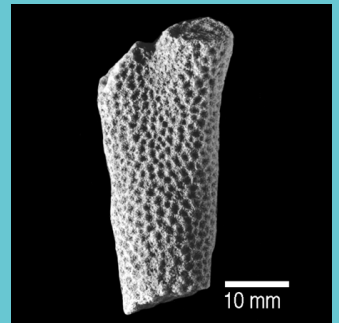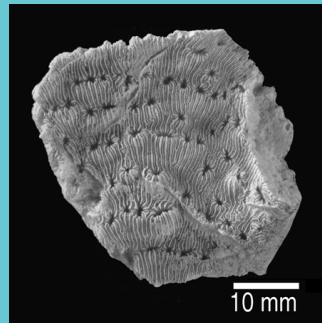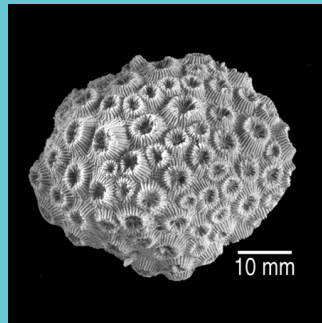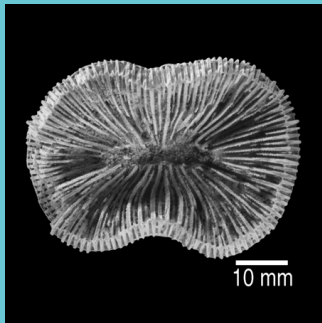# Paleoecology and Sedimentology of Ancient Coral Reefs in the Dominican Republic

Universidad Autónoma de Santo Domingo
March 16-17, 2006

Paleoecología y Sedimentología de Arrecifes Coralinos Fosiles en la República Dominicana

Paleoecology and Sedimentology of Fossil Coral Reefs in the Dominican Republic

Workshop Instructors:

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Dr. James Klaus (University of Miami)

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Dr. Francisco Geraldes (Universidad Autónoma de Santo Domingo)

Objectives of the Workshop

Our goal is to show how studies of fossil reef systems, thousands to millions of year old, are relevant to addressing modern-day issues in reef conservation. During the lecture day we will focus on questions involving past extinctions and faunal turnover on coral reefs and their relationship to changes in climate and tectonics. We will focus on the evaluation of community change on Caribbean reefs during an episode of biotic turnover that occurred between 6-1 Ma in association with the closure of the Central American isthmus and the onset of Northern Hemisphere glaciations. An overview of our project on fossil reefs of the northern Dominican Republic will show how our work is relevant to understanding the biodiversity of modern Caribbean reef systems. A fieldtrip to the uplifted Holocene reefs of Enriquillo Valley will provide a hands-on example of changes in reef communities.

Objectivos de la Taller

Nuestro objetivo es demonstrar como el estudio de sistemas arrecifes fósiles es relevante para resolver problemas en conservación de arrecifes modernos. Durante el dia de clases nos enfocaremos en preguntas que involucran extinciones del pasado, cambio de fauna dominante en arrecifes y su relación con cambios climaticos y tectonicos globales y regionales. Nos enfocaremos en la evaluación de arrecifes del Caribe durante un episodio de cambio ocurrido entre 6-1 Ma, y su relación con el cierre del istmo Centroamericano y el inicio de las glaciaciones del hemisfero norte. Un vistazo a nuestro proyecto en arrecifes fósiles del norte de la Republica Dominicana mostrará la relevancia de nuestro trabajo para comprender la biodiversidad de los sistemas arrecifes modernos en el Caribe. Una salida de campo a los arrecifes emergidos del Holoceno en el valle Enriquillo proveerá con ejemplos de cambios en comunidades arrecifales.

Acknowledgements

Agradecimientos

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9:15 – 9:45	Geology and Tectonics of the Dominican Republic and Greater Caribbean Region
9:45 – 10:00	Break
10:00 – 10:30	General Ecology of Coral Reefs
10:30 – 11:00	Extinction Events on Caribbean Reefs: The Past 10 Million Years
11:00 – 12:00	Exercise: Interpreting Fossil Reef Assemblages
12:00 – 1:00	Lunch
1:00 – 2:00	Evolutionary History of Caribbean and Pacific reefs
2:00 – 2:30	Reefs of the northern Dominican Republic: Geologic Setting
2:30 – 3:00	Reefs of the northern Dominican Republic: Corals-I
3:00 – 3:30	Reefs of the northern Dominican Republic: Corals-II
3:30 – 4:00	Question/Answer (refreshments)
4:00 – 5:00	Holocene Reefs of the Enriquillo Valley and Fieldtrip Preparation
8:00 – 10:00	Dinner and Reception

Fieldtrip Itinerary – Friday March 17
(see figure 20 for a map of localities)

7:30 – 8:00   Meet at Bus (coffee, juice and rolls)

8:00   Bus Departs for Lago Enriquillo

Stop 1   Scenic Overlook of Lago Enriquillo (approximately 150 km from UASD)

Stop 2   Cervicornis Quarry (8 km west of Duvergé)

Stop 3   Flood Plain Deposits (exposures in Caño Ramillo)

Stop 4   Lunch near Los Rios (lunch provided to all students)

Stop 5   Cañada Honda (4 km west of Los Rios)

Stop 6   Brief stop for refreshments

Return to Universidad Autónoma de Santo Domingo

Geology of the Caribbean

The Caribbean region is geologically complex. The relatively small Caribbean Plate (Figure 1) interacts with the surrounding North American, Cocos, Nazca and South American plates through a variety of plate boundary interactions (Draper et al., 1994). There is active subduction along the lesser Antilles and Central America, Strike-slip motions on the northern and southern boundaries, and sea floor spreading in the Cayman Trough.

The Caribbean Plate is moving eastwards with respect to both North and South America at a rate of about 1 to 2 cm yr^{-1} (Mann et al., 1990). The eastward movement of the Caribbean Plate has resulted in subduction of the Atlantic Ocean crust under the eastern margin of the Caribbean, producing the lesser Antilles island arc system. Eastward motions of the Pacific and Cocos Plates with respect to the Caribbean and North America have resulted in subduction of these plates beneath the western margin of the Caribbean in Central America.
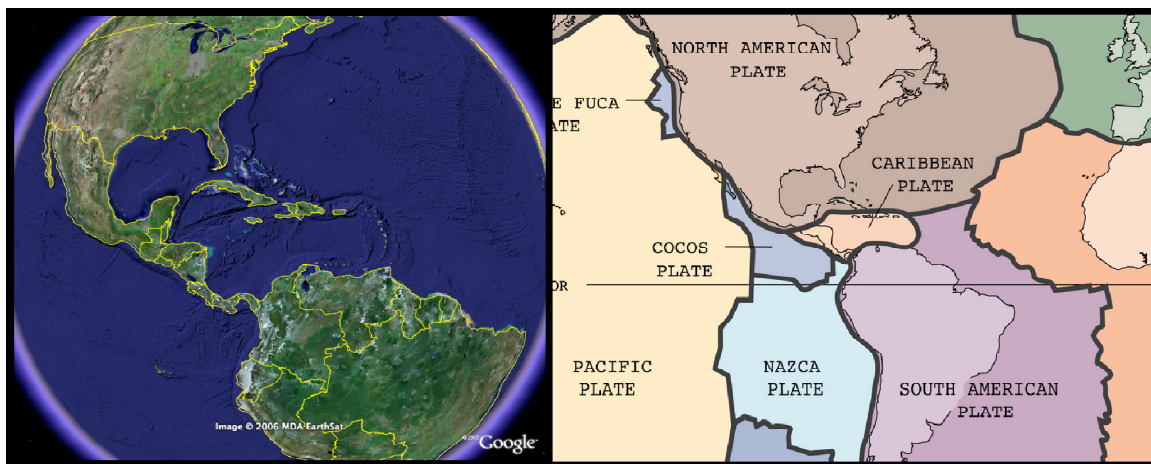
Figure 1 – A.) Satellite image of the Caribbean region with Hispaniola centrally located. B.) Map showing the Caribbean and surrounding tectonic plates.

Figure 2 provides a summary of an evolved plate tectonic model for the Caribbean by Pindell et al. (1994). One hundred and sixty million years ago, the super continent Pangea had just recently started to separate, and the Proto-Caribbean Seaway was beginning to emerge. At 120Ma the region looked much as it does today. However, much was about to change. By 90 Ma the Proto-Caribbean Seaway was being subducted beneath and consumed by what was to become the Caribbean plate. While the Caribbean plate continued to migrate eastwardly, by 70 Ma the Costa Rica – Panama island arc had emerged. By 35 Ma the Caribbean region had nearly assumed its modern configuration. Central America had spanned the gap between North and South America, and strike-slip motion characterized the northern and southern boundaries of the Caribbean. By 10 Ma the Caribbean region had nearly assumed its modern configuration.
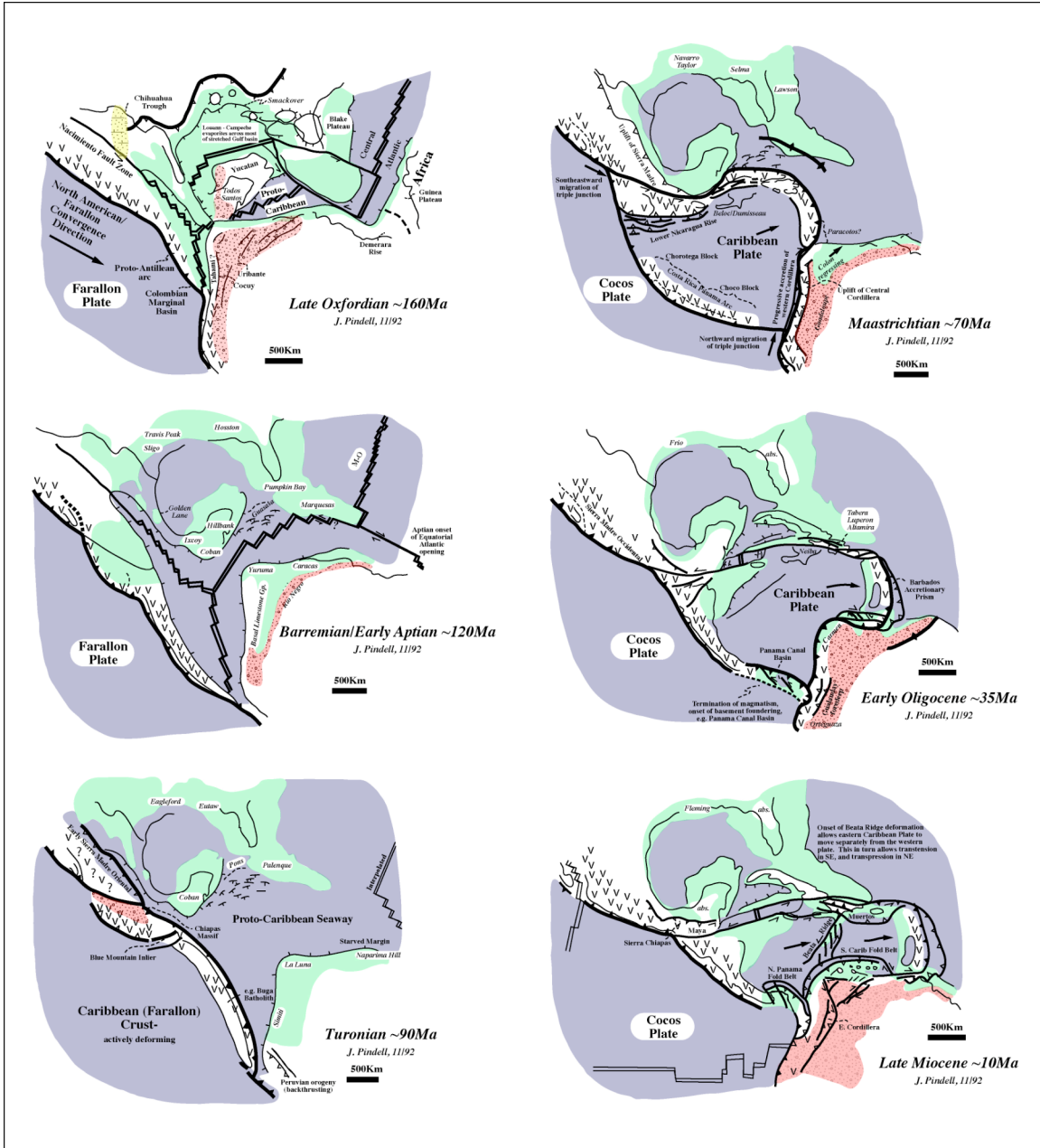
Figure 2 – Paleoreconstructions of the Caribbean region over the past 100 million years. Light green represents shallow marine environments, dark blue represents deep water environments, and red represents arid red beds (compiled from Pindell, 1994).

