ABSTRACT

A Comparison of the Cretaceous (Albian) Edwards Limestone Bioherms of Central Texas with the Holocene Coral Reefs of Bermuda

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The Edwards Limestone of Central Texas is comprised of numerous rudist-dominated patch reefs that are collectively referred to as the Central Texas Reef Trend. These bioherms were protected by the Stuart City barrier reefs along the Texas Gulf Coast. The Stuart City reefs have been compared with the modern barrier reefs of Australia and Belize, but there is currently no modern analog for the Central Texas bioherms.

Bermuda was chosen for a modern analog study based on the existence of a protective rim reef system, its low biodiversity, and a slower reef growth rate as compared with other modern reefs. Although the patch reefs of Bermuda were determined to be “similar” to the Central Texas Edwards Limestone bioherms in many respects, the high temperatures and unique oceanographic conditions of the Cretaceous likely means that no exact modern analog for the rudist-dominated Edwards bioherms exists

A Comparison of the Cretaceous (Albian) Edwards Limestone Bioherms of Central Texas with the Holocene Coral Reefs of Bermuda

by

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A Thesis

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CHAPTER 1

Introduction

Purpose

The deposition of the Lower Cretaceous Edwards Limestone in Texas is the result of reef formation on a broad, shallow, carbonate platform created during the development of the Western Interior Seaway. Along the Texas Lower Cretaceous shelf margin, the Edwards Limestone displays features characteristic of a barrier reef system. This barrier reef system, known as the Stuart City Reef Trend, is extensively studied because of its hydrocarbon productivity, and is currently compared with the modern barrier reefs of Australia and Belize (Kirkland and others, 1987; Waite, 2009) and the Florida Keys (Griffith and others, 1969). Further landward, a series of circular and elongate patch reefs formed behind the Stuart City Reef Trend in what is now Central Texas. These patch reefs comprise what is called the Central Texas Reef Trend. These reefs are not as intensely studied, and have yet to be successfully linked to a modern analog. The purpose of this investigation is to compare the Cretaceous patch reefs of the Central Texas Reef Trend with modern Bermudian coral reefs to explore the possibility that the reefs of Bermuda are an appropriate modern analog.

Significance

If successful, this project will determine whether the Bermudian reefs are in fact, a modern analog for the Central Texas Edwards reef trend. By linking the Edwards and

Bermudian reefs, this relationship will aid us in understanding the paleo-oceanographic conditions of Central Texas during the Cretaceous (Albian), and will be complementary to our knowledge of the Edwards Limestone of the Stuart City barrier reefs.

To accomplish this study, investigating Cretaceous rudists and modern Bermudian corals is essential. The relationship between rudists and corals is poorly-understood, but furthering our understanding of this relationship may prove to be instrumental in interpreting Cretaceous facies. Exploring this relationship requires the examination of rudist and coral zonation, and the ecological niche that each organism occupies. By the conclusion of this study, the relationship between these organisms will hopefully be more clearly defined.

Methods

Extensive field work for this project was conducted both in the Edwards Limestone of Central Texas and in the modern reefs of Bermuda. Reconnaissance of potential Central Texas field sites included roughly 40 outcrops that were interpreted to be elongate or circular reefs. These sites were narrowed down to six on the basis of outcrop size, preservation, and accessibility: 1) Mosheim-1, 2) Mosheim-2 3) Lake Whitney-1, 4) Lake Whitney-2, 5) Childress Creek, and 6) Coon Creek (Figure A1).

At the Mosheim 1 and Mosheim 2 outcrops, hand samples were taken using a hammer and chisel along a measured grid (Appendix A). This grid was not possible at the other sites. At Lake Whitney, the Lake Whitney Dam is federal property, and the Homeland Security Act forbids digging or hammering close to the structure. However, permission was granted by the U.S. Army Corps of Engineers to take loose-lying surficial material for examination. At Coon Creek, the flat topography of the site made samples difficult to obtain and only select samples were collected. Also, samples were not taken from Childress Creek at the request of the property owner; however, a Master's thesis by Roberson (1972) contained the necessary data. The samples from the sites were slabbed and then polished using a polyurethane coating. Chosen slabs were made into thin sections for petrographic analysis (Table A1) and point-counts were performed to determine changes in biotic distribution and sediment texture across the outcrops (Tables A2, A3).

Field work in Bermuda was completed with assistance from the Bermuda Institute of Ocean Sciences (BIOS), and was conducted at patch, rim, and terrace reef sites (Table A1). SCUBA was used to conduct coral zonation transects at each site. A total of 15 coral transects were performed by observing coral species within a 2m radius of a 30m-long transect line. In addition, twelve 30m underwater video transects were filmed. The random dot technique (Aronson and others, 1994) was used on the video transects to document coral and algal zonation (Tables, B2, B3, B4). The videos were obtained through BIOS and were taken back for further analysis at Baylor University.

Approximately 50mL of reef sediment was taken at 3m depth intervals at each reef site. The water for each sample was poured and the sediment was dried prior to transport to Baylor University for analysis under a binocular microscope. The sediment samples were analyzed and point-counted to determine biotic components, sediment textures, and any existing trends (Tables B1, B5).

Previous Works

Literature used in this project can be divided into four groups: 1) papers and theses pertaining to the Edwards Limestone, 2) previous works concerning the modern reefs of Bermuda, 3) resources used to understand the general depositional system of modern and ancient coral reefs, and 4) paleontological and paleoecological works concerning Cretaceous rudist bivalves.

A Baylor University Master's Thesis by Linda Whigham (1981) contains a thorough list of previous works pertaining to the Edwards Limestone and the Fredericksburg Group through 1979. The most important works are listed below.

In 1852, Ferdinand Roemer, a German geologist, was the first to study the Fredericksburg Group, which contains the Edwards Limestone. The outcrops Roemer studied were in the New Braunfels and Fredericksburg area of South-Central Texas and he divided the Fredericksburg strata into "beds at the foot of the highlands," and "beds of the highlands." The "highlands" that Roemer referred to would later become known as the Balcones fault scarp along which there are numerous outcrops of the Edwards Limestone. Roemer published his findings as "*Die Kreidebildungen von Texas und ihre organischen Einhiusse*."

B.F. Shumard (1860) was the first to name and describe three formations of the Fredericksburg Group. Shumard described the Edwards Limestone, which he originally named the "Caprina" Limestone, as a white to yellow, massive limestone that is a cliff-former. Shumard also described the underlying Comanche Peak and Glen Rose Formations. In his study, he provided the first stratigraphic column for the Fredericksburg Group.

R.T. Hill and T.W. Vaughan (1898) published a paper that changed the nomenclature of the "Caprina" Limestone to what is now the Edwards Limestone. They also proposed that the Goodland Limestone of North Texas was stratigraphically equivalent to the Edwards and Comanche Peak Limestones. Hill published an additional paper in 1901 that mapped the extent and thickness of the Edwards Limestone.

W.H. Matthews (1957) developed a comprehensive phylogenetic list of fossils found within the Edwards Limestone facies. The facies are categorized as: 1) marginal or littoral facies that consist of sand, sandstone, and sandy shale, 2) neritic facies that are made up of marls, marly limestones, and chalky limestones, and 3) biostrome facies that are dominated by coquinas and shell fragments. Matthews used these fossils to determine the paleoecology of the biostromal facies. The criteria used to identify biostromal deposits can be found in Matthews' earlier 1951 publication.

In 1959, the Bureau of Economic Geology at the University of Texas compiled papers by H.F. Nelson, F.E. Lozo, and K.P. Young. This compilation is one of the most extensive studies of the Edwards Limestone in Central Texas. Nelson investigated the contacts between the Comanche Peak Limestone, the Edwards Limestone, and the Kiamichi Shale. He described the Comanche Peak Limestone as being both gradational and non-gradational into the Edwards Limestone depending on the location, and the Edwards-Kiamichi contact as being unconformable. Evidence that the boundary is unconformable includes: 1) oxidation and case-hardening of the top of the Edwards Limestone, which indicates sub-aerial exposure, 2) borings filled with Kiamichi Shale, 3) onlap of higher lithological units of the shale upon the Edwards Formation, and 4) the pinching out of the Kiamichi Shale near the rudist reefs. Nelson also described the rudistid reef core, reef flank and the inter-reef depositional environments within the Edwards Limestone.

F.E. Lozo (1959) studied the stratigraphy of the Fredericksburg Group in the Waco area and northward up to Fort Worth. He stated that Fredericksburg deposition began with an influx of terrestrial sediment that is represented by the Paluxy Sand and culminates in the carbonate deposition of the Edwards Limestone.

K.P. Young's (1959) contribution focused on using pachydont mollusks as depth indicators in the Cretaceous rocks of Central Texas. Young studied the zonation and distribution of the mollusks and discovered that in general, Monopleurid and Toucasid rudists are found in the lower part of the Edwards, Caprinids and Eoradiolites rudists in the middle and upper portions, and *Chondrodonta* mollusks at the top.

In 1963, J.G. Frost investigated the Edwards Limestone from Waco to Abilene and identified three facies: 1) an inter-reef dolomite facies, 2) a massive reef facies, and 3) a fine-grained dolomite facies. Through petrographic analysis, Frost determined that dolomite within the inter-reef facies is secondary. The position of the inter-reef facies relative to the massive reef facies suggests that the inter-reef was restricted and hypersaline.

C.H. Moore (1967) described the stratigraphy and petrography of the Edwards Limestone. Moore noticed that the Edwards Limestone is heavily recrystallized in the south and up to just north of the town of Moffat. Farther north however, Moore realized that the Edwards Limestone was much less altered. Also, Moore recorded a south to north thinning trend of the Edwards, but this thinning had a punctuated thick interval at Moffat where the limestone is 125 feet thick and much of the Edwards at this outcrop lies above where the Fredericksburg Group should terminate stratigraphically. The cause of this was unknown to Moore. He described several Edwards facies: 1) rudistid limestone,

2) miliolid biomicrite and biosparite, and 3) rudistid shell-fragment biomicrite, with nodular chert and other rocks resulting from post-depositional diagenesis.

A thesis by J.B. Marcantel (1968) involved the study of dolomite within the Edwards Limestone. Marcantel attributed the presence of the dolomites to supratidal, intertidal and shallow subtidal formation during a possible regression in the time of Fredericksburg Group deposition.

W.L. Fisher and P.U. Rodda published a paper in 1969 detailing the facies and dolomitization of the Edwards Limestone. They divided the Edwards into three primary facies and one diagenetic facies: The rudist biohermal-biostromal facies had a reef core that was composed of large rudists in growth orientation contained within a mudstone matrix. The flank deposits of this facies are coarse and have poorly-sorted shell fragments and the inter-reef deposits were well-sorted and contain nodular or bedded chert. The platform facies have well-sorted carbonate grainstones that are cross-bedded and have miliolid forams, and the lagoonal facies consist of thinly-bedded to nodular carbonate mudstone with occasional gypsum preservation. The evaporites are a result of the proximity to the Kirschberg Lagoon. The diagenetic facies contains dolomite that Fisher and Rodda divided into two categories: stratal dolomite (finer-grained) and massive dolomite (coarse-grained). They interpreted that the dolomites were the result of contact with magnesium-rich brine waters.

A Baylor University Master's Thesis by Dana Roberson in 1972 investigated the paleoecology, distribution, and significance of circular bioherms in Central Texas. The bulk of Roberson's work focused on the circular bioherms of Childress Creek in which each bioherm contains 14 to 15 concentric "rings" in plan view. Roberson claimed these rings were representative of periods of increased terrestrial sediment influx. Roberson also inferred that caprinid rudists formed the original mounds that created the reef cores and that they survived in hypersaline conditions. More normal-marine conditions on the reef flanks were dominated by radiolitids. Petrographic and paleontological evidence suggested that the elongate and circular bioherms formed in calm to intermittently-agitated waters.

In 1972, Wayne Mudd performed a detailed study on the contact between the Comanche Peak and Edwards Limestones. Mudd noticed abundant *Cladophyllia* corals within the upper portions of the Comanche Peak Limestone in Coryell County, Texas. According to Mudd, these corals, along with the foraminifer *Dictyoconus walnutensis*, formed mats suitable for the attachment of pioneering *Eoradiolites* rudists and helped initiate biohermal development. The presence of these corals and forams suggest that prior to Edwards deposition, there were clear, normal-marine conditions with strong water circulation and low rates of sedimentation.

P. R. Rose (1972) published a detailed study of the Edwards “Group” of Central Texas. Rose treats the Edwards as a “group” because he includes the Kainer and Person Formations of south-central Texas, and the Ft. Terrett and Segovia Formations of the eastern Edwards Plateau. The Person Formation replaced the “Edwards A-Zone,” and the Kainer Formation replaced the “Edwards B-Zone” nomenclature. Rose identified nine depositional environments within the Edwards Group: 1) open deep-marine, 2) open shelf, 3) moderate to high wave energy, open shallow-marine, 4) low-energy, open shelf shallow-marine, 5) restricted shallow-marine, 6) tidal flat, 7) euxinic evaporitic shelf basin, 8) evaporate-dominated supratidal flat, and 9) coastal terrigenous.

S.A. Mizell (1973) described three facies within the Edwards Limestone in McLennan County: 1) a lime wackestone-boundstone facies, 2) a fine-grained calcarenite facies, and 3) a coarse calcarenite facies. Mizell interpreted the reefs of the Edwards Limestone to have formed in shallow, normal-marine conditions behind the Stuart City Barrier Reef Trend.

In addition to Whigham's compilation, there are additional important works concerning the Central Texas Edwards Limestone. K.P. Young (1972) studied the distribution of ammonite fauna within the Cretaceous deposits of Texas. Young noticed the sparseness of ammonite species within the Edwards Limestone and attributed this to an inhospitable environment for ammonite habitation. Young maintained that many areas of Edwards Limestone deposition took place under hypersaline conditions and that any ammonite fossils were more than likely washed or carried in. However, Young also postulated that because the backreef conditions may have been so unique, they then allowed for the endemic evolution of several types of ammonites: *Oxytropidoceras, Manuaniceras, and Venezoliceras*.

A guide to the Edwards reef complex was developed by H.F. Nelson in 1973 for the Geological Society of America. Nelson differentiates between the reef, inter-reef, backreef open-marine, and backreef lagoonal facies. He described the reef facies as containing many bivalves, gastropods, and the coral *Cladophyllia*. The reef core consisted of abundant fossils in a very fine-grained micrite matrix. The flank beds of the reef facies had multiple limestone types with a high volume of shell debris. Nelson cautioned that the flank beds often appear to be more fossiliferous than the core itself because the fossils were deposited in a tightly-packed state. The inter-reef facies was composed of well-sorted to unsorted micrite, calcarenite, and shell debris, and contains chert. The grains in the interreef facies were highly abraded. The backreef open-marine facies were represented by the Paluxy, Walnut, and Comanche Peak formations, and the backreef lagoonal facies were characterized by the widespread dolomite, gypsum, and limestones of the Fredericksburg Group.

Bebout (1974) studied cores taken from the Stuart City Reef Trend. He recorded seven dominant facies: 1) miliolid wackestone, 2) mollusk wackestone, 3) rudist grainstone, 4) requienid boundstone, 5) coral-caprinid boundstone, 6) caprinid-coral wackestone, and 7) planktonic foraminifer wackestone. Bebout assigned each of these facies to a depositional environment. The shelf-margin deposits included the miliolid and mollusk wackestones, which were interpreted to be a shallow-lagoonal deposit, and the rudist grainstone, which was deposited along a nearshore beach, tidal bar, or spit in water that was less than 10 feet deep. The shelf margin also included the requienid and coral-caprinid boundstones, which were deposited in shallow reefs or banks in water depths of 5-15 feet. On the upper shelf slope, the coral-caprinid wackestone was formed in depths between 10-30 feet, and in the open-marine realm, the planktonic foraminifer wackestone was deposited in depths greater than 60 feet.

An Edwards reef exposure in Scurry County, west-central Texas, was studied by Jacka and Brand in 1977. They showed that the subaerial exposure of the Edwards Limestone took place soon after deposition, and that the Edwards and Kiamichi disconformity of Central Texas extended westward. Jacka and Brand also applied research from Land (1968) and Matthews (1968) concerning the Pleistocene reefs of Bermuda and Barbados in order to determine that the diagenesis of the Edwards

Limestone was the result of a subaerial freshwater environment. They observed four biofacies at their locality: 1) caprinid-*chondrodonta* zone (reef core), 2) Eoradiolites-*Chondrodonta* zone (upper forereef), 3) Toucasia-Eoradiolites-*Chondrodonta* zone (middle forereef), and 4) *Cladophyllia* zone (lower forereef). Biostromes were present below, and in proximity to the reef, and were comprised of *Eoradiolites, Toucasia, Chondrodonta*, and *Cladophyllia*.

Wooten and Dunaway (1977) performed a seismic study on the Edwards Limestone of the Stuart City Reef Trend. They were able to identify the boundaries between the shelf-lagoon, shelf-margin, and shelf-slope deposits. The shelf-lagoon and shelf-margin interface were recognized by a flattening in the reflection dip rate because the shelf-margin had a higher sedimentation rate than the shelf-lagoon. The shelf-margin and shelf-slope boundary were characterized by a sharp increase in the dip rate on the basinward side of the shelf margin.

Bebout and Loucks (1977) held a symposium and compiled a series of papers in their "Report of Investigations" of the Edwards Limestone. This extensive set of documents includes articles pertaining to the Cretaceous carbonates of South and Central Texas that address regional stratigraphy, depositional environments and facies, diagenesis, geochemistry, paleontology, seismic stratigraphy, and hydrocarbon production. This compilation also includes the first major document concerning Texas rudists (Coogan, 1977).

A Baylor University Bachelor's thesis completed by Karen Duffin in 1985 compared the circular Edwards Limestone bioherms of Childress Creek to the modern patch reefs of Jamaica. Duffin described several similarities between the two: 1) the

Jamaican patch reefs, like the Edwards patch reefs of the Central Texas Reef Trend, were deposited in a lagoonal backreef environment, 2) both developed in turbid, low-light environments, 3) the modern and ancient organisms (corals versus rudists) both relied on light, and 4) the Jamaican and Edwards patch reefs contained reefs that were semi-circular to circular in shape. Duffin also described the elongate and circular patch reefs within the Edwards. She proposed that the elongate reefs served as wave protection for the circular reefs behind them. The protected environment allowed the circular reefs to grow in a symmetrical fashion rather than forming an elongate wave–resistant structure.

D.R. Lemons (1987) studied the structural evolution of the Cretaceous Trinity Shelf and how it related to Comanche Peak and Edwards deposition. Lemons stated that the Comanche Peak and Edwards Formations “marked a time of maximum stability during Comanchean deposition on the Trinity Shelf.” He used contour maps to show that the East Texas Basin was not subsiding during the Lower Cretaceous, but that subsidence was occurring to the southeast towards the Stuart City Reef Trend. The thinning of the Comanche Peak and Edwards Limestones in North Texas and southern Oklahoma was related to transgression over the Wichita-Arbuckle-Ouachita uplift.

Dale Fritz and others (2000) performed a seismic analysis on the Edwards Limestone of the Stuart City Reef Trend in an exploratory study on hydrocarbon productivity. Through this study, Fritz and others determined that the Edwards reef margin extended nearly 3 miles farther seaward than previously thought. The investigation used data taken from six cores that contained miliolid foraminifera, rudists, and other bivalve fragments, which were supportive of the existence of reef and backreef depositional environments. In addition, Fritz and others identified six lithofacies within the Edwards Limestone: 1) backreef grainstone, 2) reef grainstone, 3) forereef packstone, 4) proximal slope wackestone, 5) distal slope wackestone, and 6) deep shelf argillaceous wackestone.

Waite, Scott, and Kerans (2007) discovered a previously unrecognized algal boundstone facies within the Stuart City Edwards Limestone. It was bound by encrusting *Lithocodium* and *Girvanella* algae and contained rudist fragments. The presence of this facies suggested there may have been a period in time where the Edwards reefs grew stagnant, possibly due to transgression. This facies may represent a maximum flooding surface for the Stuart City Reef Trend. This algal boundstone layer divided the Edwards Limestone into upper and lower units (Edwards A&B). It separated rudist-coral-stromatoporoid boundstones from the rudist packstones and skeletal grainstones above. This layer may be correlative to the Regional Density Marker Bed described by Rose (1972).

Another publication by Waite in 2009 for Pioneer Natural Resources Inc. outlined geologic controls on the Edwards reef development. He stated that the Edwards deposition was affected by basement rock structure, the areal distribution of Jurassic salt, deep-seated growth faults, faults that formed contemporaneously with the Edwards, and the topography of the underlying Sligo Reef margin. Waite also noted that the algal boundstone unit had been regionally traced.

To accurately compare the Cretaceous Edwards Limestone with the modern reefs of Bermuda, literature was reviewed on Bermuda’s reef structure, sedimentology, and ecology. The major publications used in this project are: Eugene Shinn (1971), Peter Garrett and others (1971), R.N. Ginsburg (1971), Sam B. Upchurch (1972), Clifton

Jordan Jr. (1973), Dean and Eggleston (1975), Fricke and Meischner (1985), Alan Logan (1988), Susan Wells (1988), Caroline Rogers (1990), and James Wood and Kelsie Jackson (2005).

Understanding the depositional models of carbonate systems is central to this study. Literature used pertaining to the depositional systems of modern and ancient coral reefs included works by: R.N. Ginsburg (1956), Raymond C. Moore (editor, 1969), Philip Heckel (1974), J.D. Milliman (1974), R. G. C. Bathurst (1974, 1975), J.L. Wilson (1975), R.W. Scott (1979, 1990a), Rachel Wood (1999), and George Stanley Jr. (2001).

Literature concerning the Lower-Mid Cretaceous reef fauna, particularly the paleoecology of rudist mollusks, was also heavily utilized during this investigation. Resources cited include publications by: Keith Young (1959), Klaus Vogel (1975), Robert.W. Scott (1979, 1981, 1988, 1990b, 2002), Erle Kauffman and Claudia C. Johnson (1988), Donald J. Ross and Peter W. Skelton (1993), Eulalia Gili and others (1995a, 1995b), and Javier Hernandez (2011).

CHAPTER TWO

Regional Description of the Edwards Limestone

Paleogeography

During the Early Cretaceous, the Edwards Limestone was deposited by the transgression of the Cretaceous sea over the expansive, flat, and generally shallow Comanche Platform that covered much of present-day Central Texas and Mexico. This platform has been further subdivided into smaller-platforms, which are the: 1) Central Texas Platform, 2) the San Marcos Platform of south-central Texas, 3) the Devils River Platform of southwest Texas, and 4) the Coahuila Platform of northeastern Mexico (Fisher and Rodda, 1969) (Figure 1). The Comanche Platform was 300-400 miles wide and had water depths ranging from several feet in the backreef to one or two hundred feet at the forereef basin (Bebout, 1974). At the platform margin, complexes of biogenic bars, islands, reefs and banks were constructed by rudist bivalves (Bebout, 1974).

The Comanche Platform was bounded by the open-marine, deeper-water North Texas Tyler Basin to the north and the ancestral Gulf of Mexico to the southeast. Two intermittently restricted areas developed on the Comanche Platform: the Kirschberg and McKnight lagoons. The existence of the Kirschberg Lagoon was first proposed by Fisher and Rodda (1967) based upon alternating evaporitic and shallow carbonate beds. The McKnight Lagoon (also commonly called the Maverick Basin) formed to the southwest and contains ammonite-bearing black shales, carbonate mudstones, and evaporites (Lozo and Smith, 1964) (Figure 1).

The barrier reefs of the Stuart City Reef Trend (Albian) roughly built on top of the earlier Sligo Reef margin (Neocomian-Lower Aptian) (Fritz and others, 2000; Waite, 2009) and formed at the interface of the Comanche Platform and the ancestral Gulf of Mexico. The reef system nearly outlined the entire Gulf of Mexico and stretched from southern Florida, through Louisiana, and across Texas into northeastern Mexico (Young, 1972). The barrier reefs formed a protective rim and created a vast backreef lagoon with restricted medium to high-energy patch reefs (Moore, 1996). Back-reef, elongate patch reefs may have served as a secondary protective barrier for the formation of the circular bioherms behind them (Tucker, 1962; Roberson, 1972; Duffin, 1983).

The time of Comanche Peak and Edwards Limestone deposition represented the period of maximum tectonic stability for the Comanche Platform. Minor subsidence of the Platform was directed towards the Stuart City Reef Trend to the southeast (Lemons, 1987). The thinning of the Edwards Limestone to the north was due to the transgression of the Cretaceous sea over the Wichita-Arbuckle-Ouachita Uplift (Lemons, 1987). Because the uplift increased the angle of slope to the north, as the Cretaceous sea transgressed, the water was largely directed westward along the flat-lying plains and caused the thickness of the Edwards Limestone to increase in West Texas to over 1,000 feet in Terlingua near present-day Big Bend National Park (Mosteller, 1970; Whigham, 1981).

Regional Stratigraphy and Correlations

The regional stratigraphy of the Edwards Limestone is relatively complex. The Edwards, depending on the location, overlies or interfingers with the Comanche Peak Limestone (Figure 2A).

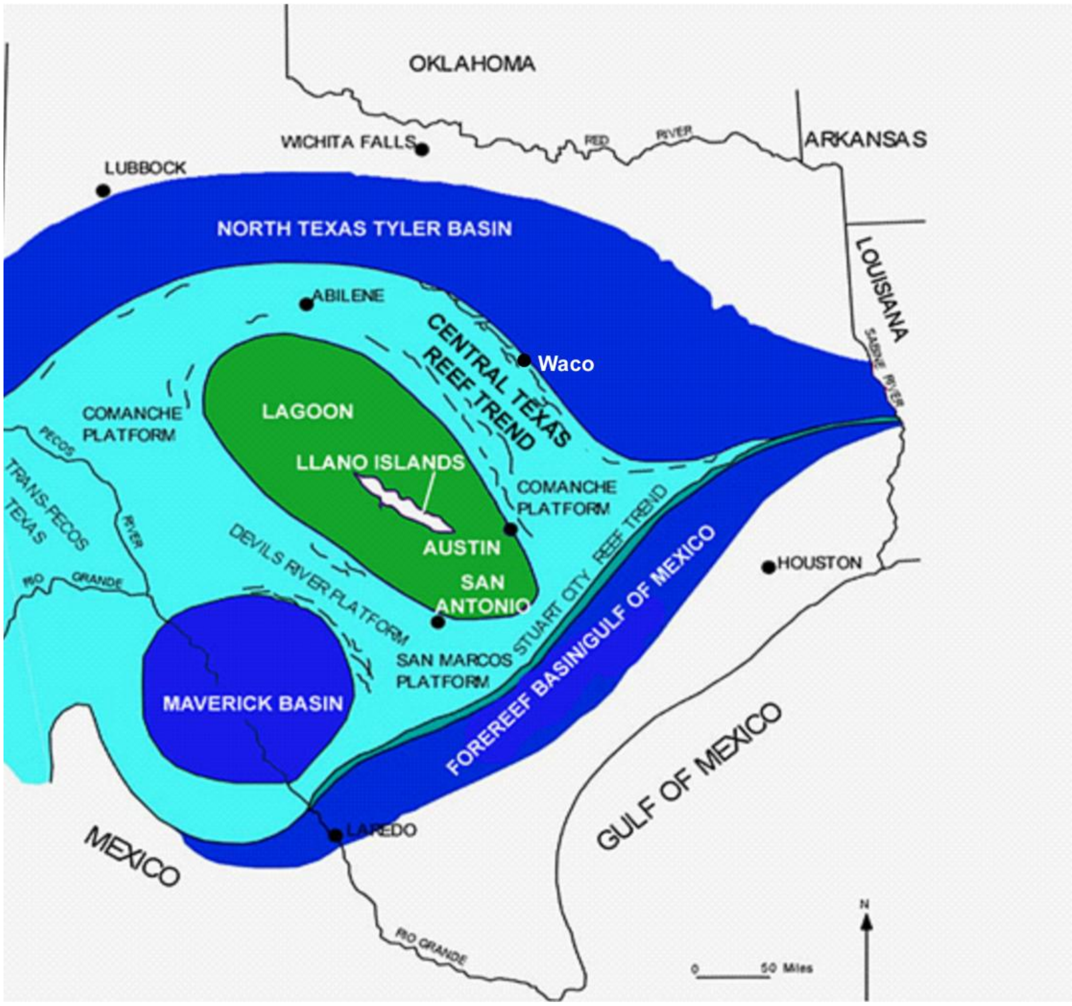

Figure 1. The paleogeography of Texas during the Cretaceous (Albian). Modified from Fisher and Rodda (1969). Dark blue=deeper waters, Light blue=shallow waters, Green=shallow lagoon.

