Diversity, Distribution and Geochemistry of Benthic Foraminifera in Holocene Lagoons of Carbonate Platforms (Belize, Central America)

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Abstract

The development of benthic foraminiferal assemblages during the past 6,000 yrs was investigated in Holocene sediment cores from three carbonate platforms (Turneffe Islands, Lighthouse Reef, and Glovers Reef) of Belize, Central America. Foraminiferal assemblages and their diversity were determined in different time periods to identify their dependence on environmental factors, such as lagoonal age, lagoonal depth, water circulation, substrate, bottom-water temperature, and salinity. Geochemical proxies ($\delta^{18}O$ and $\delta^{13}C$), obtained from the common larger foraminifer *Archaias angulatus* were used to estimate Holocene seasonal BW-temperatures and climate variabilities. A total of 51 samples were taken from 12 vibracores for taxonomic determination and 10 to 15 subsamples of 32 tests of *Archaias angulatus* were used for stable oxygen and carbon isotope analyses.

Based on cluster analyses, seven benthic foraminiferal assemblages are distinguished during the Holocene. The three platforms exhibit characteristic differences in benthic foraminiferal fauna and diversity, which are controlled by their respective environments during the last 6,000 yrs. Turneffe Islands has four benthic foraminiferal assemblages, which are typical for restricted lagoons with fluctuating salinity. Lighthouse Reef is inhabited by two benthic foraminifera associations, which are characteristic of high water exchange with the surrounding ocean and clear waters. Glovers Reef is characterized by two benthic foraminiferal assemblages, which occur in deeper lagoons with slow water circulation. In general, during the Holocene, the highest mean diversity, evenness, and richness of benthic foraminifera were found in the Turneffe Islands and the lowest occurred at Glovers Reef. The foraminiferal faunas of the Lighthouse and Glovers Reefs had been in a “Diversification Stage” since 6,000 yrs, whereas the foraminiferal fauna of the Turneffe Islands reflects the development from a “Colonisation” (~4,000 yrs BP) to a “Diversification Stage” (~2,000 yrs to present time). Lagoonal depth, water circulation, substrate, and BW-temperature have higher influence on foraminiferal diversity as compared to lagoonal size and age. The negative correlation between diversity and lagoonal depth is based on differences in light intensity and substrate. In contrast to Lighthouse Reef, the Turneffe Islands and Glovers Reef show decreasing diversity of benthic foraminifera with increasing lagoon depth, due to finer sediment, turbid waters and/or dense mangrove growth, which reduce the light intensity and the number of species. Water Circulation also affected the benthic foraminifera modes of living and their diversity during the last 6,000 yrs. Increasing abundances of infaunal taxa refer to restricted circulation and/or lower oxygen conditions, as assumed for the Turneffe Islands and Glovers Reef. Increasing abundances of epifaunal foraminifera, as observed in the Lighthouse Reef indicate better circulation and/or higher oxygen conditions.

Holocene BW-temperature reconstructions based on $\delta^{18}O$ of single *Archaias angulatus* tests do not correspond to typical Holocene climate models of the Caribbean. In the Belize area, mean BW-temperature trends indicate local climate variations. A decrease of $\delta^{13}C$ values during the last 1,000 yrs could be related to the “Suess Effect”. The seasonal BW-temperature variations within single large benthic foraminifera tests correspond to present-day temperature fluctuations in the lagoons, and indicate higher temperatures in Summer and Autumn and lower temperatures in Winter and Spring.

Kurzfassung

Die Entwicklung von benthischen Foraminiferen Gesellschaften der letzten 6,000 Jahre wurde anhand von holozänen Sedimentkernen aus drei Karbonatplattformen (Turneffe Islands, Lighthouse Reef und Glovers Reef) aus Belize, Zentralamerika, untersucht. Für verschiedene Zeitintervalle wurden Foraminiferen-Gesellschaften identifiziert und deren Diversitäten ermittelt, um deren Abhängigkeit von Umweltbedingungen wie Lagunenalter, Lagunentiefe, Wasserzirkulation, Substrat, Bodenwassertemperatur (BW-Temperatur) und Salinität zu bestimmen. Geochemische Analysen ($\delta^{18}O$ und $\delta^{13}C$) an der häuftig vorkommenden Großforaminifere *Archaias angulatus* wurden zur Bestimmung von holozänen saisonalen BW-Temperaturen und Klimavariabilitäten benutzt. Insgesamt 51 Proben wurden aus 12 Vibrationskernen entnommen und taxonomisch bestimmt. An 10 bis 15 Einzelproben von 32 *Archaias angulatus*-Gehäusen wurden stabile Sauerstoff- und Kohlenstoffisotope gemessen.