Geology of Hispaniola

As illustrated in the previous section, the island of Hispaniola can be considered part of a mature island arc formed in an intra-oceanic setting (Bowin, 1966). Physiographically, Hispaniola is comprised of four Northwest-Southeast trending mountain ranges (Cordillera Septentrional, Cordillera Central, Sierra de Neiba, and Sierra de Bahoruco) and separated by three lower lying valleys (Cibao Valley, San Juan Valley, Enriquillo Valley) (Figure 3, 5). The twin peaks of Pico Duarte and La Pelona (3087 m) within the Cordillera Central mark the highest elevation of the Greater Antilles. Lithologically, the island is composed of Cretaceous-Early Eocene igneous, metamorphic and sedimentary substrate that forms the basement for late Tertiary sedimentary basins. The basement of Hispaniola is made up of several fault-bounded blocks, or geological terranes (Draper et al., 1994) (Figure 4). The geologic history of adjacent terranes is often quite distinct (Draper et al., 1994). Basement rock south of the Cordillera Central formed as part of a Cretaceous Caribbean Oceanic Pleateau. Basement rock underneath the C. Central is associated with Cretaceous-Eocene volcanic arcs. Rocks underlying the Cordillera Septentrional are additionally associated with a Cretaceous-Eocene forearc.

The island remains tectonically active today, with reports of major earthquakes (magnitude 6.5) occurring as recently as 2003 and smaller earthquakes occurring quite frequently.
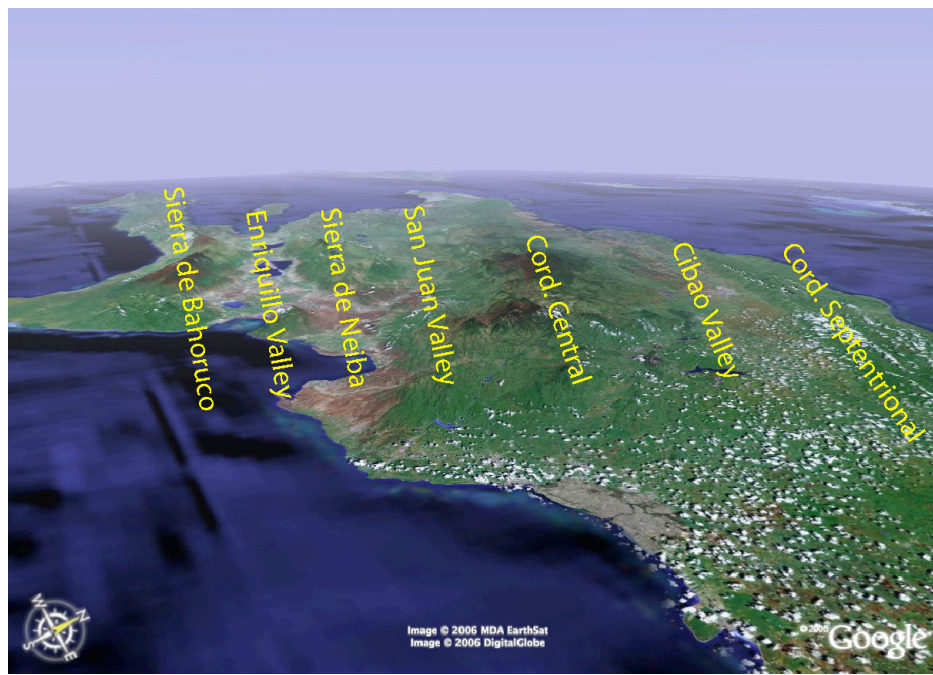
Figure 3 – Satellite image showing the alternating mountains and valleys of Hispaniola.

MORPHOTECTONIC ZONES

ATLANTIC OCEAN

GULF OF GONAVE

Haiti
Dom. Rep.

CARIBBEAN SEA

100 km

TECTONIC ZONES

SFZ

RGFZ

SFZ

GFZ

SJRFZ

LPSJFZ

EPGFZ

HAFZ

BFZ

HFZ
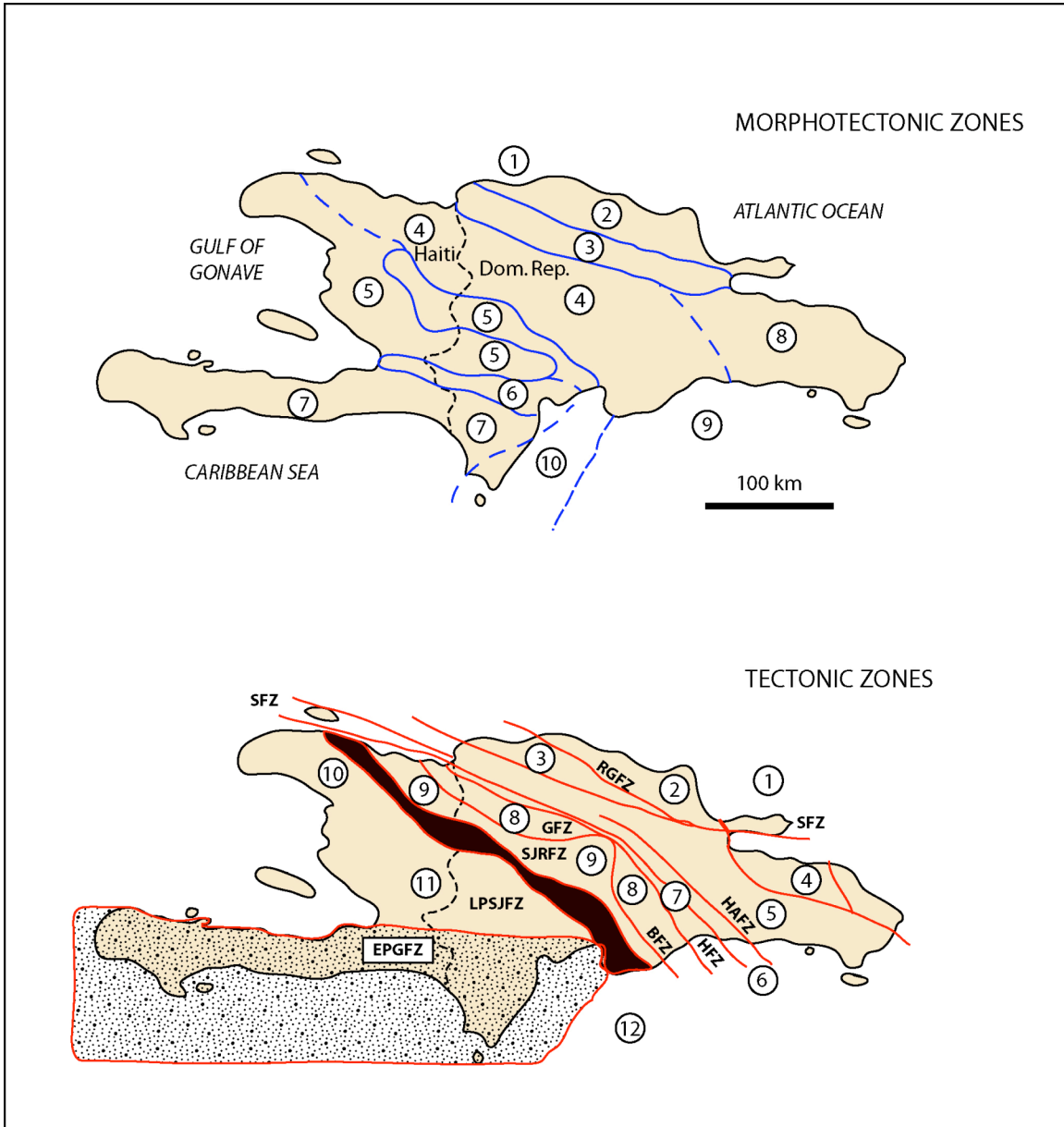
Figure 4 – Morphotectonic and tectonic zones of Hispaniola (Draper et al., 1994).