This is because Comanche Peak is the backreef facies of the Stuart City Reef trend while the Edwards Limestone is the patch reef complex (Nelson, 1973). The relationship between the two units causes the Edwards and Comanche Peak contact to occur in four ways: 1) the Edwards and Comanche Peak are not gradational, 2) the Comanche Peak is gradational into the Edwards, as evidenced by an increase in rudist abundance in the upper Comanche Peak, 3) the Comanche Peak grades into the Edwards through an increase in grain size and decrease in nodular structure, and 4) the Comanche Peak and

Edwards Limestones interfinger H.F. Nelson (1959). Typically, when the contact is gradational or interfingering, the definitive boundary can be difficult to determine.

The Edwards Limestone is the uppermost deposit of the Fredericksburg Group (Figures 2A, 2B). Outcrops of the Edwards Limestone occur in a line that passes to the west of Fort Worth, south to Waco, Austin, and San Antonio, and southwest to the Eagle Pass-Del Rio area (Payne, 1960). In the subsurface, the Edwards Limestone can be found in a band stretching from Del Rio to northwest of Laredo, and to the east-central and southeast portions of Texas (Rose, 1972). The Edwards Limestone thins both to the north (the effect of the Wichita-Arbuckle-Ouachita Uplifts) where it pinches out just south of Fort Worth, and basinward to the southeast as the Comanche Peak Limestone thickens (Tucker, 1962; Roberson, 1972; Lemons, 1987). South of the Colorado River, near Kerrville, rather than the Comanche Peak Limestone, the Edwards Limestone lies unconformably on top of the Glen Rose Limestone of the Trinity Group (Roberson, 1972; Lock and Roberts, 1999). To the east, the extent of the Edwards Limestone roughly coincides with the Balcones-Mexia fault zone in East Texas (Mosteller, 1970).

To the southeast, the stratigraphy of the Edwards becomes increasingly complicated. A thin, widely traceable, argillaceous limestone bed known as the “Regional Dense Marker” divides the Edwards into three sections on the San Marcos Platform: the Edwards A-Zone, the middle Edwards (the Regional Dense Marker), and the Edwards B-Zone (Keahey, 1962; Knapp, 1962, Rose, 1972). In 1972, the Person and Kainer Formations replaced the Edwards A-Zone and Edwards B-Zone nomenclature respectively (Figure 2B); (Rose, 1972). The Regional Dense Marker was originally thought to be correlative to the Kiamichi Shale (Tucker, 1962), but the recent discovery of an algal boundstone unit within Stuart City reefs of the Fashing-Person fields in southeast Texas, suggests that the Regional Dense Marker, is in fact, stratigraphically older than the Kiamichi (Waite and others, 2007). Waite and others (2007) also suggested that the Regional Dense Marker is stratigraphically equivalent to the newly-found algal unit, and that this has since been verified through additional coring (Figure 2B); (Waite, 2009).

Another dividing marker bed, a marly, mollusk and ammonite-rich layer called the “Dr. Burt ammonite zone,” (Hazzard, 1959), was found in the eastern Edwards Plateau and separates the Edwards Limestone into the Fort Terrett and Segovia Formations (Rose, 1972). Lozo and Smith (1964) believe the “Dr. Burt ammonite zone” was subaerially exposed on the basis of borings and iron staining found on the surface. C.H. Moore (1967) traced the “zone” 50 miles farther north, which indicates that all or part of the Central Texas Platform may have been subaerially exposed. Fisher and Rodda (1967, 1969) concluded that the Dr. Burt ammonite zone, the Regional Density Marker, and the Kiamichi Shale were stratigraphically equivalent; however, with the recent discovery of Waite (2007, 2009), this premise may no longer be accurate.

In addition to the Person, Kainer, Fort Terrett and Segovia Formations, the Edwards Limestone has also been correlated with: the Goodland Limestone of North Texas and southern Oklahoma (Hill, 1891), the University Mesa Clay at Fort Stockton (Adkins, 1927), the Finlay Formation near Sierra Blanca (Brand and DeFord, 1958), the West Nueces Formation of West Texas, the Lower Devils River Formation in South Texas, and parts of the Acatita, Aurora, Tamaulipas, Tamabra, and El Abra Formations of East-Central Mexico (Wilson and Ward, 1993).

The Kiamichi Shale of the Washita Group lies unconformably above the Edwards Limestone in Central Texas (Figure 2A). The Kiamichi Shale extends as far north as Kansas and Colorado, east to Arkansas, and west to New Mexico (Blank, 1995). The surface between the Edwards and Kiamichi represents a period of prolonged subaerial exposure. Jacka and Brand (1977) estimate that the Cretaceous seas must have dropped by approximately 40m (130ft) to account for this exposure. Evidence of subaerial exposure includes oxidation and case hardening, borings, and the presence of Terra Rossa soils at the top of the Edwards Limestone. This exposure surface has been traced as far north as Whitney Dam, extends far south (Nelson, 1959) and into west Texas (Jacka and Brand, 1977). It does not extend far to the North Texas Tyler Basin (Nelson, 1959). The Edwards and Comanche Peak Limestones combine to form the Goodland Limestone in North Texas, and the unconformity surface is still present (Laali, 1973). The Kiamichi onlaps the Edwards Limestone, thins to the south where it terminates in Round Rock, Texas (Dowling, 1981; Blank, 1995), and pinches out along a line from Gatesville to southeast Coryell County (Nelson, 1959). South of the line, the Duck Creek Limestone takes the stratigraphic position of the Kiamichi Shale. The Kiamichi may be absent over some of the patch reefs in the Central Texas area because of the variable relief of the Edwards reefs (Nelson, 1959).

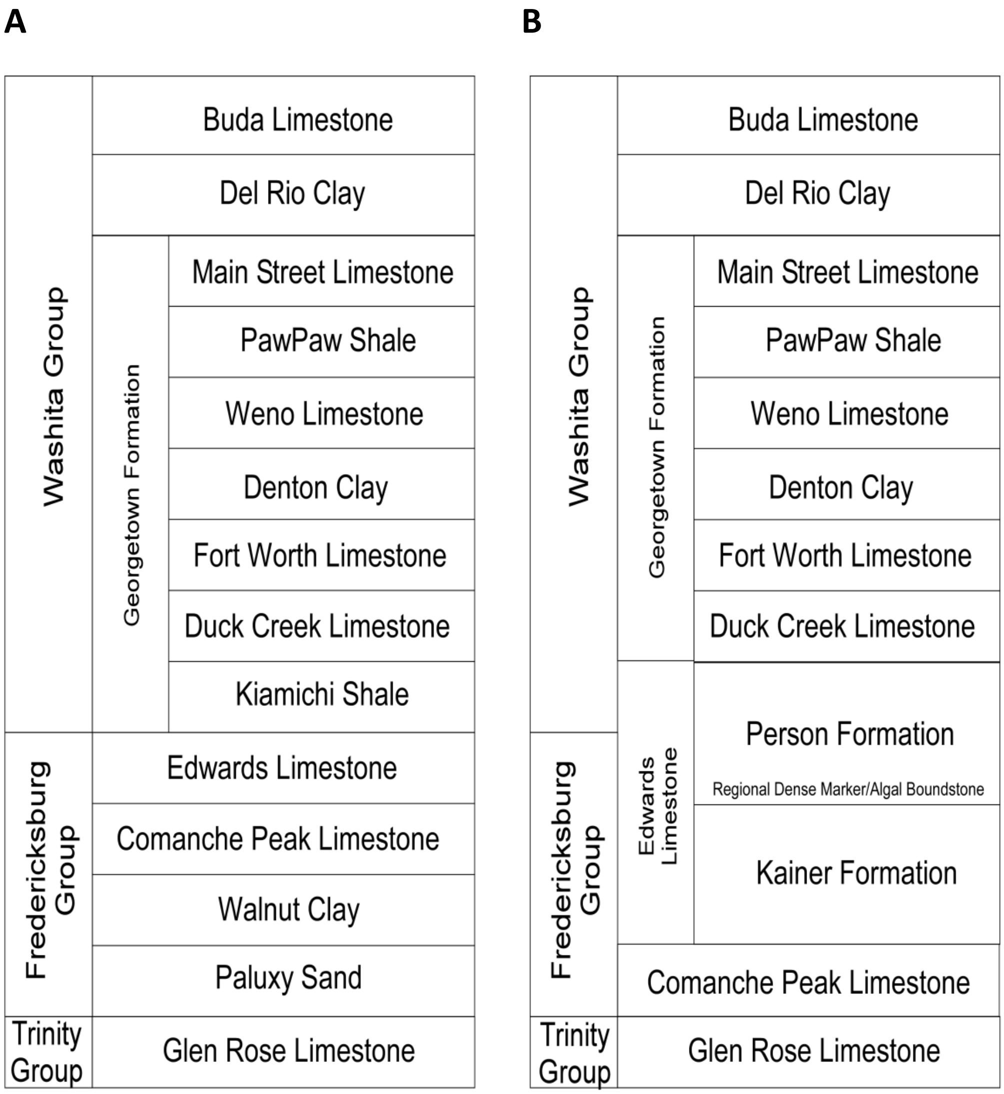

Figure 2. A) Stratigraphic column for the Comanchean Series of Central Texas, B) Stratigraphic column for the Comanchean Series of South, South-Central Texas.

CHAPTER THREE

Description of the Study Area

Mosheim

Mosheim-1

The Mosheim-1 outcrop displays three stacked, elongate reefs (Figure 3A) exposed in a small hillside about 5 kilometers southeast of the FM 217 and FM 215 intersection (Figure A1). The outcrop is approximately 76m in length and reaches a maximum height of 4.5m. The lowest 1.5m of the section consists of the argillaceous, nodular Comanche Peak Limestone, which is non-gradational with the overlying (Lower) Edwards Limestone (Figure 4).

The Edwards Limestone attains a maximum thickness of approximately 3m. The Edwards Limestone is massive and thickly-bedded, with conspicuous flank beds. It weathers gray and is commonly iron-stained, but is white to yellow when freshly exposed. The limestone is heavily recrystallized with coarse calcite spar, and the dissolution of the rudist shell material has led to the creation of and moldic porosity. A thin, argillaceous layer separates each bioherm and represents a period of increased sediment influx that suffocated the previous reef system. The next bioherm grew in succession over the remnants of the earlier reef.

The rudist population of the outcrop is comprised of solely *Eoradiolites davidsoni* (Figure 5). The stratigraphic position of Mosheim-1 to Mosheim-2 suggests that the *Eoradiolites* were the original mound-building taxa for the area. *Eoradiolites* is considered to be a normal-marine taxon.

Thin-section analysis reveals that the Edwards Limestone has diverse fauna and flora. In addition to rudist and other mollusk fragments, echinoderms, bryozoans, *Cladophyllia* corals, gastropods, ostracodes, *Dictyoconus walnutensis*, and miliolid forams are all abundant (Tables A1, A2; Figure A2, A3, A4). In the algal community, dasyclad, codiacean, and crustose coralline red algae are all well-represented (Table A3; Figure A4). *Cladophyllia* coral and *Dictyoconus walnutensis* are more heavily concentrated in the lower 1.5m of the Edwards (Tables A2, A3). They likely formed hard mat which acted as the attachment surface for the core-building *Eoradiolites* rudists (Mudd, 1972; Roberson, 1972).

The Edwards Limestone at this location can be divided into three facies: a rudist-foraminiferal-algal rudstone, a rudist-foraminiferal-algal floatstone, and a rudist-bryozoan-algal-*Dictyoconus* boundstone (Tables A1, A2, A3). The fossil communities found within all beds are essentially the same, and with the exceptions of *Cladophyllia* and *Dictyoconus walnutensis*, no discernable distribution trends are observable (Tables A2, A3).

Many crushed rudist and mollusk shells, occasional coated grains (Table A2), and the presence of mud within the matrices, suggests that the Mosheim-1 reefs were a moderate energy environment.

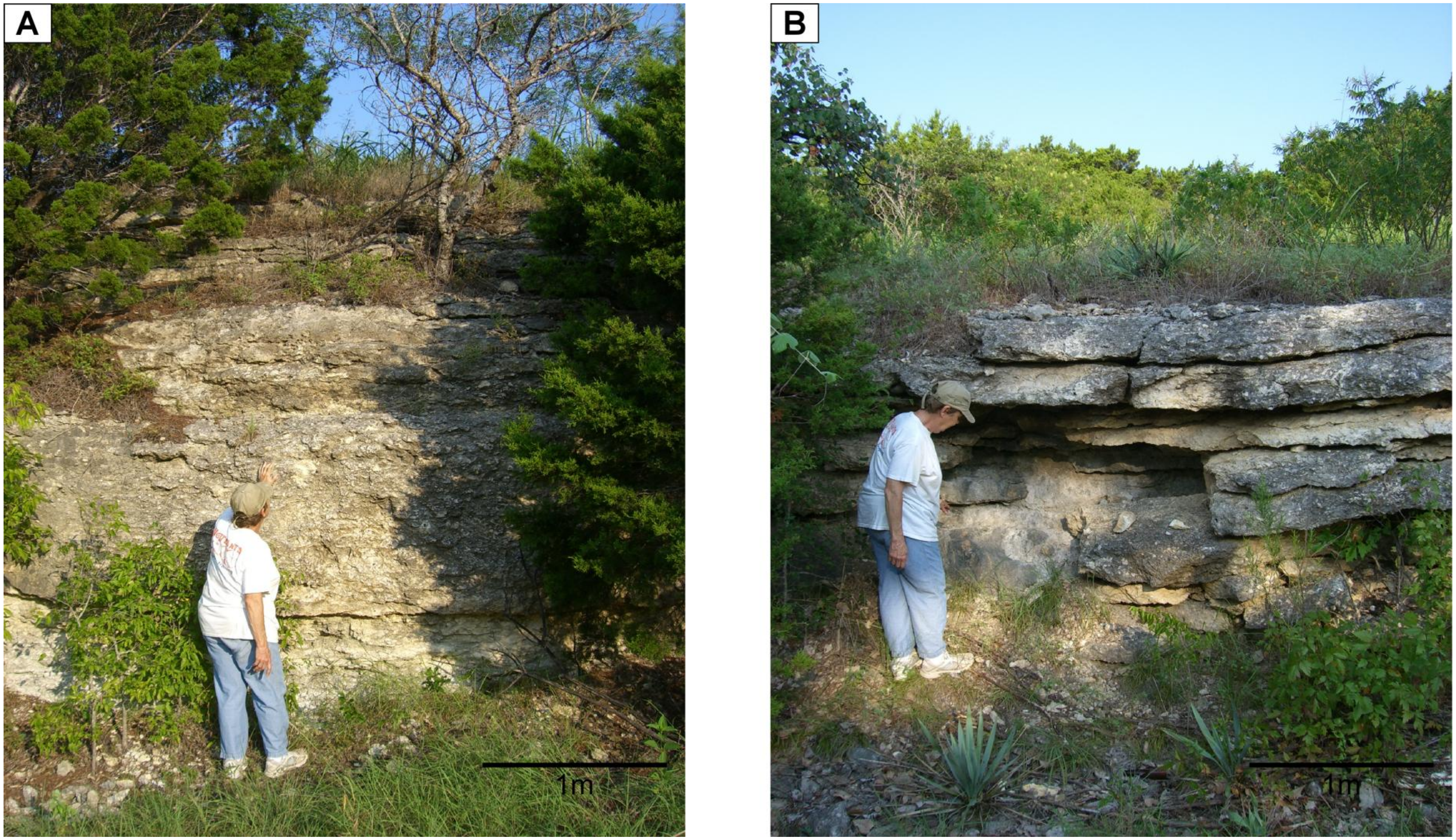

Figure 3. A) Stacked elongate bioherms at Mosheim-1. B) Well-defined flank beds at Mosheim-1.

Figure 4. The Comanche Peak and Edwards Limestone contact at Mosheim-1. The Comanche Peak is the white, argillaceous, nodular limestone unconformably underlying the gray, massively-bedded Edwards .

Figure 5. A close-up of the Edwards Limestone at Mosheim-1. It is almost entirely comprised of *Eoradiolites davidsoni* rudists that have been recrystallized, or have been filled with calcite spar.

Mosheim-2

The Mosheim-2 outcrop is a road cut located just around the corner from Mosheim-1 farther down FM 215, after a major curve in the road (Figures 6, A1). This section is the stratigraphic continuation of the top of the Mosheim-1 outcrop and contains several elongate, and possibly some circular bioherms. Evidence supporting circular bioherms lies on the opposite side of the road where there are several smaller reefs with well-defined flank beds, and by the appearance of what may be circular rings on the top surface; however, it is not clear how these reefs are correlate to the larger outcrop (Figures 7, 8). Portions of the larger outcrop have flank beds coalescing from multiple contemporaneously-existing bioherms (Figure 9).

The outcrop measures approximately 1/2km in length and reaches a maximum height of about 6m. The Edwards is massively-bedded and can be dark gray, brown, or yellow-white in color, and may have hematite staining. Significant recrystallization and moldic porosity have developed. Polished slab and thin-section studies reveal the same fossil assemblage exists here as at Mosheim-1(Tables A1, A2, A3) with one notable exception: Mosheim-2 contains a high density of caprinid rudists.

In the lower part of the section, the *Eoradiolites* reefs are displayed from Mosheim-1. As the *Eoradiolites* reefs continued to grow and relative sea level decreased, the shallow, energy-tolerant caprinid rudists took over the core as evidenced by the loss of *Eoradiolites* up-section. The *Eoradiolites* reef likely did not completely die off because *Eoradiolites* are still occasionally found to be intermixed with the caprinid rudists, albeit in low abundance. The coexistence of *Eoradiolites* and caprinids also suggests a normal-marine environment. After the caprinid colonization, the *Eoradiolites* rudists were relegated to the flank beds along with a sparse scattering of *Toucasia texana*. In the uppermost bed of the Edwards Limestone, the caprinids are joined by *Chondrodonta munsoni* bivalves suggesting the reef continued to grow until the waters became very shallow. *Chondrodonta* are very commonly associated with caprinids in the shallowest of deposits, but the can occupy multiple zones of the reef; this suggests that *Chondrodonta* are highly adaptable (Bebout and Loucks, 1974). Caprinid rudists, which needed a substrate for attachment, may have used *Chondrodonta* shells. This explains why the two organisms are usually found in association. The smaller roadside bioherms also exhibit the change from *Eoradiolites* to caprinid/*Chondrodonta*-dominated reefs.

Ooids and coated grains are present throughout the outcrop but are generally low in abundance. However, at several locations along the section, coated grain concentrations increase dramatically (Table A2). These areas are postulated to be small, high-energy caprinid shoals and these shoals may account for the dispersal of coated grains throughout the outcrop. With the exception of the caprinid shoals, the bioherms of Mosheim-2 are interpreted to be moderate energy; as at Mosheim-1, there are many crushed rudist and mollusk fragments with mud present in the matrix.

Figure 6. A portion of the Mosheim-2 outcrop located on FM 215. The outcrop extends for nearly 0.5km. To view complete outcrop see Appendix A for a series of panoramic photos.

Figure 7. The flank beds of the smaller roadside reefs of Mosheim-2. These reefs may/may not be correlative to the larger outcrop.

Figure 8. Possible circular rings at the top of the roadside bioherms at Mosheim-2.

Figure 9. Coalescing flank beds at the bioherms at Mosheim-2. Note the change in the slope direction of the flank beds from the right to left sides of the photograph.

Lake Whitney

Lake Whitney -1

Lake Whitney sites 1 & 2 are located at Soldiers Bluff Park near the Whitney Dam (Figures 10, 11, A1). These sites provide both plan and cross-sectional views of two elongate bioherms. The Upper Edwards Limestone of Lake Whitney-1 is immediately adjacent to the dam (Figure 10). It has weathered dark gray and contains abundant molds of caprinids, along with scarce *Eoradiolites davidsoni* and *Toucasia texana*. The caprinid molds exhibit either a semi-coiled or elongated growth habit and can be quite large, attaining lengths in excess of 1m. Many of the molds contain the fossilized fibrous canals that run along the inside of the caprinid shell.

The reef core consists of larger caprinids whereas the smaller caprinids are found on the reef flanks along with rare *Eoradiolites* and *Toucasia* rudists (Figure 12). Scattered *Chondrodonta* can be found along the entire reef (Figure 12). Many of the *Eoradiolites* and *Toucasia* shells may have been transported in by wave action. The wave energy in the area was at least substantial enough to transport in the large-shelled *Oxytropidoceras* ammonites, which are used as a biochronological marker for the Early Albian Stage of the Cretaceous (Young, 1959; Roberson, 1972).

Other fossil constituents of Whitney-1 are similar to those of the Edwards Limestone at the Mosheim locations and include: echinoderms, bryozoans, gastropods, ostracodes, *Texigryphaea* oysters, *Cladophyllia* coral, *Dictyoconus walnutensis*, miliolids, dasyclad, crustose coralline red, and codiacean (*Halimeda?*) algae (Figures A2, A3, A4; Tables A1, A2, A3).

The upper surface of Whitney-1 has evidence of subaerial exposure, including the presence of Terra Rossa soils, case hardening, and numerous borings. Evidence of this exposure, taken together with the sparseness of *Eoradiolites* and *Toucasia* rudists, suggests that the reefs at Lake Whitney formed under hypersaline conditions. Caprinids thrived in the shallowest water, withstood high-energy, and were much more tolerant of hypersaline conditions than other rudist taxa.

Rudist growth orientation is preserved at this locality. The larger caprinids of the reef core have oriented themselves parallel to the paleocurrent in order to minimize their exposure to higher-energy conditions. Most of the core-caprinids are oriented east to west implying an east-west flowing paleocurrent (Figure 13). At the west edge of the reef, the orientation is more random but has a general trend towards north-south (Figure 14). This change in orientation can be explained by considering the position of the caprinids on the reef. These caprinids would have been situated on the lee-side of the reef, and would have be cut-off from the east-west-flowing current. Because of this, the energy level would correspondingly decrease, and they would be able to orient in a more random fashion. The north-south general trend is probably the result of water constriction between bioherms, and some rudists chose to orient themselves parallel to the localized direction of flow.

Only loose-lying samples were able to be taken from the site because of restrictions by the U.S. Army Corps of Engineers at Whitney Dam. Too few samples were obtainable to determine any significant distribution changes in the fossil assemblage across the reef (Tables A2, A3).

Figure 10. The Whitney-1 elongate bioherm adjacent to the Lake Whitney Dam. It contains caprinid rudists up to 1m in length and has substantial moldic porosity resulting from rudist dissolution.

Figure 11. A view of the Whitney-2 locality across from Whitney-1. Remnants of flank beds are in the foreground.

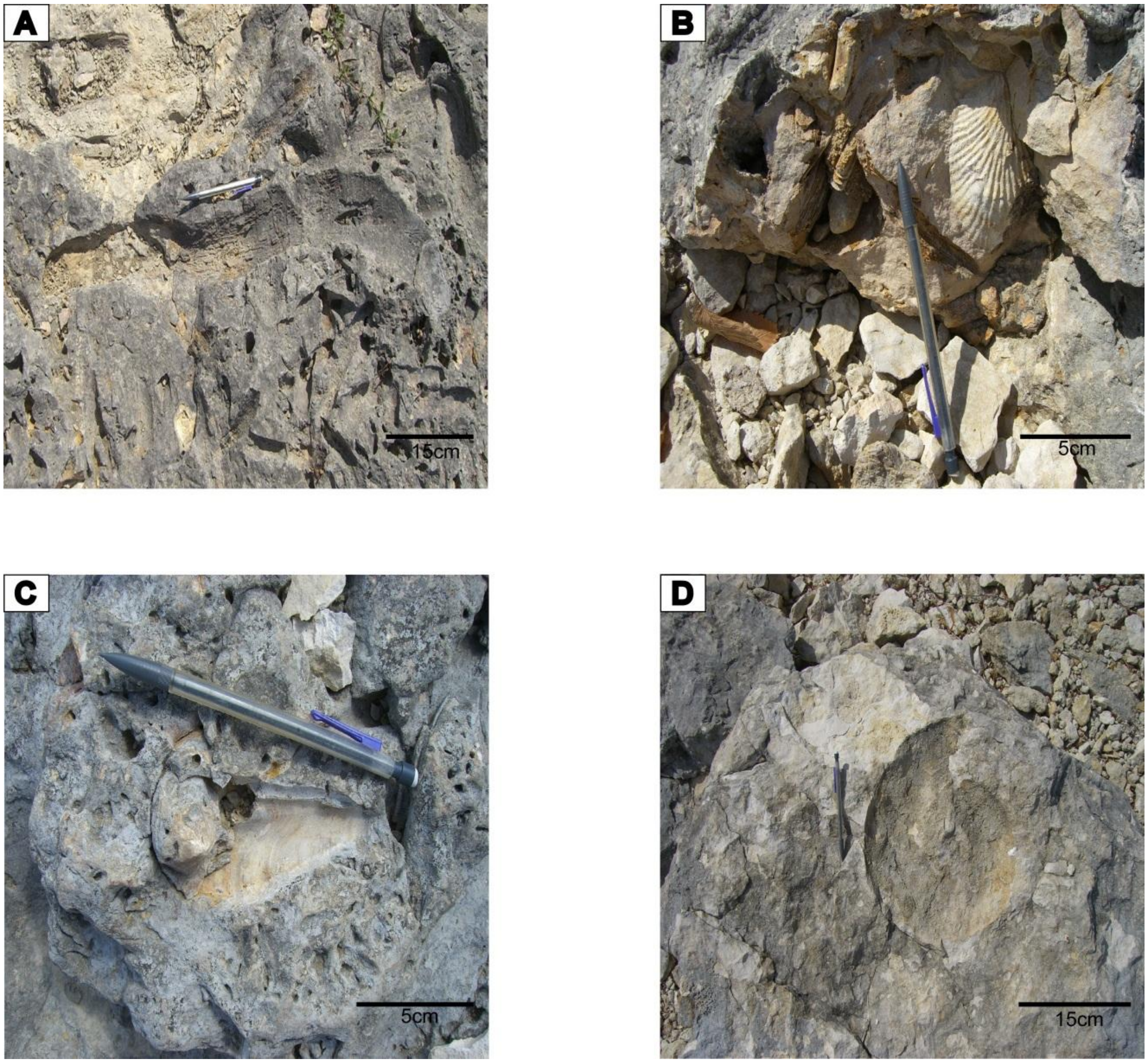

Figure 12. Fossils of Whitney-1: A) caprinid mold preserved with the characteristic fibrous canals, B) *Chondrodonta* bivalve, C) *Eoradiolites* rudist, D) washed-in *Oxytropidoceras* ammonite which is used as a biochronological constraint.

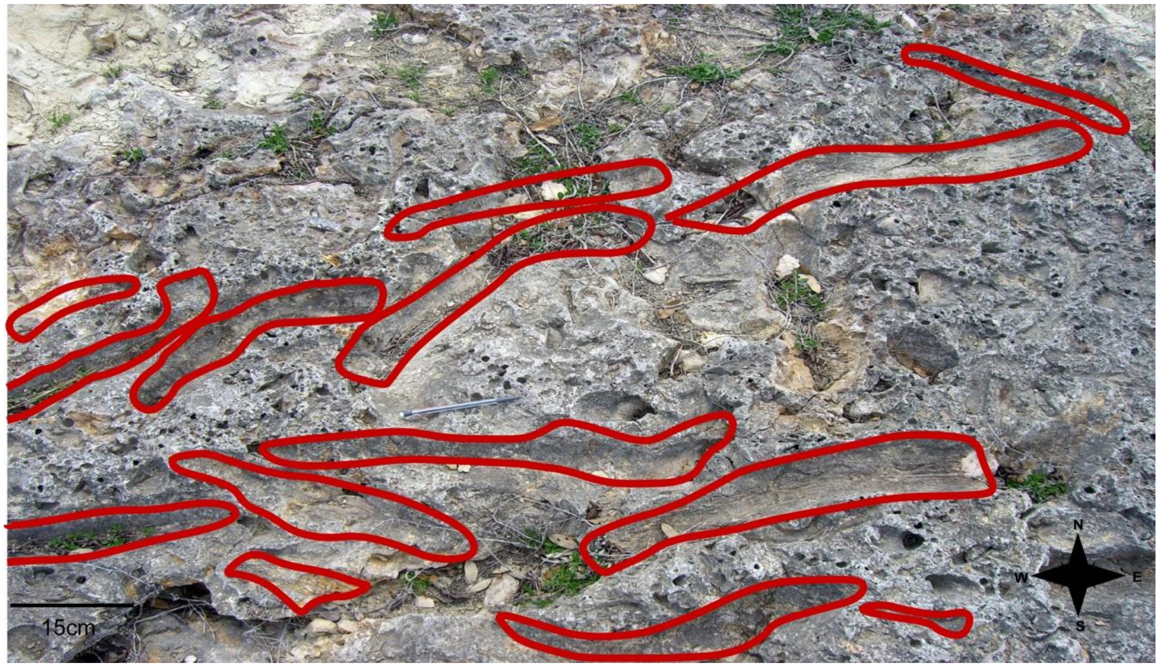

Figure 13. The orientation of the caprinid rudists in the reef core of Whitney-1 suggests an East-West flowing paleocurrent. The caprinids aligned themselves parallel to the current to receive nutrients while minimizing their exposure to high energy.

