidence that reef-dwelling grazers or predators suffered increased levels of extinction during the Oligocene-Miocene coral extinctions. Indeed, gastropods in particular continued to increase their diversity in reefs and level-bottom habitats (see chapter 6). The only organisms which suffered in this extinction were zooxanthellate organisms, animals with endosymbiotic algae. Rather than a general trophic level effect, this pattern appears to be a specific bias agains zooxanthellate organisms, based on their opposite response to upwelling and nutrification from strictly autotrophic plants or strictly heterotrophic animals. Zooxanthellate constructors of reefs appear to be a special case, rather than an example of a general trophic level effect on survivorship in mass extinctions.

7.9 Biogeography and Implications for Evolution of Cenozoic Reefs

The Oligocene-Miocene extinction was the first step in the division of a Paleogene cosmopolitan reef fauna into its modern provinces. The history of the Indo-Pacific reef faunas since that time has been markedly different from that of Caribbean reef faunas. Indo-Pacific reef corals (e.g. Rosen, 1984), molluscs (e.g. Vermeij, 1987), irregular echinoids (e.g. Ghiold, 1989), have all greatly diversified at the generic, and in some cases, the familial level. All of these groups have their current centres of diversity in the continental archipelagoes of Southeast Asia (Briggs, 1987).

Post-Oligocene diversification among coral associates has been almost entirely at the species level; most genera, and several species are cosmopolitan (see tables 7.4 to 7.6). The biogeography of boring sponges is poorly known, but nearly all genera are cosmopolitan, as are several species. Their species-level taxonomy is somewhat controversial, and there may be several synonyms listed in table 7.5. *Cliothosa* has a disjunct distribution, possibly dating from the Oligocene-Miocene extinction in the Caribbean. Endolithic bivalves are all cosmopolitan at the genus level, and a few species are cosmoplitan (table 7.4)

Table 7.4: Biogeography and Habit of Modern Lithophaginae and Gastrochaenidae.

Species		IP	Car	Med	Ob Dead	Ob Live	Fac.
Lithophaginae							
Botula fusca		X	X	X	X		
Fungiacava (2)		X				X (4)	
Gregariella (1)		X	X		X		
Lithophaga lithophaga				X	X		
L. antillarum		X	X		X		
L. nigra	X	X			X		
L. aristata			X				d>l
L. bisulcata			X				l>d
L. dixonae			X			X	
L. divaricalx		X			X		
L. (l.) malaccana		X			X		
L. (l.) obesa		X			X		
L. teres		X			X		
L. zitteliana		X			X		
L. (l.) nasuta		X					l>d
L. hanleyana		X					l>d
L. (l.) curta		X				X (1)*	
L. (l). keuhnelti		X				X (2)	
L. (l.) laevigata		X				X (m)	
L. (l.) lessespiana		X				X (m)	
L. (l). lima		X				X (m)	
L. mucronata		X				X (m)	
L. (l). purpurea		X				X (2)	
L. simplex		X				X (m)	

Table 7.4 (continued)

Species	IP	Car	Med	Ob Dead	Ob Live	Fac.
Gastrochaenidae						
Gastrochaena hians		X		X		
G. ovata		X		X		
G. mobrarii		X**		X		
G. stimpsoni		X**		X		
G. carteri	X			X		
G. cuneiformis	X			X		
G. dentifera	X			X		
G. dubia	X	X?		X		
G. gigantea	X			X		
G. inaequistriata	X			X		
G. intersepta	X			X		
G. laevigata	X			X		
G. pexiphora	X			X		
G. retzii	X***			X		
G. ruppellii	X***			X		
Spengleria rostrata		X		X		
S. apertissima	X			X		
S. plicatilis	X			X		

* Number in parentheses indicates number of coral species into which this species bores; (m) indicates more than 5 host spp.

For facultative borers, d>l indicates that boring in dead substrates is more common than in live; l>d indicates opposite.

L. (l). indicates Lithophaga subgenus Leiosolenus.

** Not strictly from Caribbean: G. mobrarii occurs in Bermuda, G. stimpsoni occurs off North and South Carolina.

*** Occur in the Red Sea only.

Compiled from: Bromley, 1978; Carter, 1978; Evseev, 1982; Kleeman, 1980, 1984; Nielsen, 1985; Scott, 1986, 1987, 1988; Morton and Scott, 1980; Morton, 1983; Wilson and Tait, 1984; Wilson, 1985;

Table 7.5 Modern Boring Sponge Biogeography

Species	IP	Car	Med	TA	TP
Alectona jamaicensis		X			
Alectona sp.	X				
Anthosigmella varians		X		X	
Cliona amplicavata		X			
C. aprica*		X			
C. caribbea*		X		X	
C. carpenteri				X	
C. carteri			X	X	
C. celata	X	X	X	X	X
C. delitrix		X			
C. ensifera	X				
C. flavifodina		X			
C. lampa	X	X	X		
C. langae*		X			
C. laticavicola	X	X	X		
C. lobata				X	
C. nigricans*			X		
C. peponacea**		X			
C. raphida		X		X	
C. rhodensis			X		
C. robusta				X	
C. schmidti	X	X	X		
C. spirilla				X	
C. truitti				X	
C. vastifica	X	X	X	X	
C. vermifera		X	X	X	
C. viridis	X	X	X	X	
Cliothosa hancocki	X		X		
Siphonodictyon brevitabulatum		X			
S. cachocrouensis		X			
S. coralliphagum		X			
S. mucosum	X	X			
S. siphonum			X		
Siphonodictyon sp.	X	X	X		
Thoosa bulbosa	X				
T. mollis	X				

IP: Indo-Pacific; Car: Caribbean; Med: Mediterranean; TA: Temperate Atlantic; TP Temperate Pacific.

* Possible synonyms of C. viridis (K. Rutzler, pers. comm. to MJ Risk, 1985; Rutzler, 1973 (C. nigricans).

** Possible synonym of C. laticavicola (MJ Risk, pers. comm., 1990).

Bromley and D'Alessandro (1989) suggest that C. celata may be a species complex of several morphologically convergent species.