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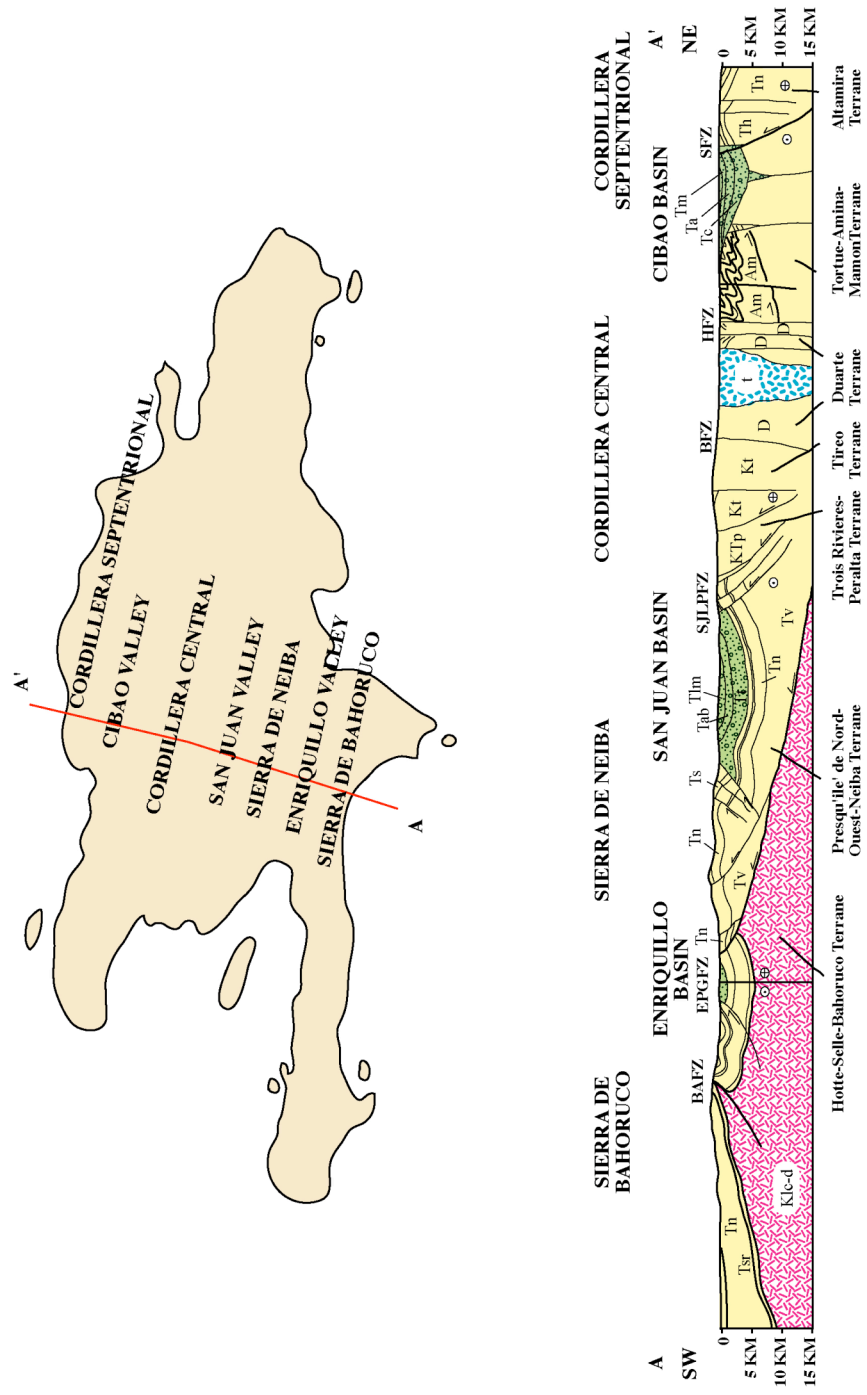
Figure 5 – Regional cross section across central Hispaniola (Dominican Republic) showing the relation between morphotectonic zones and tectonic terranes (Draper et al., 1994).

Ecology of Modern Reef Corals

Hermatypic scleractinian corals are sessile colonial organisms with a symbiotic relationship with photosynthetic algae (zooxanthellae), an aragonite skeletal mineralogy, and a delicate filter-feeding system. Under ideal conditions, these attributes allow corals to thrive and provide the structure for one of the most diverse and plentiful ecosystems on our planet. However, these same attributes limit the distribution of coral reefs, and make them sensitive to changes in environmental conditions. In this section we will discuss environmental controls on coral reef formation, and how human activities can potentially harm coral reef ecosystems.

Figure 6 graphically illustrates the "modern reef growth window". Coral reefs are most common in warm, shallow tropical waters with limited sediment and nutrient inputs.
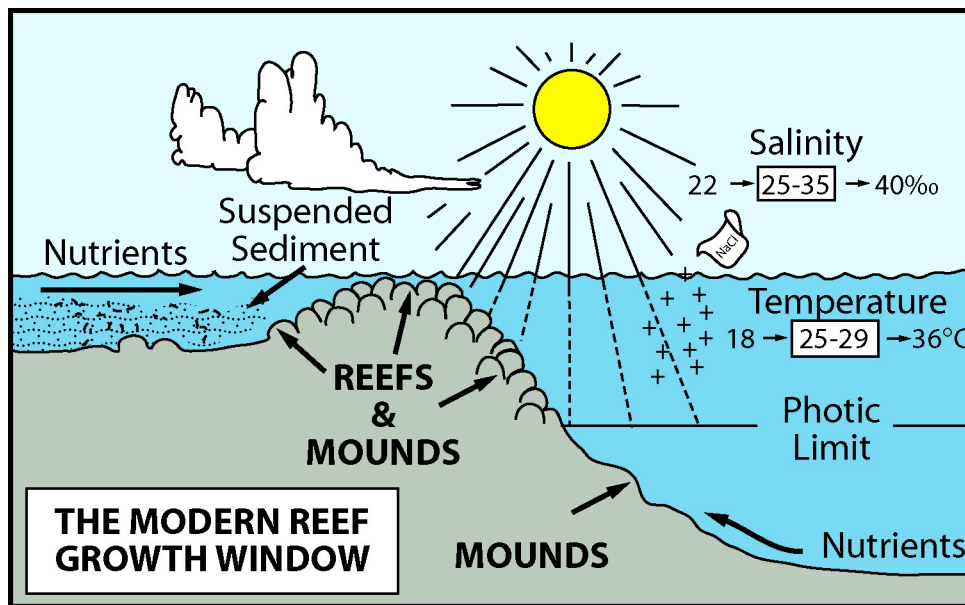
Figure 6 – Diagram illustrating the constraints and ideal growth conditions of modern coral reefs. Numbers outside of the arrows illustrate the limitations of coral growth. Values within the boxes represent the ideal conditions. (James and Bourque, 1992).

Temperature – Few photosymbiotic corals grow below 18ºC. Due to this temperature constraint, most coral reefs are confined to low latitudes (28 ºN to 28 ºS). The limiting high temperatures for corals are sustained maxima of 30-34ºC (Glynn, 1984). Heat stress can cause a breakdown in the coral-photosymbiosis leading to the loss of algal symbionts and coral death; a phenomenon known as coral bleaching.

Light – Growth of corals that obtain most of their metabolic requirements from their photosymbionts is clearly light-limited. The depth to which light can penetrate water is dependent upon water clarity. Water clarity is influenced by the amount of suspended plankton, dissolved substances, and particulate organic matter. In general,

photosymbiotic corals are rarely found below 100 m (Figure 7; Goreau and Wells, 1967), with reef development rarely below 30 m.
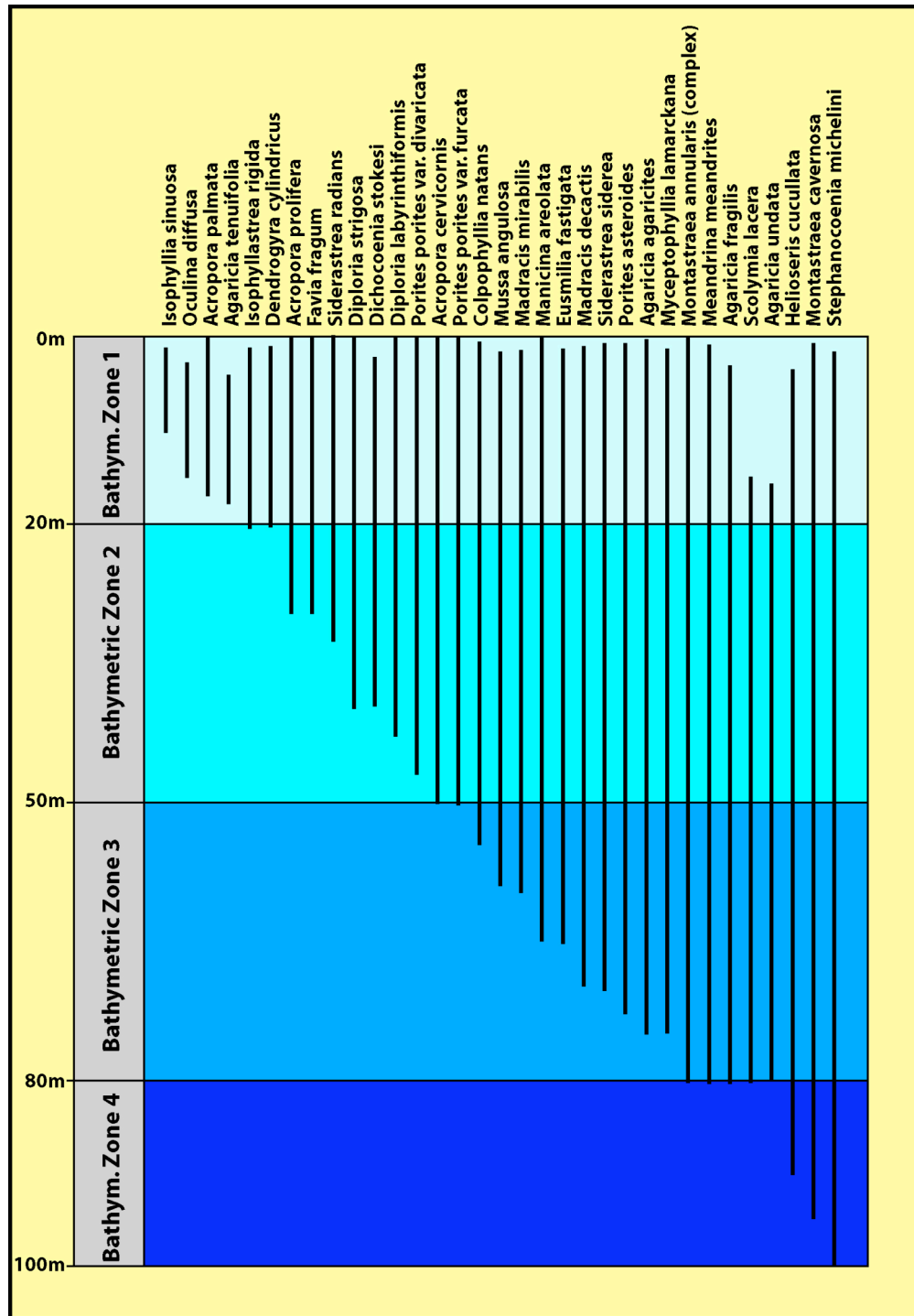
Figure 7 – Depth distribution of Modern Caribbean reef corals (Goreau and Wells, 1967).

Nutrients – High nutrient levels enhance the growth of benthic macroalgae, which compete with corals for space and light. Most coral reef growth occurs when annual average concentrations of nitrate are less than 2.0 μmol L^{-1}, and phosphate is less than 0.20 μmol L^{-1} (Kleypas, 1995).