Aufgrund von Cluster Analysen konnten sieben benthische Foraminiferen-Gesellschaften im Holozän unterschieden werden. Die drei Plattformen zeigen charakteristische Unterschiede in der benthischen Foraminferenfauna und -diversität in den letzten 6,000 Jahren, die durch entsprechende Umweltbedingungen kontrolliert wurden. Turneffe Islands besitzt vier benthische Foraminiferen-Gesellschaften, die typisch sind für Lagunen mit eingeschränktem Meerwasseraustausch und variabler Salinität. Lighthouse Reef beherbergt zwei Gesellschaften, die einen hohen Wasseraustausch mit dem umgebenden Meer und sehr klares Wasser bevorzugen. Glovers Reef zeigt zwei Gesellschaften, die in tieferen Lagunen vorkommen und eine geringe Wasserzirkulation benötigen. Generell wurden die höchsten durchschnittlichen Werte für Diversität, Abundanz und Artenzahl für Turneffe Islands und die niedrigsten Werte für Glovers Reef berechnet. Die Foraminiferenfauna in Lighthouse- und Glovers Reef befindet sich seit 6,000 Jahren in einem „Diversifikations -Stadium“, während die Foraminiferen in Turneffe Islands die Lagunenentwicklung, vom Stadium der „Kolonisation“ (vor ~4,000 Jahren) zu „Diversifikation“ (~2,000 Jahre bis heute) widerspiegelt. Lagunentiefe, Wasserzirkulation, Substrat und Bodenwassertemperatur haben einen größeren Einfluss auf die Foraminiferen Diversität als Lagunengröße und -alter. Die negative Korrelation zwischen Diversität und Lagunentiefe beruht auf Unterschieden in den Lichtverhältnissen am Lagunenboden und dem Substrat. Im Gegensatz zu Lighthouse Reef, sinkt die Diversität mit steigender Wassertiefe in Turneffe Islands und Glovers Reef, bedingt durch feines Sediment, trüberes Wasser und/oder dichtem Mangrovenbewuchs die die Lichtintensität und die Anzahl der Arten reduzieren. Auch der Zirkulationsgrad beeinflusst die Lebensweise und die Diversität der Foraminiferen in den letzten 6,000 Jahren. Zunehmende Häufigkeiten infaunal lebender Taxa verweisen in Turneffe Islands und Glovers Reef auf eingeschränkte Zirkulation und/oder niedrigere Sauerstoffbedingungen. Zunehmende Häufigkeiten epifaunal lebender Foraminiferen in Lighthouse Reef hingegen deuten auf bessere Zirkulation und Durchlüftung in den letzten 6,000 Jahren hin.

Holozäne Temperaturrekonstruktionen anhand von $\delta^{18}O$ Werten der Großforaminifere *Archaias angulatus* korrelieren nicht mit typischen karibischen Klimamodellen. Unterschiede in den Temperatur-Trends und Schwankungen spiegeln lokale Klimavariationen in Belize wider. Eine Abnahme von $\delta^{13}C$ in den letzten 1,000 Jahren deutet auf den sog. „Suess Effect“ hin. Saisonale BW-Temperaturrekonstruktionen der $\delta^{18}O$ Werte entsprechen dem modernen Jahrestemperaturverlauf in den Lagunen mit höheren Temperaturen im Sommer und Herbst und niedrigeren Temperaturen im Winter und Frühling.

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Kurzfassung

1 Introduction

The aim of this work is to record Holocene paleoenvironmental change for three carbonate platforms (Turneffe Islands, Lighthouse Reef and Glovers Reef) off the Belize Barrier Reef in the Caribbean Sea (Central America). For this, the appearance, distribution and diversity of the benthic foraminiferal assemblages from cores, and isotopic ratios ($\delta^{18}O$, $\delta^{13}C$) in the larger symbiont-bearing miliolid foraminifera *Archaias angulatus* were investigated.

1.1 Distribution and Use of Benthic Foraminifera in Shallow Caribbean Environments

The composition of a fossil faunal assemblage can be used to reconstruct habitat conditions. Benthic foraminifera have been used as useful facies indicators in recent and ancient carbonate depositional environments (e.g. FROST & LANGENHEIM 1974, HALLOCK & GLENN 1986). MURRAY (1991) investigated the ecology of benthic foraminifera in shallow environments. CEBULSKI (1969) and WANTLAND (1975) described the distribution of benthic foraminifera on the shelf of Belize, and WALLACE & SCHAFERSMAN (1977) studied the foraminiferal fauna in Glovers Reef. GISCHLER et al. (2003) compared the recent foraminiferal distribution on the carbonate platforms off Belize, from the Turneffe Islands, Lighthouse Reef and Glovers Reef and presented different depositional areas within the lagoons.

There are many publications on benthic foraminifera from shelf regions in the Caribbean Sea (e.g. HOFKER 1964, 1969, 1971, 1976; BOCK et al. 1971, BROOKS 1973, ROSE & LIDZ 1977, MARTIN & WRIGHT 1988, MARTIN & LIDELL 1988, 1989, LIDZ & ROSE 1989, & LI et al. 1997), however a limited number of studies are available for the benthic foraminifera distribution in isolated carbonate platforms and atolls. Those that do exist (e.g. MCKEE et al. 1959, STREETER 1963, DAVIS 1964, BICCHI et al. 2002, YAMANO et al. 2002, GISCHLER et al. 2003) are mainly concerned with the modern distribution of benthic foraminifera but not with foraminifera in the Holocene period.

Benthic foraminifera inhabit different characteristic environmental associations. They are abundant an all marine environments, can have good test preservation, have relative short life span, and occur in communities that are sensitive to, and react to environmental change. At different periods within the Holocene, foraminifera assemblages have varied in response to changes in environmental parameters such as water temperature, water depths, salinity (BANDY 1954, 1964), lagoonal size, lagoonal age and type of substrate (CULVER 1990). BICCHI et al. (2002) described a positive correlation between distribution of benthic foraminifera and lagoonal size, lagoonal depth and water circulation. YAMANO et al. (2002) quantified the richness of benthic foraminifera in Holocene lagoons, but neglected changes in diversity.

1.2 Geochemistry of Foraminifera Tests

The tests of benthic foraminifera are built near isotopic equilibrium of ambient sea-water conditions (WEFER et al. 1981). Therefore, stable isotopes of oxygen (^{18}O and ^{16}O) and carbon (^{13}C and ^{12}C) can be used 1) to study changes in paleoceanographic conditions and climatic variabilities, and 2) to interpret life processes of benthic foraminifera during the Holocene. Exact information on temperature, salinity and oxygen conditions, as well as reconstructions of changes within a seasonal cycle can be derived. The δ^{18}O signal can be used as a proxy for water temperature, whereas δ^{13}C helps to interpret metabolic activities (UREY et al. 1951, BUCHARDT & HANSEN 1977).