Sources: Volz, 1939; Wells, et al., 1960 (North Carolina); Evans, 1969 (Newfoundland); Pang, 1973 (Jamaica); Rutzler, 1973 (Tunisia); Rutzler, 1971 (Caribbean, Palau); Hechtel, 1976 (Brazil); Bromley, 1978 (Bermuda); Ricketts, et al., 1985 (California); Bromley and D'Alessandro, 1989 (Mediterranean); Smyth, 1990 (Guam), MJ Risk, pers. comm., 1990.

Table 7.6 Biogeography of Coral-Inhabiting Barnacles

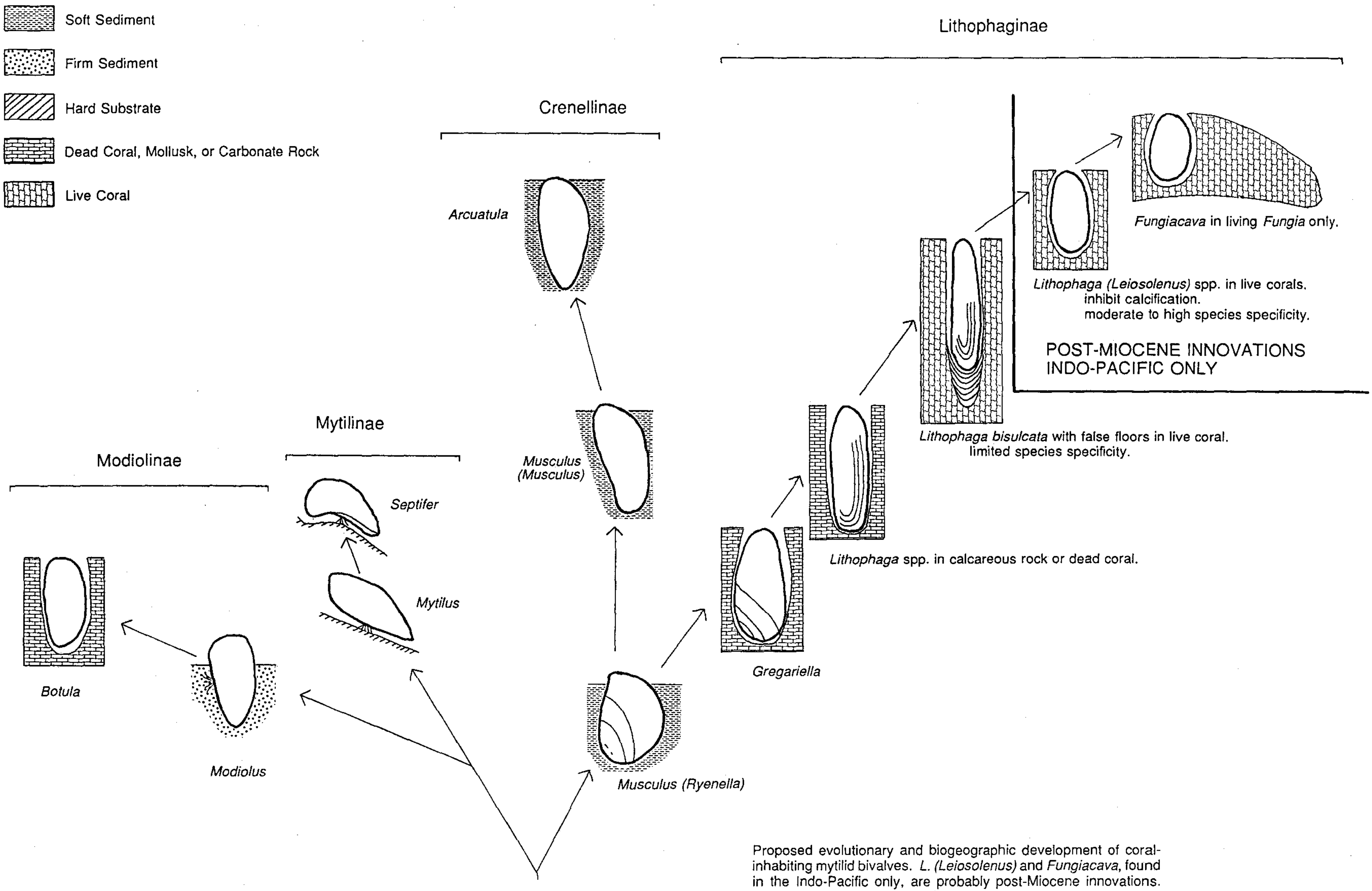
Genus	IP	Car
Boscia	X	X
Cantellius	X	
Cetatoconcha		X
Creusia	X	
Hiroa	X	
Hoekia	X	
Nobia	X	
Pyrgoma	X	
Pyrgopsella	X	
Savignium	X	
	9	2

Compiled from Ross and Newman, 1973; Newman, et al., 1976.

The only coral associates which are mostly not cosmopolitan at the genus level are coral-inhabiting barnacles (table 7.6). Two genera are extant in the Caribbean, and 7 in the Indo-Pacific; only one (Boscia) is cosmopolitan (Ross and Newman, 1973; Newman, et al., 1976); the most speciose genera all inhabit the Indo-Pacific. The oldest known coral-inhabiting barnacles are from the Miocene of the Caribbean; their fate during the Plio-Pleistocene extinction is unknown (Newman and Ladd, 1974; Newman, et al., 1976). These animals do not truly bore into the coral skeleton, but rather, inhibit calcification such that the coral grows around them, and eventually overgrows them. Likewise, the bivalves which exclusively inhabit live corals (Lithophaga, subgenus Leiosolenus; Wilson and Tait, 1984) do not bore, but inhibit calcification (Morton and Scott, 1980; Morton, 1983).

The coral-inhabiting barnacles and live-coral inhabiting Lithophaga (Leiosolenus) are the only coral associates which show a high degree of species specificity (see tables 7.4, 7.6; Ross and Newman, 1973; Kleeman, 1980). Many of these species occur in only a few species of coral, and a few are restricted to a single coral species (see table). Apparently, only these groups have undergone significant coevolution with their host species. This diversification is only found in the Indo-Pacific, and is probably post-Miocene, if not younger (fig. 7.3). If the coral-inhabiting

Figure 7.3. Proposed evolutionary and biogeographic development of coral-inhabiting mytilid bivalves. *L. (Leiosolenus)* and *Fungiacava*, found in the Indo-Pacific only, are probably post-Miocene innovations. Modified from Wilson and Tait (1984). *Lithophaga dixonae*, convergent with *L. (Leiosolenus)* and found only in live Caribbean *Madracis* spp., also has no known fossil record.