Sedimentation – High rates of sedimentation can be damaging to corals in several ways. High sedimentation can block out available light, clog the delicate filter-feeding apparatus of corals, and prevent coral larvae from attaching to the substrate. Furthermore, if sedimentation rates are high enough, corals can become literally buried in the sediment.

One way in which corals have adapted to different environmental conditions is through variation in colony morphology. As depicted in Figure 8, different colony morphologies tend to dominate in different environmental conditions. Free-living corals, delicately branching, and thin plate-like corals tend to be most common in low energy environments. Massive, encrusting, and robust branching corals tend to be more common in high-energy environments. Variations in colony morphology also influence a corals ability to harness available light, and effectively remove large amounts of sediment. Platy or tabular corals can be more effective at collecting light while branching corals are more effective at removing sediment from their polyps.

GROWTH FORM AND ENVIRONMENT OF REEF BUILDING SKELETAL METAZOA			
Growth Form		**Environment**	
		Wave Energy	**Sedimentation**
	Delicate, banching	low	high
	Thin, delicate, plate-like	low	low
	Globular, bulbous, columnar	moderate	high
	Robust, dendroid, branching	mod-high	moderate
	Hemispherical, irregular, massive	mod-high	low
	Encrusting	very high	low
	Tabular	moderate	low

Figure 8 – Diagram showing the distribution of coral colony growth morphologies (James and Bourque, 1992).

Due to the combined adaptations of different coral species, different coral species tend to prefer different reef environments. Based on the distribution of different coral species, as well as other physical and chemical aspects, a typical coral reef can be divided into zones (Figure 9). A typical barrier reef can be subdivided into 5 zones: (1) lagoon; (2) back reef; (3) reef crest; (4) reef front; and (5) fore reef. The corals occurring in each of these zones are predictable both in terms of their colony morphology and their species composition.
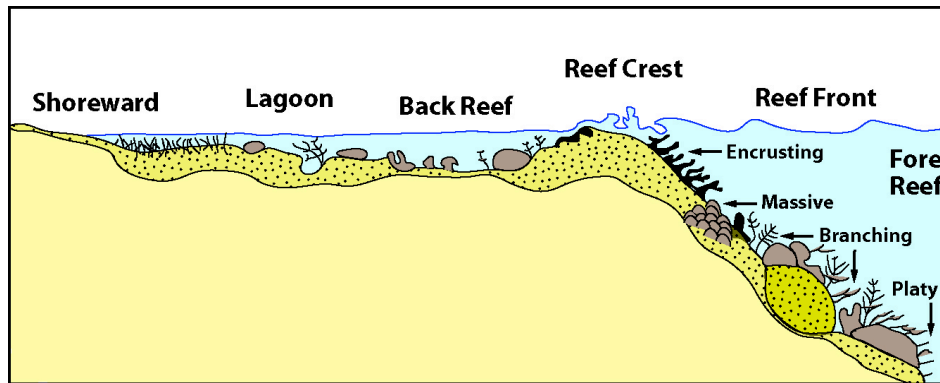
Figure 9 – Diagram showing the dominant coral reef environments (facies).

Based on the distributional patterns of corals, 6 common reef types can be characterized for Caribbean reefs. These different reef types occur as a result of differing exposure to wave energy (Figure 10; Geister, 1977). These reef types can be recognized by their dominant coral species.
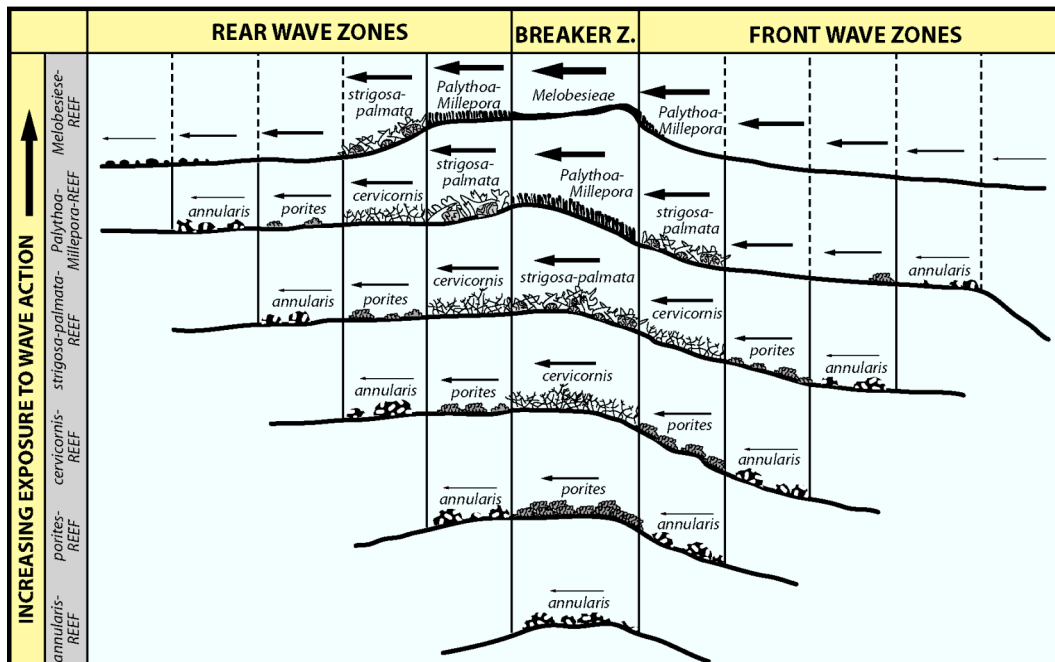
Figure 10 – Diagram showing the most common Caribbean reef types (Geister, 1977).

Evolution of Cenozoic Reef Corals

The fossil record provides a unique and valuable perspective on the maintenance of biological diversity on a scale of thousands to millions of years (Sepkoski, 1997). Within marine benthos, reef-building organisms have experienced six primary phases of high diversity through earth history: Early Cambrian, Siluro-Devonian, Permian, Triassic, Cretaceous, and Eocene to Recent (Newell, 1971; Copper, 1988, 1989) (Figure 11). The six phases were each approximately 30±50 million years in length, and were separated by intervals of low diversity that followed high extinction and lasted as long as 8±20 million years. The extinction episodes corresponded with those in other marine shelf communities and were associated with global climatic cooling and oceanic regression (Sheehan, 1985). However, the recovery intervals were unusual in their extended duration, and suggest that reef ecosystems are especially sensitive to large-scale environmental perturbations (Copper, 1989).
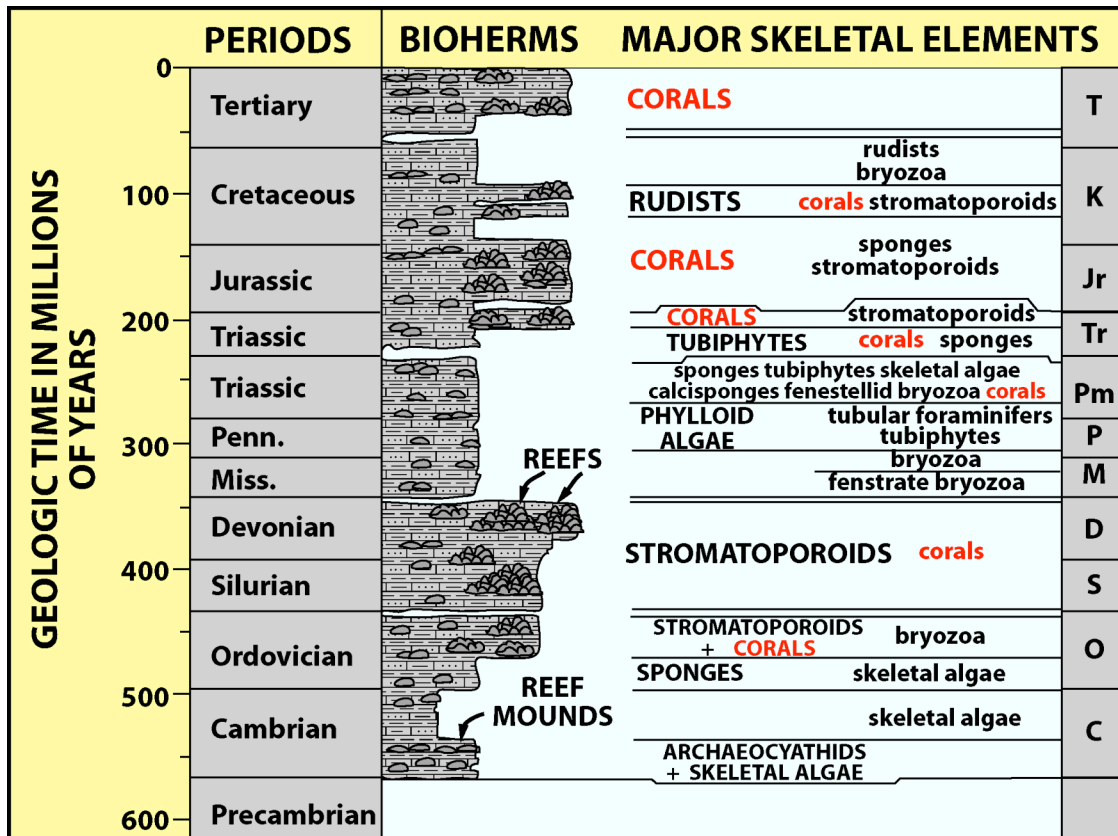
Figure 11 – An idealized stratigraphic column representing geological time and illustrating periods when there were either reefs or mounds and the major reef/mound builders (James and Bourque, 1992).

The purpose of this section is to provide a synthesis of the Cenozoic evolution of scleractinian reef corals in the Caribbean region. As part of the synthesis, three sets of interrelated questions will be addressed:

1. How has taxonomic diversity changed within the Caribbean region over the past 50 million years? Since its initial Eocene rise, has biodiversity remained constant, or has it significantly increased and/or decreased?

2. Have distinct episodes of accelerated origination and/or extinction occurred within the Caribbean region over the past 50 million years? If so, how do these episodes correspond with reported environmental changes in the Caribbean region? What is the relative timing of peaks of extinction and origination? What impact did they have on regional biodiversity?

3. How have reef communities changed over the past 50 million years? Has turnover been episodic or gradual? Have new species been added to pre-existing communities, and how has extinction affected community structure?

Occurrences of reef corals are examined at Caribbean fossil localities to determine how biodiversity has changed within the region over the past 50 million years (Figure 12). Analyses of 294 species (66 genera) at 58 fossil localities show that Caribbean generic diversity rose to 44 between 50 ± 22 Ma, ranged from 32 ± 39 between 22 ± 2 Ma, and dropped to 25 afterwards. Regional species diversity was high at 40 ± 36 Ma, 28 ± 22 Ma, and 5 ± 2 Ma (Figure 13). Origination rates were elevated throughout each high diversity interval, but extinction was concentrated near the end of each interval (Figure 14). Regional highs of origination and extinction, therefore, differed in timing and duration, causing the observed regional diversity increases during the three remarkably long intervals of turnover.