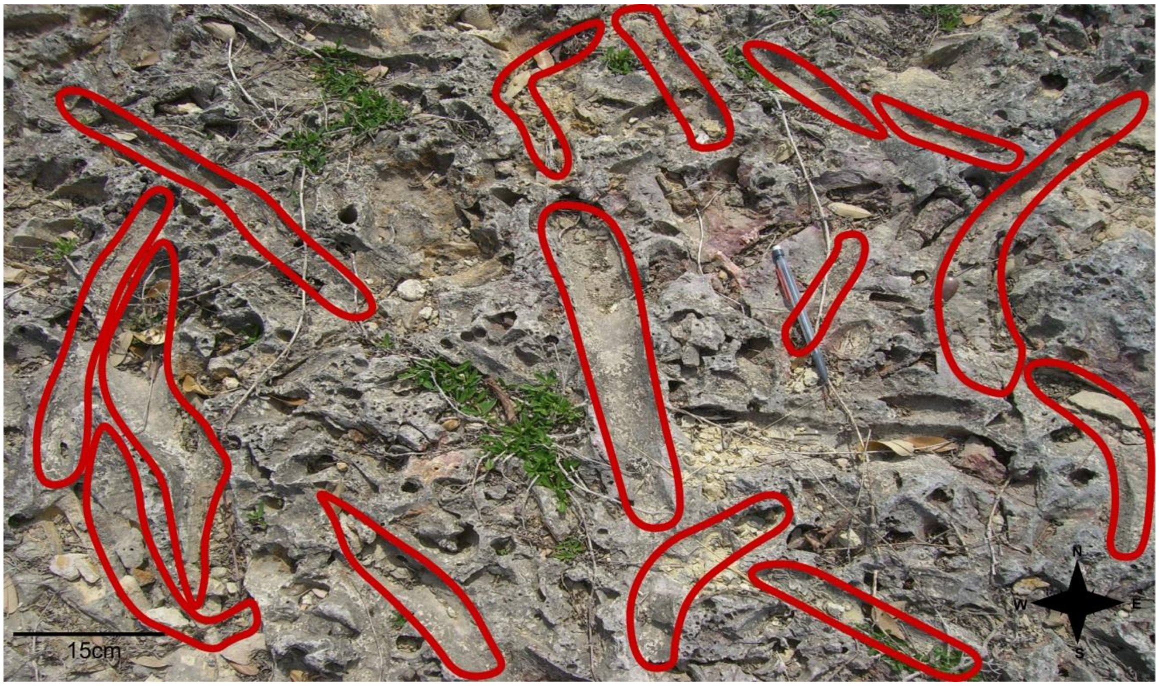

Figure 14. The caprinids on the flanks of the elongate reef at Whiney-1 display a north-south trend. The north-south orientation is contrary to the dominant paleocurrent, but could be explained if the caprinids were situated on the lee-side of the reef or in an area protected from the current-flow.

Lake Whitney-2

Whitney-2 is located just west of Whitney-1 on the other side of the embayment and presents an elongate bioherm with an interreef talus slope. The core of the reef is composed of large caprinids, *Chondrodonta* bivalves, and gastropods, and the flank beds are made up of smaller caprinids and large *Texigryphaea* oysters. As at Whitney-1, the orientation of the caprinids generally trends east-west, and evidence of subaerial exposure suggests hypersaline conditions.

Farther down-section, a topographic break occurs in the outcrop and presents a view of the flank beds with depositional relief. The flank beds dip downward into the "break," which contains many *Chondrodonta* fragments and other finely-crushed, poorly-sorted shell debris (Figure 14). This debris was washed off of the reef and into an interreef channel. The poorly-sorted shell debris constitutes the interreef deposit of the Edwards Limestone, which is also present at the Coon Creek location (Figure A1). The debris continues on the other side of the channel where there are small, interspersed groupings of caprinids. These groupings are interpreted to be localized inter-reef caprinid shoals or small knob reefs (Figures 15, 16).

The Terra Rossa soil which is present in portions of the surface at Whitney-1 is found in a greater amount at Whitney-2 (Figure 16). Terra Rossa soil is created by the clays left behind during the subaerial weathering of limestone. Fe-oxides form when the clays are left above the water table under oxidizing conditions; this gives the soils their characteristic red-orange color. The presence of these soils indicates a regression that terminated the deposition of the Edwards Limestone and left the irregular upper surface of the Edwards exposed. This marks the northern-most extent of the unconformity surface between the Kiamichi Shale and the Edwards Limestone, which was recorded by Nelson (1959).

Beneath the unconformity surface, there is a non-rudist bearing mudstone bed roughly 0.5m thick (Figure 17A). Because this bed is stratigraphically just below the Edwards-Kiamichi contact, this is interpreted as an interval of heavy sedimentation that effectively smothered the bioherm. The mudstone bed is mainly comprised of some small oysters and gastropods. The miniature size may be evidence for less than ideal conditions created by an increase in terrigenous sedimentation. The top surface of the mudstone (synonymous with the unconformity surface of the Edwards-Kiamichi) regains some caprinid rudists, and suggests a very short-lived episode of reef reestablishment.

An 8cm-thick bed of *Texigryphaea* oysters is directly above the unconformity surface indicating a post-Edwards transgressive event (Figure 17B). This thin unit is believed to represent one of the basal beds of the Kiamichi Shale. *Texigryphaea* oyster beds were documented by Nelson (1959) in the lowest parts of the Kiamichi. Above the Kiamichi Shale is the ammonite-bearing Duck Creek Limestone. This indicates an eventual return to normal-marine conditions during the Albian.

Only one sample was obtainable from the Whitney-2 bioherm due to the lack of loose material. The surface had been cleared by the Army Corps of Engineers. No conclusions can be made with regards to the complete fossil assemblage or distribution, but echinoderms, gastropods, bryozoans, *Cladophyllia* coral, ostracodes, and coralline red algae were present (Tables A1, A2,A3; Figures A2, A3, A4).

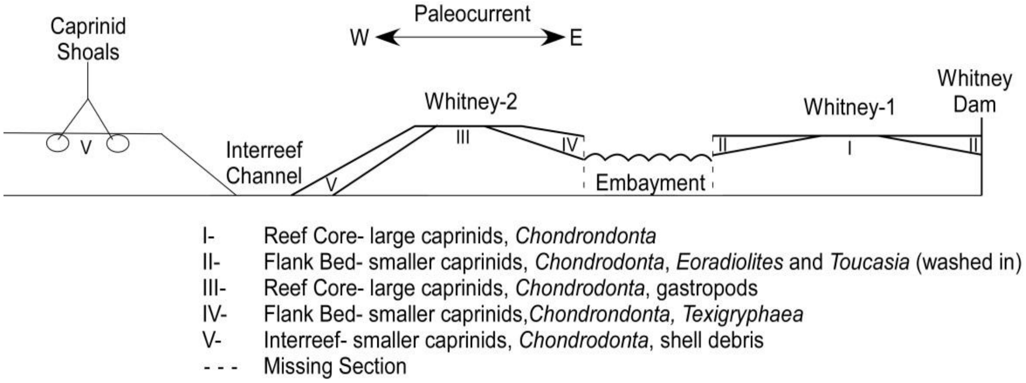

Figure 15. The relationship between Whitney-1 and Whitney-2. This figure illustrates the biotic zonation of each reef. Not drawn to scale.

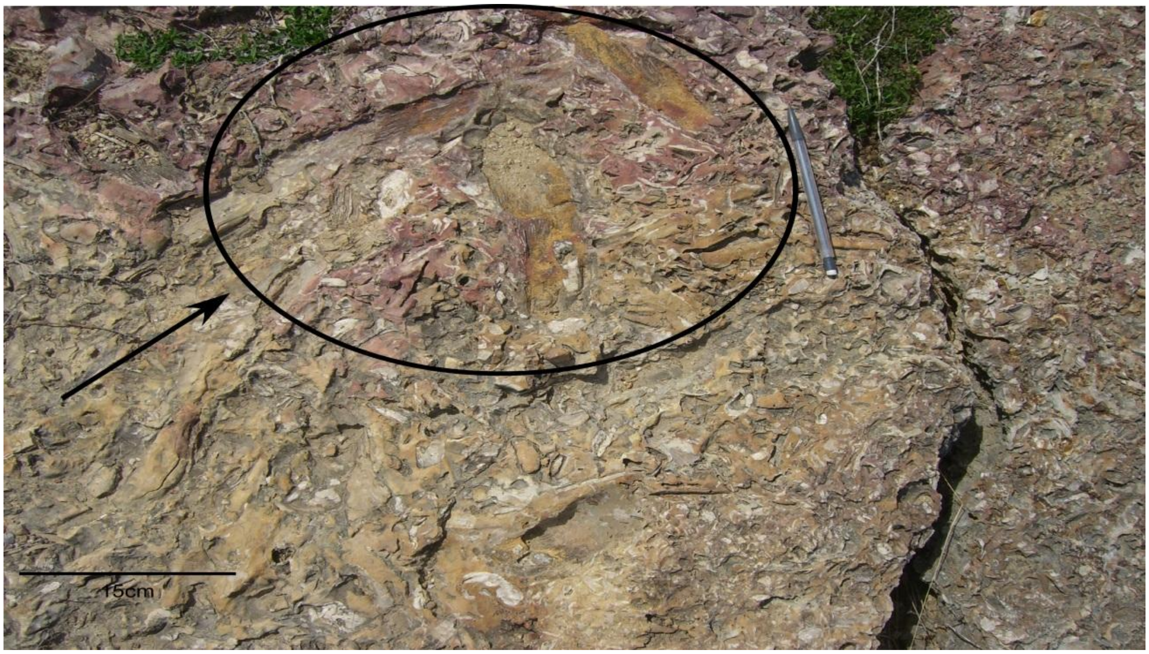

Figure 16. Caprinid shoal or knob reef at Whitney- 2. The red-purple coloration is due to the infilling of the Edwards by Terra Rossa soils.

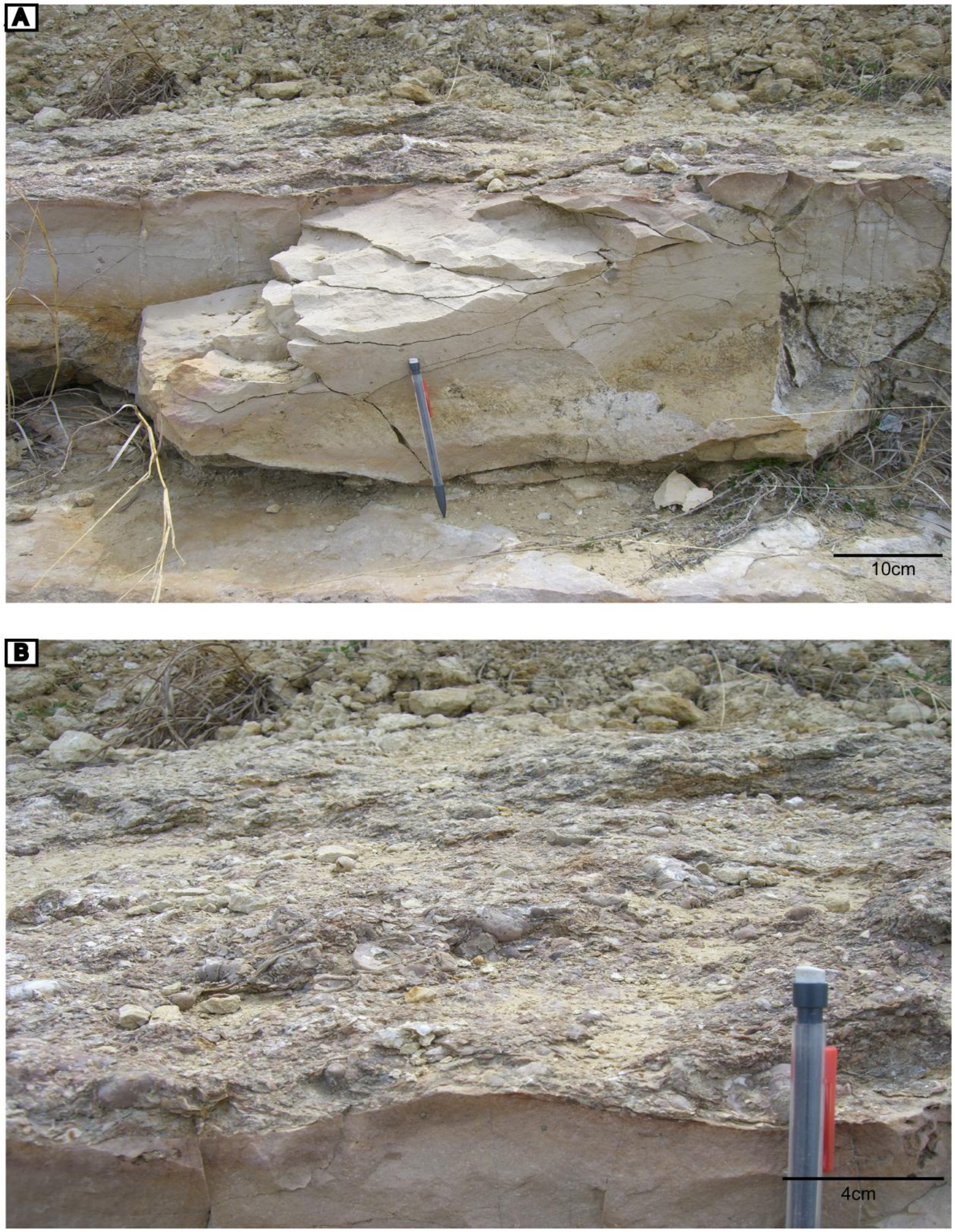

Figure 17. A) The non-rudist-bearing mudstone of Whitney-2. This represents an interval of heavy terrigenous sedimentation that suffocated the Edwards reefs. B) Basal *Texigryphaea* beds of the Kiamichi Shale at Whitney-2. Only this basal bed of the Kiamichi is present at Lake Whitney. The surface between the Edwards Limestone and the Kiamchi Shale is a subaerial exposure surface. Prior to Kiamchi deposition, this surface contains some rudists, likely a brief period of reef re-growth before the influx of the Kiamichi occurred.

Coon Creek

The Coon Creek site is located on FM 2114 (Gholson Rd.) about 2km from the FM 56-CR 3615 split (Figure A1). This locality contains a larger exposure of the inter-reef deposit than that at Whitney-2 and has several caprinid-C*hondrodonta* interreef mounds. Many of the rudist molds and body fossils have been heavily-stained by hematite. The Edwards here (like the other localities) has weathered dark gray and is yellow to brown when freshly exposed. The Edwards is unconformably overlain by the ammonite-bearing Duck Creek Limestone (the Kiamichi Shale is not present). The most noticeable aspect of the Coon Creek site is a large central mound (Figure 18). It is unclear whether this mound represents depositional relief, or if it is the result of erosion during periods of high creek flow. The caprinids near this "mound" are oriented east-west, consistent with the paleocurrent flow at Lake Whitney.

Behind the central mound, there are two pipeline trenches that allow for a small-scale cross-sectional view of the outcrop (Figure 19). The Edwards visible in these trenches is comprised of shell hash. At the base of the trenches, small current ripples are present. The wavelengths of the current ripples increase in size further up and suggest an increase in flow velocity.

Only caprinid rudists and Chondrodonta bivalves are present at Coon Creek; *Eoradiolites* and *Toucasia,* are noticeably absent. The abundance of caprinids and *Chondrodonta,* the proximity of the Coon Creek site to Lake Whitney, and the presence of current-ripples within the trenches, suggest a hypersaline-stressed, moderate-energy environment during the deposition of the Edwards Limestone at Coon Creek. The outcrop is devoid of any other sedimentary features to better constrain the energy regime.

Only a few samples were collected from this site because of the dominance of a single bed of Edwards Limestone at this location. Fossils here are consistent with the assemblages from the other localities, however they occur in a lower abundance, possibly the result of weathering from flowing creek waters (Tables A1, A2). They include: echinoderms, bryozoans, *Cladophyllia*, gastropods, *Dictyoconus walnutensis*, miliolids, and ostracodes (Tables A1, A2; Figures A2, A3, A4). Coralline red algae were documented, and while dasyclad and codiacean algae were not observed in the few hand samples, they are likely present (Table A3).

Figure 18. The central mound of Coon Creek. This may be the depositional relief of the bioherm, or may just be an artifact of erosion.

Figure 19. These trenches located behind the central mound give a small-scale cross-sectional view of the inter-reef deposits of Coon Creek. At the base of the trenches are small current ripples (not visible in photo). The wavelengths of these current ripples increase towards the top trench indicating an increase in energy. Trench is approximately 1m in depth.

Childress Creek

The Childress Creek site is located on CR 3550 and contains five end-member circular bioherms (Figure 20, A1). The cores of the circular bioherms are surrounded by a series of very well-defined, concentric beds. In between the concentric rings are clay layers several centimeters thick that represent periods of increased terrigenous sediment influx. This influx either slowed the growth of the reefs or caused them to die off completely. If the reef died, organisms would have settled on the remnants to initiate a period of regrowth. The outermost ring has a layer of marine clay, 15cm-thick that separates it from the rest of the reef. The clay contains sharks teeth, echinoid spines, and ostracodes (Roberson, 1972) and indicates either a more voluminous or prolonged period of sediment input. The reefs were able to splay out circularly because they were protected behind the seaward elongate reefs described by Roberson (1972).

The cores of the bioherms are dominantly composed of caprinids, with a few scattered *Monopleura* rudists and *Chondrodonta* bivalves. The caprinid and monopleurid core suggests that the initial mounds of the circular bioherms grew in hypersaline waters. After the establishment of the core, either a return to normal salinities or an increase in relative sea level, allowed *Eoradiolites, Toucasia,* and *Monopleura* beds to start growing out from the original mound (Figure 21). Most proximal to the core and throughout the ringed beds, *Eoradiolites* is the dominant rudist taxon, whereas on the outer flanks, while *Eoradiolites* is still the most common, *Toucasia* and *Monopleura* rudists increase in abundance (Figure 21).

Samples were unobtainable from this section as per request of the property owner, however earlier studies by Roberson (1972) and Duffin (1985) recorded many of the biota present at Childress Creek. The fossils include whole or fragmented *Neithea duplicosta* bivalves, *Ostrea* and *Texigryphaea marcoui* oysters, *Cyphosoma* echinoids, and *Tylostoma tumida* gastropods. These organisms are considered to be normal-marine fauna and are found with *Eoradiolites* on the flank beds. All of the shell material, including the rudists, has either been recrystallized, infilled by calcite spar or Terra Rossa soils, replaced by limonite or pyrite, or has been completely dissolved resulting in extensive moldic porosity.

The Childress Creek locality presents a rare opportunity to measure the dimensions of circular bioherms. The diameters of four of the five bioherms fall within the range of 40-45m. The uniformity of the diameters suggests that these bioherms formed contemporaneously behind the protection of the elongate reefs described by Roberson (1972). The fifth and largest bioherm measures 65m in diameter. The larger size could possibly be explained by 1) reef maturity, 2) increased accessibility to reef-building organisms, or 3) because it was located in slightly deeper waters and its growth was not limited by wave-base until later in its development.

Figure 20. The circular bioherms of Childress Creek. The bioherms can be found on either side of the CR 3550 bridge. The ringed structure of the bioherms is the result of the preferential weathering of mud-rich carbonate or clay which represented periods of increased terrestrial influx.

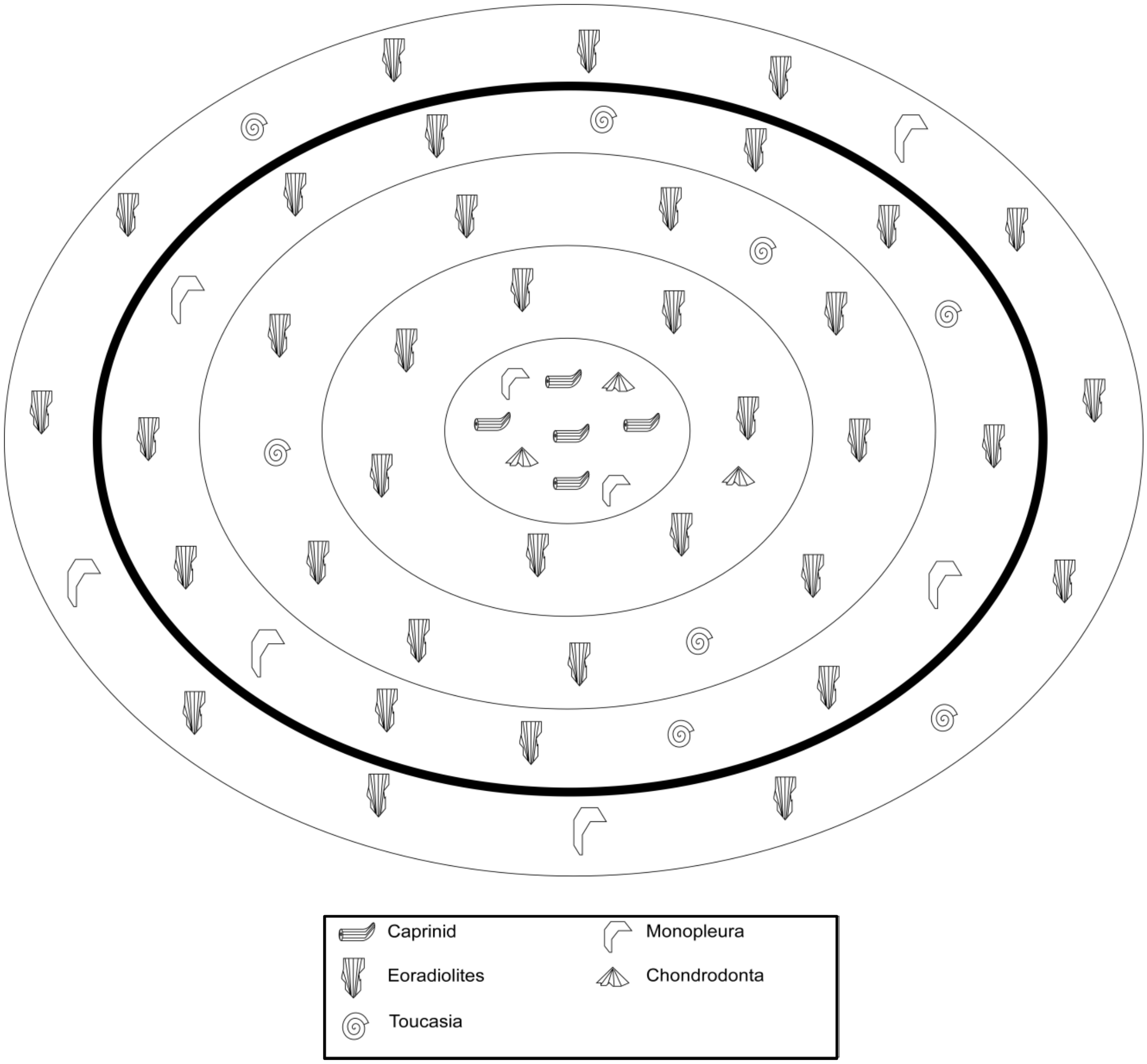

Figure 21. The zonation of the circular bioherms of Childress Creek. The symbols represent a change in the relative abundance. These bioherms were initially established by a core consisting of caprinids, *Monopleura*, and *Chondrodonta* in stressed, possibly hypersaline conditions behind seaward elongate reefs. The concentric rings are dominated by *Eoradiolites davidsoni* rudists with *Toucasia* and *Monopleura* increasing towards the flanks as normal marine conditions returned and/or relative sea level increased. The dark ring represents the 15cm-thick bed of marine clay that separates the outermost flank bed from the rest of the bioherm.

CHAPTER FOUR

Bermuda’s Coral Reefs

Geography and Geology

The British colony of Bermuda consists of a group of 130-150 islands with a total landmass of 53.7km^2 in the Sargasso Sea (North Atlantic) between 32° 10’N and 32° 30’N (Wells, 1988; Logan, 1988; Wood and Jackson, 2005). It is positioned roughly 960km east of Cape Hatteras, North Carolina and 1,400km from the nearest coral reefs in Florida and the Bahamas (Figure 22) (Garrett and others, 1971; Wood and Jackson, 2005). Geographically, Bermuda should be located too far north to be able to support a coral reef community, but the islands are located about 320km east of the warm waters of the Gulf Stream (Figure 22) (Jordan, 1973). The Gulf Stream warms the air and sea temperatures to create the subtropical climate necessary for the coral reefs to flourish (Jordan, 1973; Wells, 1988; Smith, 1998; Wood and Jackson, 2005).

Because of Bermuda’s distance from the Gulf Stream, there is no dominant current on the Bermuda Platform; instead, water circulates irregularly (Jordan, 1973; Wells, 1988). The lagoonal waters are freely exchanged over the outer reefs with semi-diurnal tides that have a mean daily range of 0.75m, a spring range of 1.3m, and a neap range of 0.3m (Garrett and others, 1971; Smith, 1998). Seawater temperatures fluctuate seasonally in Bermuda’s expansive north lagoon (14°-31°C) and in the outer reefs (18-29°C) (Smith, 1998). The salinity of Bermuda’s open ocean varies only slightly with an average of 36.5‰ (although inshore basins can be fresher) (Schroeder and Stommel, 1969; Beers and Herman, 1969; Smith, 1998).

Bermuda is unique in that it is not situated in the tradewind belt, but it is between the trade wind belt and the belt of westerlies and it is strongly affected by the Bermuda-Azores High (Garrett, 1971). In the summer, the north lagoon and northern reefs are on the lee-side of the island because south and southwesterly winds predominate and produce large swells on Bermuda's south shore (Jordan, 1973). In the winter months, southwesterly, north, and northwesterly winds dominate and bring frequent storms (Jordan, 1973; Wells, 1988).

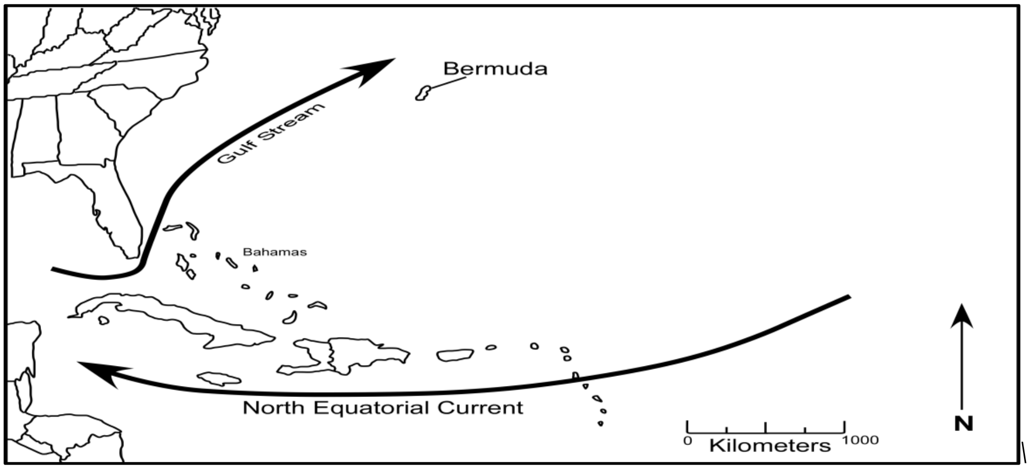

Figure 22. The geographic position of Bermuda. The Gulf Stream current warms air and sea temperatures to produce a subtropical climate.

The islands of Bermuda are the exposed portions of the 2000 meter-high Bermuda Seamount, one of three volcanic seamounts (Challenger and Argus) located on the Bermuda Rise (Logan, 1988; Wells, 1988; Wood and Jackson, 2005). The top of the Bermuda Seamount forms the Bermuda Platform, which has an area of roughly 775 km^2 (Wells, 1988). During the Pleistocene, much of the Bermuda Seamount was eroded to below sea level and corals began growing around the margins to form an “atoll-like” structure (Garrett and Scoffin, 1977).

Bermuda is generally considered to be an atoll, but more accurately, it is classified as a “pseudo-atoll” (Verrill, 1900). Bermuda has several characteristics that are not indicative of the true Pacific-style (Darwinian) atoll (Samantha DePutron and Kaitlin Baird, personal communication, 2011; Rosen, 1982). One significant difference is that Bermuda has considerably more island formation and relief than do true atolls (Logan, 1988; Samantha DePutron and Kaitlin Baird, personal communication, 2011). The islands are built by large, cross-bedded, aeolianite sand dunes that have been cemented into limestone rock (Smith, 1998). Most of the limestone is Pleistocene in age (1.7m.y.a.) and is the result of glacio-eustatic sea level change, which caused the Bermuda islands to repeatedly submerge and re-emerge (Vacher, 1973). Most of the aeolian dune deposition took place during interglacial periods when sea-level was high and the Bermuda Platform was flooded (Smith, 1998). During glacial sea-level lows, the aeolianite sand deposition ceased and vegetation and soil development began (Vacher, 1973). Interbedded limestones and paleosols can be found throughout the island.