Proposed evolutionary and biogeographic development of coral-inhabiting mytilid bivalves. *L. (Leiosolenus)* and *Fungiacava*, found in the Indo-Pacific only, are probably post-Miocene innovations. Modified from Wilson and Tait, 1984.

Lithophaga (Leiosolenus) arose only in the Pleistocene (Scott, pers. comm., 1990). It is in these groups that we might expect to see the effects of mass extinctions on coral associates, but we will probably have to wait for the next mass extinction to test this hypothesis. If current rates of human-induced reef destruction continue (e.g. Brown, 1988), however, we may not have to wait too long.

In summary, the last 25 Ma of evolution on coral reefs indicate which portions of the reef fauna have rapid rates of diversification and which are more conservative. The Oligo-Miocene and Plio-Pleistocene extinctions in the Caribbean give us some indication of which organisms are sensitive to which kinds of stresses on an evolutionary time scale. Corals and gastropods have diversified immensely in the Indo-Pacific, but only to a limited extent in the Caribbean since the Oligocene-Miocene extinctions. With the exception of coevolved coral-inhabiting (but not boring) bivalves and barnacles, coral associates have experienced little or no extinction, and only limited (species-level) diversification during this time.

Chapter 8: Conclusions

The Oligocene-Miocene extinction of Caribbean reef corals was the first of two regional extinctions which together reduced Caribbean coral diversity by about 60%; the second event occurred around the Plio-Pleistocene boundary. The Oligocene-Miocene extinction did not affect bioeroding coral associates, as measured by diversity of trace fossils and body fossils of endolithic bivalves. Other reef associated invertebrates, such as bivalves, gastropods, and echinoids, were similarly unaffected, but large benthic foraminifera (Lepidocyclinidae) suffered a sharp decline in diversity during the Late Oligocene and Early Miocene. The extinction thus appears to have primarily affected zooxanthellate organisms, but not affected those which lack photosymbionts. Of the coral genera which became extinct in the Caribbean, about 2/3 are extant in the Indo-Pacific.

Miocene reefs in the Caribbean are primarily patch reefs on shallow carbonate platforms or embayments; no shelf-edge buildups have been reported. All of the Oligocene species which in this study occurred only (or primarily) on shelf-edge reefs became extinct or restricted to the Indo-Pacific; these species, however, only account for about half of the generic extinctions. Environmental tolerance of modern congeners of the survivors of this extinction suggest that tolerance of turbid and/or cold water conditions were important factors in survival. This suggestion is consistent with the lack of turnover in coral associates, which are generally tolerant of cold water and moderate (but not heavy) sediment loading. The poor development of Miocene reefs, and the apparent high intensity of bioerosion on them, suggest eutrophication as an additional stress on Miocene reefs of the Caribbean.

Coral associates suffered almost no effects in this extinction, with the possible exception of the elimination of Cliothosa from the Caribbean. Their differential survival from corals probably stems from their habitat characteristics, specifically, their greater tolerance of cold, turbid, and nutrient rich water, and their ability to bore into non-coral hosts. There is no evidence for a general trophic level effect on survivorship, but rather, a specific bias against zooxanthellate organisms, which are intolerant of cold, turbid, and nutrient-rich conditions.

Bioeroding coral associates are an extinction-resistant guild of reef organisms. There is no evidence of coevolution between corals and associates in the fossil material, with the possible exception of Lithophaga bisulcata, which bores into only a few species of live corals. Whatever coevolution may be occurring did not affect survivorship of the bivalve when its host corals Diploastrea (Oligocene) and Coscinaraea (Miocene) became locally extinct. All of the coral associate genera observed in this study except for coral-inhabiting barnacles, which arose in the Miocene, were also present on Cretaceous reefs, where they mostly inhabited shells of rudists and other non-coral substrates. Coral associates are thus a poor group for examining evolutionary dynamics in the fossil record.

There is no evidence for a major regression at the Oligocene-Miocene boundary in the Caribbean. Patterns of selective extinction among the corals suggest that regional cooling, and perhaps nutrient enrichment, combined to drastically restrict or eliminate shelf-edge reef habitats in the Caribbean. Together, these environmental changes probably caused the coral extinction (and perhaps the extinctions among giant forams). Oceanographic models suggest deep circulation from the Eastern Pacific into the Caribbean beginning at the Oligocene-Miocene boundary, coincident with the closure of the Eastern Tethys and the opening of Drake Passage to deep circulation. Upwelling of this cold, nutrient-rich water in the Caribbean could have caused the environmental changes which are apparently responsible for the extinction.

Direct paleoceanographic evidence for this proposed major change in Caribbean oceanography at the Oligocene-Miocene is presently lacking, due to a paucity of unaltered material of Late Oligocene to Middle Miocene age in Caribbean DSDP cores. Geochemical tracers to examine for evidence would be $\delta^{18}O$, $\delta^{15}N$, and Cd, all as indicators of the cool temperatures and nutrient abundance normally associated with deep ocean waters.

Life history characteristics, particularly mode of larval nutrition and dispersal, are correlated with survivorship of corals, but not of coral associates. Corals whose modern congeners brood their larvae survived in greater proportion than those whose modern congeners broadcast their larvae. This pattern is reversed from that seen in molluscs, and is probably related to the greater dispersal ability of brooded coral larvae, made possible by their inheritance of zooxanthellae in the egg cell. Brooding corals may be more common in the relatively turbid conditions of in-shore patch reefs, so the reproductive bias may be an effect, rather than a cause, of selective extinction.

There is no evidence for a general trophic level effect on survivorship in this extinction. Rather, zooxanthellate organisms were the primary victims of the extinction, while heterotrophic organisms at various trophic levels were not differentially affected.