Highs of generic origination decreased in magnitude as immigration from the Mediterranean ceased, but speciation highs increased in association with emergence of the Central American isthmus. Peaks of extinction coincided with regional changes in climate and oceanic circulation.

Maximum species diversities within assemblages increased to 40 ± 60 between 50 ± 36 Ma, and have remained relatively constant ever since. Assemblage compositions differed among localities having similar ages and environments, suggesting that the timing and pattern of turnover varied across the region. Stable diversities but variable compositions within assemblages suggest that dispersal and recruitment influenced the pattern of faunal change during turnover.

Figure 12 – Ranges of all known reef coral genera (total = 66) within in the Caribbean region during Cenozoic time. The ranges are based on occurrences in the 57 localities listed in Table 1. Ends of range lines are maximum age estimates for localities in which first and last occurrences take place. Taxa are arranged in order of origination (Budd, 2000).

Figure 13 – Estimated numbers of taxa living in the entire Caribbean region over the past 50 million years. The data consist of faunal lists for the 57 localities listed in Table 1. The estimates were made using 1-million-year intervals. A.) Genus richness. B.) Species richness (Budd, 2000).

Evolutionary Rates in Cenozoic Caribbean Reef Corals
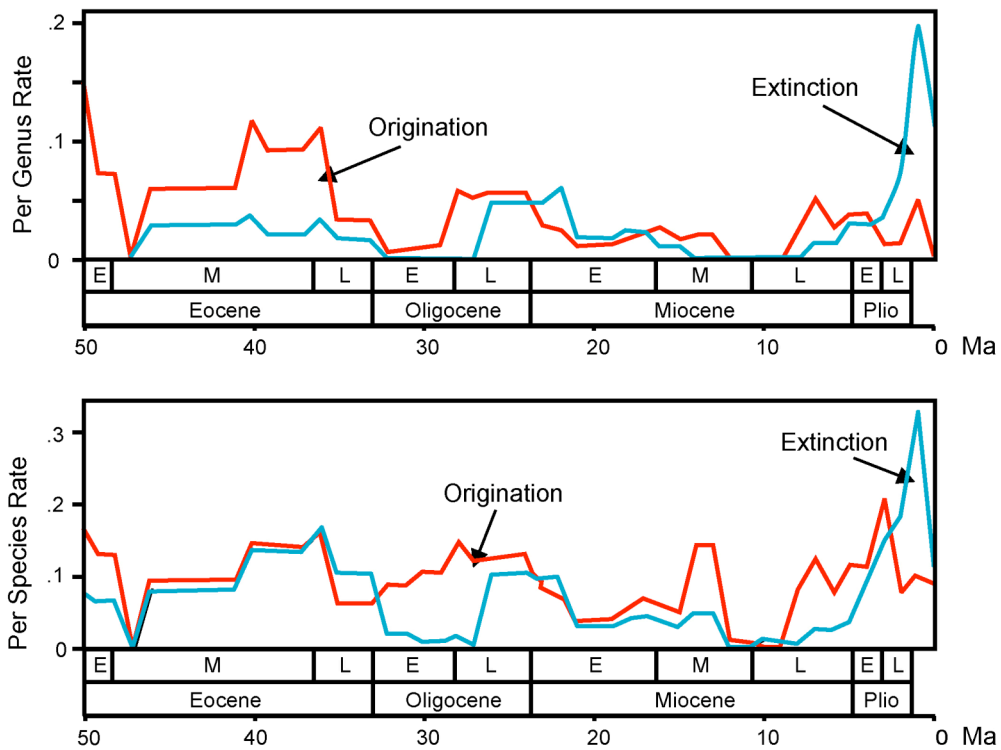
Figure 14 – Evolutionary rates of Caribbean reef corals over the past 50 million years, based on faunal lists for 57 localities. The estimates were made using 1-million-year intervals, and occurrences within each interval were weighted relative to the duration of the locality in which they occurred. Extinction rates are indicated by blue lines; origination rates are indicated by red lines. A Genus rates. B Species rates (Budd, 2000).

Exercise: Holocene Reef Coral Exercise

For this exercise we will split into 4 teams. Each team will identify the corals found in two reef assemblages. We will use these assemblages to interpret the reef environments that the corals were collected from.

1.) Use the identification keys to identify the specimens in your assemblage. After 15 minutes we will switch assemblages. Feel free to work together. Once your group has completed two assemblages, share your answers with the other groups.

2.) Calculate the percent abundance of each species in your assemblages.

3.) Determine the colony growth form for each species in your assemblages.

4.) Calculate the species richness (diversity) and percent abundance of each growth form in your assemblages (Summary data table).

5.) Use figure 7 and 8 to determine which reef environment each assemblage represents. Discuss amongst your group what criteria were most important in determining the environment.

Assemblage A

Sample	# of individuals in assemblage	% abundance	Growth form	Taxonomic ID
1	23			
2	5			
3	6			
4	4			
5	11			
6	13			
7	14			
8	6			
9	2			
10	3			
11	1			
12	3			
13	1			
14	2			
15	6			
	Total = 100			

Assemblage B

Sample	# of individuals in assemblage	% abundance	Growth form	Taxonomic ID
16	45			
17	11			
18	3			
19	15			
20	2			
21	4			
22	1			
23	1			
24	3			
	Total = 85			

Assemblage C

Sample	# of individuals in assemblage	% abundance	Growth form	Taxonomic ID
25	10			
26	7			
27	18			
28	22			
29	12			
30	11			
31	5			
32	2			
33	3			
34	6			
35	2			
	Total = 98			

Assemblage D

Sample	# of individuals in assemblage	% abundance	Growth form	Taxonomic ID
36	15			
37	9			
38	1			
39	17			
40	1			
41	1			
42	2			
43	7			
44	1			
45	3			
46	20			
47	1			
48	9			
49	4			
50	6			
	Total = 97			

Summary Data

Assemblage	Species richness	% branching	% massive	% freeliving	% platy
A					
B					
C					
D					

Caribbean Reef Coral Communities and the Origin of the Modern Eastern Pacific Coral Fauna

Hermatypic coral studies in the eastern Pacific have focused mainly on the distribution, abundance, ecology, and biogeography of modern species, but relatively few of these works have studied fossil corals. The objective of this talk is to present the recent advances in: a) coral reef species taxonomy and b) community-level analysis, in order to disentangle the evolutionary history of coral reef communities in the Gulf of California and explore its possible implications for understanding the origin of the eastern Pacific coral fauna.

Even though the eastern Pacific hermatypic coral fauna has a long evolutionary history, its current composition was determined during the last 6.5 million years. Specifically, the evolution of the eastern Pacific coral fauna has been closely linked to the formation of the Gulf of California, the extinction of Caribbean related species, and to closure of the Central American Isthmus and its subsequent environmental related changes.

The Gulf of California has a complex geological history commonly summarized in three developmental phases occurring between Miocene, ~ 25 million years ago (Ma) to Recent times. Nevertheless age determinations of the oldest coral-bearing units deposited in the California area suggest that coral settlement and development occurred over approximately the last 12 Ma of formation of the Gulf of California. In general, Gulf of California coral bearing units are small and represent single spatio-temporal growth episodes ranging in age between late Miocene to late Pleistocene. Identification of recently collected specimens based on morphometric techniques and by the qualitative comparison with previously described fossil and Recent species reveals that, previously recognized coral species probably represent ~ 50 % of the Gulf of California fauna.

Multivariate analysis of data derived from the species recognition techniques demonstrated that Gulf of California coral reef assemblages experienced larger temporal differences in species composition and relative abundance than expected by chance. Origination rate metrics demonstrated that coral species originated and were added to the Gulf of California species pool during late Miocene-early Pliocene and Pleistocene (Figure 15A). Morphologic analysis of the material suggested that Gulf of California assemblages consisted of locally originated Caribbean-like species between late Miocene and late Pliocene. During the Pliocene assemblages consisted of a mix of extinct and living species co-occurring within and among localities, but immediately after the demise of pre-turnover taxa (Figure 15B), living Indo-Pacific immigrant species dramatically increase in number and relative abundance ruling out ecological replacement as the key factor in pre-turnover species extinction (Figure 16). The turnover is unique in that pre-turnover species origination resulted from the formation of the Gulf of California, and instead of reducing species richness, the extinction event triggered the long-distance colonization of species.
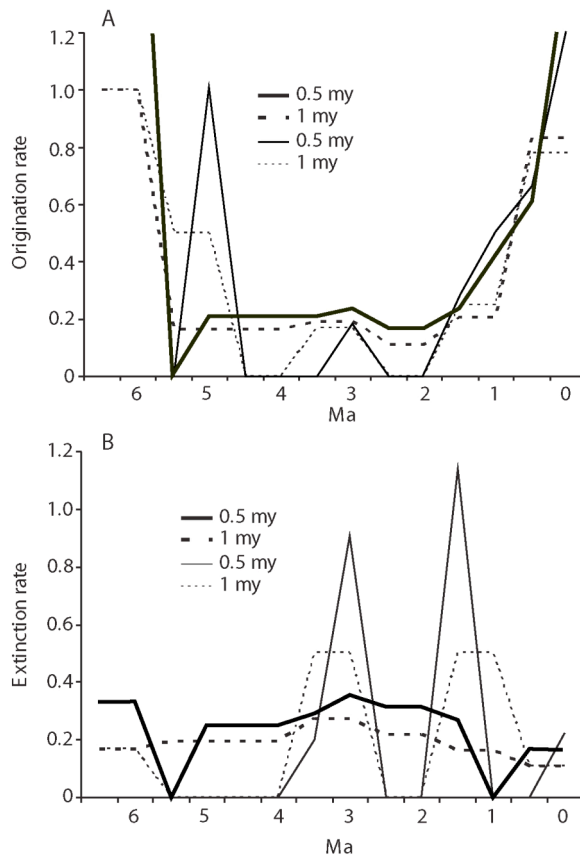
Figure 15 - Species evolutionary rates (A, origination; B, extinction) of Gulf of California reef corals from late Miocene to Recent. Each plot shows patterns calculated with interval durations of 0.5 and 1 million years (my).
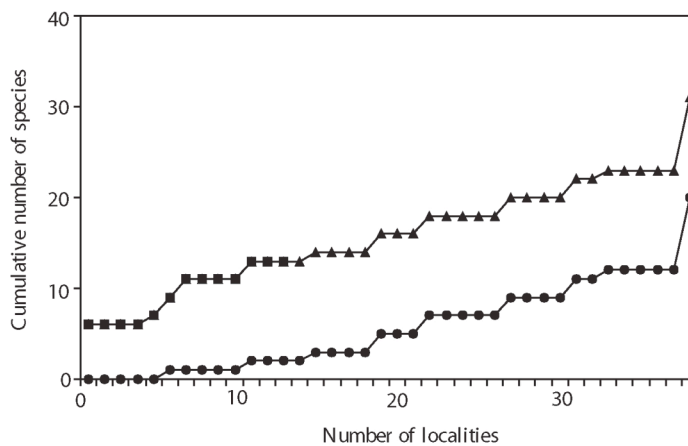
Figure 16 - Cumulative number of species curves assessing sample adequacy. Curve constructed by adding localities in stratigraphic order. Each point represents an assemblage. Squares = pre-turnover taxa; triangles = post-turnover taxa; circle = post-turnover taxa alone.