Another distinctive feature of the Bermudian pseudo-atoll relates to the subsidence rate of Bermuda and its effect on reef development; Bermuda has four main reef types: 1) terrace reefs, 2) rim reefs, 3) boiler reefs, and 4) patch reefs (Figure 23). According to Rosen (1982), the island of Bermuda has had a very slow rate of subsidence since 45 million years ago (Moniz, 2010). In fact, Rosen also stated that subsidence is so minimal that Bermuda is used as a “gauge” for changes in sea level (Moniz, 2010). Bermuda is bound by a large, wide, terrace reef, which would drown if the island was subsiding like a true Pacific atoll. The terrace reefs probably formed at a period of low sea-level and then managed to maintain vertical growth during sea-level rise because of the lack of subsidence (Samantha DePutron, personal communication, 2011).

In contrast to true Pacific atolls, Bermuda also has a lack of algal ridge formation. An algal ridge is the highest point of the reef and is exposed at low tide (Garrett and others, 1971). Atolls are encircled by well-developed algal ridges, however, rather than having these algal ridges, Bermuda has rim reefs which lay at depths of 2-6m and are rarely, if ever, exposed (Logan, 1988). The closest features Bermuda has to true algal ridges are the red-algal boiler reefs on Bermuda’s south side (Figures 24) (Garrett and others, 1971; Samantha DePutron, personal communication, 2011).

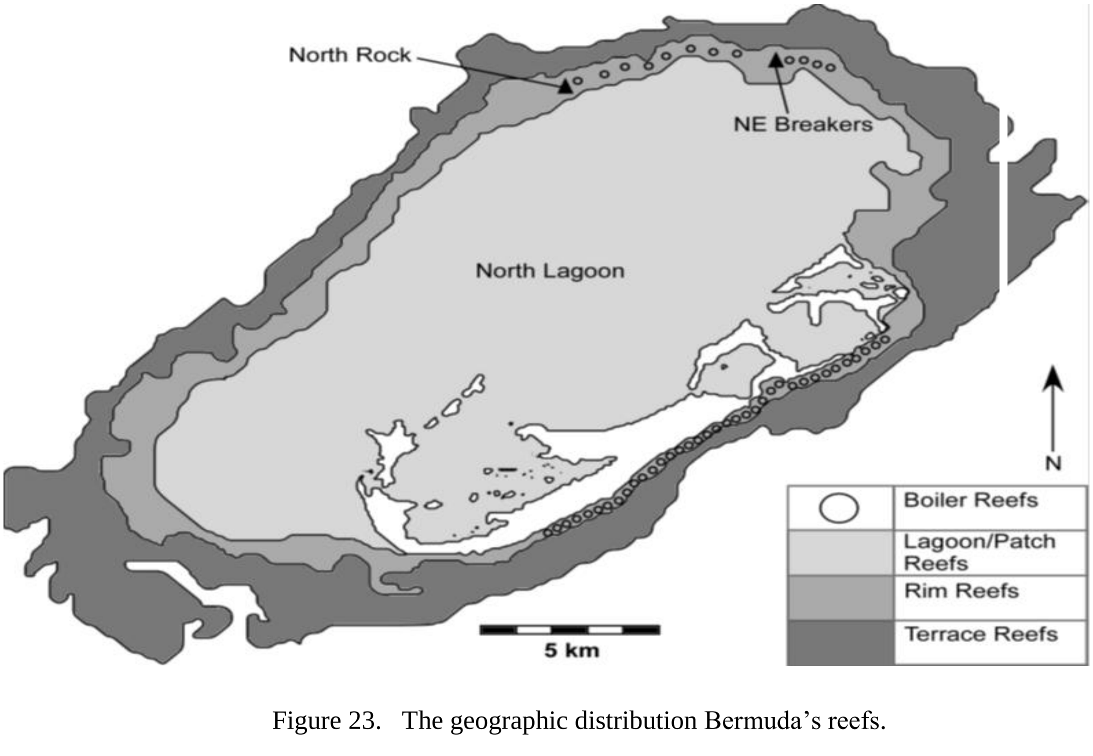

Figure 23. The geographic distribution Bermuda’s reefs.

Structure and Biodiversity

Bermuda has one of the northernmost coral reef ecosystems in the world, which limits its diversity of coral species. The coral species in Bermuda are transported from the Caribbean by the North Equatorial and Gulf Stream currents (Figure 22) (Garrett and others, 1971). Of the 72 known Caribbean hard coral species, only 26 are found in Bermuda (Logan, 1988; Wells, 1988; Wood and Jackson, 2005). The most notable absence from Bermuda's coral reef community is *Acropora* spp. which is a fast-growing, dominant reef-builder in Caribbean reefs (Garrett and others, 1971; Wells, 1988; Logan, 1988; Wood and Jackson, 2005; personal observation). The lack of *Acropora* spp. in Bermuda may actually influence the geological structure of Bermuda's reefs. The rapid growth of such a species would enhance the 'building up' of a true algal ridge. The actual algal ridge is often only colonized by non-coral species, but the area around it would be built up by the *Acropora* reef builders (Samantha DePutron, personal communication, 2011). Also, if Bermuda had fast-growing *Acropora* spp., the terrace would be closer to sea level and would be eroded similar to the rim reef. This would likely result in more lagoonal patch reefs and greater rim reef development, as opposed to having terrace reefs (Samantha DePutron, personal communication, 2011).

Bermuda's coral reefs may be low in diversity for two reasons: 1) Bermuda has low winter seawater temperatures (16-19°C), which most Caribbean corals cannot tolerate (Morris and others, 1977) and 2) the Caribbean coral species not present in Bermuda may have too short a free-swimming stage to survive transportation a long distance (approximately 1400km) (Glynn, 1973).

Terrace Reefs

The terrace reef structure differs on the north and south sides of the island. The northern terrace reefs have an average depth between 15-25m and can be up to 1-6km in width (Samantha DePutron, personal communication, 2010). The terrace reefs have a very distinctive spur-and-groove structure, with the grooves (sand channels) containing coarse, rippled sands (Figure 24A). The ridges have about 2-4m of relief and are oriented perpendicular to the platform margin (Wells, 1988). The southern terrace reefs have the same spur-and-groove structure, but they exhibit up to 10m of relief and have numerous pillars, arches, and overhangs (Logan, 1988).

The terrace reefs are Bermuda's most densely-populated reefs, with hard coral coverage of 40 to 60% (Wells, 1988; Logan, 1988; personal observation). The most common corals of the terrace reefs include *Diploria strigosa*, *Diploria labyrinthiformis*, *Montastrea franksii*, *Montastrea cavernosa*, *Porites astreoides*, *Gorgonia ventalina*, and *Millepora alcicornis* (Table B4); (Wells, 1988; Logan, 1988; personal observation). Smaller understory corals include *Dichocoenia stokesii*, *Stephanocoenia michelinii*, *Favia fragum*, and *Siderastrea radians* (Logan, 1988; personal observation). These reefs also have the lowest amount of *Halimeda* green algae and the highest concentrations of the pink, encrusting *Homotrema rubrum* foraminifera (Tables B5, B6)

Rim Reefs

The rim reefs (Figures 23, 24B) are located on the platform margin and form a near-complete annular tract around Bermuda. The rim reefs are between 0.5 to 1 km wide and are very shallow, ranging from just 2 to 6 meters deep (Garrett, 1971; Wells, 1988; Logan, 1988). The reefs are dissected by many coarse-grained sand channels that average about 10m in depth (Wells, 1988; Logan, 1988). The sand channels become progressively larger moving lagoonward and the rim reefs become less connected and more isolated (Wells, 1988).

Hard coral coverage in the rim reefs is considerably lower because of the increased wave disturbance. Hard coral coverage estimates range from 22-35% and it is dominated by the *Diploria* spp., *Montastrea spp.*, *Porites astreoides*, and *Millepora alcicornis* assemblage (Table B3); (Wells, 1988; Logan, 1988; personal observation). Common understory corals include *Agaricia fragilis*, *Madracis decactis*, *Stephanocoenia michelinii*, *Dichocoenia stokesii*, *Isophyllia sinuosa*, *Meandrina meandrites*, and *Siderastrea radians* (Wells, 1988; Logan, 1988; personal observation). The rim reefs have a healthy population of coralline red algae and of *Homotrema rubrum* foraminifera, and *Halimeda* algae is noticeably scarce (Tables B5, B6)

"Boiler" Reefs

High energy reefs called "boilers", named for the boiling appearance caused by the waves breaking over the reefs, form near the platform edge and grow up from depths of 8 to 10m to be exposed at low tide (Figures 23, 24C); (Shinn, 1971; Dean and Eggleston, 1975; Logan, 1988; Wells, 1988, personal observation). Boiler reefs may also be known as: algal cup reefs (Ginsburg, Shinn, and Schroeder, 1967), algal/vermetid reefs (Logan, 1988), micro-atolls (Boyd, Kornicker, and Rezak, 1963), and mini-atolls (Scheer, 1972; Scoffin and Stoddart, 1978). These reefs are circular to ellipsoidal in shape and can reach widths of up to roughly 65m (Shinn, 1971). They are part of the rim reef system and can be found dominantly on the south side of the island, though there are a few scattered boilers on the north side between North Rock and the Northeast Breakers (Figure 22); (Shinn, 1971; Logan, 1988; personal observation).

The boilers mainly consist of the coralline red algae *Lithothamnion* and *Millepora alcicornis* corals, together which form stromatoporoid-like sheets and encrustations (Shinn, 1971; Dean and Eggleston, 1975). Also very abundant are the encrusting foraminifera *Homotrema rubrum*, and the vermetid worms *Dendropoma corrodens* (Shinn, 1971; Logan. 1988). Hard corals are rare on the boiler reefs, but small specimens of *Diploria* spp., *Porites astreoides,* and *Siderastrea* spp., may be found around the rim or in the mini-lagoon (Logan, 1988).

Patch Reefs

Over 1,500 patch reefs (Figures 23, 24D) are located in Bermuda's protected North Lagoon and they occur in a variety of shapes and sizes: 1) knob reefs, 2) pinnacle reefs, 3) linear-cellular reefs, and 4) mini-atolls or circular lagoonal patch reefs (Garrett and others, 1971; Logan, 1988). Garrett and others (1971), note that there is a correlation between water depth and patch-reef size. In the deeper parts of the North Lagoon (15 to 20m) the patch reefs are larger and have a diameter of 75-400m; in the shallower areas, the reefs are smaller and are more numerous.

Knob reefs are described as juvenile reefs that have dimensions between 1-5m in width and up to 3m in height (Logan, 1988). They will grow vertically and laterally as new coral recruits settle. Pinnacle reefs form from the vertical growth of knob reefs during periods of rapid sea-level rise (Logan, 1988). They can be 10-150m wide and 6-20m in height, with steep sides. The linear patch reefs grow laterally in shallow water that is only several meters deep (Logan, 1988). Anastomosing linear reefs may occasionally become linked and form an enclosed lagoon (Garrett and others, 1971; Logan, 1988). These interconnected reefs are known as “cellular reefs” and are basically the shallow-water equivalent of micro-atolls (Garrett and others, 1971; Logan, 1988). The mini-atoll patch reefs (different from the mini-atoll term used for boiler reefs because there is no aerial exposure), are circular lagoonal patch reefs that have a marginal ridge with abundant coral growth (Garrett and other, 1971; Logan, 1988). On the inside of the mini-atoll ridge however, reef corals are sparse or absent and sandy sediment dominates; Garrett and others (1971) liken this to a small lagoon within a lagoon.

The hard coral coverage of the patch reefs is low at about 15-20%, but the diversity of coral and invertebrate species is higher than that of the platform margin reefs (Logan, 1988; Wells, 1988). The two most abundant corals are *Montastrea franksii* and *Porites astreoides* which form the framework of the patch reefs (Table B2) (Garrett and other, 1971; Logan, 1988). Other common corals include *Diploria* spp., *Millepora alcicornis*, *Oculina diffusa*, *Madracis decactis*, and *Agaricia fragilis* (Table B2) (Logan, 1988). It is also worth noting that *Porites porites* (growth habit similar to Cretaceous *Eoradiolites* rudists) is found in higher abundance in the lagoonal patch reefs than anywhere else on the Bermuda platform (Logan, 1988). The patch reefs contain the most *Halimeda* green algae, sponge spicules, and miliolid forams of the various reefs types (Tables B5, B6).

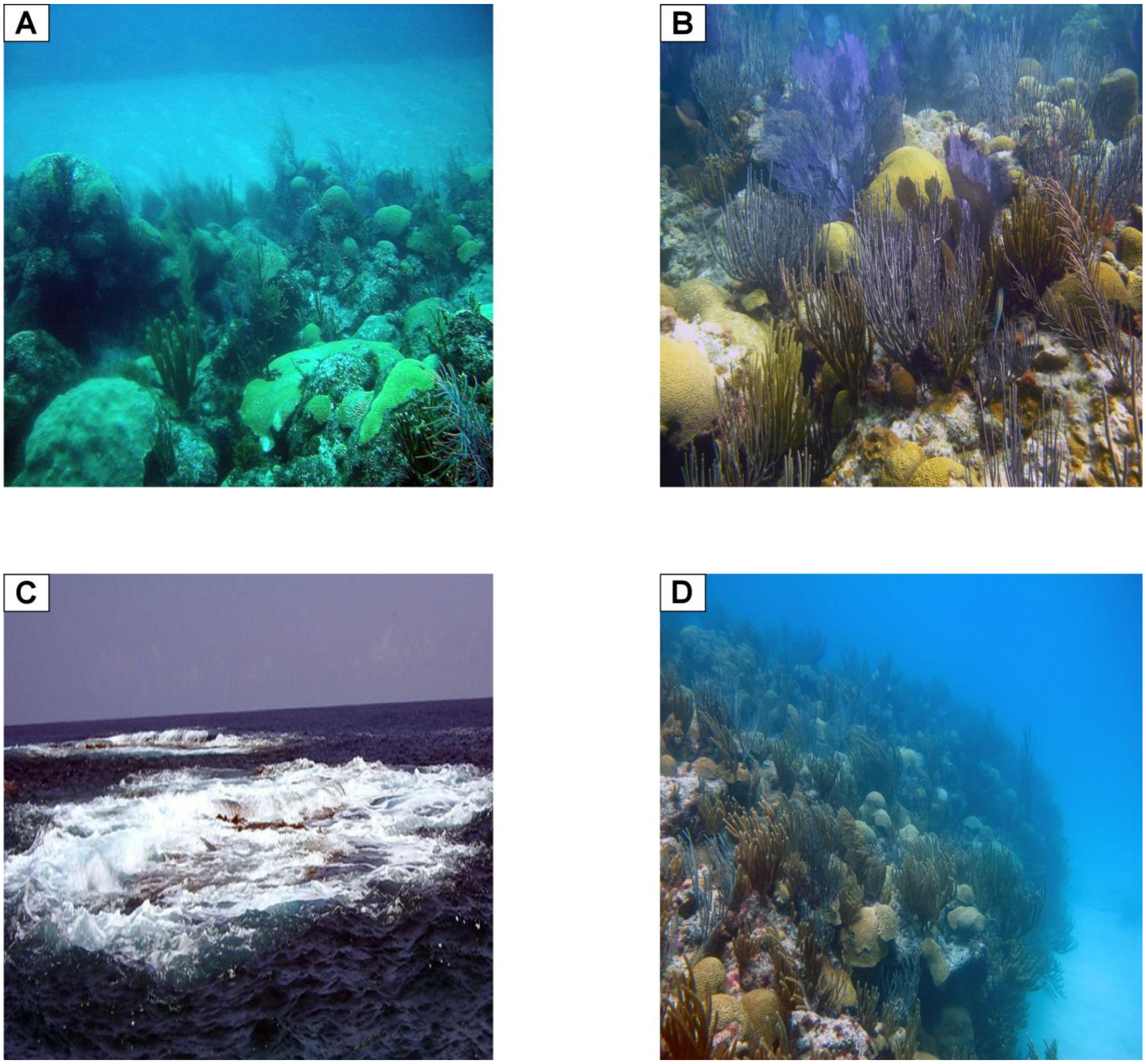

Figure 24. The four main reef types of Bermuda: A) the terrace reef with the distinctive "ridge and valley" structure (the coral-covered ridge is in the foreground), B) the annular rim reef is dominated by the *Diploria* spp., *Montastrea* spp., *Porites astreoides*, and *Millepora alcicornis* assemblage, C) a boiler/algal cup reef constructed by *Lithothamnion* algae, *Homotrema rubrum* foraminifera, and *vermetid* worms as seen from the surface, D) a lagoonal patch reef with abundant *Montastrea* spp., *Porites astreoides*, and *Diploria* spp.

CHAPTER FIVE

Cretaceous Rudists

Rudist Distribution, Evolution and Diversification

Rudists were a group of heterodont bivalves that first appeared during the Late Jurassic (mid-Oxfordian) Period and became so abundant by the Early Cretaceous that they were the dominant reef-builders until their extinction at the K/T boundary (Hut and others, 1987; Kauffman, 1988; Kauffman and Johnson, 1988; Ross and Skelton, 1993). Rudist-dominated reefs were generally limited to the tropics and subtropics although extremely rare clusters (small bioherms) have been known to exist in more temperate areas (Kauffman and Johnson, 1988). Rudists have been found in North and South America (Caribbean), Europe (Mediterranean), the Middle East, North Africa, and Southeast Asia.

The expansion of rudists began in the Mediterranean during the Berriasian Age and their larvae were likely carried by ocean currents to the proto-Gulf of Mexico. This initiated a second expansion event in the Caribbean during the Albian-Cenomanian (Kauffman, 1973). In Texas, Nelson (1973) observed that the Caribbean Albian rudists migrated northward via two main pathways: 1) northwestward around the flanks of the Llano islands, and 2) northward over the Sabine Uplift as far as southwestern Arkansas and southeastern Oklahoma.

Rudists were sessile, epifaunal suspension feeders (Skelton, 1978; Ross and Skelton, 1993) that commonly possessed bi-mineralic shells composed of aragonite and calcite (Al-Aasm and Veizer, 1986). They had a calcitic outer wall and an aragonitic inner wall (Skelton, 1976). The ratio of aragonite to calcite in rudist shells varied through time as outlined by Kauffman and Johnson (1988). During the Barremian-Aptian interval, rudists with thick, dominantly calcitic shells, which included early monopleurids and toucasids, were abundant. In the Albian (Edwards age)-Turonian interval, the more aragonitic rudists such as Caprinidae, Caprotinidae and early Hippuritidae increased; although during the Albian-Cenomanian calcitic radiolitids also emerged. In the Coniacian-Santonian interval, aragonite depletion allowed for calcitic radiolitid dominance, and in the final Campanian to Maastrichtian interval, the more aragonitic Hippuritidae rudists diversified and the caprinid population was partially re-established.

A study of Mg/Ca ratios and strontium concentrations in seawater by Steuber (2002) yielded similar results. The major difference between the findings of Steuber and Kauffman was that calcitic rudists dominated from the Turonian to the Maastrichtian rather than aragonitic rudists.

Rudists are believed to have been related to the Megalodontidae bivalves from the Silurian-Lower Jurassic, from whom they retained important evolutionary traits (Kauffman and Sohl, 1979; Kauffman and Johnson, 1988). Rudists had 1) very large, thick shells, which indicated they had a very high calcification rate compared to other bivalves, 2) they had an extended mantle, which increased exposure to light and possibly signified that some rudists had a relationship with symbiotic zooxanthellae, 3) they had epifaunal to semi-infaunal modes of life, and kept their feeding and respiratory margins above the sediment-water interface, and 4) they formed a means with which to attach to the substrate (Kauffman and Sohl, 1979; Kauffman and Johnson, 1988).

Rudists have been subdivided into three functional growth forms: elevators, clingers, and recumbents (Figure 25); (Skelton, 1978, 1979a; Skelton and Gili, 1991; Ross and Skelton, 1993; Gili and others, 1995a; Hernandez, 2011). Hernandez (2011) replaced the term "clingers" with "encrusters." Elevator rudists were elongate in shape and oriented themselves vertically by attaching to a hard substrate via a small attachment surface at the tip of their shell (Figure 25A). This growth habit allowed for dense clustering and the formation of "organ-pipe" colonies (Figure 25A); (Ross and Skelton, 1993). Elevators were better adapted to muddier, low-energy environments than other rudists because their vertical orientation would allow them to keep their feeding and respiratory apparatuses above the accumulating sediment. Elevators were mainly comprised of radiolitid, and hippuritid rudists (Ross and Skelton, 1993), though caprinids and monopleurids also had the ability to do so (Gili and others, 1995a).

Clingers (or encrusters) rested directly on, or partially buried in the substrate and relied either on frictional contact or on attachment to keep them in place (Figure 25B) (Skelton and Gili, 1991; Ross and Skelton, 1993; Gili and others, 1995a). A stable substrate or hardground was required so that the sediment upon which the rudist rested/attached would not be winnowed away or deflated by traction currents. Areas with high sediment accumulation would have not been conducive to clinger habitation because the motile sediment would increase the potential for mass-wasting or suffocation. The clinger group includes *Toucasia* and some radiolitids (Ross and Skelton, 1993; Gili and others, 1995a).

Recumbent rudists had large, arcuate or stellate shaped-shells that may (Kauffman and Johnson, 1988) or may not (Skelton and Gili, 1991; Ross and Skelton, 1993) have attached to mobile carbonate sand and other shells (ex. *Chondrodonta*) in high-energy, low-sedimentation environments (Figure 25C). The large size and the unique shape of the shells made the rudists less susceptible to being overturned by waves while living on the softer, more dynamic substrates (Hernandez, 2011). If the recumbent rudists lived unattached to the substrate, they were extremely vulnerable to the effects of storms (Skelton and Gili, 1991; Ross and Skelton, 1993). Recumbents were made up of dominantly caprinid and some radiolitid rudists.

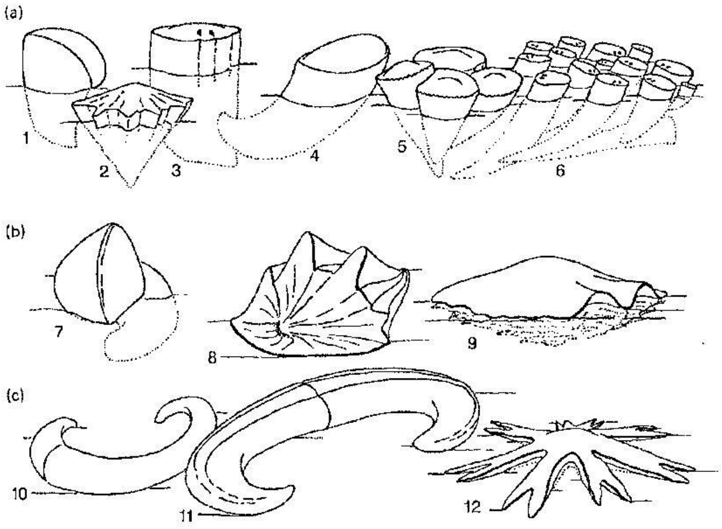

Figure 25. The three growth forms of rudist bivalves: A) elevator rudists can be solitary or colonial and include (1) caprotinids, (2,5) radiolitids, (3,6) hippuritids, and multigeniculate forms (4). B) clinger rudists could rest on the substrate (7,8) laterally or (9) radially and consist of (7) toucasids (requieniids) and (8,9) radiolitids. C) Recumbent rudists have (10,11) arcuate or (12) stellate shapes and include caprinids (10,11) and (12) radiolitids (from Ross and Skelton, 1993).

The abundance and diversity of rudists fluctuated throughout the Cretaceous, with four diversification and three extinction events (Figure 26); (Masse and Philip, 1986; Ross and Skelton, 1993; Philip, 1998; Steuber and Löser, 2000; Höfling and Scott, 2003). This closely parallels the calcite-aragonite trends seen by Kauffman and Johnson (1988).

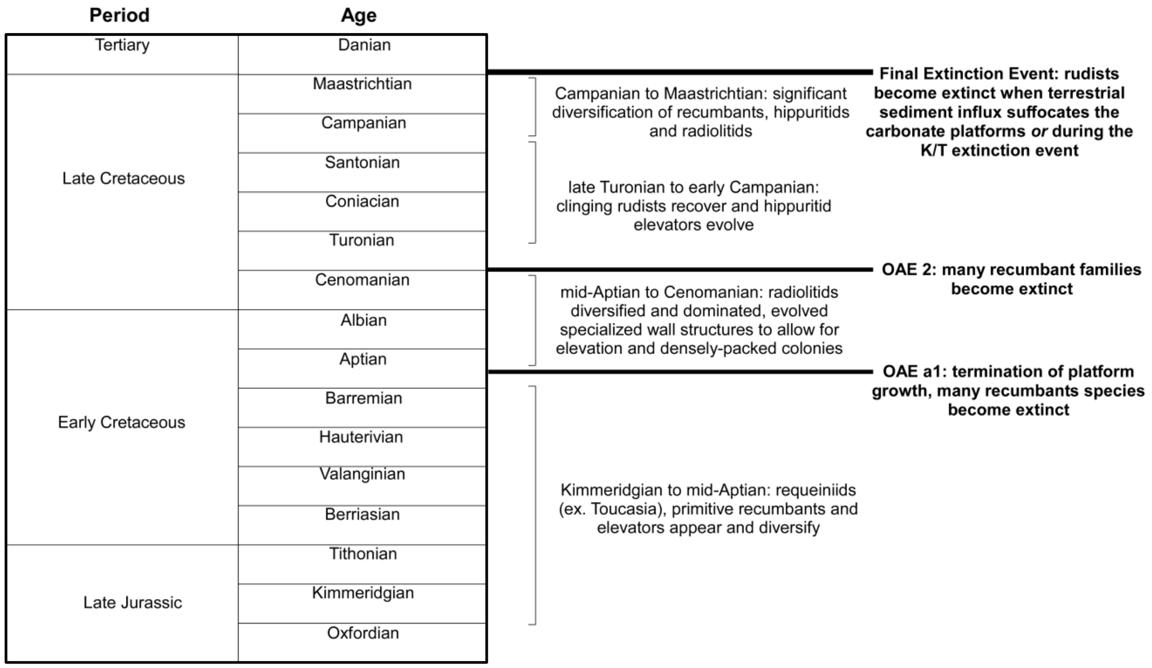

Figure 26. Rudist diversification and extinction events.

Rudists as Reef Builders

Whether or not rudist bivalves were true reef-builders is a point of contention among the paleoecological community. One definition of a reef is an "[organic], rigid, mound-like structure having bathymetric relief and having a framework of densely-intergrown, mainly calcareous colonial organisms and marine cement" (Fagerstrom, 1987). The possibility that rudists did not form "true reefs" mainly stems from the argument for attachment and whether or not they developed a true framework. Many believe most rudists lived at least part of their adult lives attached to the substrate, though others disagree with this assertion (Ross and Skelton, 1993; Gili and others 1995a). It has been proposed that rudists were substrate-dependent organisms and that only juvenile rudists needed to attach. While some rudist taxa retained this ability, others lost this attachment mechanism as adults (Gili and others, 1995a) or grew too large to remain attached (Scott, 1981). Recumbents, such as caprinids, are suggested to be among those who have lost or grown out of this mechanism. Some radiolitid rudists, on the other hand, did attach, but because their attachment surface was so small they were easily overturned. Because caprinid and radiolitid rudists were the major “reef-builders,” the lack of, or weakness of attachment as adults meant that they actually did not form a rigid framework. Instead, these mounds were easily destroyed by storms (Scott, 1988; Gili and others, 1995a). Proponents of this idea suggest that the recent and Pleistocene *Crassostrea* oyster beds of Littlewood and Donovan (1988) and Demarq and Demarq (1992) are more suitable analogs than scleractinian coral reefs.

There is no universally accepted definition for a reef. Kiessling and others (1999) subdivided reefs into four categories in an attempt establish one based on 1) biological control by sessile benthic organisms, 2) laterally confined structures, and 3) inferred rigidity of the structure. A “true reef,” is defined as having a rigid framework of skeletal organisms with depositional relief, a “reef mound,” is a structure with depositional relief that has skeletal organisms as abundant as matrix and cement, and does not have a rigid framework, a “mud mound” is a mud-dominated structure with depositional relief, but has only minor skeletal components, and a “biostrome” is a structure with no depositional relief that has abundant skeletal organisms; biostromes may or may not have a rigid framework.