This extinction was the first step of a two-stage division of a cosmopolitan Palaeogene coral reef fauna into its highly provincial modern state. Corals have undergone considerable generic, and exponential species, diversification in the Indo-Pacific since the time of this extinction, but Caribbean coral diversity is still less than its Oligocene high. Most coral associates are cosmopolitan at the genus level, and, to a lesser extent, at the species level; their primary diversification predates the Oligocene-Miocene extinction, with the exception of coral-inhabiting barnacles, which arose and diversified in the Miocene, and the live-coral inhabiting lithophagids (subgenus Leiosolenus), which may be as young as the Pleistocene.

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Appendix 1: Catalogue of Fossil Specimens.

All specimens are housed in the Dept. of Geology, McMaster University.

GU-1*	Siderastrea conferta	15 upright	nearly complete, sampled left 1/4.
GU-1B*	S. conferta	30 overturned	largely complete, sampled lower 1/4.
GU-2*	S. conferta	40 upright	largely complete; sampled 2 pc. from upper left corner.
GU-3*	S. conferta	30 overturned	largely complete, somewhat abraded, in place.
GU-4	Montastrea tampaensis	10 on side	incomplete, in channel fill between large colonies 3,5, and 7.
GU-5*	Antiguastrea cellulosa	30 overturned	fairly complete.
GU-6*	Porites waylandi	15 overturned	surrounded by rhodoliths, other rubble in channel fill.
GU-7	Stylocoeniella lobatorotund	50 upright	pseudomassive, fairly complete, collected 2 small fragments, with rhodoliths and coralline algal crusts.
GU-8*	S. lobatorotundata	15 upright	pseudomassive, fairly complete, just above and left of #7.
GU-9*	Antiguastrea cellulosa	15 upright	fairly complete, missing one edge, heavily bored.
GU-10*	Goniopora hilli	15 ?	incomplete, fragment of larger colony, slightly abraded.
GU-11*	G. hilli	15 upright	complete, domal head, well-preserved, encrusted by epilithic barnacles.
GU-12*	G. hilli	15 upright	complete, domal head, well preserved, in channel fill.
GU-13	Porites ?waylandi	10 ?	incomplete, rhodolith with adhering Porites.
GU-14	Porites waylandi	40 upright	fairly complete, heaviy recrystallized, collected 2 small fragments from lower right corner, with several Lithophaga holes.
GU-15	Goniopora hilli	15 ?upright	well preserved portion of domal head, slightly encrusted with red algae.
GU-17	Porites waylandi	60 upright	small piece collected for identification only.
GU-B1	Siderastrea conferta	15 ?	incomplete, fragment of massive S. conferta.
GU-B2	Porites baracoaensis	5 on side	three relatively complete branches, 1-2 cm diameter, not complete colony, branches broken in collection.
GU-B3	Astreopora	5 ?	small fragment, with Porites baracoaensis
GU-B4	Acropora saludensis	5 on side	complete branches, not whole colony, with fragment of Antiguastrea cellulosa.
GU-B5	Stylophora imperatoris	5 ?	internal mold, incomplete.
GU-B6	Goniopora hilli	10 upright	small domal coral, complete.
GU-B7	Stylophora imperatoris	5 on side	complete branches, well preserved.
GU-B8	S. imperatoris	5 on side	complete branch, well preserved.
GU-1-1	Stylocoeniella lobatorotund	5 upright	encrusting on rhodolith.
GU-1-2	Siderastrea conferta	5 on side	on rhodolite, fairly complete.
GU-1-6*	Goniopora hilli	7 overturned	small domal coral, mostly complete, well preserved, heavily bored.
GU-2-1	S. conferta	5 upright	encrusting on rhodolith.
GU-2-3	Porites baracoaensis	1 ?	small fragment of branching coral, incomplete.
GU-2-4	Porites waylandi	5 upright	encrusting on rhodolite which grew on fragment of Montastrea tampaensis.
GU-2-6	P. waylandi	5 upright	incomplete, fragment of colony.
GU-2-7	P. waylandi	10 upright	incomplete, somewhat abraded, heavily bored by worms and bivalves.
GU-2-8	P. waylandi	5 ?	incomplete, with fragment of S. conferta.
GU-2-9	Stylophora cf. granulata	5 on side	two small branches, .5 cm diameter.
GU-2-10	Antiguastrea cellulosa	5 on side	corallith, complete, well preserved, bored by sponges.
GU-3-1	Stylocoeniella lobatorotund	5 on side	incomplete branch fragment
GU-3-2	Antiguastrea cellulosa	5 on side	corallith, complete, well-preserved.
GU-U8.a	Caulastrea portoricoensis	5 upright	fragments of two branches, well preserved, found near base of unit 8.
GU-X*	Hydnophora sp.	15 ?	incomplete, somewhat abraded, heavily bored.