Reefs of the Northern Dominican Republic

Geologic Setting

     The Cibao Basin lies between the Cordillera Central and the Cordillera Septentrional in the northern Dominican Republic. Together the Cibao Basin and Eastern and Central Cordillera Septentrional define a large synclinal structure with its axis approximately parallel to that of the Cibao Basin (Mann et al., 1991, 1999). The Cibao Basin is traversed by the Río Yaque del Norte, which along with 4 smaller streams (Río Gurabo, Río Cana, Río Mao, Río Amina), exposes Eocene to Pliocene mixed siliciclastics and carbonates. The bulk of the thick (~5000 m) and well-preserved sequence (Mann et al., 1991) is composed of Miocene-Pliocene deposits of the Cercado, Gurabo, and Mao Formations, which span a time interval of 5-10 million years. Collectively these formations make up the Yaque Group, a remarkably continuous northward (seaward)-prograding wedge of sediments shed off the Cordillera Central, which deepens upward from depths interpreted as < 10 m to > 300 m (Bold, 1988).
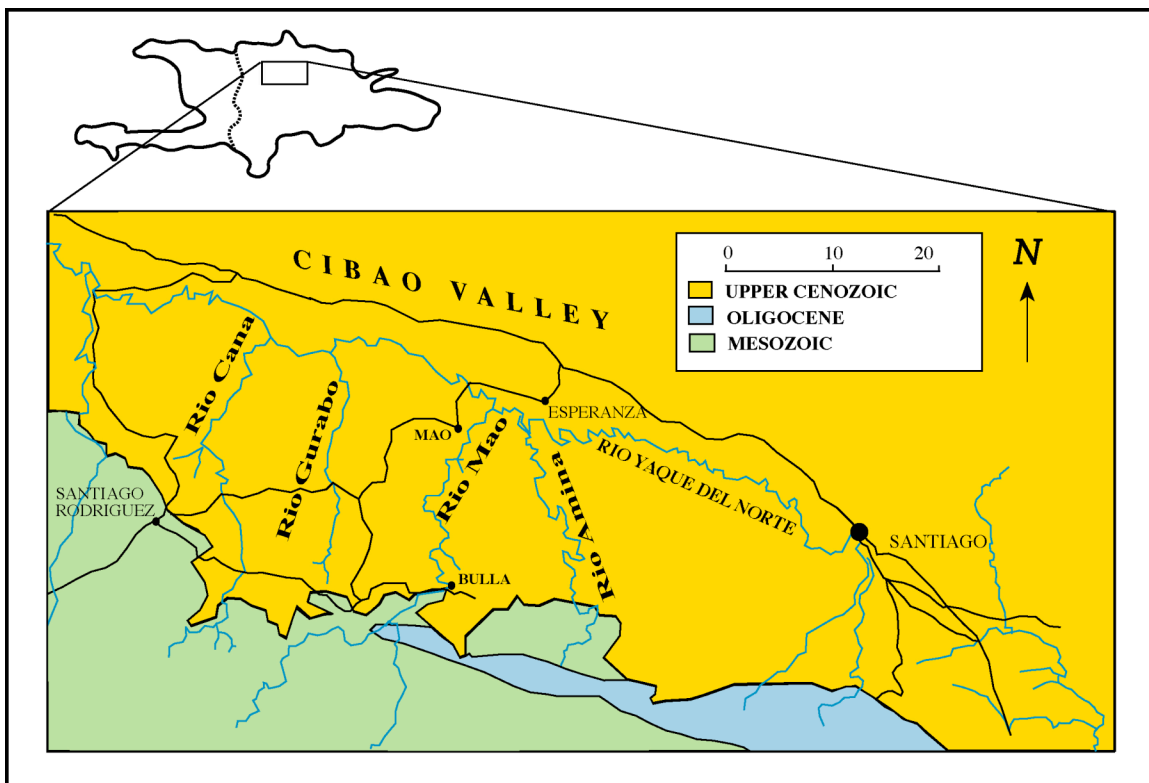
Figure 17 – Geological map of the Cibao Valley, northern Dominican Republic showing rivers from which samples for this project were collected.

     The two most recent and comprehensive chronostratigraphic studies (Saunders et al., 1986; Vokes, 1989) provide strikingly different age models. Our chronostratigraphic efforts will resolve this age controversy and provide a definitive age model for the

sections of community interest within the Cibao Basin. Existing paleoenvironmental interpretations for the sequence are sketchy and inconclusive. Saunders et al. (1986) prepared detailed maps and stratigraphic sections of the river sections, and provided bed-by-bed descriptions of lithologies, sedimentary features, and fossil content. Evans (1986a, b) performed a preliminary study of the sedimentology of the sequence and interpreted patterns within the context of depositional models. We will build on these two earlier works to redefine the depositional setting using water-depth indicators based on benthic foraminifers and re-evaluation of the sedimentology in light of subsequent advances in understanding upper slope lithofacies (based on a U. Miami submersible dives on modern tropical slopes; Grammer 1991). After the ages of the key sections are determined, the benthic foraminifers will allow us to compare time-equivalent sections to determine the relative depth of the setting and provide a baseline indicator of the paleo-shelf configuration.

Corals-I: Communities

Assemblages of reef corals from the Late Miocene to early Late Pliocene of the northern Dominican Republic have been statistically analyzed to document patterns of community change during the 4 my period leading up to the Late Pliocene Caribbean-wide episode of accelerated faunal turnover. The sections analyzed were part of a thick sedimentary wedge (as much or more than 1000 m thick) that prograded north forming a thin shelf and slope along a narrow eastward-opening trough located north of the rapidly uplifting Cordillera Central. Exposures were examined along five rivers of the Cibao Valley: the Rio Gurabo, Rio Cana, Rio Mao, Rio Amina and Rio Yaque del Norte. Two approaches were utilized to characterize reef coral assemblages and assess community stability.

In the first approach stratigraphic variations in coral occurrences were determined from over 2,900 coral samples collected by haphazardly extracting well-preserved material from the surface of the outcrop. Sampling therefore was roughly representative of species composition, but not of abundance. Analysis of the occurrence matrix (91 species X 20 lithostratigraphic units) was performed using average linkage clustering of Bray-Curtis similarity coefficients. At the coarsest level assemblages were categorized as either free-living communities (>35% free-living taxa) or mixed-shape communities (<30% free-living taxa). Grassflat and mixed-shape communities were stratigraphically scattered throughout the section, reflecting variations in environment rather than temporal changes in communities. To independently test each community type for temporal changes over the 3 my interval, the Bray-Curtis similarity coefficient between all locality-group pairs within each community was regressed over the estimated age difference between locality-groups. Results suggest that despite background levels of origination and extinction reef coral assemblages were fairly stable.
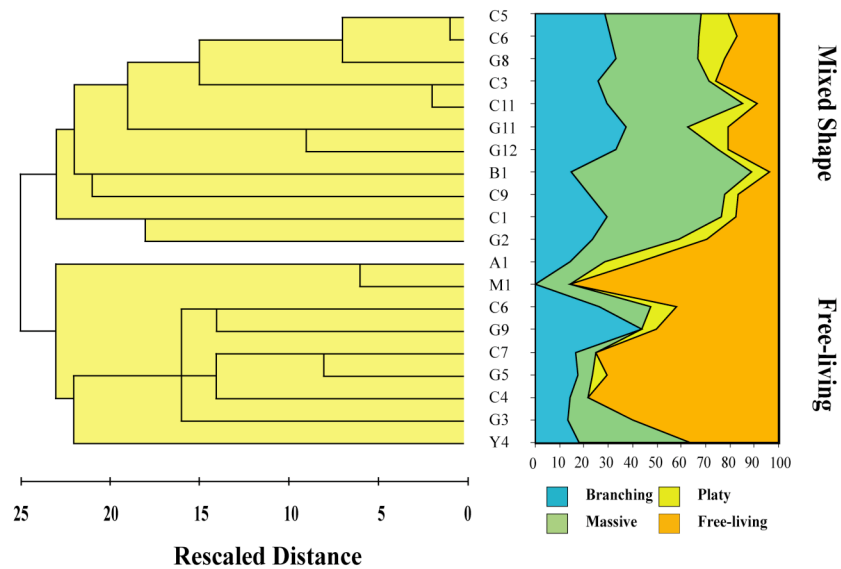
Figure 18 – Results of cluster analysis on species occurrences in different lithostratigraphic units in the northern Dominican Republic. Two clusters are suggested; one dominated by massive corals, and one dominated by free-living corals.

In the second approach mixed-shape coral communities were compared using transect samples from three areas of exceptional reef development which collectively spanned roughly the entire 3 my sequence. The composition and relative abundance of taxa were compared using the same techniques as above. This approach allowed characterization of pre-turnover coral reef zonation patterns and provided insights into the ecological role of several dominant taxa. A comparison of communities from strictly defined reef zones suggests more significant changes in community structure during this 3 my interval than previously determined from the presence/absence data of broadly defined locality groups.

Corals-II: The early evolution of a common modern Caribbean reef coral

Morphometric analyses show that more than nine species existed within the *Montastraea "annularis"* complex during its early evolution in the Mio-Pliocene of the Dominican Republic, and many had durations of up to 2-5 million years. In addition to higher diversity, comparisons with modern members of the complex show that the Dominican Republic species were more variable both within and among colonies, suggesting less colony-wide coordination and fewer growth-related morphologic constraints during the early evolution of the species complex. Speciation within the complex has resulted in continued narrowing of this initial morphologic variability, both within and among species. Phylogenetic analyses

further indicate that the three modern members of the complex are not sister species but belong to different clades, two of which diverged during the early to middle Pliocene prior to Plio-Pleistocene reef coral turnover (Figure 19). The three modern members of the *M. "annularis"* complex are thus survivors of previously more diverse, distinct evolutionary groups.