First studies of oxygen and carbon isotopes on large benthic foraminifera tests from carbonate platforms were published by VINOT-BERTOUILLE & DUPLESSY (1973), WEFER & BERGER (1980), WEFER et al. (1981), and LUZ et al. (1983). WEFER & BERGER (1980) and WEFER et al. (1981) showed that oxygen isotope signals in single shells of larger foraminifera such as *Archaias angulatus* and *Cyclorbiculina compressa* largely reflect annual seasonal water temperature fluctuations. The δ^{18}O signals of *A. angulatus* are 0.9‰ lighter than ambient seawater temperatures, whereas the δ^{13}C values show a much wider range of 1.3 - 4.0‰ when compared to average water variations (WEFER et al. 1981). BRASIER & GREEN (1993) investigated the δ^{18}O and δ^{13}C values of *Archaiasinae* from South Florida. Their bulk material shows low oxygen variations but a high variance in carbon isotope signals, which was assumed to be a consequence of metabolic effects or differences in CO_2 concentration of different micro habitats.

1.2.1 Background on Stable Isotopes (δ^{18}O and δ^{13}C)

Stable isotopes are atoms of the same element that differ in their number of neutrons but have equal numbers of protons and electrons. This results in different atomic masses and thus in different chemical and physical properties of elements (UREY 1947).

Oxygen has three naturally occurring isotopes: ^{16}O with 8 protons and 8 neutrons and an average abundance of 99.759%, ^{17}O with 8 protons and 9 neutrons, and an average abundance of 0.037%, and ^{18}O with 8 protons and 10 neutrons, and an average abundance of 0.204% (Table 1). Ratios of stable isotopes are usually expressed as deviations of ratios of the heavier to lighter isotopes (e.g. O^{18}/O^{16}) relative to the same ratio of a reference material.

Carbon has two naturally occurring isotopes: ^{12}C with 6 protons and 6 neutrons, and an average abundance of 98.89%, and ^{13}C with 6 protons and 7 neutrons, and an average abundance of 1.11%. The ^{12}C and ^{13}C isotopes are stable, while ^{14}C decays radioactively to ^{14}N with a half life of 5,730 years.

Symbol	**Atomic Number**	**Mass Number**	**Abundance (per cent)**	**Atomic Weight (^{12}C = 12)**
H	1	1	9.985	1.007825
D	1	2	0.015	2.0140
C	**6**	**12**	**98.89**	**12**
		13	**1.11**	**13.00335**
N	7	14	99.63	14.00307
		15	0.37	15.00011
O	**8**	**16**	**99.759**	**15.99491**
		17	**0.037**	**16.99914**
		18	**0.204**	**17.99914**

Table 1:
Isotopic abundances and relative atomic masses of the described elements and hydrogen in stable isotope geochemistry.

1.2.2 Isotope Fractionation

During isotope fractionation, heavy and light isotopes partition differently between two compounds or phases. This occurs because the bond energy of each isotope is slightly different, with heavier isotopes having stronger bonds and slower reaction rates. The difference in bonding energy and reaction rates is proportional to the mass differences between isotopes. The dependency on mass is referred to isotope effects or isotope fractionation. There are two categories of isotope effects: kinetic and equilibrium fractionation.

Kinetic effects are associated with fast, incomplete, or unidirectional processes such as evaporation, diffusion, dissociation reactions (HOEFS 1997), and biologically mediated reactions (WHITE 1997). A kinetic isotope fractionation occurs when one isotope reacts more rapidly than the other in an irreversible system or a system in which the products are swept away from the reactants before they have the opportunity to come to equilibrium. Normally, the lighter isotope reacts faster than the heavier and the product will be lighter than the reactant. This occurs for example, during the evaporation of water from the ocean into the atmosphere. Water molecules that contain the heavier isotope ^{18}O move slower than molecules comprising the light isotope ^{16}O. Lighter isotopes or molecules cross phase boundaries (e.g. liquid to vapour) at higher rates than the heavier isotopes. Due to these different reaction rates the vapour is enriched in isotopically lighter water molecules, leaving seawater enrichment of the heavier ^{18}O istotopes.

Large kinetic effects are associated with biologically mediated reactions or metabolic effects, which are mainly caused by photosynthesis and respiration. They result from changes in the δ^{13}C of dissolved inorganic carbon (DIC) in the vicinity of the precipitated carbonate (MCCONNAUGHEY 1989a and b). Photosynthetic organisms in seawater are enriched in ^{12}C relative to atmospheric CO_2

(GROSSMAN 1987, MCCORKLE et al. 1990) because ^{12}C is incorporated into organic tissue during photosynthetic reactions. Thus, photosynthetic activity in the upper water column causes a depletion of ^{12}C and an enrichment of ^{13}C. When organic matter is remineralized at depth, the opposite occurs. Biological activity imposes a gradient in $\delta^{13}C$ in the water column. The extent of depletion of ^{12}C in surface waters will depend on biological activity: $\delta^{13}C$ will be higher in productive waters than in unproductive waters. The extent of enrichment of ^{12}C in deep water, depends on the age of the deep water; „Old“ deep water will have lower $\delta^{13}C$ than „young” deep water (WHITE 1997). During an increase in temperature an enrichment in the heavier isotope ^{13}C occurs in contrast to oxygen isotopes. According to EMRICH et al. (1970), the carbon isotope fractionation between HCO_3^- and $CaCO_3$ is 0.035‰ per 1°C.

Most fractionations arise from equilibrium effects. Equilibrium fractionation describes isotopic exchange reactions that occur between two different phases of a compound, as in the transformation of water vapour to liquid precipitation. The rate of these exchanges varies and the result is an enrichment of one of the isotopes (WHITE 1997). One example is the condensation of water from a vapour phase (opposite to evaporation). During the condensation process the liquid phase represents the phase with the lower energy stage, whereas the vapour has a higher energy stage. As a consequence isotopically heavy molecules tend to be more abundant in the liquid phase. These fractionation effects make rainwater isotopically heavier than condensed water from the clouds.