Number	Species	Size	Orientation	Comments
L-1*	Porites waylandi	20	overturned	collected 1 small piece, heavily recrystallized.
L-3*	P. waylandi	30	?	collected left 1/2 of colony, heavily recrystallized.
L-4*	Acropora saludensis	20	?	pseudomassive, fairly complete.
L-5*	Montastrea costata	60	upright	complete, large colony, edges are heavily bored. subsampled in P.R. branching coral rubble above, #7 is below.
L-6*	Porites waylandi	20	on side	fairly complete, columnar, heavily bored.
L-7*	Colpophyllia willoughbiensi	20	?	incomplete, heavily bored.
L-7A*	Porites waylandi	10	?	stout branching colony.
L-8*	P. waylandi	15	?	stout branching, heavily recrystallized.
L-9*	P. waylandi	20	on side	complete, columnar, well preserved.
L-10	Montastrea costata	50	upright	large domal colony, 2 small pieces collected.
L-11*	M. costata	60	overturned	large domal colony, subsampled in P.R., edges are lightly bored.
L-11B*	M. costata	30	overturned	incomplete domal colony, heavily bored, with small adhering Agathiphyllia
L-12*	Porites waylandi	15	on side	pseudomassive - multilobate, complete, heavily bored.
L-13	P. waylandi	8	?	incomplete, stout branching colony, heavily recrystallized.
L-14	Diploastrea crassolamellata	50	upright	large domal colony, impossible to collect.
L-15*	Porites waylandi	15	on side	fairly complete, columnar, heavily bored.
L-16*	Pironastrea sp.	10	?	incomplete, small domal corallith, encrusted with rhodoliths, heavily bored.
L-17*	Montastrea tampaensis	20	upright	incomplete, heavily weathered, heavily bored.
L-18*	Antiguastrea cellulosa	40	upright	large massive colony, complete, sampled outer 1/4.
L-19*	Acropora saludensis	10	?	pseudomassive, incomplete, heavily bored.
L-19B*	Porites waylandi	30	?	large pseudomassive colony, nearly complete, sampled lower 1/3.
L-20*	P. waylandi	30	on side	complete domal colony, heavily recrystallized, heavily bored.
L-20A*	P. waylandi	30	upright	complete domal colony, heavily recrystallized, heavily bored, subsampled in P.R.
L-21	P. waylandi	40	upright	fairly complete domal colony, heavily recrystallized, subsampled in P.R.
L-22*	Antiguastrea cellulosa	40	upright	mostly complete, slightly abraded at edges heavily bored, subsampled in P.R.
L-24	Porites waylandi	15	on side	stout branch, 5 cm diameter, nearly complete.
L-B2	P. waylandi	6	on side	stout branches, incomplete, above and behind massive #2.
L-B8*	P. waylandi	15	on side	stout branching, nearly complete.
L-1-1*	Porites baracoaensis		on sides	many branch fragments, gen. 2-3 cm diameter, incomplete.
L-1R	P. baracoaensis	10	on side	two branches, relatively complete, 2-3 cm diameter.
L-U1	P. waylandi	10	on side	stout branching, diameter 5 cm., incomplete.
L-u1mtx	Cladocora sp.	8	on side	plocoid, in wackestone matrix, branches ca. 1 cm diameter.
L-2M*	Stylophora imperatoris	5	?	complete branch, recrystallized, well-preserved.
L-2-1R	Diploastrea crassolamellata	5	?	incomplete fragment
L-2-2*	Porites baracoaensis	5	on side	complete branches, with adhering branch of Actinacis.
L-2-3*	Antiguastrea cellulosa	20	rubble	loose fragment next to large head of Antiguastrea (#32).
L-U2.4.a	Diploastrea crassolamellata	10	upright	incomplete, fragment of larger colony, heavily weathered.
L-U2.4.b	Montastrea tampaensis	20	?	fragment of large colony, heavily weathered.
L-U2.4.c	Porites sp., foliose	8	?	incomplete, foliose colony.
L-U2.4.d	Stylophora imperatoris	8	upright?	external mold, incomplete, semi-foliose.
L-U2.4.e	Alveopora tampae	7	?	incomplete, fragment of larger colony.
L-U3	Diploastrea crassolamellata	5	?	incomplete, two small fragments, abraded.
L-U3.mtx	Cladocora sp.	8	?	plocoid, branches ca. 1 cm diam., wackestone-packstone matrix.
L-U4.a*	Diploastrea crassolamellata	40	?	large massive colony, complete, heavily bored. subsampled in P.R.
L-U4.b	Antiguastrea cellulosa	20	?	incomplete, massive colony, heavily bored.
L-U4.c	Alveopora tampae	25	?upright	weathered fragment of larger colony, fairly complete.
L-U6.a	Antiguastrea cellulosa	40	rubble	complete, domal colony, heavily bored, subsampled in P.R.
L-U6.b	Diploastrea crassolamellata	15	?	domal colony, fairly complete, subsampled in P.R.
L-U6.c	Colpophyllia willoughbiensi	60	upright	complete, large massive colony, small portion collected.
L-U6.d	Goniopora hilli	10	?	incomplete, fragment of domal colony.
L-flt.1	Diploastrea crassolamellata	15	rubble	domal colony, upper half, well-preserved, lightly bored.
L-flt.2	Montastrea tampaensis	15	rubble	incomplete domal colony, outer surface well-preserved, probably from unit 4.
L-flt.3	Colpophyllia willoughbiensi	20	rubble	complete, tabular-domal colony, well-preserved, probably from unit 4.
L-129.a	Montastrea tampaensis	10	rubble	small corallith, heavily bored.
L-129.b	Siderastrea siderea	10	rubble	two small coralliths, lightly bored.