Samples consist of 208 colonies of *M. "annularis"*-like corals (less than four septal cycles), which were collected along four river sections in the Cibao Valley of the northern Dominican Republic. Five stratigraphic intervals are represented, ranging from approximately 17.3-13.1 Ma to 3.7-3.4 Ma (with a gap at ~13.1-8.3 Ma). Data for morphometric and phylogenetic analyses are based on coordinates of 27 spatially homologous points or landmarks, which define the thickness and structure of the corallite wall and associated costosepta. Numbers of septa, relative development of septal cycles, and measures of colony growth form are also recorded. Species are recognized using Bookstein size and shape coordinates as variables in cluster and canonical discriminant analyses. Variation within and among colonies is estimated using principal component analysis. Cladistic analyses are based in part on characters derived from morphometric data.
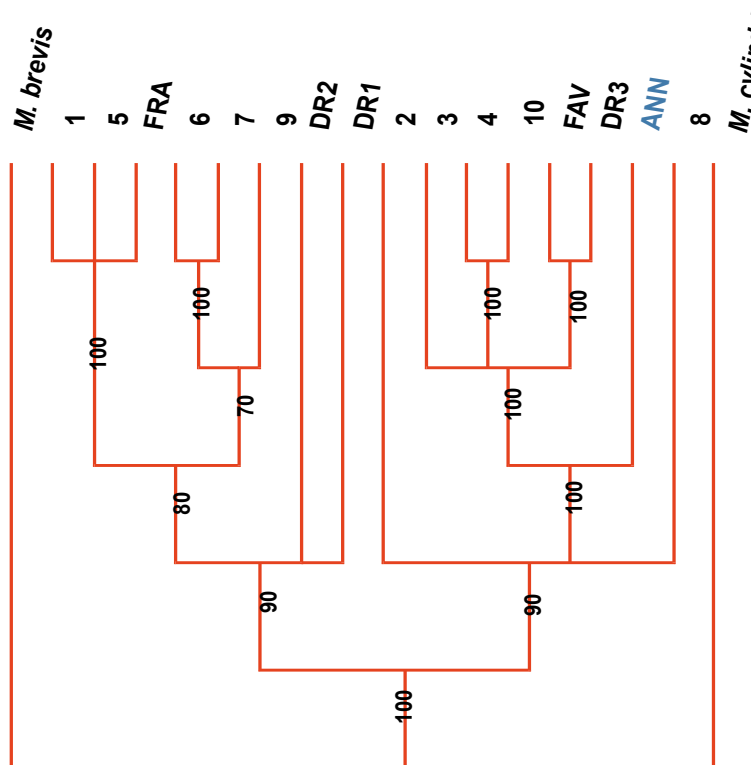
Figure 19 – 50% majority rule consensus of ten trees showing that the three modern members of the *M. annularis* species complex are not sister species but belong to different clades, two of which diverged during the early to middle Pliocene.

Holocene Reefs of the Enriquillo Valley (Stemann et al., 1992: Lethaia, 25)

The Enriquillo Valley is the eastern portion of an east-west trending depression that extends 150 km across southern Hispaniola (Figure 16). Over 50% of the valley lies below sea-level. Lago Enriquillo, at 43 m below mean sea-level (b.s.l.), is separated from Bahia de Neiba to the east by a topographic sill that extends just 4 m above mean sea-level (a.s.l.). The area has been termed a compressional ramp valley (Mann et al., 1984) with blocks to the north and south of Lago Enriquillo moving together along thrust faults and depressing the valley floor. Relative rates of tectonic uplift of the valley walls may be as high as 0.4 mm/yr (Taylor et al., 1985).

Figure 20 – Satellite images of the Enriqillo Valley. A.) Looking west from the Bahia de Neiba. B.) Looking west, just east of Lago Enriquillo.

Figure 21 – Geology of the central and western Enriquillo Valley, Dominican Republic. (Modified from Mann et al., 1984).

A sequence of Neogene and Quaternary carbonate, siliciclastic and evaporitic sediments suggests a series of marine transgressions into the valley (Mann et al., 1984). During the latest of these marine incursions in the Early to Middle Holocene, luxuriant coral growth thrived along the edges of the valley (Figure 2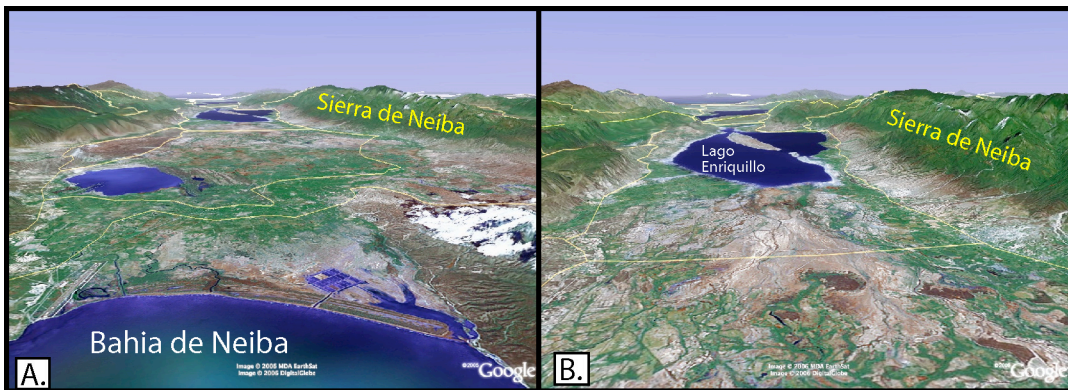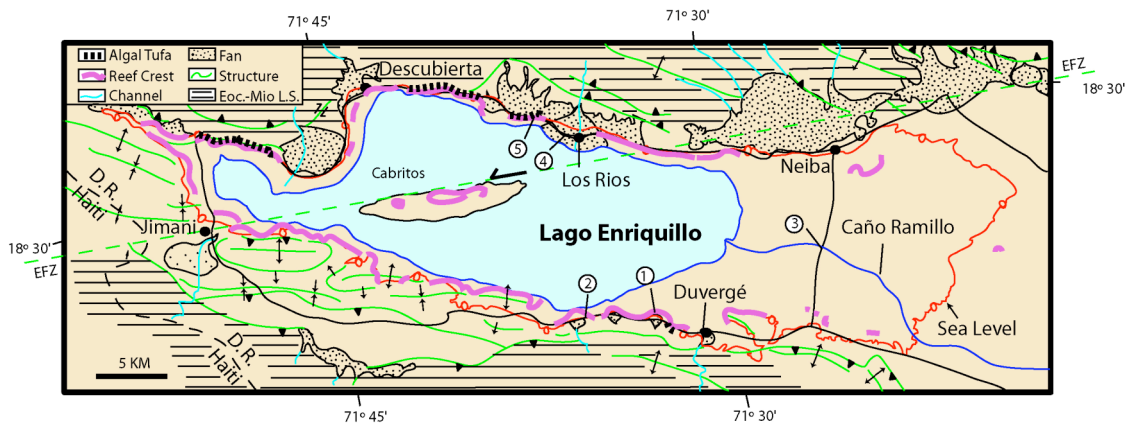0). Based on carbon-14 dates obtained by Taylor et al. (1985) and Mann et al. (1984), coral growth in the Enriquillo Basin began around 9020 BP and ended 4760 BP. The demise of the reef tract probably resulted from the constriction of the valley's eastern connection to the sea by the build-up of the delta of the Rio Yaque del Sur. Mann et al. (1984) suggest that brackish water conditions created by the influx of fresh water from the Yaque del Sur ended reef growth approximately 4700 BP.

The Holocene reef rock in the Enriquillo Valley is mostly coral bafflestones and framestones with exquisitely preserved, in place scleractinians and hydrocorals (95-100% aragonite) and locally abundant mollusks and echinoids. The matrix is uncemented calcareous mud, silt and sand. Reefal deposits are found along a belt fringing the northern, western and southern sides of the valley within the Dominican Republic, as well as on Isla Cabritos and as patches scattered across the eastern part of the valley floor (Mann et al., 1984). The reef rock overlies both alluvial fan deposits and beds of abundant intertidal bivalves. In some areas, the reefal deposits are capped by brackish water and lacustrine sediments that mark the end of marine conditions in the valley. Alluvial fan sediments and coralliferous colluvium overlie coral at several sites. Taylor et al. (1985) found reef rock exposed from 2 m b.s.l. to 35.7 m b.s.l.

The reef itself is composed of a rich fauna of 30 species of scleractinians and hydocorals, (Table 1) all of which are also common on modern Caribbean reefs. The total number of species found is comparable to that noted from living reefs on the Alacran and Campeche bank (Chavez et al., 1985) and is actually greater than that recorded from many Pleistocene reefs (Geister, 1982).
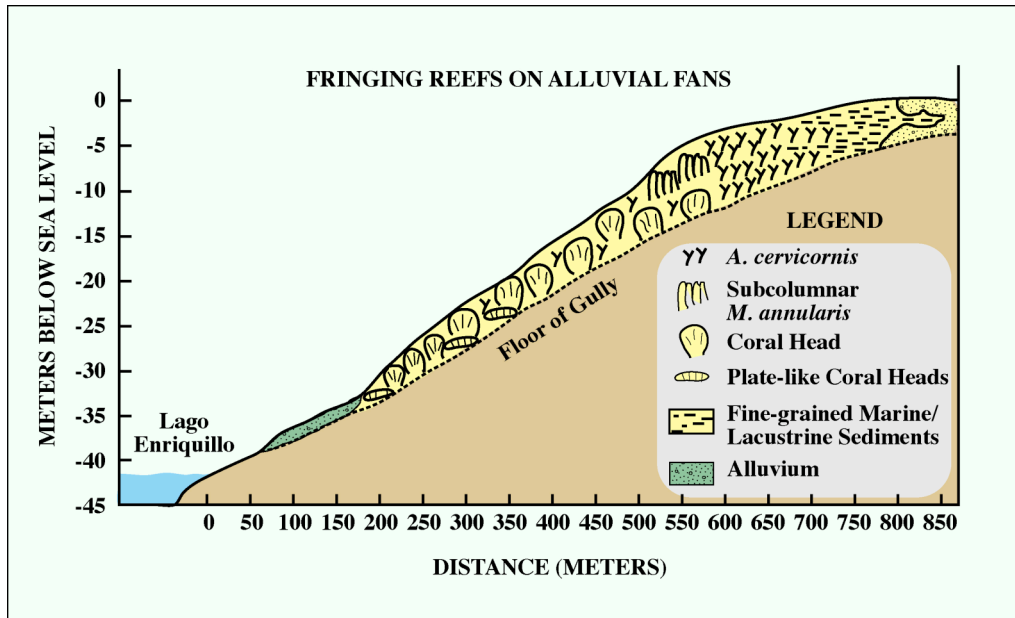
Figure 22 – Representative cross section of the Enriquillo fringing reef. After Taylor et al. (1985).
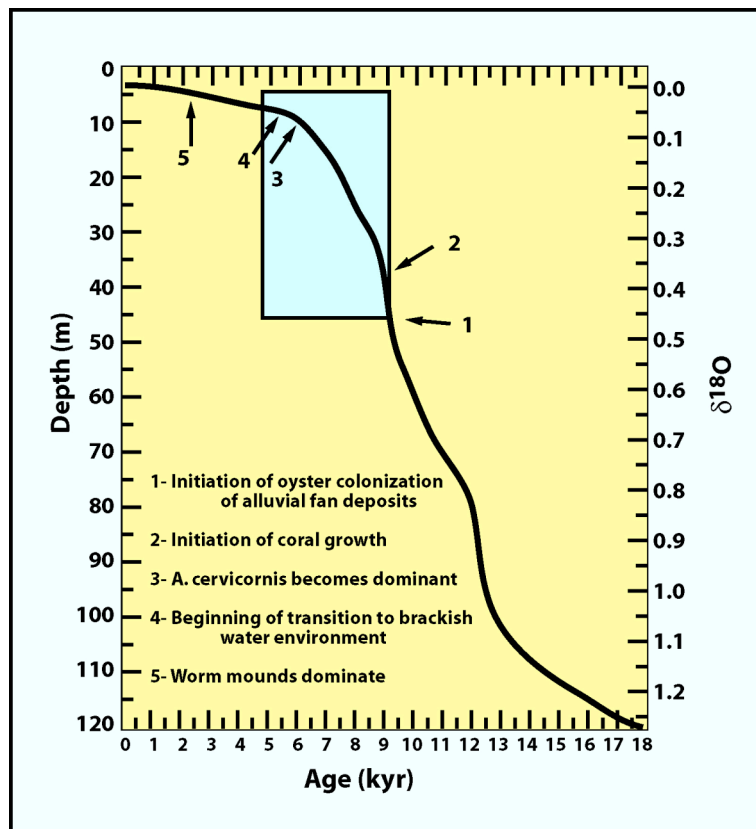
Figure 23 – Modified sea-level curve from Fairbanks (1989) based on radiocarbon-dated Acropora palmata data. The rectangle encompasses the portion of the sea-level curve represented by corals from the Enriquillo Valley.