Scott (1988) claimed that on the shelf margins, ramps, and atolls of the Early and Mid-Cretaceous, rudists and corals formed “true reefs,” and that within carbonate shelves, and on high-energy shelf margins, rudist-dominated associations formed reef mounds and biostromes. If this were the case, then the Edwards Limestone of Central

Texas formed on a large Cretaceous carbonate shelf and the Central Texas circular and elongate bioherms might well be “reef mounds”.

Based on personal observations in the field and the findings of numerous other authors at localities within the study area, the rudist build-ups were capable of breaking wave energy and their densely packed- colonies formed rigid growth frameworks. Quite commonly, the rudist colonies were so densely-packed that the rudists were stacked on top of each other. Another relevant observation is that rudist shells were deformed by the close proximity of neighboring rudists during growth. The rudists formed sturdy, elongate reefs which dissipated wave action to create a calm, low-energy environment for the circular bioherms.

The argument that rudist accumulations should not be considered reefs because they were often overturned or destroyed by storm waves is weak. In modern-day coral reefs, corals are broken and overturned as well, but often the corals manage to re-orient themselves. The resistance to being overturned or broken should not be used as a criterion to identify a rigid framework. Nevertheless, whether or not the rudist accumulations of Central Texas were “true reefs” or “reef mounds” it appears to be strictly a matter of semantics. For the scope of this project, this controversy does not need to be resolved. Both “true reefs” and “reef mounds” performed the same wave-baffling function.

Rudists and Zooxanthellae

Living zooxanthellae symbionts of the genus *Symbiodinium* are found in clear, tropical waters with low nutrient levels and low plankton density (Muscatine and Porter, 1977; Yellowlees and others, 2008). Evidence supporting a rudist relationship with these symbionts includes: 1) the large size and thickness of rudist shells, 2) an epi-benthic mode of life, and 3) the development of structures that allowed for the expansion of mantle tissue (where the zooxanthellae would have resided) increasing its exposure to light (Kauffman and Sohl, 1979). It is likely that rudists, like modern scleractinian corals, had hermatypic and non-hermatypic forms. Hermatypic rudists would have had zooxanthellae symbionts.

Primitive rudists such as early monopleurids and toucasids had very thick shells, but they were small in size and slow-growing. Perhaps not coincidentally, these rudists also lacked the structures necessary for the extension of the mantle, which indicates zooxanthellae were not present in these primitive forms (Kauffman and Johnson, 1988). By contrast, other rudists such as caprinids, caprotinids, and radiolitids, grew much larger, had an expanded mantle, and possessed thinner, smaller free-valves to allow for more light exposure and penetration (Kauffman and Johnson, 1988).

The symbiotic relationship with zooxanthellae would have had similar effects on rudists, as it does today on modern corals. The presence of zooxanthellae would significantly increase calcification and growth rates, and their photosynthate product would provide an alternate energy source for the rudists in low-nutrient seas (Kauffman and Johnson, 1988). Indirectly, the expansion of the mantle to accommodate the zooxanthellae could also allow the mantle to be used for physical and chemical sensing (Kauffman and Johnson, 1988).

Exactly how zooxanthellae increased calcification rates is still unresolved. There are three mechanisms proposed that potentially explain how the presence of zooxanthellae influence coral calcification: 1) the removal of carbon dioxide in photosynthesis allows for the precipitation of calcium carbonate, 2) the consumption of phosphates by the zooxanthellae, which acts as a growth-inhibiting “crystal poison,” and 3) photosynthetic nutrients provided by the zooxanthellae may somehow increase the calcification rate (Pearse and Muscatine, 1971).

The larger mantle in rudists not only could have increased their ability to gather food, but it could also have been used as a chemical receptor or fouler to ward off predation, encrusters, and shell borers, offering a significant competitive advantage (Skelton, 1979b; Kauffman and Johnson, 1988). Kauffman and Sohl (1974) studied numerous specimens of rudist bivalves and found no signs of predation. This ability to deter predators could account for the low biodiversity on Cretaceous reefs. Employing the Intermediate Disturbance Hypothesis (Grimes, 1973), low predation would lead to the dissemination of the dominant, more competitive organisms, in this case rudists, because there would be few population-limiting controls.

Symbiotic zooxanthellae exist in various clades (A-H) with each clade specializing to life under certain conditions. In modern corals, clades A (also found in *Tridacnid* clams) and B are high-light specialists, clade C thrives in low-light and is also present in tridacnids (Rowan and Knolton, 1995; Baker, 2003), and clade D is comprised of stress-tolerant (particularly thermal stress) zooxanthellae (Riddle, 2006; Rowan, 2008). Clade E does not exist in corals and most species have been reclassified (Riddle, 2006). Clade F zooxanthellae are usually found in foraminifera and are light-sensitive, and clade G is found in some soft and hard corals, sponges, and sea anemones, though its function is not yet completely understood (Riddle, 2006). Clade H is a rare zooxanthellae clade and more research is necessary to resolve its functionality and affiliations (Riddle, 2006).

Given that the Cretaceous seas were warm, and that rudists survived in shallow, occasionally hypersaline waters, if rudists possessed *Symbiodinium*, they probably did so in some ratio of clades A, C, and D. Rudists in clear, warm waters likely were affiliated with clades A and D. Rudists in more turbid waters or in darker, protective pockets may have contained clade C symbionts. Perhaps rudists, as has been documented in modern-day corals and in the large bivalve *Tridacna gigas* (Belda-Baillie and others, 1999), possessed the ability to "shuffle" or "switch" clades to withstand changes in water chemistry and temperature. "Shuffling" refers to the host modifying the ratio of the zooxanthellae clades; "switching" is a near complete replacement of the clade (Baker, 2003).

In muddy, high-turbidity, possibly nutrient-rich environments; the rudists would rely exclusively on their ability to filter-feed. Hippuritid rudists, in particular, had a well-developed "pore and canal" system very efficient for filter feeding (Skelton, 1976; Gili and others, 1995a).

Under more ideal environmental settings, many rudists likely had a symbiotic relationship with zooxanthellae. Vogel (1975) compared the mantle of radiolitid rudists with that of the modern zooxanthellae-hosting *Corculum* bivalves and found that both organisms could support zooxanthellae. Steuber (2000) determined that the calcification rates of Cretaceous rudists matched those of the extant *Tridacna gigas* giant clams; both are/were characterized by exceptionally high calcification rates. Within the study area, *Eoradiolites* rudists have definitively-flared mantles where the zooxanthellae would have resided. The flaring allows for increased light exposure. Also, it cannot be coincidental that rudists are only found within the photic zone in shallow waters. Since rudists were primarily filter-feeders, they conceivably should have occupied marginally deeper waters as well.

If rudists were symbiotic with zooxanthellae, then it is reasonable to assume they would be zoned in a fashion similar to modern corals. Water depth, light penetration, wave energy, and salinity would have played crucial roles in establishing rudistid biozones. For a thorough description of zooxanthellae-invertebrate interactions, see Yellowlees and others (2008) and Baker (2003).

The Rudist Succession of Scleractinian Corals

The definitive explanation for the rudist succession of scleractinian corals during the Cretaceous is not known. The three mostly widely proposed ideas are 1) rudists competitively displaced corals through convergent evolution with successful Phanerozoic reef-building organisms, (Kauffman, 1977, 1986; Kauffman and Johnson, 1988), that 2) rudists were more tolerant of variations in water chemistry caused by cyclic changes in oceanic productivity (Scott, 1988; Kauffman and Johnson, 1988; Scott, 1990, 1995; Gili and others, 1995b; Höfling and Scott, 2002), and that 3) a climatic change in the tropics caused the formation of a proposed “Supertethys zone” (Kaufmann and Johnson, 1988 . It might have been a combination of these factors that allowed for the rudist takeover of Cretaceous reefs (Kauffman and Johnson, 1988).

The convergent evolution hypothesis involves the development of new morphological traits ideal for reef-building. The greatest morphological change occurred in the Aptian-Albian interval when rudists became the primary reef builders at the expense of scleractinian corals and algae (Kauffman and Johnson, 1988). The appearance of new traits in rudists and the drastic reduction of corals during this time suggested that the decline was at least partially due to competitive displacement (Kauffman and Johnson, 1988).

The evolved traits, as detailed by Kauffman and Johnson (1988) are: 1) an increase in the size of the rudists' attachment surface to better resist wave and current energy, 2) the uncoiling of the attached valve to a more conical or tubular shape to allow for dense, upright clustering, 3) the uncoiling of the free valve to lower the center of gravity and to expose the mantle to more light necessary for zooxanthellae symbionts (larger mantle may have also acted as a chemical-producing deterrent), 4) the development of stronger shell ornamentation to increase the shell strength and stability for clingers and recumbents, 5) the shells became thicker, stronger, and dominantly aragonitic (not for monopleurids or radiolitids), 6) an increase in rudist growth rates due to the effects zooxanthellae symbiosis (up to 5cm/yr, faster than many corals) and 7) the appearance of pseudo-colonial growth which helped create rigid wave-resistant structures.

There are a few timing issues with rudist evolution when correlated with the disappearance of corals from shallow water (Kauffman and Johnson, 1988). Following the rudist evolutionary timescale, rudists in shallow, high-energy reefs in the tropics had displaced corals much earlier (Barremian-Aptian) than those in the marginal tropical areas (Late Albian-Cenomanian) (Kauffman and Johnson, 1988). Also, rudists were dominant in the Aptian- Albian before they had fully evolved traits to augment their success in spatial competition. The fact that better-adapted corals were relegated to deeper waters, while only scattered clusters of rudists took over the shallows, does not make much sense; this likely means that environmental controls were also involved (Kauffman and Johnson, 1988).

There were many changes in oceanic chemistry and climate in the 30 Ma between the Hauterivian and the end of the Albian (Scott, 1988). The transgression of the Cretaceous seas flooded nearly 20% of the continental landmass (Barron and others, 1980) and sea level was 100-200m higher than present day (Höfling and Scott, 2002). This created very large, broad carbonate shelves and intrashelf basins. Initially, this transgression would have resulted in a period of high productivity because of the re-sedimentation and erosion of the newly-flooded landscape (Scott, 1988; Scott, 1995). The high productivity would have resulted in algal blooms inhibiting rudist and coral reef growth by blocking out sunlight. Over time, the prolonged submersion of land, coupled with the retention of soil nutrients by the expanding angiosperm population (Tappan, 1986), caused the net continental nutrient runoff to decrease. This created a period characterized by low-productivity and high oceanic CO_2 levels. Intense global tectonics and seafloor spreading during the Cretaceous also played a major part raising atmospheric CO_2 (Berner and others, 1983). Under this scenario, the coral and rudists reefs thrived (Scott, 1988).

As the rest of the Cretaceous ensued, cyclic sea-level fluctuations caused periods of high and low productivity; with the lowest productivity occurring in the Albian when the Mg/Ca ratio was at its most depleted level in the Phanerozoic (Hardie, 1996; Steuber, 2002). This is supposedly when rudists began overtaking corals (Scott, 1988). These productivity cycles may have stressed the deeper platy corals and left the more turbid, and hypersaline-tolerant rudists as the major reef builders in the shallow water by default

(Scott, 1988; Scott and others, 1990; Scott, 1995). The cycles in productivity may have also caused the redoxicline (oxygen-minimum zone) to fluctuate in depth, likewise stressing the relatively deeper-living corals and leaving the shallow rudists unharmed (Thierstein, 1989; Scott, 1990; Scott, 1995). Of the three proposed hypotheses, this seems to be the more widely- accepted view among the scientific community.

Kauffman (1973) and Kauffman and Johnson (1988) proposed that a new tropical climatic zone, termed “Supertethys” formed during the Cretaceous under eustatic sea-level rise and global warming. The long-term highstand, the drowning of land, warmer seas, and the lack of ice caps during the Cretaceous could have caused the tropical zone to expand by a factor of 25% or more (Kauffman and Johnson, 1988). These conditions, in conjunction with the flux of CO_2 into the atmosphere through strong global tectonics and volcanism, may have created this warmer, high-salinity “Supertethys” zone. The corals within this zone would have been thermally and chemically stressed, and over millions of years corals may have eventually retreated to the deeper, cooler waters (Kauffman and Johnson, 1988).

CHAPTER SIX

Comparison of the Edwards and Bermudian Patch Reefs

Temperature and Biodiversity

There are many similarities between the Edwards Limestone bioherms of Central Texas and the patch reefs of Bermuda (Table 1). One substantial difference, however, is the disparity between seawater temperatures. The high-latitude reefs of Bermuda are commonly referred to as “cold-water” reefs. Winter sea-water temperatures on the outer patch reefs (study area) can fall to as low as 18°C. For much of the year however, they are a warm 25°C to 28°C (Table 1) (Forbes, 2011), even occasionally exceeding 30°C (Smith, 1998). These warmer temperatures are actually comparable to those of the “warm-water” reefs in the Caribbean.

By contrast, the mid-Albian age of the Edwards Limestone is regarded as being one of the warmest periods of the Cretaceous. Using an organic geochemical proxy, average annual seawater temperatures were calculated to be between 32-34°C, although temperatures may have been even higher (Table 1) (Wilson and Norris, 2001; Forster, 2007). To determine seasonal fluctuations, Steuber and others (2005) used intra-shell variations of oxygen and carbon isotopes from rudist bivalves to find relatively low seasonal differences of ±12°C between the tropical and polar waters; thus implying warm waters year-round.

The average sea temperatures of the Albian would have exceeded the thermal tolerances of most corals, as most corals begin to bleach in temperatures greater than

30°C (Glynn, 1973). The prolonged thermal stress to corals, in all likelihood, is at least partially responsible for their demise and relegation to deeper waters. In the Edwards Limestone this is illustrated by the gradual increase in coral abundance and diversity to the southeast towards the deeper waters near the Stuart City shelf margin. At the margin, corals, particularly *Microsolena* and *Actinastrea*, were integral in the formation of the marginal reef and the seaward bioherms (Archauer and Johnson, 1969; Scott, 1990a). In the Central Texas bioherms, *Cladophyllia* is the only coral found. The lack of other corals species found in association with *Cladophyllia* implies that it was more temperature-resistant than the corals to the south.

Versus other modern reefs, Bermudian reefs have a very low biodiversity. Likewise, the Cretaceous rudist reefs had low biodiversity, but they had an even lower biodiversity than coral-algal reefs (Kauffman and Johnson, 1988). Within the patch reefs of Central Texas only 18 rudist species have been identified (Davis, 1976); this is in relation to the 792 total species of rudists found in the Middle East and Mediterranean (Steuber, 1999) and the 214 species found in the Caribbean (Kauffman and Johnson, 1990). Alongside rudists, a few species of echinoderms, bivalves, gastropods, bryozoans, foraminifera, and algae can be found (Tables A1, A2, A3; Figures A2, A3, A4). The low biodiversity of the Edwards bioherms suggests that rudists could withstand conditions not conducive to most organisms.

Periodic restriction caused by cyclic sea-level fluctuations, sluggish currents, or the formation of protective elongate reefs may have also isolated the Edwards reef communities from other settling biota. The restriction and isolation hypotheses are supported by the endemic evolution of the European-derived *Oxytropidoceras* ammonites

(Young, 1972). Once inside the expansive backreef lagoon, *Oxytropidoceras* evolved into several species that are not found outside of Texas or northern Mexico.

Bermuda's low diversity is due to a combination of low winter temperatures and distance from the reefs of the Caribbean. Much of the biota in Bermuda's reefs is derived from the Caribbean via the Gulf Stream. Of the 72 known Caribbean hard coral species, only 26 are found in Bermuda (Logan, 1988; Wells, 1988; Wood and Jackson, 2005). Though the Bermudian reefs are obviously more diverse than the Edwards bioherms, their relatively low biodiversity makes them a more accurate comparison than the more diverse communities of other modern reefs.

The absence of *Acropora* corals in the Edwards and Bermudian reefs is significant. *Acropora*, a very fast-growing coral, is one of the dominant reef-builders in the Caribbean, which is where some suggest a potential modern analog for the Edwards Limestone bioherms exists. Its absence in Bermuda has a profound impact on the geological structure of the reefs because the reefs are actually growing upwards at a slower rate than most Caribbean reefs (Samantha DePutron, personal communication, 2011). The reefs of the Edwards Limestone did not contain *Acropora*, (or any fast-growing corals) because it did not evolve until the Paleocene. Acropora corals on grow on average between 5-20cm/yr (Toda and others, 2007), while rudists by comparison are estimated to have grown between 1-5 cm/yr (Steuber, 2000). It is reasonable to assume that since the Edwards patch reefs were constructed by rudist mollusks, that the vertical growth rate would have been slower than that of the coral-algal Caribbean reefs and instead closer to that of the reefs of Bermuda.

Reef Structure

Bermuda was chosen for the modern analog study because its reef structure and development appear to be very similar to that of the Edwards Limestone bioherms. Both reef systems formed on a high-energy, low-relief, broad, shallow carbonate platform (Table 1). The Edwards Limestone patch reefs were protected by the Stuart City barrier reefs. Likewise, the reefs of Bermuda are surrounded by a shallow, annular rim reef system that encompasses the entire Bermuda platform and protects the reefs from the energy of the Sargasso Sea (Table 1).

The existence of these protective barriers is paramount to the development of the backreef lagoonal bioherms. Both the Edwards and Bermuda reefs exhibit similar growth tendencies. Lagoonward of the rim reefs are moderate-energy, elongate patch reefs, which protect low-energy, circular to irregularly-circular bioherms (Figure 27). This is analogous to the relationship between the elongate and circular bioherms at Childress Creek as observed by Roberson (1972) and Duffin (1983).

The size of the Edwards bioherms was likely a function of water depth. Larger bioherms probably existed in deeper waters because their growth would not be limited by wave-base early in their development. The largest definitive measurement obtained within the study area was a diameter of 65m at a concentric circular bioherm in Childress Creek. The elongate reefs at Mosheim may be larger, but their dimensions are difficult to determine given the available outcrops. The diameters of Central Texas Edwards bioherms observed by Roberson (1972) ranged from 10-100m in plan view.

The estimated water depth of the Central Texas Platform during Edwards Limestone deposition is less than 6-7m (Table 1; Young, 1959; Bebout and Loucks, 1974).

By comparison the lagoonal patch reefs of Bermuda exist at depths from 8 to 18m (Table 1). The deeper lagoonal waters at Bermuda allow the patch reefs to grow to sizes of 75 to 400m (Garrett, 1971), although the patch reefs are typically less than 200m in diameter (Table 1) (Jordan, 1973). The shallow waters of the Central Texas Platform likely did not permit growth to this size. Instead, the shallow waters are more conducive to expansive biostromal or low-relief biohermal growth. Because of the deeper Bermudian waters, the patch reefs exhibit more relief than the shallow water-limited bioherms of the Edwards Limestone.

Sediment

The grain size ranges of the Edwards Limestone bioherms and the reefs of Bermuda are very comparable. The sediment samples obtained from Bermuda are poorly-sorted and have grain sizes ranging from fine carbonate sand to gravel (Table 1; Table B1). The Edwards Limestone bioherms similarly have grain sizes ranging from carbonate mud to gravel, but the Edwards reefs have a higher carbonate mud concentration as evidenced by predominantly wackestone to packstone textures (Table A1).

The grain size variations within the reef partly determined the zonation of the rudists. In the Edwards Limestone, *Eoradiolites* and *Monopleura* were elevating rudists that required a hard substrate, such as limestone or shell fragments, to which the tip of the shell could securely attach. Recumbent caprinid rudists preferred to attach to or live on soft carbonate sands or shell fragments such as those of *Chondrodonta*, and *Toucasia* was a clinging rudist that required a firm substrate that would be created by mixing finer and coarser-grained material.

Table 1. The Albian Edwards Limestone patch reefs of Central Texas versus the Holocene patch reefs of the Bermuda Platform.

Category	Albian Edwards Limestone Patch Reefs	Holocene Patch Reefs of Bermuda
Climate	Subtropical	Subtropical
Sea Temperature	32-34°C (Wilson and Norris, 2001; Forster, 2007) Low seasonal variability from tropics to the poles <12°C (Steuber and others, 2005)	Outer patch reefs (study area): 18-30°C (Smith, 1998) High seasonal variability up to 16°C within lagoon (Smith, 1998)
Salinity	36.2-36.6 ppt. (Poulsen and others, 2001) Occasionally hypersaline (Roberson, 1972; Rose, 1972)	36.5 ppt., no hypersalinity because of freely-exchanged waters (Garrett and others, 1971; Smith, 1998).
Energy	Elongate reefs-low-moderate Circular reefs- low Medium to high energy platform (Fisher and Rodda, 1969)	Elongate reefs-low-moderate Circular reefs- low High energy platform (Stanley and Swift, 1968)
Turbidity	Generally low-turbidity and low terrigenous sedimentation Turbidity and influx increased during final stages of Edwards deposition (ex. Whitney mudstone, Childress Creek rings)	Low turbidity and low terrigenous sedimentation
Current	Dominant east-west/southeast to northwest flowing current (Figure 12; Young, 1955)	Season-dependent current, irregular water circulation (Wells, 1988)
Reef Shapes	Circular, biostromal, or elongate (Nelson, 1973)	Circular, irregular circular, elongate (Jordan, 1973)
Patch Reef Size	Dependent on water depth? Up to 65m at Childress Creek 10-100m (Roberson, 1972)	Dependent on water depth 75-400m in diameter in deeper water (Garrett and others, 1971) Typical patch reefs <200m (Jordan, 1973)
Reef Depth	< 6-7m (Young, 1959; Bebout and Loucks, 1974)	< 12m at study sites (Table B1) 8-18m deep within platform (Garrett and others, 1971)
Reef Protection	Stuart City barrier reef	Annular rim reef system
Biodiversity	Lower diversity than coral-algal reefs (Kauffman and Johnson, 1988) No *Acropora* sp. (evolves in Paleocene)	Low relative diversity compared with modern reefs No *Acropora* sp.
Zonation factors	Substrate, water depth, and energy-controlled	Substrate, water depth, and energy- controlled
Grain Size	Carbonate mud to gravel (shell hash)	Fine carbonate sand to gravel (Table B1)

Figure 27. The elongate and circular to irregular-circular patch reefs of Bermuda (from Jordan, 1973; photo courtesy of Dr. Robert Ginsburg).

The sediment of Bermuda's reefs becomes increasingly coarser with depth (Table B1). The finer, more mobile material of the reef crest would provide a suitable substrate for recumbent caprinids, and the mixture of fine and coarse sands on the reef flanks would have been conducive for *Toucasia*. Bermuda's reefs also have abundant limestone surfaces and coarse shell fragments that would be used by the elevating *Eoradiolites*, and *Monopleura* rudists.

Sediment algal abundances differ between the Edwards Limestone and Bermudian reefs: Bermuda has higher volumes of both crustose coralline red algae and of codiacean algae (*Halimeda*) (Tables A3, B6). The difference in algal composition between the two reefs is environmentally significant because it indicates that the Edwards Limestone bioherms developed in lower-nutrient seas than those of the modern Bermudian reefs. Hardie (1996) and Steuber (2002) used Mg/Ca ratios to show that oceanic productivity levels were the lowest in the Phanerozoic during the Albian period of the Cretaceous. Algal density increases moving towards the Stuart City Reef Trend. This could be the result of very low nutrient waters, or a higher number of algal grazers, particularly gastropods, within the Central Texas area.

With the exception of rudists and corals, the other biotic constituents of the Edwards and Bermuda sediments are similar and no significant trends between the two are discernable from the data (Tables A1, A2, A3, B1, B5, B6). The organisms of the Edwards and Bermudian sediments are commonplace in both the Cretaceous and modern normal-marine environments.

Very little terrigenous sedimentation is present in either of the reef systems. The Edwards Limestone within the study area is a clean, pure limestone. The regional deposition of the clay partings within the Edwards Limestone (not present in all outcrops), for example at Childress Creek, are macroscale events created either by an increase in runoff due to regression, storm events, or by fluvial sedimentation. These clays are not considered to be indicative of the clean, carbonate lithology of the Edwards Limestone. Likewise, the non-rudist-bearing mudstone bed at Lake Whitney is also a product of regression because it was immediately followed by the deposition of the Kiamichi Shale. In Bermuda, the distance of the patch reefs from the island has kept them free of terrigenous sediment (Table B6).

Zonation

The zonation of the Edwards and Bermudian patch reefs is primarily controlled by substrate, water depth and wave/current energy (Table 1). The patch reefs of Bermuda are dominated by *Diploria* sp., *Montastrea* sp., and *Porites astreoides* corals; all three can be found in abundance on each part of the reef (Table B2). It was initially hoped that correlations could be made in the zonation patterns of specific rudist and coral species; however the zonation on the Bermudian patch reefs is not as pronounced as that of the Edwards Limestone. The dominance of the *Diploria-Montastrea-Porites* assemblage makes any trends difficult to identify.

Within the Central Texas study area, the caprinid rudists are the principal reef-builders for bioherms developing in shallow, moderate to high-energy, hypersaline, waters (Figure 28) (Childress Creek and Lake Whitney). The euryhaline caprinids however are also able to thrive in normal-marine environments. For example, at the normal-marine Mosheim-2 location, caprinids replaced *Eoradiolites* rudists as the dominant core-formers when relative sea level decreased.

Eoradiolites is one the more versatile rudists within the study area. It is the pioneering taxon for the slightly deeper, lower-energy circular and elongate reefs. In caprinid-built reefs, *Eoradiolites* dominates the upper to middle reef slope (Figure 28). *Eoradiolites* seems to have existed within a buffer zone between the extremely shallow caprinids and the deeper-dwelling toucasids and monopleurids (Figure 28). The presence of *Eoradiolites* signifies normal-marine conditions, as evidenced by its coexistence with normal-marine fauna. Together, caprinids and *Eoradiolites* are, by far, the most common rudist types found within Central Texas.

Ideally, *Toucasia* and *Monopleura* are found on the lower reef slope possibly accompanied by a few *Eoradiolites* rudists and *Cladophyllia* corals (Figure 28). *Monopleura* is found slightly farther down the slope than *Toucasia* towards the base of the reef; however, as mentioned before, *Monopleura* zonation is problematic. Perplexingly, the bioherms at Childress Creek contain both caprinids and monopleurids at the reef core. *Monopleura* was likely more tolerant of the hypersaline conditions that existed at Childress Creek during the time of core-formation (Figure 29). An ensuing return to normal-marine conditions would have allowed for the settlement of *Eoradiolites* and *Toucasia* on the flanks. There have been sites to the south of the study area found to have toucasid or monopleurid cores (Nelson, 1959; Roberson, 1972). This is likely a function of deeper water depth during the initial stages of reef growth.

Though not a rudist, *Chondrodonta* is a very important constituent of the Edwards Limestone bioherms. It is present at each site except for Mosheim-1. *Chondrodonta* is commonly found associated with caprinid rudists in the cores of very shallow patch reefs and it can occasionally be found scattered on flanks. *Chondrodonta* has been found attached to not just caprinids, but to all rudist types as well as *Cladophyllia* coral (Jacka and Brand, 1977). This may indicate that *Chondrodonta* is a “keystone” species with respect to reef development on the basis of providing a suitable attachment substrate.

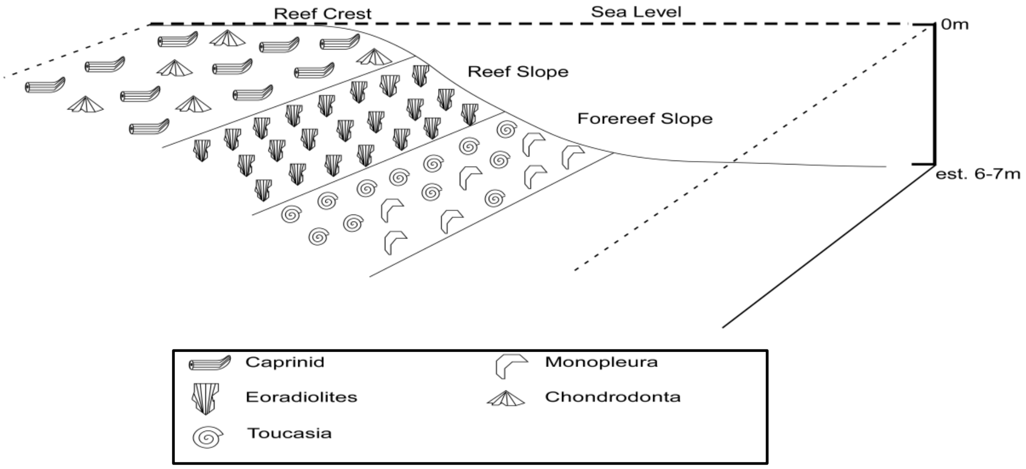

Figure. 28. Ideal normal-marine zonation based on substrate, energy, and water depth. Caprinids and Chondrodonta dominate high-energies; *Eoradiolites* exists within a "buffer zone" between caprinids and the *Toucasia* and *Monopleura*. *Eoradiolites* can from the core under low-energy, normal-marine conditions.