Other factors are vibrational energy, which is related to the zero-point energy difference and is dependent on temperature. Different isotopes have different zero-point energies for the vibrational mode of a bond. The zero point of energy changes with temperature increases. The difference in zero point energy between two isotopes decreases. The heavier isotope has a lower zero point energy and takes more energy to break the bond of a heavy isotope compared to the light isotope (WHITE 1997).

1.3 *Archaias angulatus* as $\delta^{18}O$ Proxy

Stable isotope investigations were measured in tests of the large miliolid foraminifera *Archaias angulatus*. *A. angulatus* (FICHTEL & MOLL, 1798) is a large (<7 mm) symbiont-bearing porcellaneous foraminifera and belongs to the suborder *Miliolina* and the family *Soritidae* (Fig. 1a). The test surface is densely covered with pseudopores (Fig. 1b). *A. angulatus* possesses pseudopodia, which are used for attachment on different substrates. The tests are planispiral and involute to evolute towards the margin (LOEBLICH & TAPPAN 1988 a and b).

A. angulatus has a mean life span of one to one-and-a-half years (HALLOCK et al. 1986), and WEFER et al. (1981) assumed a reproduction stage in early spring. MURRAY (1991) found *A. angulatus* living epifaunally, free or clinging on seagrass (*Thalassia testudinum*), in water depths less than 12 m and in low energy regimes. ROSE & LIDZ (1977) found *A. angulatus* living on mud flats of Andros

Island in the Bahamas that are periodically exposed by tides or on carbonate sands. HALLOCK et al. (1986) described the occurrence of live *A. angulatus* on rocky substrates, algal-seagrass substrates, and seagrass substrates, but most abundantly on the mixed algal-seagrass substrate. In the Northern Florida Keys, MARTIN (1986) found *A. angulatus* is confined to seagrass blades, in eutrophic conditions with extreme salinities, light intensities and wave energy.

According to LEE et al. (1974), *A. angulatus* lives in symbiosis with the green alga *Chlamydomonas hedley* and preserves oxygen conditions of more than 4 ml/l (BANDY 1964), and shows high tolerance to sea-level fluctuations (MURRAY 1991). BANDY (1964) reported that a very large part of the marine carbonate shelf of Batabanó Bay, Cuba, is characterized by an *A. angulatus* assemblage in which one species comprises up to 80% of the foraminiferal population. BANDY (1964) assumed that the total populations represented living populations and concluded that *A. angulatus* is a stenohaline species, because its endosymbionts limit it to depths of <20 m (LEE et al. 1974, MARTIN 1986). Tests of *Archaias* are strong and resistant to abrasion and dissolution (COTTEY & HALLOCK 1988) and cause a dominance of dead specimens in the respective areas (MARTIN 1986). The calcite shells of the miliolid species *A. angulatus* contain two-to-three times more magnesium in their tests, which ranges from 10 – 14%, than the benthic rotaliid foraminifera (MACINTYRE & REID 1998). These high-magnesium calcite tests have to be corrected in typical paleo water-temperature calculations, which based on calcite shells (TARUTANI et al. 1969, WEFER & BERGER 1980; Chapter 3.7.2).

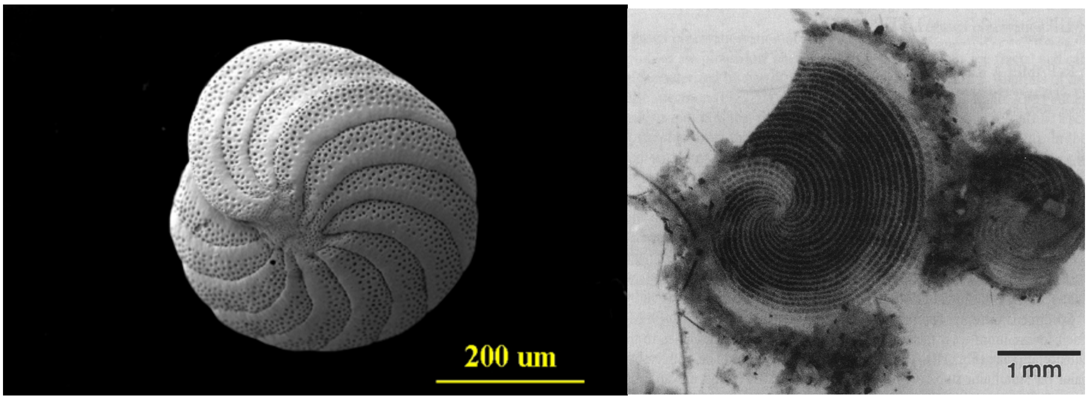


Figure 1.1:
(a) Juvenile specimen of *Archaias angulatus* (photo: P. Hallock), (b) adult *A. angulatus* with pseudopodia, which include grains or particles of various materials (MACINTYRE & REID 1998).

2. Study Area: Turneffe Island, Lighthouse Reef and Glovers Reef

2.1 Geographic Setting

The three carbonate platforms Turneffe Islands, Lighthouse Reef and Glovers Reef are located in the Caribbean Sea east of the Belize Barrier Reef (Fig. 2.1). The country of Belize (15°45′ and 18°30′N, and 87°30′ and 89°15′W) is situated in the Central American mainland, forming part of the Yucatán peninsula and comprises approximately 22,960 km^2 (including territorial sea). Mexico is bordering to the north and Guatemala to the west and south of Belize. The three isolated platforms are part of a 600 km long reef system offshore from Belize which contains several isolated reef-fringed and drowned platforms e.g. Arrowsmith Bank, Cozumel Island and Banco Chinchorro in the north.

Broadleaf tropical moist forest covers approximately 60% of Belize's mainland. The topographic relief ranges from <60 m above mean sea level in the north to 1,095 m in the southern Maya Mountains.