Table 1 – Frequency of categories found in quadrat counts of Enriquillo fringing reefs (Stemann et al., 1992).

Class	Frequency (%)
Acropora cervicornis	42.1
Leptoseris cucullata	1.1
Agaricia agaricities	1.9
Agaricia tenuifolia	0.5
Agaricia lamarcki	2.7
Siderastrea siderea	13.1
Siderastrea radians	*
Porites asteroids	0.9
Porites divaricata	0.8
Porites furcata	0.8
Porites porites	0.7
Madracis spp.	0.2
Manicina areolata	0.4
Favia fragum	0.1
Montastraea annularis	3.6
Montastraea cavernosa	2.9
Colpophyllia natans	2.7
Colphphyllia breviserialis	*
Cladocora arbuscula	*
Stephanocoenia intersepta	1.2
Eusimilia fastigata	0.8
Oculina diffusa	0.4
Dichocoenia stokesi	0.4
Mussa angulosa	0.3
Myceptophyllia danaana	0.1
Myceptophyllia lamarckiana	0.4
Isophyllastrea rigida	*
Scolymia spp.	0.1
Millepora complenata	1.8
Millepora alcicornis	1.2
Clam	1.9
Oyster	1.3
Gastropoda	0.8
Serpulid worm	*
Sediment	14.7
Cobble	*

Detailed Field Trip Itinerary

Stop 1: Scenic overlook of Lago Enriquillo
This stop will provide us a view of the Enriquillo Valley. Looking towards the west (Haiti), the mountains along the southern shore of Lake Enriquillo are the Baoruco Mountains. The mountains along the northern shore are the Sierra de Neiba. The valley between these two mountain ranges is filled with extensive flood plain deposits originating from the surrounding mountains. During the Holocene, this flood plain would have been below sea-level, and formed the bottom of a shallow seaway.

Stop 2: Cervicornis Quarry (N 18°24.135', W 71°35.382')
The unique geologic setting of the Enriquillo Valley has led to preservation and exposure of fringing reefs that formed 5,000 to 9,000 years before present. Several distinct coral biofacies can be detected in the outcrops fringing lago Enriquillo. The reef exposed approximately 8 km west of Duvergé is dominated by the branching coral *Acropora cervicornis*. The outcrop consists of an approximately 10 meter thick accumulation of *A. cervicornis* with numerous other massive and branching corals amongst this *in situ* coral thicket. In addition to *A. cervicornis*, *Manicina aerolata*, *Siderastrea siderea*, *Favia fragum* and *Millepora* spp. are common.

Stop 3: Enriquillo Valley Flood Plain
The bridge crossing the Caño Ramillo provides excellent exposures to the flood plain deposits associated with the Rio Yaque del Sur. The demise of the reef tract probably resulted from the constriction of the valley's eastern connection to the sea by the build-up of the delta of the Rio Yaque del Sur.

Stop 4: Lunch (near Los Rios)

Stop 5: Cañada Honda (N 18°31.914', W 71°37.094)
The Cañada Honda outcrop contains a spectacular example of several stages of the history of the Enriquillo reef development. During the early portion of the Enriquillo record, this reef experienced open marine conditions. As the extent of the Cañada Honda gully is traversed, stages of reef colonization, reef shallowing, and reef demise are encountered.

The southern portion of the gully contains pristine *in situ* corals, and shells with morphologic detail and color still evident (Figure 24a). Corallites are excellently preserved and small colonies of branching corals are intact. The coral communities are diverse (~30 species), but dominated by the genera *Siderastrea*, *Porites*, *Stephanocoenia*, *Montastraea*, *Agaricia*, and *Colpophylia*, with thin *Oculina* beds and other corals scattered throughout the outcrop. Some massive corals exhibit drape morphology at this site with annual bands of skeletal carbonate layered continuously at the core of the colony but laid discontinuously along outer edges. Hypotheses for the origin of the drape

morphology include excess sedimentation or shading by soft corals and colonies of filamentous algae during growth.

The more northern portion of gully is characterized by deposits of sand and mud-sized carbonate grains with an abundant molluscan fauna. Polychaete worm mounds are found capping deposits of the gully (Figure 24e). Individual subspherical worm mounds commonly reach heights of greater than 2 m and have diameters of more than 3 m.

These large mounds were previously reported as being "calcareous tufa of probable algal origin" (Mann et al., 1984) or as "thrombolitic algal stromatolites" (Taylor et al., 1985). The internal structure of the mounds sometimes is thrombolitic and microbial activity likely was important in their formation, but many mound specimens exhibit a prominent framework formed by small (1-2 mm diameter), intertwining tubes of serpulid worms (Polychaeta) (Greer, personnel communication). The serpulid worm tubes were effective as binders of sand-sized carbonate grains as well as shell fragments, commonly including small (2-4 mm) whole hydrobiid snail shells.

The hydrobiid snails preserved within the serpulid mounds and the molluscan fauna of the overlying and possibly underlying beds suggest onset of brackish-water conditions. However, modern serpulid worm mounds found in Laguna Madre, Texas, have developed under variable salinity conditions, including hypersaline intervals (Fagerstrom, 1987).

Stop 6: Refreshments
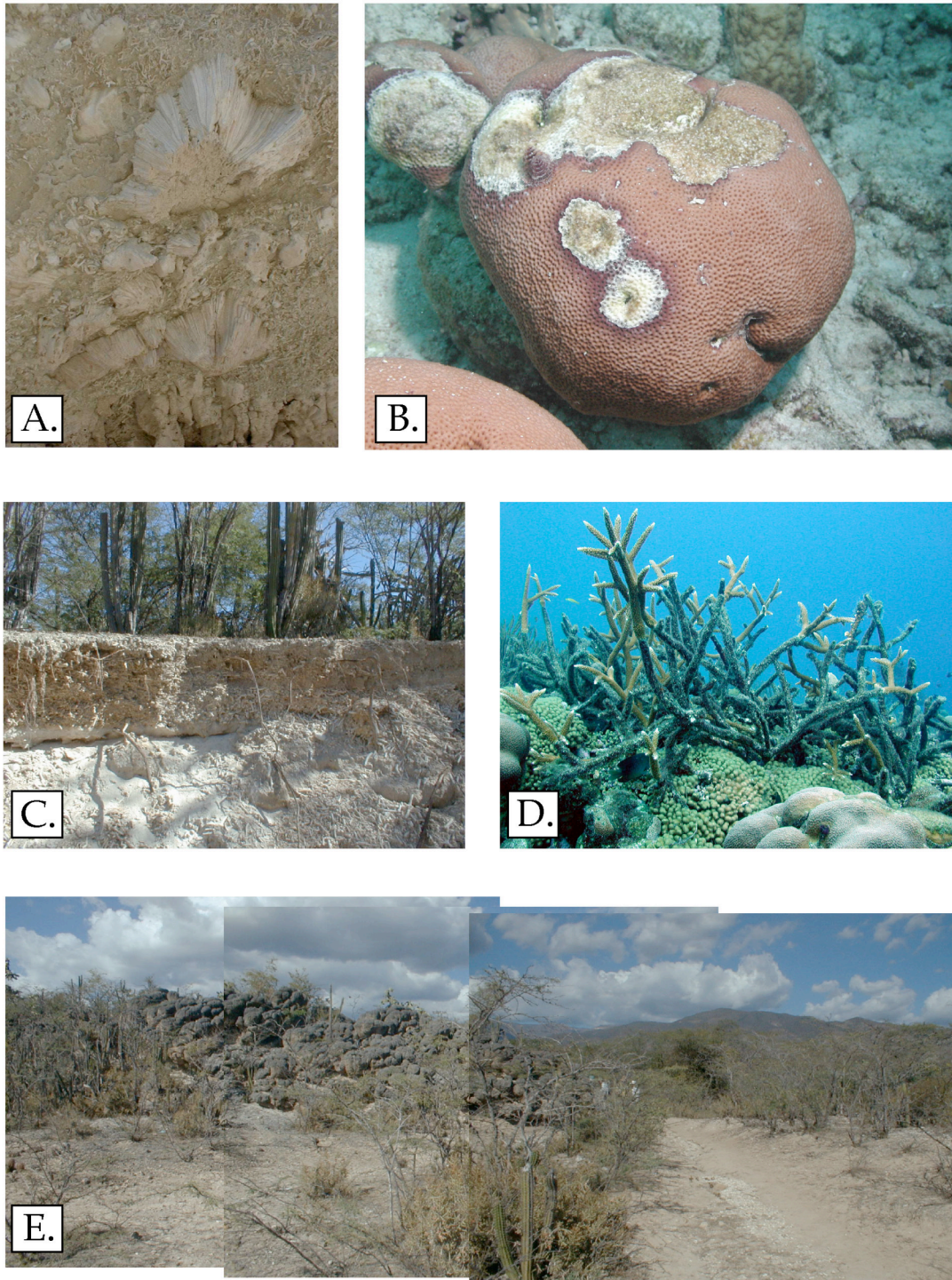
Figure 24 - A.) Holocene Siderastrea siderea exposed in outcrop at Las Clavallinas. **B.)** Modern *S. siderea* from Curaçao, N.A., showing signs of dark spot disease. **C.)** Holocene *Acropora cervicornis* exposed in outcrop at Las Clavallinas. **D.)** Modern *A. cervicornis* from Curaçao showing signs of recent mortality. **E.)** Holocene worm mounds exposed at Cañada Honda.

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