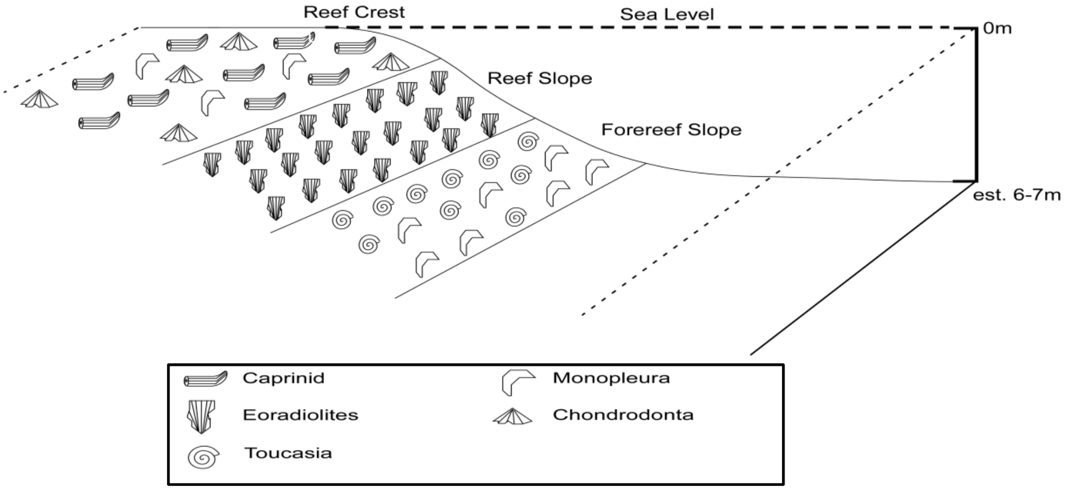

Figure 29. Hypersaline zonation model. *Monopleura* appears to more hypersaline tolerant than *Eoradiolites* and *Toucasia* and can be found in cores alongside caprinids. This can be observed at Childress Creek and Lake Whitney. *Eoradiolites* and *Toucasia* are normal-marine and will only be present at the reef if normal salinity returns.

Summary

As outlined in Table 1 there are similarities between the patch reefs of the Edwards Limestone and the patch reefs of Bermuda. The similarities identified are: 1) both reefs developed in subtropical regions, 2) the existence of protective barriers which created a large backreef for low-moderate energy elongate and low-energy circular biohermal growth, 3) both reef systems received little to no terrigenous sediment influx and had low-productivity waters, 4) the salinities of the Albian and modern Bermudian seawater are comparable, though the Edwards Limestone had hypersalinity, (theoretically Bermuda's irregular water circulation could create isolated hypersaline pockets), 5) the grain sizes present on the Bermudian reefs would create substrates habitable by all Central Texas rudists, 5) the Edwards and Bermudian reefs both have very low biodiversity, thought the rudist reefs are even less diverse than coral-algal reefs, 6) the zonation on both reefs is controlled by substrate, water depth, and wave/current energy, and 7) the growth rate of Bermudian reefs may be closer to that of the Cretaceous rudist bioherms because it lacks reef-building *Acropora* spp. and other fast-growing coral species.

The most problematic attribute is the difference in temperatures (Table 1). The Cretaceous seas were substantially warmer than the reefs of Bermuda, and for that matter warmer than any modern reefs today. The Albian temperatures thermally-stressed corals and relegated them to deeper, somewhat cooler waters. In light of the temperature disparity (and other Cretaceous environmental factors), it is believed that no "exact" modern analog for rudist reefs exists. Instead, a "similar" modern analog should be identified using characteristics such as substrate, wave-energy, turbidity, reef size, water depth, biodiversity, and zonation controls. It is in the author's opinion, that whereas Bermuda fits in the "similar analog" category, it is not an exact modern analog for the Edwards Limestone bioherms.

CHAPTER SEVEN

Conclusions

The orientation of caprinid rudists at Lake Whitney demonstrates that the paleocurrent flowed from the southeast (proto-Gulf of Mexico) to the northwest (Western Interior Seaway) during the time of Edwards Limestone deposition. This determination is supported by Young (1959) and through an Albian paleo-oceanographic reconstruction by Poulson (2003). This current might have carried terrigenous sediment originating from the Llano Islands to the south. This sediment may be partially responsible for creating the rings of the concentric bioherms at Childress Creek; however, the most likely source appears to be from the Wichita-Arbuckle-Ouachita Uplift to the north as evidenced by the northward thickening of the Kiamichi Shale. The deposition of this terrestrial material either severely slowed reef growth, or smothered the reef entirely, as evidenced by the lack of rudists within the rings.

The zonation of the rudists in the Central Texas Edwards bioherms was dependent on substrate, water depth and wave or current energy. Zonation models were constructed by observing the distribution patterns of each taxon within the study area (Figures 28, 29). Caprinid rudists lived in the shallowest, highest-energy environments of the various rudist taxa. This can be observed at the Mosheim-1 and Mosheim-2 field sites where *Eoradiolites* rudists formed the original mound. As the reef continued to grow, relative sea-level decreased and the reefs became caprinid-dominated, while *Eoradiolites* become much less abundant.

At Childress Creek, caprinids were found with the usually deeper-dwelling *Monopleura* in the reef cores. This suggests that caprinids and monopleurids were hypersaline-tolerant, and that there were hypersaline conditions at the time of initial reef development. The strictly normal-marine *Eoradiolites* and *Toucasia* are found on the flanks and signify an eventual return to normal salinities (Figure 29). *Chondrodonta* bivalves, observed at Childress Creek, Lake Whitney, and Coon Creek, may have been a keystone organism in the Edwards bioherms with respect to reef growth. The euryhaline *Chondrodonta* are found in caprinid cores and acted as attachment substrates, which aided in biohermal growth or establishment. *Cladophyllia* coral and all rudists types have been found attached to *Chondrodonta* (Jacka and Brand, 1977).

During the Edwards time, rudist bivalves likely succeeded scleractinian corals and algae through a combination of convergent evolution and environmental factors. High temperatures, coupled with cyclic periods of high and low productivity, eventually stressed the corals and algae and forced them to deeper, cooler waters. This can be seen in Texas as coral and algal density increase to the south where water depth increased towards the Stuart City Reef Trend.

In terms of a modern analog, Bermuda has many similarities with the Central Texas Edwards Limestone bioherms (Table 1). The zonation of both the Edwards and Bermudian reefs is controlled by substrate, water depth, and wave energy. The presence of fine and coarse sands, and numerous hard surfaces on Bermuda's reefs, would create suitable substrates for all Central Texas rudist types. The softer muds and sands of the reef crest are ideal for recumbent caprinid colonization. The clinging *Toucasia* would utilize mixed, fine and coarse sands for a firm, stable substrate, and elevating *Eoradiolites* and *Monopleura* would use limestone or shell fragments to attach.

The Edwards and Bermudian reefs both had/have protective barriers (the Stuart City barrier reefs and the annular rim reefs) which rim medium to high-energy, low-relief carbonate platforms. The existence of these barriers created a large backreef in which low-moderate energy elongate reefs formed. These elongate reefs in turn, protected low-energy, circular to irregularly-circular reefs.

The biodiversity of the Bermudian reefs, while higher than that of the Edwards rudist reefs, is more comparable than that of any extant coral-algal reef. In particular, the lack of *Acropora* corals at Bermuda and within the Edwards Limestone suggests that the growth rate of the Edwards and Bermudian reefs may be more comparable than that of other modern coral reefs.

Though the Edwards and Bermudian reefs are "similar," in many respects, Bermuda is not an "exact" analog for the Edwards bioherms in Central Texas (Table 1). Because of the high temperatures and unique oceanographic conditions of the Cretaceous, it is likely that no exact modern analog for the Edwards bioherms currently exists.

APPENDICES

APPENDIX A

Field Data from the Edwards Limestone of Central Texas

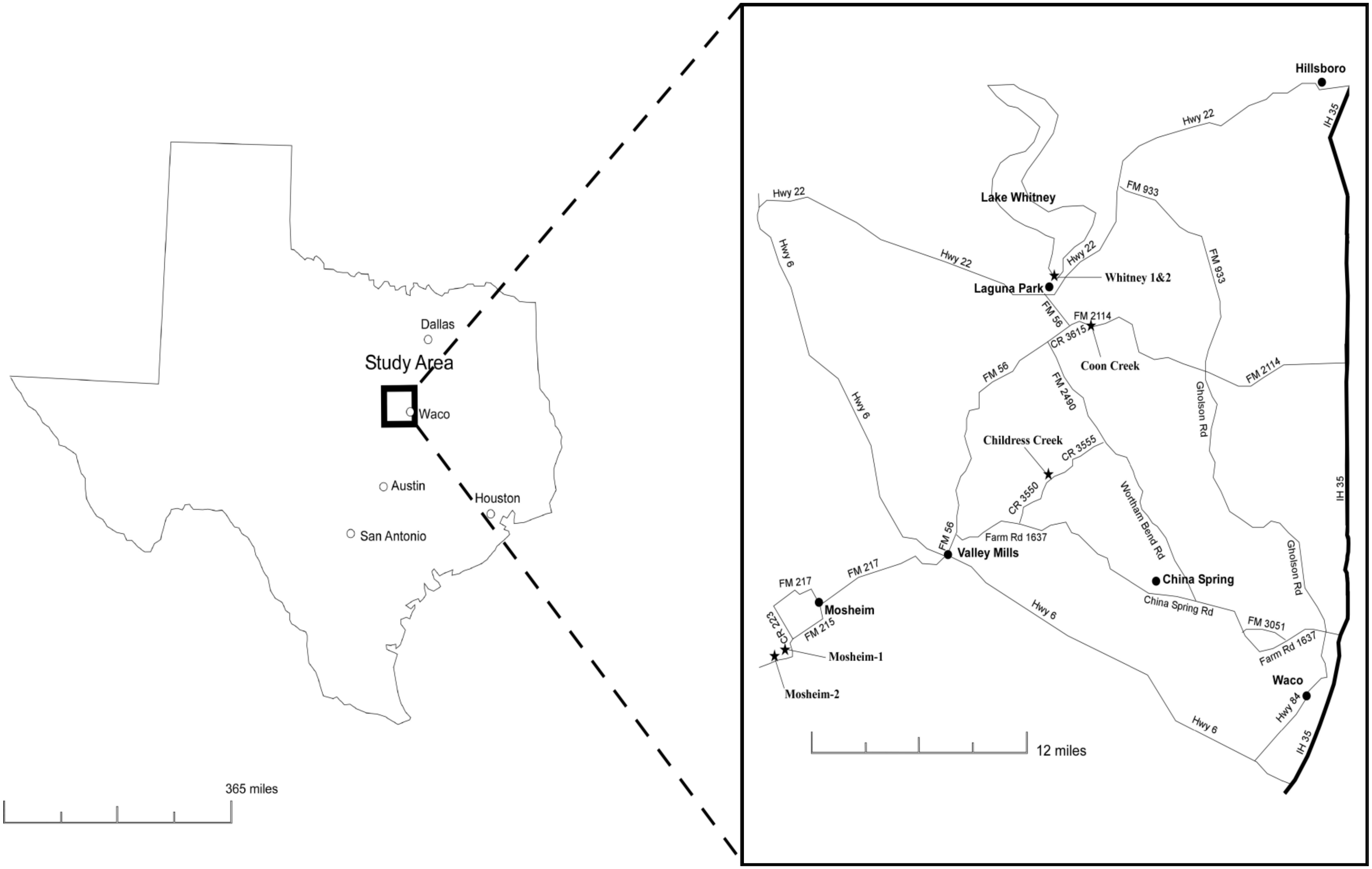

Figure A1. Edwards Limestone study area in North-Central Texas

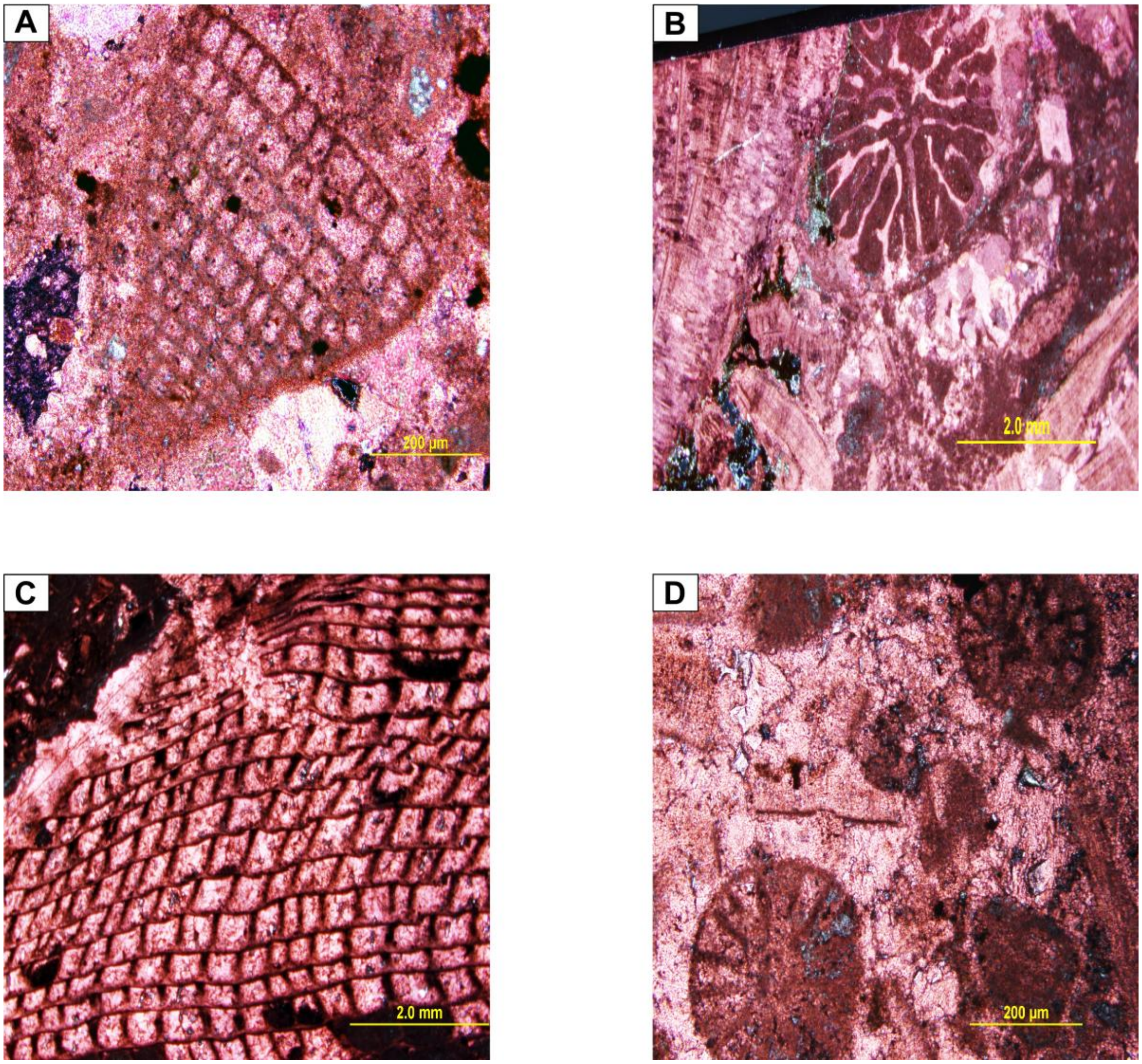

Figure A2. Fossils of the Edwards Limestone: A) *Dictyoconus walnutensis*, B) *Cladophyllia* coral corallite, C) typical rudist fabric, D) echinoderm spines. Stained with Alizarin red S, XPL.

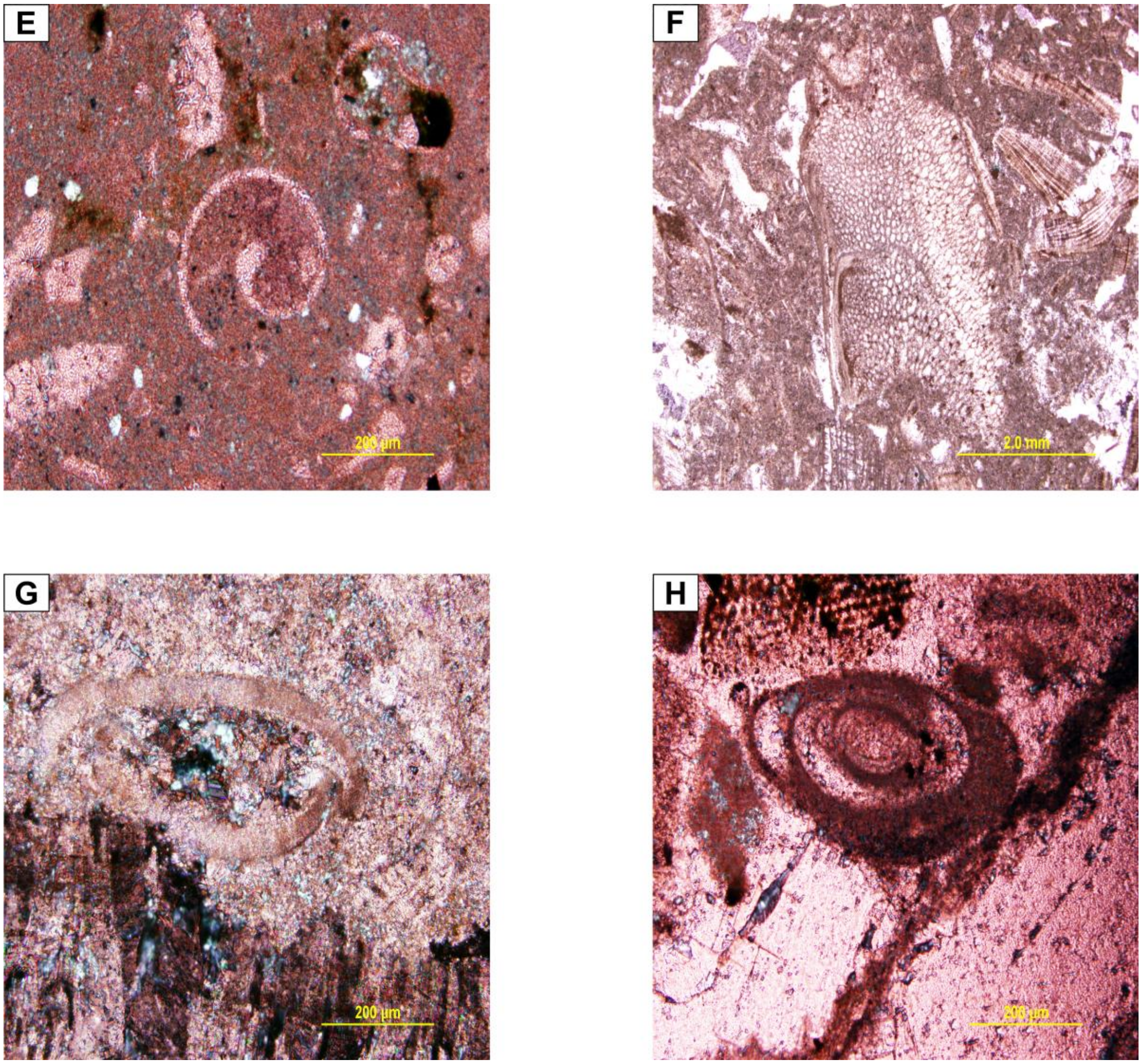

Figure A3. Fossils of the Edwards Limestone: E) gastropod, F) bryozoan, G) ostracode, H) miliolid foram. Stained with Alizarin red S, XPL.

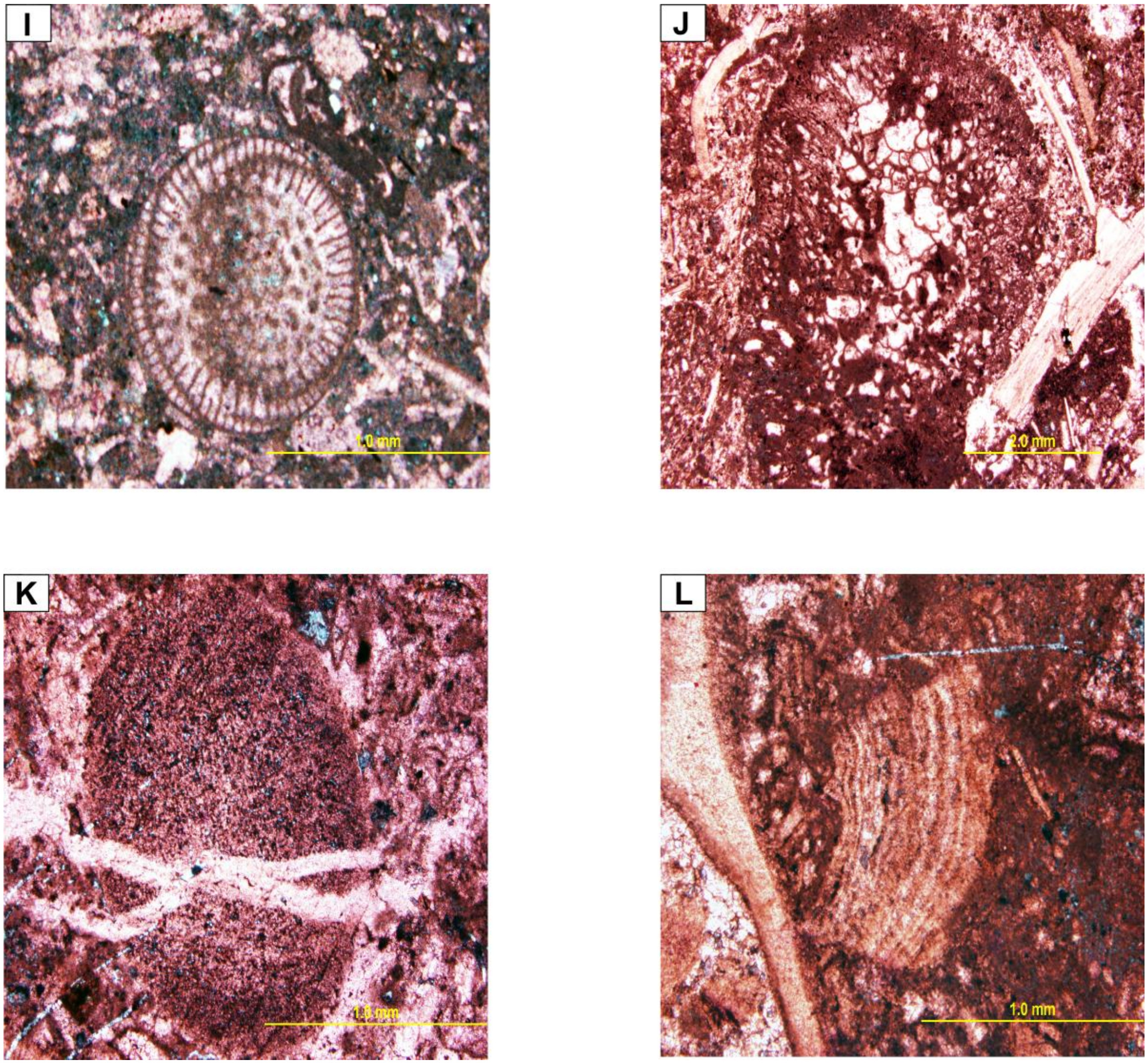

Figure A4. Fossils of the Edwards Limestone: I) dasyclad algae, J) codiacean green algae, K) phylloid algae across an echinoderm fragment, L) *Lithopyhllum* red algae. Stained with Alizarin red S, XPL.

Table A1. Results of the thin section analysis of the Edwards Limestone.

Sample ID	Location	Texture (Matrix)	Fossil Biota	Other
M1-1(1)	Mosheim 1	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, *Dictyoconus walnutensis*, miliolid foraminifera, ostracodes, dasyclad algae, red algae	recrystallization, iron-staining
M1-1(3)	Mosheim 1	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, *Cladophyllia coral*, red algae, green algae	recrystallization, iron-staining, some original shell material
M1-2(1)	Mosheim 1	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments, pteropods, ostracodes, *Dictyoconus walnutensis*, miliolids, other foraminifera, dasyclad algae, other green algae	recrystallization, coated grains
M1-2(4)A	Mosheim 1	boundstone (packstone)	rudist and mollusk fragments, echinoderm fragments, encrusting bryozoans, *Dictyoconus walnutensis*, green algae?	recrystallization, iron-staining, stylolites
M1-2(4)B	Mosheim 1	boundstone (packstone)	rudist and mollusk fragments, encrusting bryozoans, *Dictyoconus walnutensis*, coralline red algae, green algae	recrystallization, iron-staining, stylolites, coated grains
M1-3(1)	Mosheim 1	rudstone (packstone)	rudist fragments and mollusk fragments, echinoderm fragments, bryozoans, pteropods, *Dictyoconus walnutensis*, miliolids, dasyclad algae	recrystallization, iron-staining, stylolites
M1-4(5)	Mosheim 1	rudstone (packstone) boundstone?	rudist and mollusk fragments, encrusting bryozoans, green algae	recrystallization, iron-staining
M1-5(2)	Mosheim 1	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, *Dictyoconus walnutensis*, bryozoans, miliolids, dasyclad algae	recrystallization, iron-staining

Table A1. Results of the thin section analysis of the Edwards Limestone- continued.

Sample ID	Location	Texture (Matrix)	Fossil Biota	Other
M1-6(2)	Mosheim 1	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, ostracodes, green algae	recrystallization, iron-staining
M1-6(3)	Mosheim 1	rudstone (packstone to grainstone)	rudist and mollusk fragments, green algae	recrystallization, iron staining
M1-6(4)	Mosheim 1	floatstone (wackestone)	rudist and mollusk fragments, bryozoans, *Cladophyllia coral*, gastropods	recrystallization, iron staining, carbonate sand, some original shell material
M2-1(3)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, *Dictyoconus walnutensis*, miliolid forams, coralline red algae, green algae	recrystallization, calcite twinning
M2-1(4)	Mosheim 2	rudstone (packstone)	rudist and mollusk fragments, dasyclad algae	recrystallization, iron-staining
M2-1(5)	Mosheim 2	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans?, red algae	recrystallization, iron-staining, ooids
M2-2(2)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, miliolid foraminifera, coralline red algae	recrystallization, iron-staining stylolites
M2-2(4)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, organic worm tubes, coralline red algae, green algae?	recrystallization, iron-staining, ooids

Table A1. Results of the thin section analysis of the Edwards Limestone- continued.

Sample ID	Location	Texture (Matrix)	Fossil Biota	Other
M2-2(5)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, bryozoans, green algae?	recrystallization, iron-staining, ooids
M2-2(6)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, coralline red algae	recrystallization, iron-staining, some original shell material
M2-3(1)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, bryozoans	recrystallization, iron-staining, stylolites, some original shell material
M2-3(2)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, ostracodes, dasyclad algae?, other green algae	recrystallization, iron-staining, intraclasts?
M2-3(4)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, bryozoans, ostracodes? red algae, dasyclad, other green algae	recrystallization, some original shell material , iron staining, peloids
M2-4(3)	Mosheim 2	rudstone (packstone)	rudist and mollusk fragments, bryozoans	recrystallization
M2-5(1)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, bryozoans, ostracodes, red algae, dasyclad algae	recrystallization, calcite twinning, coated grains?
M2-5(2)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, bryozoans?	recrystallization, possible coated grains

Table A1. Results of the thin section analysis of the Edwards Limestone- continued.