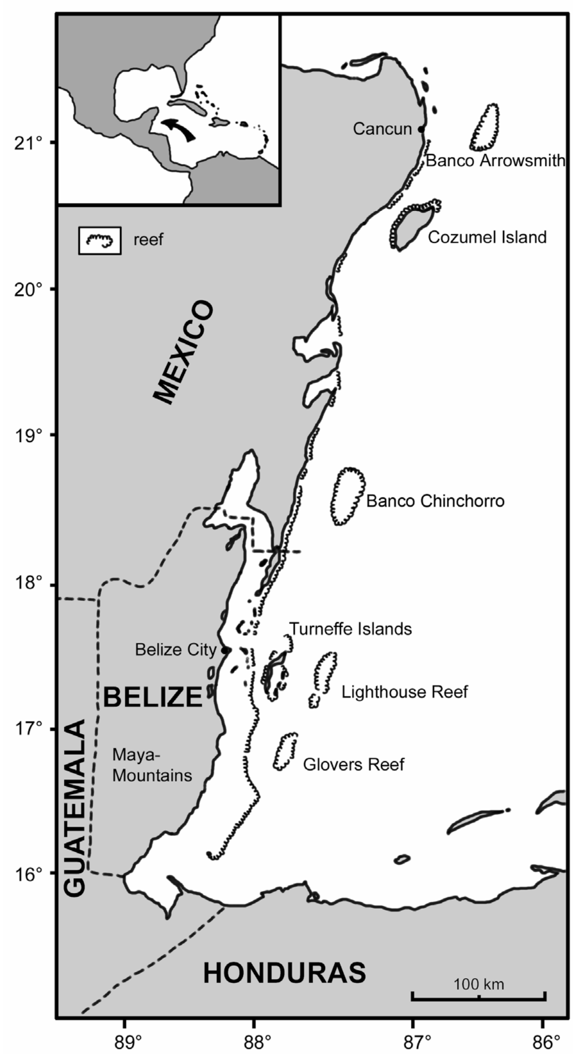


Figure 2.1:
Location of the study area in the Caribbean Sea: Belize and the three isolated carbonate platforms (GISCHLER & LOMANDO 1999).

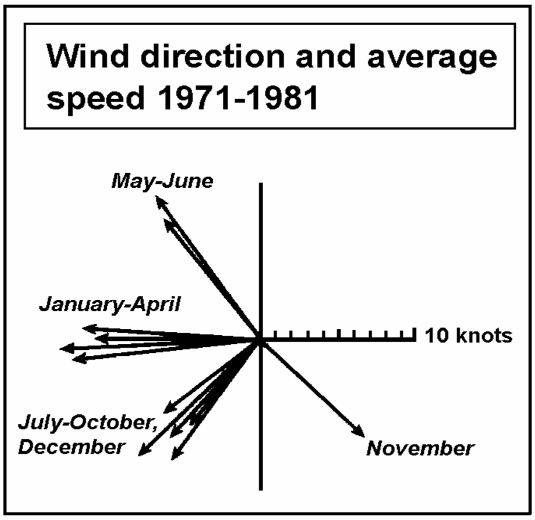


Figure 2.2:
Main wind direction (data from GISCHLER & HUDSON 1998).

2.2 Climatic and Oceanographic Setting

The climate of Belize is subtropical with average air temperatures of approximately 24°C in winter and 27°C in the summer (PURDY et al. 1975). It is characterized by two annual seasons: a rainy and a dry season. Most of the year`s rainfall occurs between June and November. Mean annual rainfall in Belize ranges from 124 - 178 cm/y in the north to more than 380 cm/y in the south (STODDART 1962, PURDY et al. 1975, Belize Weather Bureau 2000).

Belize is located in the trade wind belt and shows wind directions from the East (January - April) and from the NE (July - December) for most of the year (Fig. 2.2). Wind directions affect the main wave direction (BURKE 1982). During May and June the wind blows from the SE and in November from the NW. Average wind speeds range from 7 knots in October to 13 knots in March. From November to February tropical storms and hurricanes (from E - SE) may affect Belize and cause major damage to the reefs and coast; hurricanes Chantal and Iris hit Belize during the sampling period between 2000 and 2001. Within the last 50 years, around 20 hurricanes have hit Belize.

The tidal range is microtidal at ~0.3 m (STODDART 1962). The Caribbean Current flows westward and is diverted to the north into the Gulf of Honduras and results in a southward-flowing Counter Current along the shelf and the platforms (WALLACE & SCHAFERSMAN 1977, GISCHLER & LOMANDO 1999).

2.2.1 Present-Day Bottom-Water Temperature and Salinity

The Turneffe Islands show highest yearly bottom-water temperatures of 21.7 to 31.8°C. Lighthouse Reef shows BW-temperatures between 23.1 and 31.3°C and Glovers Reef has BW-temperatures between 23.5 and 30.4°C (Tab. 2.1).

Highest salinity fluctuates between 34.2 - 42.5‰ in Turneffe Islands and from 37.7 - 41.6‰ in Lighthouse Reef and from 38.6 - 42‰ in Glovers Reef (GISCHLER et al. 2003). Temperature and salinity fluctuations (Figs. 2.3 and 2.4) are highest in the Turneffe Islands (ΔT= 8.3 - 10.1°C, ΔS= 5 - 8‰), lowest in Glovers Reef (ΔT= 6.9°, ΔS= 3.4‰), and intermediate in Lighthouse Reef (ΔT= 6.7 - 7.4°, ΔS= 3.9‰).

Position	Depth (m)	BW-Temperature(°C)	ΔT(C°)	Salinity (‰)	ΔS (‰)
T-North	3.60	21.7 - 31.8	10.1	34.2 - 42.2	8.0
T-South	7.80	22.5 - 30.8	8.3	37.5 - 42.5	5.0
L-North	6.00	23.1 - 29.8	6.7	no data	no data
L-South	3.00	23.9 - 31.3	7.4	37.7 - 41.7	3.9
G-North		lost - no data			
G-South	10.50	23.5 - 30.4	6.9	38.6 - 42.0	3.4

Table 2.1: Bottom-water temperature and salinity ranges for the three platforms, as measured from December 2000 to December 2001 (GISCHLER et al. 2003).