Number	Species	Size	Orientation	Comments
BR-1*	Montastrea limbata	15	on side	nearly complete, heavily leached
BR-2	M. limbata	15	?	moldic, poorly preserved, heavily bioeroded, incomplete.
BR-3*	Agaricia sp.	8	?	internal mold, heavily bored.
BR-3A	mix of coral fragments			
BR-4	Porites trinitatis	25	upright	knobby domal-branching coral, leached, several complete branches.
BR-5*	Porites trinitatis	25	?	pseudomassive, complete, rather leached.
BR-6*	Coscinaraea colei	15	upright?	incomplete, upper part of domal colony.
BR-6A*	C. colei	30	upright	large domal head, nearly complete, subsampled in P.R.
BR-7*	C. colei	70	upright	large domal head, nearly complete, subsampled in P.R.
BR-7B*	C. colei	15	upright	incomplete, but with intact upper edge.
BR-8*	C. colei	50	upright	large domal head, nearly complete, subsampled in P.R.
BR-8B	Agaricia sp.	5	?	internal mold, lightly bored, incomplete.
BR-9*	Coscinaraea colei	25	upright	columnar, complete, only collected top half.
BR-9A*	C. colei	25	upright	domal colony, nearly complete, well-preserved.
BR-9B*	C. colei	15	on side	incomplete, but with intact outer edge.
BR-9C*	Agaricia sp.	10	on side	internal mold, heavily bored.
BR-11*	Porites trinitatis	15	upright	nearly complete, somewhat leached.
BR-12*	Coscinaraea colei	20	upright	incomplete, but with intact outer edge.
BR-13*	C. colei	50	upright	top half of large domal head, complete, well-preserved.
BR-14*	C. colei	60	upright	two fragments of nearly complete large domal colony, subsampled in P.R.
BR-16	C. colei	20	upright	columnar colony, well preserved, top part collected.
BR-17*	C. colei	50	upright	large domal colony, complete, subsampled in P.R.
BR-17A*	Agaricia sp.	30	upright?	internal molds of 3-5 platelike colonies, heavily bored.
BR-18*	Coscinaraea colei	20	upright	columnar colony, largely complete, but leached at base.
BR-19	Montastrea limbata	15	?	incomplete, domal colony, edges missing.
BR-B2	Porites trinitatis	20	?	knobby pseudomassive, with stout branches, branches complete, well-preserved.
BR-B3*	P. trinitatis	20	on side	knobby pseudomassive with stout branches, complete.
BR-B4	Porites baracoaensis	?	?	discarded
BR-B5*	P. trinitatis	?	?	stout branches, complete, heavily bored.
BR-B6*	P. trinitatis	10	flat lying	vertical growing plates to stou branches, fragmented.
BR-B7	P. baracoaensis	10	upright	fine branches, erect, complete branches.
BR-B8	P.trinitatis	10	?	knobby-stout branching, complete branches.
BR-B9	P. trinitatis	15	?	ten stout branches, well preserved, complete.
BR-B10	P. trinitatis	12	on side	stout branches, complete, heavily bored.
BR-U1.a	Strombus	10	on side	internal mold, heavily bored by sponges.
BR-U2.1	Porites trinitatis	6	?	matrix sample"
BR-U2.2*	Colpophyllia mexicana	8	rubble	external mold, in rubble on back side.
BR-U2.3	Placocyathus barretti	5	?	internal mold, nearly complete, bored.
BR-U2.4	Clypeaster cubaensis	10	rubble	incomplete, with internal molds of sponge borings.
BR-U2.a*	Porites trinitatis	8	?	stout branching, knobby, complete.
BR-UL.1	M. limbata	20	rubble	incomplete, domal head missing edges, internal mold.
BR-UL.2	Placocyathus barretti	6	rubble	external mold, heavily bored.
BR-UL.3	Spondylus	15	rubble	well preserved, heavily cemented.
BR-UL.4	Placocyathus barretti	6	rubble	external and internal mold, heavily bored.
BR-UL.5	P. barretti	3	rubble	internal molds (2).
BR-UL.6*	P. barretti	5	rubble	internal molds (2) with Gastrochaena borings.
BR-UL.7*	Ostrea	12	rubble	incomplete, lightly bored.
BR-UL.8*	Porites trinitatis	15	rubble	fairly complete, lightly bored.
BR-UL.9	Polynisces	2	rubble	internal mold.
BR-UL.10	Placocyathus barretti	7	rubble	internal molds, incomplete.
BR-UL.11	P. barretti	5	rubble	incomplete, heavily bored.
BR-UL.12	P. barretti	5	rubble	nearly complete, internal mold, with various other corals and molluscs.
BR-UL.13	P. barretti	5	rubble	external mold, incomplete, heavily bored, with Kuphus tubes.

Number	Species	Size (cm)	Orientation	Comments
RG-1*	Montastrea limbata	15	inclined up	internal mold, heavily recrystallized, not complete.
RG-2*	M. limbata	20	inclined up	incomplete, heavily leached
RG-3*	M. limbata	15	upright	internal mold, recrystallized, not complete
RG-4	M. limbata	8	upright	incomplete, heavily leached
RG-5*	M. limbata	30	inclined up	two pieces, neither complete, missing edges, heavily recrystallized.
RG-6*	M. limbata	20	inclined up	incomplete, heavily leached and recrystallized
RG-7	M. limbata	10	overturned	incomplete, heavily leached and recrystallized
RG-8	M. limbata	8	upright	small fragment, incomplete, heavily leached
RG-9*	Solenastrea hyades	20	upright	incomplete, heavily recrystallized
RG-10	S. hyades	15	upright	incomplete, heavily recrystallized
RG-11*	S. hyades	20	inclined up	incomplete, heavily recrystallized
RG-11a*	S. hyades	20	upright	incomplete, heavily recrystallized
RG-12*	Montastrea limbata	25	inclined down	incomplete, heavily leached and recrystallized
RG-13*	M. limbata	20	inclined down	internal mold, incomplete, heavily leached and recrystallized
RG-14	M. limbata	10	overturned	internal mold, incomplete, heavily leached and recrystallized
RG-16*	M. limbata	15	inclined down	incomplete, heavily leached and recrystallized, heavily bored
RG-18	M. limbata	20	inclined down	incomplete, heavily leached and recrystallized; adhering reef rock contains Porites baracoaensis, Stylophora, mollusc molds.
RG-19	M. limbata	15	?	cemented reef rock with knobby M. limbata, Stylophora, external molds, heavily bored.
RG-20*	Favia mexicana	5	?	external mold, heavily leached
RG-22*	Montastrea limbata	15	inclined up	incomplete, heavily leached and recrystallized
RG-23	Porites baracoaensis	5	?	external mold, incomplete, heavily bored
RG-24*	Montastrea limbata	20	upright	heavily leached and recrystallized, incomplete
AY-X*	M. limbata	20	rubble	incomplete, heavily recrystallized, heavily bored, with adhering fragment of Siderastrea siderea.
RG-X.a*	Goniopora hilli	25	rubble	incomplete, heavily recrystallized, subsampled in P.R.
RG-X.b*	Colpophyllia mexicana	6	rubble	external mold on cemented reef rock with Porites trinitatis, not complete, bored.
RG-X.c*	Siderastrea siderea	20	rubble	incomplete, heavily recrystallized, subsampled in P.R.
RG-X.d	Porites ?trinitatis	8	rubble	incomplete, encrusting morph., heavily recrystallized.
RG-X.e	Placocyathus barretti	4	rubble	internal mold, nearly complete
RG-X.f	Porites trinitatis	5	rubble	incomplete, heavily leached and recrystallized
RG-X.g	Colpophyllia mexicana	5	rubble	incomplete, external mold
RG-X.h	Favia mexicana	3	rubble	external mold, incomplete, poorly preserved, adhering Placocyathus barretti, internal mold.
RG-X.i	Placocyathus moorei	6	rubble	external and internal mold, nearly complete
RP-P1*	Porites trinitatis	10	rubble	incomplete massive head, recrystallized, lightly bored.
RG-U3.a	Strombus sp.	10	inclined down	internal mold, heavily bored, nearly complete
RG-U3.b	Agaricia sp.	10	overturned	external mold, incomplete
RG-B1*	Stylophora imperatoris	10	rubble	external mold, contains internal mold of ctenostome bryozoan borings; and mollusc molds.
RG-R1*	S. imperatoris	5	rubble	external mold, contains internal molds of bryozoan and sponge borings, incomplete.
RG-R2*	S. imperatoris	10	rubble	external molds, incomplete
RG-R3*	Favia mexicana	10	rubble	internal mold, well-preserved, incomplete, lightly bored
RG-R4*	Agaricia sp.	10	rubble	external and internal molds, with internal molds of sponge borings, incomplete.
RG-R5*	Stylophora imperatoris	5	rubble	external mold, with internal molds of sponge borings, incomplete
RG-R6	S. imperatoris	10	rubble	external mold, heavily bored, incomplete
RG-S2*	Stylophora imperatoris	10	rubble	external molds with internal molds of bryozoan and sponge borings,