Sample ID	**Location**	**Texture (Matrix)**	**Fossil Biota**	**Other**
M2-7(1)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments, red algae	recrystallization, some original shell material , iron-staining
M2-7(4)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments	recrystallization, iron-staining
M2-8(1)	Mosheim 2	wackestone	rudist and mollusk fragments, echinoderm fragments, ostracodes	recrystallization, some original shell material , iron-staining
M2-8(4)	Mosheim 2	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, ostracodes, miliolids, other foraminifera, coralline red algae	recrystallization, iron-staining, some clastic sediment, ooids?
M2-9(1)	Mosheim 2	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, ostracodes, miliolid forams, coralline red algae, dasyclad algae	recrystallization, some original shell material, iron-staining, ooids?
M2-9(3)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments, ostracodes, red algae, *Halimeda?* green algae	recrystallization, some clastic material, iron-staining, ooids
M2-9(4)	Mosheim 2	floatstone (wackestone)	rudist and mollusk fragments, echinoderm fragments, coralline red algae, dasyclad algae	recrystallization, iron-staining, pyrite, ooids
W1-1(2)	Lake Whitney 1	wackestone to packstone	rudist and mollusk fragments, echinoderm fragments, bryozoans, gastropods, dasyclad algae	recrystallization, iron-staining, ooids?
W1-2(2)	Lake Whitney 1	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, miliolids?, other foraminifera?, codiacean green algae?	recrystallization, iron-staining

Table A1. Results of the thin section analysis of the Edwards Limestone- continued

Sample ID	**Location**	**Texture (Matrix)**	**Fossil Biota**	**Other**
W1-2(3)	Lake Whitney 1	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, ostracodes, miliolids, other foraminifera	recrystallization, iron-staining
W1-2(4)	Lake Whitney 1	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, ostracodes, coralline red algae	recrystallization, iron-staining, abundant ooids
W1-3(2)1	Lake Whitney 1	rudstone (packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, ostracodes, gastropods, miliolids, dasyclad algae	recrystallization, heavy iron-staining, ooids?, pellets?
W1-3(2)2	Lake Whitney 1	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans, ostracodes, gastropods, miliolid forams, dasyclad algae?	recrystallization, heavy iron-staining, ooids?
W2-1(1)	Lake Whitney 2	mudstone to wackestone	rudist and mollusk fragments, echinoderm fragments, gastropods, bryozoans? *Dictyoconus walnutensis*?, miliolids? Other foraminifera, coralline red algae?	recrystallization, iron-staining
C1-1(3)	Coon Creek	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, *Cladophyllia coral*, gastropods, miliolids, other foraminifera?, coralline red algae	recrystallization, iron-staining, some original shell material
C1-3(1)	Coon Creek	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, ostracodes?, *Dictyoconus walnutensis*?, coralline red algae	recrystallization, heavy iron-staining, coated grains?
C2-1(1)	Coon Creek	floatstone to rudstone (wackestone to packstone)	rudist and mollusk fragments, echinoderm fragments, bryozoans?, ostracodes, green algae?	recrystallization, heavy iron-staining, ooids?

Table A2. The distribution of the common invertebrates in the Edwards Limestone. Results determined through the point counting of polished slabs. If the organism was present within the .64cm x.64cm square it received a value of “1”, if not present it received a value of “0”. The total value for each organism was divided by the number of squares per slab. For the Mosheim-1and Mosheim-2 samples, the first number represents the column and the second number represents the row from which the sample was taken from on the outcrop. Because no grid was possible for Whitney-1, Whitney-2, and Coon Creek, the first number of the sample ID represents the bed, and the second number is the relative position of the sample to the others from that bed.

Sample ID	**Squares**	**Matrix**	**Bryozoan**	**Rudist/Mollusk**	**Echino.**	**Coral**	**Gastropod**	**Ostracode**	**Coated Grain**	**Spar**	**Unknown**
M1-1(1)	72	94.44%	7.35%	100.00%	4.17%	0.00%	6.94%	11.11%	5.56%	36.14%	13.89%
M1-1(2)	107	84.11%	18.89%	73.83%	0.93%	0.00%	1.87%	3.74%	0.00%	55.14%	10.28%
M1-2(1)	60	91.67%	0.00%	66.67%	15.00%	5.32%	6.67%	6.67%	3.33%	46.67%	38.33%
M1-2(2)	61	100.00%	0.00%	31.15%	1.64%	0.00%	0.00%	0.00%	0.00%	4.92%	11.48%
M1-2(3)	93	94.62%	0.00%	60.22%	0.00%	0.00%	0.00%	0.00%	1.08%	32.26%	9.68%
M1-2(4)A	86	100.00%	0.00%	97.67%	3.49%	0.00%	0.00%	2.33%	3.49%	66.28%	6.98%
M1-2(4)B	96	72.92%	0.00%	72.92%	1.04%	0.00%	0.00%	0.00%	0.00%	67.71%	3.13%
M1-2(5)	195	88.21%	5.23%	55.90%	0.51%	0.00%	0.00%	0.51%	0.00%	13.33%	14.36%
M1-3(1)	100	97.00%	1.03%	99.00%	7.00%	7.10%	4.00%	5.00%	3.00%	21.00%	17.00%
M1-3(2)	93	98.92%	0.00%	51.61%	1.08%	0.00%	0.00%	1.08%	1.08%	5.38%	5.38%
M1-3(3)	99	96.97%	0.00%	100.00%	0.00%	0.00%	1.01%	0.00%	0.00%	50.51%	5.05%
M1-4(1)	133	87.97%	1.71%	84.21%	1.50%	4.20%	9.02%	3.76%	0.00%	27.82%	6.02%
M1-4(2)	78	100.00%	0.00%	62.82%	0.00%	0.00%	0.00%	0.00%	0.00%	26.92%	6.41%
M1-4(3)	207	70.05%	0.00%	88.89%	0.48%	0.00%	0.97%	0.00%	0.48%	45.89%	2.90%
M1-4(4)	171	87.13%	0.00%	82.46%	2.34%	0.00%	1.17%	1.17%	0.00%	32.75%	12.87%
M1-4(5)	95	98.95%	13.83%	94.74%	3.16%	0.00%	1.05%	0.00%	0.00%	25.26%	14.74%
M1-5(1)	211	100.00%	5.56%	91.94%	0.00%	0.00%	0.00%	0.47%	0.00%	37.91%	6.64%
M1-5(4)	152	88.16%	7.46%	71.05%	1.32%	0.00%	0.66%	0.66%	0.00%	30.92%	7.89%
M1-5(5)	165	96.36%	4.40%	85.45%	1.21%	0.00%	0.00%	0.00%	0.00%	27.27%	8.48%
M1-6(1)	107	97.20%	12.50%	92.52%	3.74%	0.00%	0.00%	0.00%	0.00%	45.79%	11.21%
M1-6(2)	96	86.46%	4.82%	96.88%	8.33%	0.00%	0.00%	2.08%	0.00%	63.54%	8.33%

Table A2. The distribution of the common invertebrates in the Edwards Limestone- continued.

Sample ID	**Squares**	**Matrix**	**Bryozoan**	**Rudist/Mollusk**	**Echino.**	**Coral**	**Gastropod**	**Ostracode**	**Coated Grain**	**Spar**	**Unknown**
M1-6(3)	85	95.29%	2.47%	94.12%	1.18%	0.00%	0.00%	10.59%	4.71%	16.47%	10.59%
M1-6(4)	83	97.59%	0.00%	95.18%	0.00%	0.00%	1.20%	3.61%	2.41%	32.53%	10.84%
M2-1(1)	88	92.05%	1.23%	82.95%	0.00%	0.00%	0.00%	0.00%	0.00%	43.18%	10.23%
M2-1(3)	102	84.31%	0.00%	94.12%	2.94%	0.00%	0.00%	0.98%	1.96%	58.82%	6.86%
M2-1(4)	96	97.92%	2.13%	100.00%	4.17%	0.00%	3.13%	3.13%	4.17%	21.88%	9.38%
M2-1(5)	96	88.54%	2.35%	100.00%	6.25%	0.00%	0.00%	5.21%	7.29%	25.00%	17.71%
M2-2(1)	135	86.67%	0.85%	85.93%	2.22%	2.96%	0.00%	1.48%	2.22%	25.93%	17.04%
M2-2(2)	84	100.00%	2.38%	92.86%	2.38%	0.00%	2.38%	2.38%	3.57%	22.62%	11.90%
M2-2(3)	84	98.81%	0.00%	94.05%	2.38%	0.00%	0.00%	2.38%	4.76%	39.29%	21.43%
M2-2(4)	96	87.50%	0.00%	67.71%	0.00%	0.00%	0.00%	0.00%	0.00%	23.96%	15.63%
M2-2(5)	96	90.63%	3.45%	94.79%	1.04%	0.00%	0.00%	0.00%	0.00%	27.08%	10.42%
M2-2(6)	96	86.46%	4.82%	93.75%	1.04%	1.04%	0.00%	2.08%	3.13%	28.13%	20.83%
M2-3(1)	225	96.44%	0.46%	95.56%	2.22%	0.44%	3.11%	6.22%	0.00%	32.89%	11.56%
M2-3(2)	96	81.25%	1.28%	95.83%	5.21%	0.00%	0.00%	2.08%	1.04%	59.38%	9.38%
M2-3(3)	225	85.78%	0.52%	68.44%	0.44%	0.00%	0.00%	0.00%	0.00%	33.78%	6.67%
M2-3(4)	96	94.79%	0.00%	39.58%	4.17%	0.00%	3.13%	2.08%	0.00%	38.54%	11.46%
M2-3(5)	225	84.89%	0.52%	84.00%	1.78%	0.44%	6.67%	3.11%	0.00%	23.56%	15.11%
M2-4(1)	128	85.16%	2.75%	92.19%	6.25%	2.34%	2.34%	3.91%	1.56%	72.66%	20.31%
M2-4(2)	126	88.89%	0.89%	73.02%	6.35%	1.59%	3.97%	0.00%	0.00%	15.08%	16.67%
M2-4(3)	119	87.39%	0.96%	57.14%	1.68%	0.00%	0.00%	0.00%	0.00%	29.41%	10.92%
M2-4(4)	156	90.38%	1.42%	52.56%	5.13%	0.64%	0.00%	0.64%	1.28%	35.26%	8.97%
M2-5(1)	116	77.59%	0.00%	56.90%	3.45%	0.00%	1.72%	0.00%	26.72%	42.24%	8.62%
M2-5(4)	225	81.33%	1.09%	74.67%	0.89%	0.44%	0.00%	0.00%	0.00%	22.22%	9.33%
M2-5(5)	197	90.36%	1.69%	67.51%	2.54%	0.00%	0.00%	1.52%	0.00%	11.68%	6.09%
M2-6(1)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table A2. The distribution of the common invertebrates in the Edwards Limestone- continued.

Sample ID	Squares	Matrix	Bryozoan	Rudist/Mollusk	Echino.	Coral	Gastropod	Ostracode	Coated Grain	Spar	Unknown
M2-6(2)	180	96.67%	3.45%	76.11%	0.56%	2.78%	1.11%	0.56%	1.11%	13.89%	6.11%
M2-6(3)	217	88.02%	1.57%	72.81%	0.00%	0.00%	0.00%	0.00%	0.00%	9.22%	9.22%
M2-6(4)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
M2-6(5)	225	90.22%	0.99%	72.89%	0.89%	0.44%	0.00%	1.78%	0.00%	22.22%	12.44%
M2-7(1)	96	87.50%	1.19%	94.79%	0.00%	0.00%	1.04%	1.04%	0.00%	42.71%	6.25%
M2-7(2)	218	95.41%	0.48%	76.15%	0.46%	1.83%	0.92%	2.75%	0.00%	20.64%	6.42%
M2-7(3)	224	92.41%	0.00%	96.88%	0.00%	1.34%	0.00%	1.79%	1.79%	41.07%	7.59%
M2-7(4)	116	98.28%	1.75%	68.97%	0.00%	0.00%	0.00%	5.17%	0.00%	31.90%	20.69%
M2-8(1)	108	100.00%	0.00%	75.00%	0.00%	0.00%	0.00%	1.85%	0.00%	10.19%	12.96%
M2-8(2)	225	87.56%	2.54%	76.00%	0.44%	4.44%	1.78%	1.78%	0.00%	20.89%	8.89%
M2-8(3)	225	96.00%	0.46%	46.67%	1.78%	0.00%	0.44%	0.89%	0.00%	12.89%	13.33%
M2-8(4)	108	93.52%	0.99%	74.07%	0.93%	0.00%	0.00%	0.00%	0.00%	14.81%	9.26%
M2-9(1)	108	100.00%	1.85%	63.89%	0.93%	3.70%	1.85%	3.70%	0.00%	16.67%	8.33%
M2-9(2)	222	89.19%	0.00%	52.25%	0.00%	0.45%	0.45%	0.45%	0.00%	13.96%	8.56%
M2-9(3)	96	100.00%	5.21%	64.58%	5.21%	1.04%	1.04%	1.04%	2.08%	10.42%	16.67%
M2-9(4)	96	88.54%	0.00%	66.67%	2.08%	0.00%	1.04%	3.13%	0.00%	35.42%	16.67%
W1-1(1)	223	95.96%	5.61%	56.50%	4.04%	0.00%	1.79%	1.35%	0.45%	10.76%	12.11%
W1-1(2)	108	100.00%	5.56%	47.22%	6.48%	0.00%	0.00%	2.78%	0.93%	12.04%	25.00%
W1-2(1)	154	97.40%	3.33%	55.84%	1.30%	1.30%	0.65%	0.65%	0.00%	44.81%	7.14%
W1-2(2)	96	95.83%	1.09%	39.58%	1.04%	1.04%	0.00%	2.08%	2.08%	35.42%	17.71%
W1-2(3)	96	89.58%	6.98%	50.00%	1.04%	1.04%	1.04%	4.17%	0.00%	14.58%	29.17%
W1-2(4)	108	96.30%	2.88%	32.41%	0.00%	0.00%	2.78%	0.93%	0.00%	52.78%	11.11%
W1-3(1)	216	95.83%	1.45%	49.07%	1.85%	0.00%	1.39%	0.46%	11.11%	9.26%	9.26%
W1-3(3)	225	98.67%	0.90%	34.67%	1.33%	0.00%	1.33%	1.78%	0.00%	8.89%	11.56%
W2-2(1)	157	96.82%	4.61%	45.22%	0.00%	0.64%	3.18%	1.91%	0.64%	21.02%	7.01%

Table A2. The distribution of the common invertebrates in the Edwards Limestone- continued.

Sample ID	Squares	Matrix	Bryozoan	Rudist/Mollusk	Echino.	Coral	Gastropod	Ostracode	Coated Grain	Spar	Unknown
C1-1(3)	215	93.02%	1.00%	37.21%	0.93%	0.00%	1.86%	0.47%	0.00%	22.79%	5.58%
C1-2(1)	105	91.43%	2.08%	60.95%	0.00%	0.00%	0.00%	0.00%	0.00%	6.67%	8.57%
C1-2(2)	134	92.54%	4.03%	74.63%	0.00%	0.00%	0.75%	0.00%	0.00%	23.13%	8.21%
C1-3(1)	96	80.21%	3.90%	72.92%	1.04%	0.00%	1.04%	0.00%	0.00%	10.42%	5.21%
C2-1(1)	179	96.65%	1.73%	74.86%	0.00%	0.56%	0.56%	0.56%	1.12%	9.50%	12.85%

Table A3. The distribution of forams and algae in the Edwards Limestone. Results determined through the point counting of polished slabs. If the organism was present within the .64cm x.64cm square it received a value of "1", if not present it received a value of "0". The total value for each organism was divided by the number of squares per slab. For the Mosheim-1and Mosheim-2 samples, the first number represents the column and the second number represents the row from which the sample was taken from on the outcrop. Because no grid was possible for Whitney-1, Whitney-2, and Coon Creek, the first number of the sample ID represents the bed, and the second number is the relative position of the sample to the others from that bed.

Sample ID	**Squares**	***Dictyoconus***	**Miliolid**	**Other Foram**	**Red Algae**	**Other Green Algae**	**Dasyclad Algae**
M1-1(1)	72	11.11%	4.17%	1.39%	0.00%	0.00%	2.78%
M1-1(2)	107	8.41%	8.41%	0.93%	0.00%	6.54%	13.08%
M1-2(1)	60	28.33%	26.67%	0.00%	0.00%	23.33%	25.00%
M1-2(2)	61	11.48%	1.64%	0.00%	0.00%	24.59%	8.20%
M1-2(3)	93	11.83%	13.98%	1.08%	2.16%	7.53%	5.38%
M1-2(4)A	86	4.65%	2.33%	0.00%	1.16%	9.30%	1.16%
M1-2(4)B	96	6.25%	2.08%	0.00%	1.04%	4.17%	1.04%
M1-2(5)	195	9.23%	4.10%	0.00%	1.54%	3.59%	0.51%
M1-3(1)	100	26.00%	8.00%	0.00%	7.00%	5.00%	12.00%
M1-3(2)	93	4.30%	1.08%	0.00%	1.08%	0.00%	3.23%
M1-3(3)	99	2.02%	0.00%	0.00%	2.02%	2.02%	0.00%
M1-4(1)	133	0.75%	3.76%	0.00%	0.00%	0.00%	1.50%
M1-4(2)	78	0.00%	1.28%	0.00%	1.28%	2.56%	1.28%
M1-4(3)	207	0.00%	0.48%	0.00%	0.00%	0.48%	0.00%
M1-4(4)	171	1.17%	2.34%	0.00%	0.00%	1.75%	0.00%
M1-4(5)	95	0.00%	1.05%	0.00%	2.11%	3.16%	0.00%
M1-5(1)	211	0.00%	0.00%	0.47%	0.00%	2.37%	0.00%
M1-5(3)	113	0.00%	0.00%	0.00%	0.88%	0.00%	2.65%
M1-5(4)	152	0.00%	1.97%	0.00%	1.32%	0.00%	0.00%
M1-5(5)	165	0.00%	0.00%	0.00%	0.00%	1.21%	0.00%
M1-6(1)	107	0.93%	1.87%	0.93%	2.80%	0.93%	3.74%
M1-6(2)	96	0.00%	0.00%	0.00%	0.00%	4.17%	0.00%
M1-6(3)	85	0.00%	0.00%	0.00%	0.00%	4.71%	1.18%
M1-6(4)	83	0.00%	1.20%	0.00%	0.00%	0.00%	0.00%
M2-1(1)	88	1.14%	0.00%	0.00%	0.00%	0.00%	0.00%
M2-1(3)	102	0.00%	0.00%	0.00%	0.00%	0.00%	0.98%
M2-1(4)	96	1.04%	2.08%	0.00%	1.04%	1.04%	3.13%
M2-1(5)	96	1.04%	6.25%	0.00%	6.25%	1.04%	2.08%
M2-2(1)	135	0.00%	0.74%	0.00%	1.48%	0.00%	0.00%
M2-2(2)	84	0.00%	0.00%	0.00%	2.38%	1.19%	2.38%
M2-2(3)	84	0.00%	0.00%	0.00%	7.14%	1.19%	5.95%

Table A3. The distribution of the forams and algae in the Edwards Limestone- continued.

Sample ID	**Squares**	***Dictyoconus***	**Miliolid**	**Other Foram**	**Red Algae**	**Other Green Algae**	**Dasyclad Algae**
M2-2(4)	96	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
M2-2(5)	96	0.00%	1.04%	0.00%	1.04%	0.00%	0.00%
M2-2(6)	96	0.00%	4.17%	0.00%	4.17%	0.00%	3.13%
M2-3(1)	225	1.78%	2.67%	0.00%	8.00%	0.00%	3.56%
M2-3(2)	96	0.00%	0.00%	0.00%	4.16%	3.13%	5.21%
M2-3(3)	225	0.00%	0.00%	0.00%	1.33%	0.00%	0.00%
M2-3(4)	96	0.00%	3.13%	0.00%	2.08%	2.08%	2.08%
M2-3(5)	225	0.00%	0.89%	0.00%	1.78%	0.00%	0.89%
M2-4(1)	128	0.00%	3.91%	0.78%	1.56%	0.00%	1.56%
M2-4(2)	126	0.00%	0.00%	0.00%	1.58%	0.00%	0.79%
M2-4(3)	119	0.00%	2.52%	0.00%	1.68%	0.00%	0.84%
M2-4(4)	156	0.00%	1.28%	0.00%	1.92%	1.28%	0.00%
M2-5(2)	95	0.00%	0.00%	0.00%	0.00%	1.05%	0.00%
M2-5(3)	173	0.00%	1.73%	0.00%	4.62%	0.58%	0.00%
M2-5(4)	225	0.89%	1.33%	0.00%	4.45%	0.44%	0.00%
M2-5(5)	197	1.52%	2.03%	0.00%	0.00%	0.51%	0.51%
M2-6(1)	N/A	N/A	N/A	N/A	N/A	N/A	N/A
M2-6(2)	180	1.67%	0.00%	0.00%	7.22%	0.00%	0.00%
M2-6(3)	217	0.00%	0.46%	0.00%	0.92%	0.00%	1.38%
M2-6(4)	N/A	N/A	N/A	N/A	N/A	N/A	N/A
M2-6(5)	225	0.44%	1.78%	0.89%	6.22%	0.00%	0.44%
M2-7(1)	96	0.00%	2.08%	0.00%	7.29%	0.00%	0.00%
M2-7(2)	218	0.92%	0.92%	0.00%	9.17%	0.46%	1.38%
M2-7(3)	224	1.34%	0.89%	0.00%	4.92%	0.45%	3.13%
M2-7(4)	116	0.86%	1.72%	0.00%	7.76%	0.86%	8.62%
M2-8(1)	108	0.00%	0.00%	0.00%	4.63%	0.93%	1.85%
M2-8(2)	225	0.00%	0.89%	0.00%	4.89%	0.00%	0.89%
M2-8(3)	225	1.33%	2.67%	0.00%	2.22%	0.00%	2.22%
M2-8(4)	108	0.93%	0.00%	0.00%	1.85%	0.00%	0.93%
M2-9(1)	108	1.85%	0.93%	0.00%	6.48%	0.93%	1.85%
M2-9(2)	222	1.80%	0.00%	0.00%	0.90%	0.00%	1.35%
M2-9(3)	96	6.25%	8.33%	0.00%	7.30%	1.04%	3.13%
M2-9(4)	96	0.00%	2.08%	0.00%	1.04%	0.00%	0.00%
W1-1(1)	223	5.38%	1.79%	2.24%	5.38%	0.00%	4.04%
W1-1(2)	108	1.85%	2.78%	0.00%	3.70%	0.00%	17.59%
W1-2(1)	154	1.30%	1.30%	0.00%	3.90%	3.25%	1.95%
W1-2(2)	96	1.04%	3.13%	1.04%	10.42%	1.04%	0.00%
W1-2(3)	96	3.13%	0.00%	0.00%	2.08%	0.00%	4.17%

Table A3. The distribution of the forams and algae in the Edwards Limestone- continued.

Sample ID	**Squares**	***Dictyoconus***	**Miliolid**	**Other Foram**	**Red Algae**	**Other Green Algae**	**Dasyclad Algae**
W1-3(1)	216	0.93%	0.93%	0.00%	2.78%	0.00%	0.93%
W1-3(2)	156	3.21%	1.28%	1.92%	3.84	0.64%	2.56%
W1-3(3)	225	4.00%	0.00%	0.44%	1.78%	0.44%	3.11%
W2-2(1)	157	0.00%	0.00%	0.00%	2.55%	0.00%	0.00%
C1-1(3)	215	1.40%	0.93%	0.00%	2.33%	0.47%	1.40%
C1-2(1)	105	2.86%	0.00%	0.00%	3.81%	0.00%	1.90%
C1-2(2)	134	2.24%	0.75%	0.00%	0.00%	0.00%	0.75%
C1-3(1)	96	1.04%	1.04%	0.00%	0.00%	0.00%	2.08%
C2-1(1)	179	2.79%	1.12%	0.00%	4.47%	0.00%	1.68%

Figure A5. Composite panoramic 1 of 6: South end of the Mosheim-1 section. Composite panoramic series proceeds from South to North. Vertical sampling intervals were .6m.

Figure A6. Composite panoramic 2 of 6: Mosheim-1 sampling locations 12m from previous. Vertical sampling intervals were .6m.

Figure A7. Composite panoramic 3 of 6: Mosheim-1 sampling locations 7m from previous. Vertical sampling intervals were .6m.

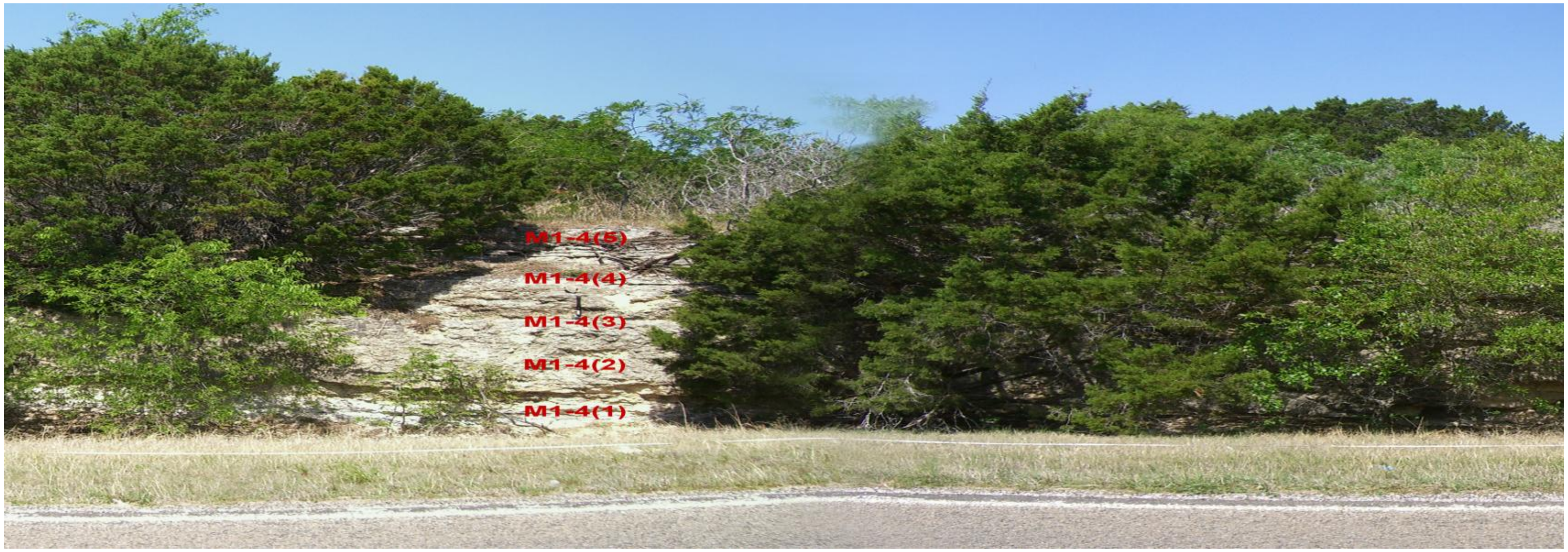

Figure A8. Composite panoramic 4 of 6: Mosheim-1 sampling locations 8m from previous. Vertical sampling intervals were .6m.

Figure A9. Composite panoramic 5 of 6: Mosheim-1 sampling locations. Column 5 is 10.8m from previous. Column 6 is 10.4m from column 5. Vertical sampling intervals were .6m for column 5 and 0.3m for column 6.

Figure A10. Composite panoramic 6 of 6: North end of Mosheim-1 location.

Figure A11. Composite panoramic 1of 10: Mosheim-2 sampling locations on the East end of the outcrop. Composite panoramic series proceeds from South to North end of the section. Column 1 is 19.8m from Column 2. Vertical sampling intervals were .6m.

Figure A12. Composite panoramic 2 of 10: Mosheim-2 sampling locations. Column 3 is 31m from Column 2. Vertical sampling intervals were .6m.

Figure A13. Composite panoramic 3of 10: Mosheim-2 between columns 3 and 4.

Figure A14. Composite panoramic 4of 10: Mosheim-2 sampling locations. Column 4 is 21.6m from Column 3. Vertical sampling intervals were .6m.

Figure A15. Composite panoramic 5of 10: Mosheim-2 sampling locations. Column 5 is 32m from Column 4. Vertical sampling intervals were .6m.

Figure A16. Composite panoramic 6 of 10: Mosheim-2 sampling locations. Column 6 is 19.8m from Column 4. Vertical sampling intervals were .6m.

Figure A17. Composite panoramic 7 of 10: Mosheim-2 sampling locations. Column 7 is 26.5m from Column 6. Vertical sampling intervals were .6m.

Figure A18. Composite panoramic 8 of 10: of Mosheim-2 between columns 7 and 8.

Figure A19. Composite panoramic 9 of 10: Mosheim-2 sampling locations. Column 8 is 24.4m from Column 7. Vertical sampling intervals were .6m.

Figure A20. Composite panoramic 10 of 10: Mosheim-2 sampling locations at West end of the outcrop. Column 9 is 30.8m from Column 8. Vertical sampling intervals were .6m.

APPENDIX B

Field Data from the Coral Reefs of Bermuda

Table B1. Common biota and grains observed in the sediment of the patch, rim, and terrace reefs of Bermuda.