Seasonal bottom-water temperatures in all lagoons were highest between May and September (Fig. 2.3). Turneffe Islands exhibits summer BW-temperatures (May to September) of 27.8 - 31.4°C and winter temperatures (October to April) of 22.7 - 27.4°C. Summer BW-temperatures for Lighthouse Reef range between 26.7 - 30.6°C and winter temperatures vary between 23.3 - 28.0°C. Glovers Reef shows summer BW-temperatures of 28.4 - 30.3°C and in winter temperatures of 23.6 - 27.4°C.

Seasonal salinities are different across the three platforms (Fig. 2.4). Turneffe-North and Lighthouse-South show high salinities (41.6 and 42.1‰) between April/May to September/November. On Turneffe-South and Glovers-South high salinity values (41.9 and 42.4‰) were measured between January and May. The significance of this data is unclear as these results indicate an opposite trend to the present-day seasonal climate patterns, as highest precipitation occurs between June and November and would exhibit low salinities.

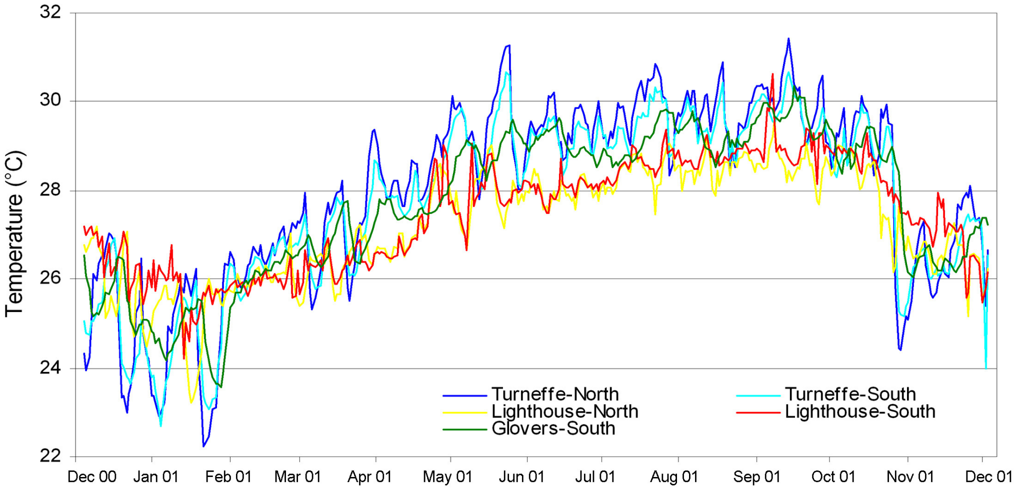


Figure 2.3: Annual bottom-water temperature measurements on all lagoons during the year 2000 and 2001. The data logger at Glovers Reef-North was lost, so no data are available for this region.

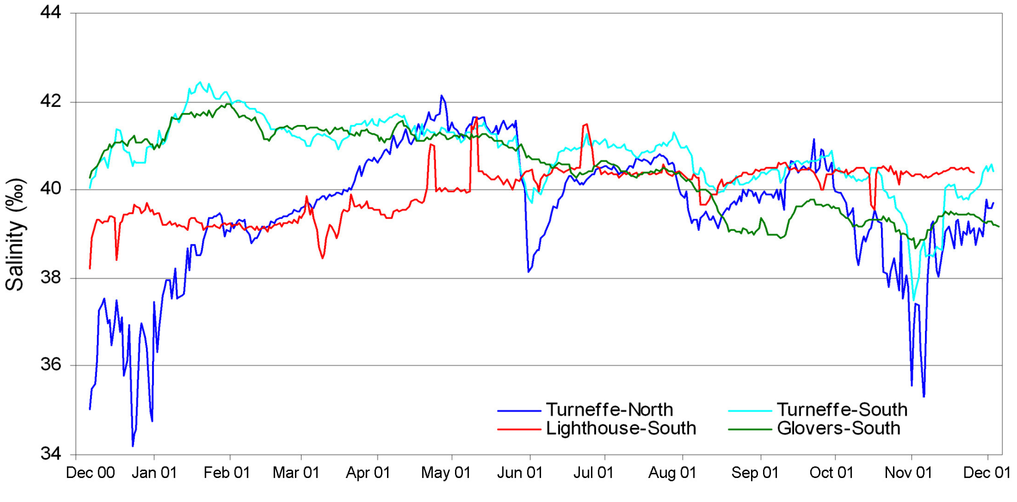


Figure 2.4: Annual salinity measurements of the three platforms in December 2000 to 2001. Data logger at Glovers Reef-North was lost, and conductivity (salinity) data at Lighthouse Reef-North yielded no results.

2.3 Geomorphology of the Platforms

The modern geomorphology of the three platforms was first described by STODDART (1962). The platforms are separated by deep water areas. Between the Belize Barrier Reef and Turneffe Islands, water depths reach ~250 m below sea level (bsl) land between Glovers Reef and the Belize Barrier Reef 450 m bsl (Fig. 2.5). Areas of maximum water depths are located between the Turneffe Islands and Lighthouse Reef with more than 1,000 m and to the east of the platforms in the Yucatan Basin, with several thousands of meters (GISCHLER & LOMANDO 1999). This abrupt increase in water depth characterizes many reefs around the world (PURDY & GISCHLER 2003).

The three platforms show morphological similarities with surface-breaking marginal reefs on their windward sides, sloping fore reefs and wide sand aprons behind the windward reefs. However they differ significantly in size and in the type of platform interior; Lighthouse Reef and Glovers Reef show more open marine conditions with coral patch reefs, whereas the Turneffe Islands show dense mangrove growth behind the rim which causes restricted circulation (GISCHLER 2003). The Turneffe Islands is the largest platform that reaches a total area of 525 km^2. Glovers Reef reaches 260 km^2, and Lighthouse Reef is the smallest atoll of 200 km^2.