Number	Species	Size	Orientation	Comments
RT-1*	Coscinaraea colei	15	upright	complete domal head, well-preserved.
RT-2*	Montastrea limbata	15	?	incomplete, internal mold, heavily bored.
GD-1	M. limbata	15	upright	internal mold, heavily recrystallized, incomplete.
GD-2	Spondylus	10	horizontal	well-preserved, complete.

Number	Species	Size	Orientation	
GN-1*	Stylocoeniella lobatorotund	30	upright	tabular, pseudomassive, well-preserved, heavily bored.
GN-3*	Favites polygonalis	15	upright	largely complete, well-preserved.
GN-4*	F. polygonalis	20	upright	largely complete, well-preserved, encrusted with red algae.
GN-5*	Colpophyllia willoughbiensi	10	?	incomplete, encrusted with red algae, 1 side well preserved.
GN-7*	Stylocoeniella lobatorotund	10	upright	psuedomassive, nearly complete
GN-8*	S. lobatorotundata	25	upright	tabular pseudomassive, complete.
GN-9*	Hydnophora sp.	60	on side	complete, weel-preserved, encrusted with Porites and red algae, subsampl
GN-10*	Montastrea tampaensis	20	on side	not complete, somewhat abraded, lightly bored.

Comments

Number	Species	Size	Orientation	Comments
CL-6*	Agathiphyllia roxboroughi	10	upright	two fragments off top of large (70-80 cm) head
CL-4a*	Leptoseris portoricoensis	30	on side	Leptoseris bafflestone, complete "leaves", lightly bored, moldic.
CL-4b*	L. portoricoensis	10	on side	Leptoseris bafflestone, including bases of colonies, moldic.
CL-4c*	L. portoricoensis	10	on side	Leptoseris bafflestone, nearly complete "leaves", moldic.
CL-4d	L. portoricoensis	5	on side	Leptoseris bafflestone, incomplete colonies, moldic.

Appendix 2: Geographic Ranges of Indo-Pacific Coral Genera.

Ranges measured from Mercator projection maps in Veron (1986). Other information includes approximate number of species per genus. Although brooding genera have a greater average number of species per genus than broadcasters, this difference is not significantly different. Genera which include both brooders and broadcasters are considered brooders.

Brooders

Pocillopora	herm	10	21.3	26625	6
Seriatopora	herm	5	13.5	16875	5
Stylophora	herm	4	16.5	20625	5.5
Palauastrea	herm	1	5	6250	4.3
Madracis	herm	1	7	8750	4
Acropora	herm	78	23	28750	5.8
Porites	gon	19	28.3	35375	5.8
Goniopora	gon	14	14	17500	4.5
Alveopora	gon	16	16	20000	5.8
Acrhelia	herm	1	5	6250	4.4
Favia	herm	12	27.5	34375	6
Euphyllia	gon	4	12.8	16000	5.7
Psammocora	gon	7	21	26250	5.8
Pavona		12	21	26250	5.8
Gardineroseris		2	20.4	25500	5.5
Leptoseris		14	22.5	28125	6
Cycloseris	gon	7	21.2	26500	5.6
Diaseris	gon	2	21	26250	5.5
AVG1.br		13.75	15.825	19781.25	5.233333
STD1.br		20.27365	7.65943	9574.288	0.713364
Na.br		12	12	12	11
AVG2.br		11.61111	17.61111	22013.89	5.388889
STD2.br		17.02984	6.754825	8443.531	0.631479
N2.br		18	18	18	17

Broadcasters

Astreopora	herm	15	16	20000	6
Fungia	gon	25	16.3	20375	5.5
Echinophyllia	herm	4	15.7	19625	5.8
Oxypora	herm	2	14.9	18625	5.5
Mycedium	herm	2	14.9	18625	5.8
Pectinia	herm	7	14.3	17875	5
Acanthastrea	herm	6	16.4	20500	5.8
Lobophyllia	herm	5	15.7	19625	5.6
Symphyllia	herm	5	13.4	16750	5.8
Hydnophora	herm	5	15.7	19625	5.6
Merulina	herm	2	14	17500	5.6
Paraclavarina	herm	1	1	1250	1.3
Scapophyllia	herm	1	7.6	9500	5.1
Caulastrea	herm	4	12.6	15750	5.6
Barbattoia	herm	3	7.5	9375	6
Favites	herm	7	16.1	20125	5.9
Platygyra	herm	5	15.7	19625	5.6
Australogyra	herm	1	1.6	2000	1.8
Leptoria	herm	1	15	18750	5.5
Oulophyllia	herm	3	13	16250	5.5
Montastrea	herm	7	20.2	25250	5.8
Oulastrea	herm	1	5	6250	4.5
Plesiastrea	herm	2	16.7	20875	6.5
Diploastrea	herm	1	13	16250	4.9
Leptastrea	herm	7	16.3	20375	5.5
Cyphastrea	herm	8	16	20000	5.9
Echinopora	herm	6	15.8	19750	5.6
Moseleya	herm	1	3.3	4125	3.8
Euphyllia	gon	4	12.8	16000	5.7
Physogyra	gon	3	13	16250	4.6
AVG.bc		4.8	12.98333	16229.17	5.236667
STD.bc		4.791659	4.722999	5903.749	1.1119
N.bc		30	30	30	30