Sample ID	**Location**	**Coordinates**	**Depth (m)**	**Grain Size**	**Dominant Grains**
PR-1(1)	Patch Reef 1	32°22'9.69"N 64°44'45.44"W	6	very fine sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, other green algae
PR-1(2)	Patch Reef 1	32°22'9.69"N 64°44'45.44"W	6	very fine sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, other green algae
PR-1(3)	Patch Reef 1	32°22'9.69"N, 64°44'45.44"W	9	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes
PR-1(4)	Patch Reef 1	32°22'9.69"N 64°44'45.44"W	9	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, other green algae

Table B1. Common biota and grains observed in the sediment of the patch, rim, and terrace reefs of Bermuda.-continued

Sample ID	Location	Coordinates	Depth (m)	Grain Size	Dominant Grains
PR-2(1)	Patch Reef 2	32°22'9.69"N 64°44'45.44"W	9	fine sand to coarse sand	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes
PR-2(2)	Patch Reef 2	32°22'9.69"N 64°44'45.44"W	12	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, serpulid worm tubes
PR-3(1)	Patch Reef 3	32°25'33.16"N 64°43'47.21"W	6	fine sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes
PR-3(2)	Patch Reef 3	32°25'33.16"N 64°43'47.21"W	6	fine sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes

Table B1. Common biota and grains observed in the sediment of the patch, rim, and terrace reefs of Bermuda.-continued

Sample ID	Location	Coordinates	Depth (m)	Grain Size	Dominant Grains
RR-1(1)	Rim Reef 1	32°28'27.12" N 64°46'6.85" W	6	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, other green algae
RR-1(2)	Rim Reef 1	32°28'27.12" N 64°46'6.85" W	9	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, miliolid forams, rotalids, , *Halimeda*, coralline red algae, serpulid worm tubes
RR-2(1)	Rim Reef 2	32°28'18.84" N 64°46'33.50" W	12	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes
RR-3(1)	Rim Reef 3	32°19'38.59" N 64°41'8.21"W	9	medium sand to gravel	bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, other forams, *Halimeda*, coralline red algae, serpulid worm tubes, other green algae
RR-3(2)	Rim Reef 3	32°19'38.59" N 64°41'8.21"W	9	medium sand to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, serpulid worm tubes

Table B1. Common biota and grains observed in the sediment of the patch, rim, and terrace reefs of Bermuda.-continued

Sample ID	**Location**	**Coordinates**	**Depth (m)**	**Grain Size**	**Dominant Grains**
RR-4(2)	Rim Reef 4	32°19'38.59"N 64°41'8.21"W	12	medium sand-sized to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, detrital sediment
RR-4(1)	Rim Reef 4	32°19'38.59"N 64°41'8.21"W	12	medium sand-sized to gravel	corals, bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, other forams, *Halimeda*, coralline red algae, triaxon sponge spicules, serpulid worm tubes, other green algae, detrital sediment
TR-1(1)	Terrace Reef	32°28'57.58" N 64°46'3.98" W	18	coarse sand to gravel	bivalves, *Homotrema rubrum*, echinoderms, gastropods, arthropods, miliolid forams, rotalids, *Halimeda*, coralline red algae, serpulid worm tubes

Table B2. The results of five coral and algal transects from the patch reefs near North Rock, Bermuda; Tr = transect.

Category	Tr 1	Tr 2	Tr 3	Tr 4	Tr 5	Sum	%Tr 1	%Tr 2	%Tr 3	%Tr 4	%Tr 5	Mean	Error
Bare Rock	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubble	9	2	32	2	13	58	3.00	0.67	10.67	0.67	4.33	3.87	1.84
Sand/sediment	37	40	28	1	18	124	12.33	13.33	9.33	0.33	6.00	8.27	2.36
Gaps	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Madracis sp.	2	8	2	0	0	12	0.67	2.67	0.67	0.00	0.00	2.40	0.49
Montastrea franksii	41	53	10	46	48	198	13.67	17.67	3.33	15.33	16.00	39.60	2.55
Montastrea cavernosa	10	0	17	16	12	55	3.33	0.00	5.67	5.33	4.00	11.00	1.01
Diploria strigosa	9	20	5	30	11	75	3.00	6.67	1.67	10.00	3.67	15.00	1.49
Diploria labyrinthiformis	9	1	16	5	32	63	3.00	0.33	5.33	1.67	10.67	12.60	1.82
Porites astreoides	10	11	8	16	3	48	3.33	3.67	2.67	5.33	1.00	9.60	0.70
Porites porites	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Favia fragum	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stephanocoenia mich.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siderastrea sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia fragilis	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scolymia sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Meandrina meandrites	0	0	3	0	0	3	0.00	0.00	1.00	0.00	0.00	0.60	0.20
Fleshy Algae	34	18	150	85	94	381	11.33	6.00	50.00	28.33	31.33	76.20	7.82
Turf Algae	107	96	6	83	54	346	35.67	32.00	2.00	27.67	18.00	69.20	6.04
Encrusting Calc. Algae	0	20	0	0	0	20	0.00	6.67	0.00	0.00	0.00	4.00	1.33
Millepora alcicornis	3	5	10	6	2	26	1.00	1.67	3.33	2.00	0.67	5.20	0.46
Sea Fan	15	1	6	8	0	30	5.00	0.33	2.00	2.67	0.00	6.00	0.90
Sea Rod	7	6	3	1	10	27	2.33	2.00	1.00	0.33	3.33	5.40	0.52
Sea Plume	5	0	0	0	0	5	1.67	0.00	0.00	0.00	0.00	1.00	0.33
Sponge spp.	1	0	2	0	1	4	0.33	0.00	0.67	0.00	0.33	0.80	0.12
Sea Cucumber	0	0	2	1	0	3	0.00	0.00	0.67	0.33	0.00	0.60	0.13
Unknown	1	19	0	0	2	22	0.33	6.33	0.00	0.00	0.67	4.40	1.22
Totals	**300**	**300**	**300**	**300**	**300**	**1500**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	-	-

Table B3. The results of five coral and algal transects from the rim reefs near North Rock, Bermuda;Tr = transect.

Category	**Tr 1**	**Tr 2**	**Tr 3**	**Tr 4**	**Tr 5**	**Sum**	**% Tr 1**	**%Tr 2**	**% Tr 3**	**% Tr 4**	**% Tr 5**	**Mean**	**Error**
Bare Rock	0	0	0	0	1	1	0.00	0.00	0.00	0.00	0.33	0.20	0.07
Rubble	0	0	0	7	0	7	0.00	0.00	0.00	2.33	0.00	0.47	0.47
Sand/sediment	0	8	1	13	4	26	0.00	2.67	0.33	4.33	1.33	1.73	0.80
Gaps	0	43	6	0	7	56	0.00	14.33	2.00	0.00	2.33	3.73	2.69
Madracis sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Montastrea franksii	30	19	38	15	15	117	10.00	6.33	12.67	5.00	5.00	7.80	1.52
Montastrea cavernosa	14	5	7	1	7	34	4.67	1.67	2.33	0.33	2.33	2.27	0.70
Diploria strigosa	32	24	17	32	64	169	10.67	8.00	5.67	10.67	21.33	11.27	2.68
Diploria labyrinthiformis	28	19	31	19	24	121	9.33	6.33	10.33	6.33	8.00	8.07	0.80
Porites astreoides	8	11	8	7	5	39	2.67	3.67	2.67	2.33	1.67	2.60	0.32
Porites porites	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Favia fragum	0	1	0	0	0	1	0.00	0.33	0.00	0.00	0.00	0.07	0.07
Stephanocoenia mich.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siderastrea sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia fragilis	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scolymia sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Meandrina meandrites	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fleshy Algae	104	67	129	105	77	482	34.67	22.33	43.00	35.00	25.67	32.13	3.68
Turf Algae	33	65	49	56	75	278	11.00	21.67	16.33	18.67	25.00	18.53	2.38
Encrusting Calc. Algae	0	13	0	1	0	14	0.00	4.33	0.00	0.33	0.00	0.93	0.85
Millepora alcicornis	12	2	3	1	0	18	4.00	0.67	1.00	0.33	0.00	1.20	0.72
Sea Fan	1	2	0	0	0	3	0.33	0.67	0.00	0.00	0.00	0.20	0.13
Sea Rod	30	20	3	3	15	71	10.00	6.67	1.00	1.00	5.00	4.73	1.72
Sea Plume	8	1	8	40	4	61	2.67	0.33	2.67	13.33	1.33	4.07	2.36
Sponge spp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown	0	0	0	0	2	2	0.00	0.00	0.00	0.00	0.67	0.13	0.13
Totals	**300**	**300**	**300**	**300**	**300**	**1500**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**-**	**-**

Table B4. The results of five coral and algal transects from the terrace reefs near North Rock, Bermuda; Tr = transect.

Category	**Tr 1**	**Tr 2**	**Tr 3**	**Tr 4**	**Tr 5**	**Sum**	**%Tr 1**	**%Tr 2**	**%Tr 3**	**%Tr 4**	**%Tr 5**	**Mean**	**Error**
Bare Rock	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubble	1	0	0	0	0	1	0.33	0.00	0.00	0.00	0.00	0.07	0.07
Sand/sediment	1	3	0	0	1	5	0.33	1.00	0.00	0.00	0.33	0.33	0.18
Gaps	2	12	10	0	2	26	0.67	4.00	3.33	0.00	0.67	1.73	0.81
Madracis sp.	0	0	0	0	1	1	0.00	0.00	0.00	0.00	0.33	0.07	0.07
Montastrea franksii	39	44	11	18	10	122	13.00	14.67	3.67	6.00	3.33	8.13	2.39
Montastrea cavernosa	0	5	19	11	7	42	0.00	1.67	6.33	3.67	2.33	2.80	1.06
Diploria strigosa	21	29	20	30	30	130	7.00	9.67	6.67	10.00	10.00	8.67	0.75
Diploria labyrinthiformis	18	21	7	22	19	87	6.00	7.00	2.33	7.33	6.33	5.80	0.90
Porites astreoides	1	1	1	5	5	13	0.33	0.33	0.33	1.67	1.67	0.87	0.33
Porites porites	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Favia fragum	1	0	0	0	0	1	0.33	0.00	0.00	0.00	0.00	0.07	0.07
Stephanocoenia mich.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Siderastrea sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agaricia fragilis	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scolymia sp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Meandrina meandrites	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fleshy Algae	91	112	102	182	186	673	30.33	37.33	34.00	60.67	60.00	44.47	6.57
Turf Algae	82	27	107	9	29	254	27.33	9.00	35.67	3.00	9.67	16.93	6.20
Encrusting Calc. Algae	14	11	0	0	0	25	4.67	3.67	0.00	0.00	0.00	1.67	1.03
Millepora alcicornis	0	5	0	0	2	7	0.00	1.67	0.00	0.00	0.67	0.47	0.33
Sea Fan	1	0	0	0	0	1	0.33	0.00	0.00	0.00	0.00	0.07	0.07
Sea Rod	11	3	9	0	0	23	3.67	1.00	3.00	0.00	0.00	1.53	0.76
Sea Plume	17	27	14	23	12	93	5.67	9.00	4.67	7.67	4.00	6.20	0.93
Sponge spp.	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown	0	0	0	0	2	2	0.00	0.00	0.00	0.00	0.67	0.13	0.13
Totals	**300**	**300**	**300**	**300**	**300**	**1471**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**-**	**-**

Table B5. Bermuda reef sediment point count data. PR=patch reef, RR=rim reef, TR=terrace reef.

Sample ID	**PR-1(1)**	**PR-1(2)**	**PR-1(3)**	**PR-1(4)**	**PR-2(1)**	**PR-2 (2)**	**PR-3(1)**	**PR-3(2)**	**RR-1(1)**	**RR-(2)**	**RR-2(1)**	**RR-3 (1)**	**RR-3(2)**	**RR-4 (1)**	**RR-4 (2)**	**TR-1(1)**
Coral	3	2	2	4	3	4	2	5	5	5	6	0	4	8	9	0
Bivalve	37	43	31	35	28	36	39	38	39	34	38	27	18	43	37	22
Homotrema rubrum	11	7	6	1	19	34	14	4	26	44	32	46	49	29	40	62
Echinoderm	6	5	2	2	10	13	3	2	3	10	7	7	5	4	5	14
Gastropod	13	13	4	3	1	2	5	2	4	4	3	8	3	1	2	5
Arthropod	0	1	2	1	2	2	2	6	3	0	0	1	3	2	1	1
Archaias angulatus	16	10	17	7	2	5	8	3	5	11	2	10	12	8	5	0
Peneropolis Proteus	6	3	4	3	0	0	1	3	0	1	0	1	0	0	1	0
Other Miliolid	5	8	8	9	3	8	9	5	2	1	4	2	2	2	1	5
Rotalid	4	8	5	2	14	11	6	5	4	4	4	0	2	4	3	1
Other Foram	4	2	2	1	5	2	0	3	1	0	0	0	0	2	1	0
Halimeda	34	57	71	72	48	30	63	62	25	23	8	35	44	14	10	2
Coralline Red	39	27	40	53	55	49	35	49	73	60	88	54	53	68	66	87
Sponge	13	7	3	4	4	0	9	8	1	0	4	0	0	1	0	0
Serpulids	8	6	3	2	3	4	4	5	2	3	1	3	3	1	2	0
Green Alg.	1	1	0	1	3	0	0	0	4	0	1	5	2	0	3	1
Detrital	0	0	0	0	0	0	0	0	3	0	2	1	0	13	14	0
Unknown	100	101	94	101	132	178	189	160	137	170	227	147	146	205	153	130
Total	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**	**200**

Table B6. The distribution of the most common constituents of the patch, rim, and terrace reefs of Bermuda. The relative percentages were calculated using the point count data from Table B4. PR=patch reef, RR=rim reef, TR=terrace reef. The first number of the sample ID is the depth (ft.) of the sample taken.

Sample ID	**PR-1(1)**	**PR-1(2)**	**PR-1(3)**	**PR-1(4)**	**PR-2(1)**	**PR-2 (2)**	**PR-3(1)**	**PR-3(2)**	**RR-1(1)**	**RR-1(2)**	**RR-2(1)**	**RR-3 (1)**	**RR-3(2)**	**RR-4 (1)**	**RR-4 (2)**	**TR-1(1)**
Coral	1.5%	1.0%	1.0%	2.0%	1.5%	2.0%	1.0%	2.5%	2.5%	2.5%	3.0%	0.0%	2.0%	4.0%	4.5%	0.0%
Bivalve	18.5%	21.5%	15.5%	17.5%	14.0%	18.0%	19.5%	19.0%	19.5%	17.0%	19.0%	13.5%	9.0%	21.5%	18.5%	11.0%
Homotrema rubrum	5.5%	3.5%	3.0%	0.5%	9.5%	17.0%	7.0%	2.0%	13.0%	22.0%	16.0%	23.0%	24.5%	14.5%	20.0%	31.0%
Echinoderm	6.0%	5.0%	2.0%	2.0%	10.0%	13.0%	3.0%	2.0%	3.0%	10.0%	7.0%	7.0%	5.0%	4.0%	5.0%	14.0%
Gastropod	6.5%	6.5%	2.0%	1.5%	0.5%	1.0%	2.5%	1.0%	2.0%	2.0%	1.5%	4.0%	1.5%	0.5%	1.0%	2.5%
Arthropod	0.0%	0.5%	1.0%	0.5%	1.0%	1.0%	1.0%	3.0%	1.5%	0.0%	0.0%	0.5%	1.5%	1.0%	0.5%	0.5%
Archaias angulatus	8.0%	5.0%	8.5%	3.5%	1.0%	2.5%	4.0%	1.5%	2.5%	5.5%	1.0%	5.0%	6.0%	4.0%	2.5%	0.0%
Peneropolis Proteus	3.0%	1.5%	2.0%	1.5%	0.0%	0.0%	0.5%	1.5%	0.0%	0.5%	0.0%	0.5%	0.0%	0.0%	0.5%	0.0%
Other Miliolid	2.0%	1.0%	1.0%	0.5%	2.5%	1.0%	0.0%	1.5%	0.5%	0.0%	0.0%	0.0%	0.0%	1.0%	0.5%	0.0%
Rotalid	2.0%	4.0%	2.5%	1.0%	7.0%	5.5%	3.0%	2.5%	2.0%	2.0%	2.0%	0.0%	1.0%	2.0%	1.5%	0.5%
Other Foram	2.0%	1.0%	1.0%	0.5%	2.5%	1.0%	0.0%	1.5%	0.5%	0.0%	0.0%	0.0%	0.0%	1.0%	0.5%	0.0%
Halimeda	17.0%	28.5%	35.5%	36.0%	24.0%	15.0%	31.5%	31.0%	12.5%	11.5%	4.0%	17.5%	22.0%	7.0%	5.0%	1.0%
Coralline Red Algae	19.5%	13.5%	20.0%	26.5%	27.5%	24.5%	17.5%	24.5%	36.5%	30.0%	44.0%	27.0%	26.5%	34.0%	33.0%	43.5%
Sponge	6.5%	3.5%	1.5%	2.0%	2.0%	0.0%	4.5%	4.0%	0.5%	0.0%	2.0%	0.0%	0.0%	0.5%	0.0%	0.0%
Serpulids	4.0%	3.0%	1.5%	1.0%	1.5%	2.0%	2.0%	2.5%	1.0%	1.5%	0.5%	1.5%	1.5%	0.5%	1.0%	0.0%
Green Algae	0.5%	0.5%	0.0%	0.5%	1.5%	0.0%	0.0%	0.0%	2.0%	0.0%	0.5%	2.5%	1.0%	0.0%	1.5%	0.5%
Detrital	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1.5%	0.0%	1.0%	0.5%	0.0%	6.5%	7.0%	0.0%

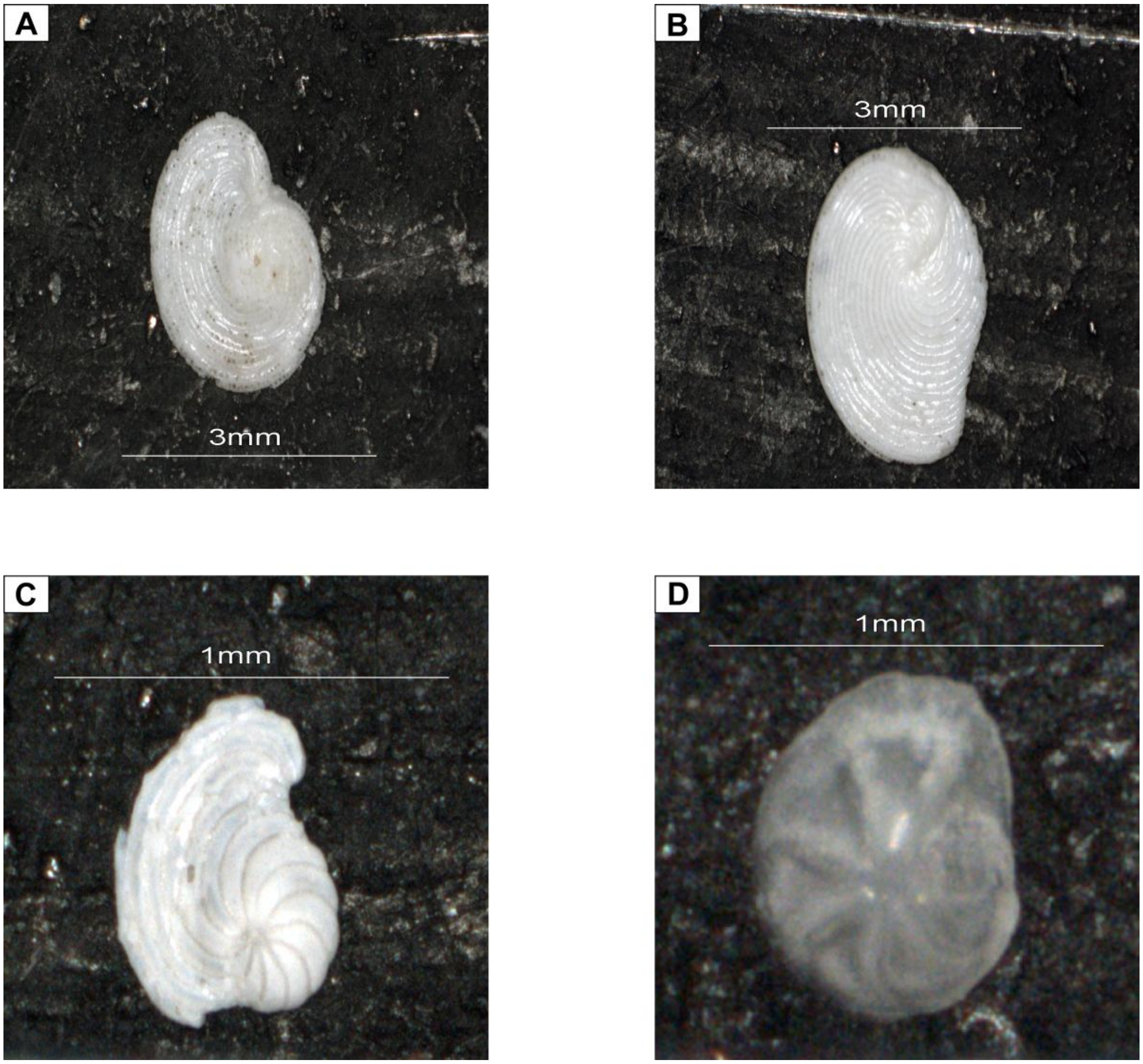

Figure B1. Common biota in the reef sediment of Bermuda: A) *Archaias angulatus, B)* weathered *Archaias angulatus*, C) *Peneropolis proteus*, D) *Eponides repandus.*

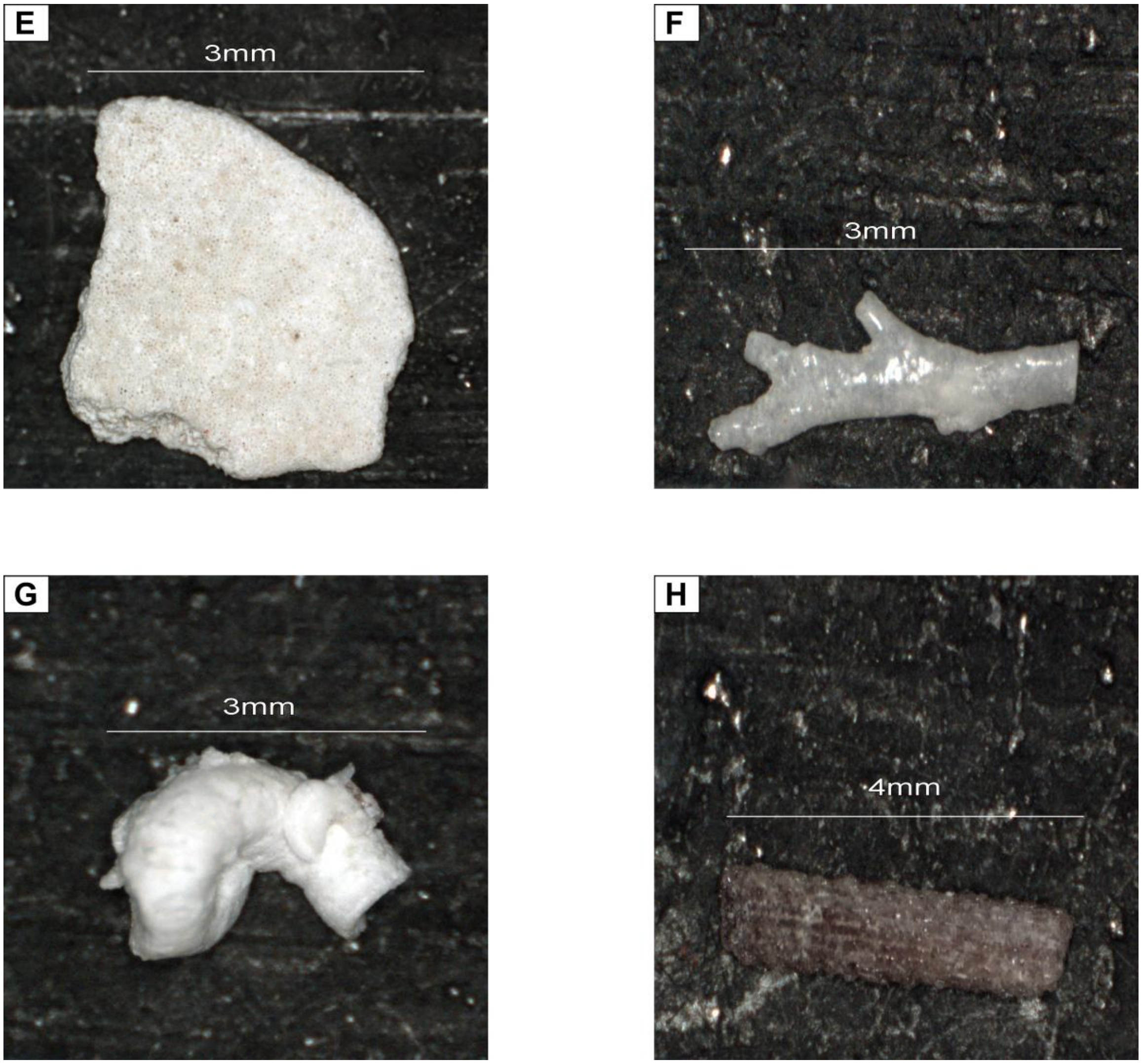

Figure B2. Common biota in the reef sediment of Bermuda: E) *Halimeda* algae plate, F) coralline red algae, G) serpulid worm tube, H) echinoderm spine.

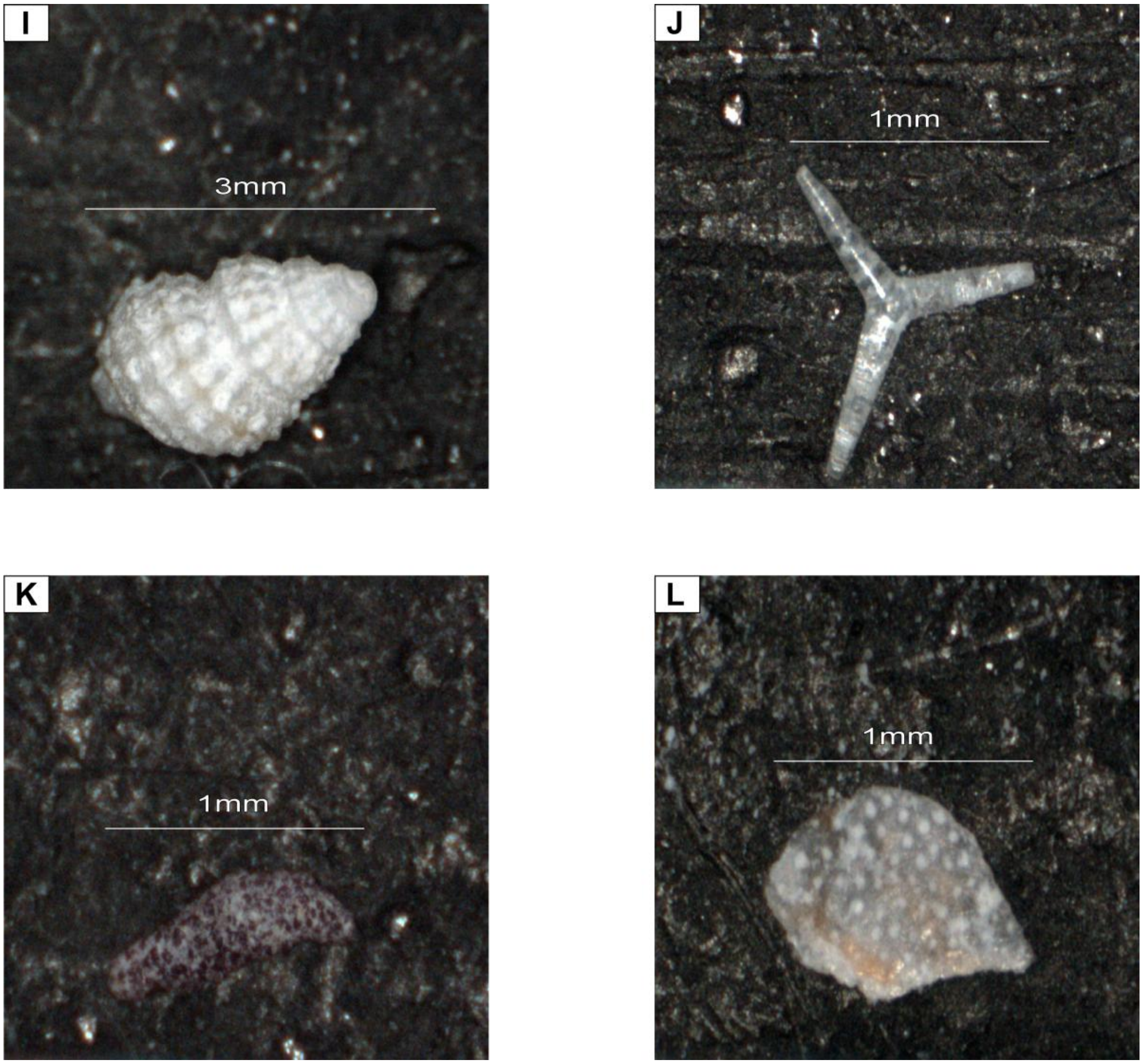

Figure B3. Common biota in the reef sediment of Bermuda: I) gastropod, J) triaxon sponge spicule, K) Gorgonian spicule, L) ostracode.

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