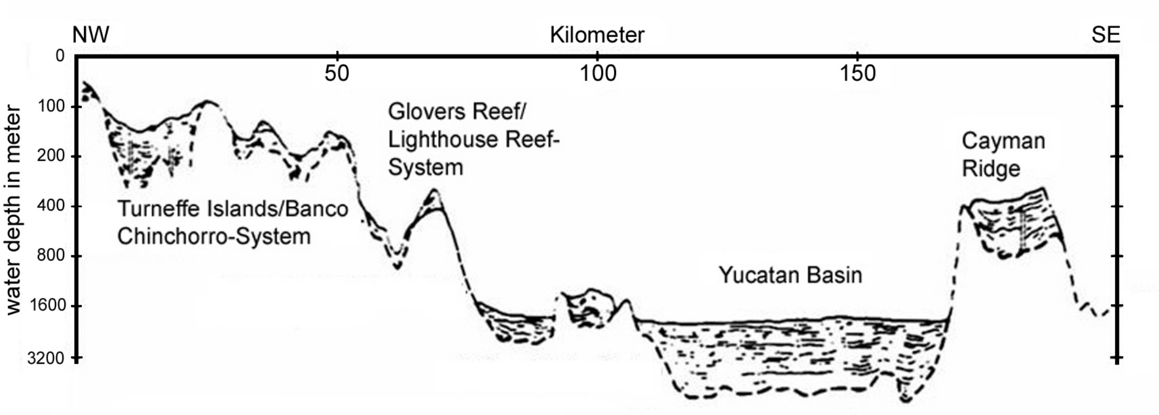


Figure 2.5: NW-SE cross section through the Yucatán reef system (modified after WEYL 1980).

Turneffe Islands are surrounded by marginal mangrove areas and show a maximum water depth of 8 m in the interior area. SMITH 1941 described that the platform is divided into two restricted sections; 1) the smaller northern lagoon, with water depths of 3 m, and 2) the larger, southern lagoon with maximum water depths of 8 m. Red mangroves (*Rhizophora mangle*) are common in the lagoons. The southern windward part of the lagoon contains several channels and in the western mangrove margin several ponds exist. They are abundantly covered by *Thalassia testudinum* (seagrass) and the green alga *Halimeda*. The bottom sediment is dominated by organic-rich sands and plates of *Halimeda*, and a low number of patch reefs are located in the northern lagoon (GISCHLER 1994).

Lighthouse Reef is divided into an eastern and a western lagoon. A NNE-striking patch reef trend (Middle Reef) separates the deeper (8 m) eastern part from the shallower (3 m) western part. The western lagoon and the patch reefs consist of the massive coral, such as *Montastraea annularis*, and the eastern lagoon is dominated by the branching coral *Acropora palmata* (GISCHLER& LOMANDO 1999). Some channels are present in the southern part of Lighthouse Reef. One characteristic part of Lighthouse Reef is the "Blue Hole". It is a sinkhole, almost perfectly circular in shape and 125 m deep, which was formed during the last glacial maximum when sea level was much lower.

Glovers Reef has an 18 m deep interior lagoon and becomes shallower to the rim. Numerous patch reefs (>860) are common. The patch reefs are dominated by the massive coral such as *Montastrea annularis*, the delicate branching corals *Acropora* sp. and *Porites* and different algae (WALLACE & SCHAFERSMAN 1977, MCCLANAHAN & MUTHIGA 1998). Three windward channels interrupt the eastern part of Glovers Reef. Clear water, light-coloured bottom sediments and the abundant patch reefs suggest open marine conditions similar to those observed at Lighthouse Reef (GISCHLER 2003).

2.4 Geology

2.4.1 Geological Background

The mainland of Belize can be divided into two structural-morphological regions (Fig. 2.6). (1) The central Maya Mountains represent the Palaeozoic core of igneous, metamorphic, and sedimentary rocks with shales, schists, granites, and porphyrites. The surrounding flat plains are underlain by Cretaceous limestones, which are characterised by tower karsts.

(2) The northern low-relief region is composed of Tertiary and Quaternary limestones. The Pleistocene rocks and modern sediments along the coast represent the youngest cycle of deposition in Belize. In the northern shelf lagoon, Pleistocene shallow-water limestones and pre-Holocene rocks underlie the onshore barrier-reef platforms (PURDY 1974) and the offshore platforms (reefs and lagoons) (GISCHLER & HUDSON 1998, GISCHLER & LOMANDO 1999). In the southern shelf lagoon, south of Belize City, pre-Holocene rocks consist of Pleistocene terrigenous clastic material (PURDY 1974).

The elevation of the Pleistocene top beneath Holocene reefs, shoals, and islands differs between 1 m above present sea level in the north of Belize to more than 25 m below present sea level in the south. In the lagoonal areas Pleistocene elevation decreases from 3-4 m below present sea level in the north to more than 50 m below present sea level in southern Belize, as suggested by drilling and seismic studies on the Belize shelf and barrier reef (PURDY 1974, HALLEY et al. 1977, SHINN et al. 1982, WESTPHAL & GINSBURG 1985, MAZZULLO et al. 1992, MACINTYRE et al. 1995).

2.4.2 Tectonic Setting

Belize is located near the junction of the North American and Caribbean tectonic plates. This in turns allows transtension in a southeast, and transpression in a northeast direction (LARA 1993). The active plate boundary between the North American and Caribbean plates is situated less than 50 km south of the Belize Barrier Reef (Fig. 2.6).

The basement of this reef system is part of a series of three parallel NNE-trending fault blocks along the passive continental margin (DILLON & VEDDER 1973, JAMES & GINSBURG 1979). These are from west to east; 1) the Ambergris Cay shoreline fault-block, 2) the Turneffe-Chinchorro fault-block, and 3) the Glovers-Lighthouse fault-block (Fig. 2.6).