Stylocoeniella		2	15.5	19375	6
Montipora		38	16.5	20625	6
Anacropora		6	10.7	13375	4.1
Stylaraea		1	4.3	5375	4.6
Pseudosiderastrea	gon	1	4.9	6125	4
Coscinaraea	gon	8	15.8	19750	6.6
Coeloseris		1	8.1	10125	5
Pachyseris		2	16	20000	5
Heliofungia	gon	1	5.3	6625	4.6
Herpolitha	gon	2	15.8	19750	4.9
Polyphyllia	gon	3	12.2	15250	4.4
Malomitra	gon	1	14.1	17625	4.2
Sandalolitha	gon	2	10.3	12875	4.7
Lithophyllon	gon	2	8.3	10375	5.1
Podabacia	gon	1	15.6	19500	5
Blastomussa		3	12.8	16000	5
Cynarina		2	12.4	15500	5.7
Scolymia		2	13.4	16750	6.3
Australomussa		1	2.5	3125	3.5
Trachyphyllia		2	11.7	14625	5
Wellsophyllia		1	3.5	4375	3.3
Catalophyllia		1	10	12500	4.8
Plerogyra		3	13.1	16375	4.7
Psammocora	gon	7	21	26250	5.8
Pavona		12	21	26250	5.8
Gardineroseris		2	20.4	25500	5.5
Leptoseris		14	22.5	28125	6
Cycloseris	gon	7	21.2	26500	5.6
Diaseris	gon	2	21	26250	5.5

AVG1.unk	4.482759	13.1	16375	5.058621
STD1.unk	7.132348	5.653135	7066.418	0.794167
N1.unk	29	29	29	30

AVG2.unk	3.73913	10.9913	13739.13	4.891304
STD2.unk	7.490385	4.323939	5404.923	0.806987
N2.ink	23	23	23	24

Avg. Long. Km. Summary Table

	br1	bc	unk1	br2	bc	unk2
AVG	19781.25	16229.17	16375	22013.89	16229.17	14000
STD	9784.29	5903.75	7066.42	8443.53	5903.75	5437.02
N	12	30	29	18	30	23
Sx	2824.481	1077.872	1312.201	1990.159	1077.872	1133.697
x+sx	22605.73	17307.04	17687.2	24004.05	17307.04	15133.7
x-sx	16956.77	15151.3	15062.8	20023.73	15151.3	12866.3

Avg N spp. Summary Table

	br1	bc	unk1	br2	bc	unk2
AVG	13.75	4.8	4.48	11.61	4.8	3.74
STD	20.27	4.79	7.13	17.03	4.79	7.49
N	12	30	29	18	30	23
Sx	5.851445	0.87453	1.324008	4.014009	0.87453	1.561773
x+sx	19.60144	5.67453	5.804008	15.62401	5.67453	5.301773
x-sx	7.898555	3.92547	3.155992	7.595991	3.92547	2.178227

Appendix 3: Designation and Description of Guayanilla Fm.

Name: Guayanilla Fm., named for nearby town of Guayanilla.

Previous designation: carbonate facies of Juana Diaz Fm.

Lower Boundary: Juana Diaz Fm.

Upper Boundary: Angola Equivalent, chalky white limestone, thinly to thickly bedded.

Type Section: Guayanilla I and II sections, published in Frost, et al., 1983. Along road into Santa Elena housing development off highway 2, approx. 1 km from Guayanilla townsite. Punta Cuchara Quadrangle, Puerto Rico.

Location: Southwestern Puerto Rico., USA.

Lithology: well indurated yellow to pink limestone, often buff coloured on weathered surface, massive to thickly bedded

Fossil Content: Scleractinian corals, including characteristic Oligocene genera Antiquastrea and Diploastrea, Lepidocyclinid large foraminifers, soritid and myolinid benthic foraminifers, calcareous algal rhodolites, gastropods, bivalves and echinoids less common.

Age: Latest Oligocene

Appendix 4: Description of *Entobia convoluta* isp. n.

Derivation of Name: Latin, *convoluta*, convolute, twisted, complex.

Type series: Holotype BR-13; Paratype BR-B3. Plate 4.5b).

Horizon and Age: Ponce Fm., Middle Miocene

Type Locality: Brizas del Caribe site, Punta Verraco Quadrangle, Puerto Rico, USA.

Collocation: Dept. of Geology, McMaster University, Hamilton, Ontario, Canada.

Material: Further specimens from the type locality and other localities in the Oligocene and Miocene carbonates of Puerto Rico.

Diagnosis: Unicamerate to occasionally bi- or tri-camerate entobian with large irregular chambers, often exceeding 15mm in diameter. Apertures large, generally not more than 2-3. Most common in scleractinian corals, but occasionally found in oysters. See fig.4.3.

Description of fossil material: Infilled boreholes in Miocene corals *Coscinaraea colei*, *Montastrea limbata*, and *Porites trinitatis*. Also occurs in a variety of Oligocene corals.

Description of recent material: Modern borings matching *E. convoluta* are made by *Cliona laticavicola*. Large, complex unicamerate to bi-camerate galleries with large apertures, bright orange tissue. *C. laticavicola* is common in Caribbean massive and branching corals.

Appendix 5: Description of *Gastrochaenolites vivus*, isp.n.

Derivation of Name: Latin, *vivus*, live.

Type series: Holotype L-U4.a. (Plate 4.8c).

Horizon and Age: Lares Fm., Late Oligocene.

Type Locality: Lares Quarry Section, Bayaney Quadrangle, Puerto Rico.

Collocation: Dept. of Geology, McMaster University, Hamilton, Ontario, Canada.

Material: Further specimens from the type locality and other localities in the Oligocene and Miocene carbonates of Puerto Rico.

Diagnosis: Clavate borehole with a series of fine arc-shaped laminations parallel to sides and base of borehole, often preserved with bivalve shell in top of boring. See fig. 4.4, plates 4.8c, 4.8d).

Description of fossil material: Infilled boreholes in Oligocene corals *Diploastrea crassolamellata* and *Montastrea tampaensis*, also in Miocene coral *Coscinaraea colei*, with arc-shaped laminations parallel to sides and bottom of borehole. Most still have bivalve shells in boreholes.

Description of recent material: Modern borings matching *G. vivus* are made by *Lithophaga bisulcata*, and always contain false floors made of calcium carbonate. Found only in those bivalves boring into the live surfaces of corals. Most commonly observed in domal corals *Siderastrea siderea* and *Stephanocoenia michelini*.