SZABO et al. (1978) dated corals from Pleistocene limestones of Cancún (Mexico) and on the island of Cozumel (~350 km in the north of the Belize Barrier Reef) at 2 - 4 m above present-day sea level to be approximately 125,000 years old. This suggested that the eastern Yucatán area has thus been tectonically stable since the last interglacial sea-level highstand. However, seismic lines along the active plate boundary (DILLON & VEDDER 1973, DILLON et al. 1987), as well as offshore wells indicate neotectonic activity (GISCHLER et al. 2000). GISCHLER (2000) and GISCHLER et al. (2000) suggest an eastward-directed subduction relative to the westward seafloor spreading of the Caribbean Cayman Ridge.

2.4.3 Holocene Development of the Carbonate Platforms

The Holocene development of the three carbonate platforms (Turneffe Islands, Lighthouse Reef, and Glovers Reef) was observed from sedimentological and stratigraphical data of GISCHLER (2000, 2003). Additional investigations based on oxygen isotopes of marine fossil corals from the Belize Barrier Reef were made (GISCHLER et al. 2000). As described above, the basement of Pleistocene reefs and limestones in the Belize area accumulated around 125-130 ka (SZABO et al. 1978). Overlying Holocene carbonate reefs increase in thickness of a few meters (in the north) to >25 m in the south of Belize and indicate a southward directed flooding of the shelf (GISCHLER & HUDSON 1998, GISCHLER 2000). A similar trend was observed for the three carbonate platforms; Turneffe Islands and Lighthouse Reef in the north indicate a lower Holocene thickness of ~3 – 8 m, whereas Glovers Reef in the south shows a Holocene thickness of ~10 - 12 m (GISCHLER et al. 2000). Due to the Holocene transgression a successive flooding of the platforms was suggested by GISCHLER & HUDSON (1998) and GISCHLER (2000); Glovers Reef was flooded ~8,500 years BP, Lighthouse Reef ~7,000 years BP, and Turneffe Islands ~6,000 years BP.

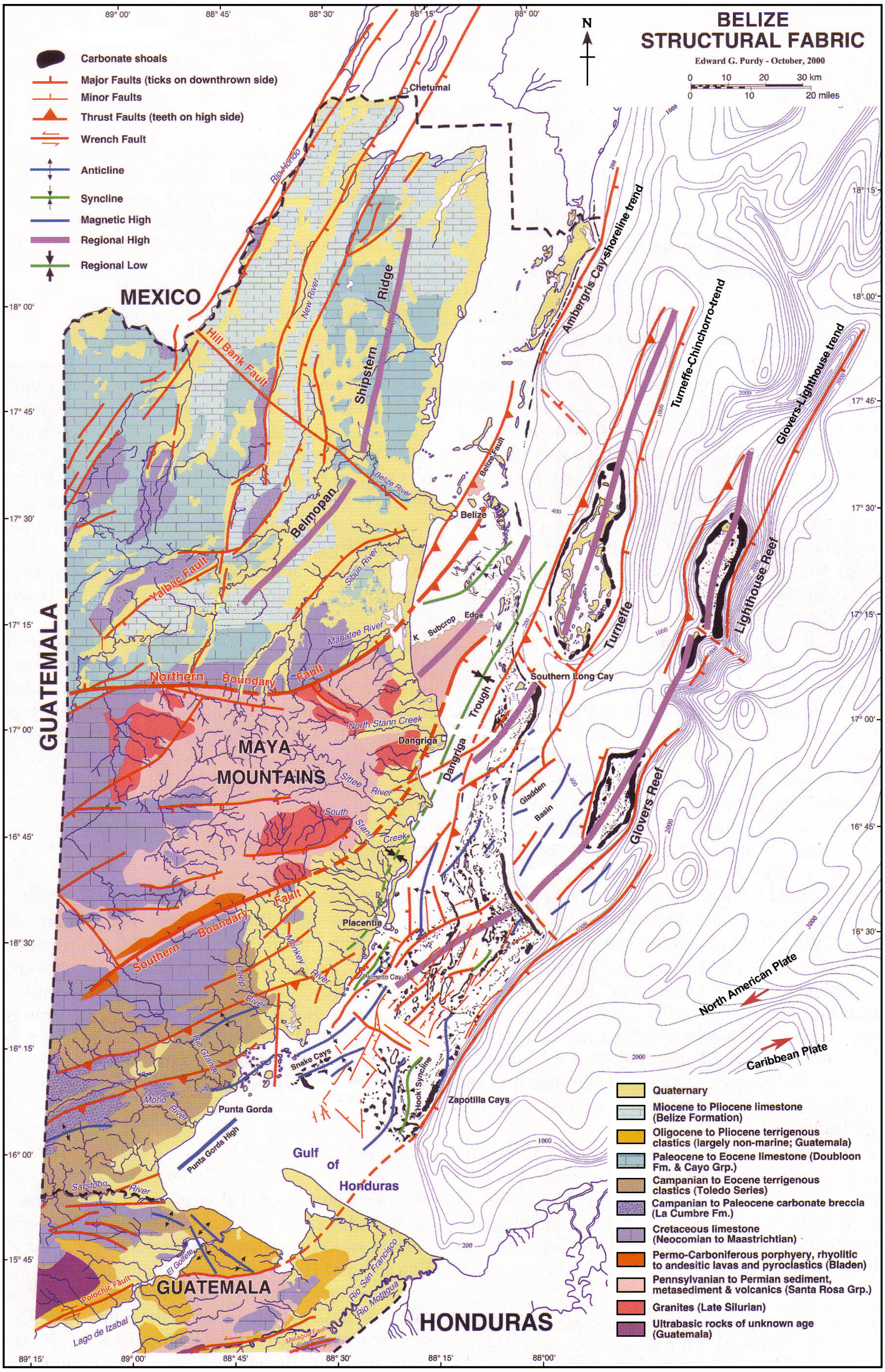


Figure 2.6:
Geological and tectonical map of Belize (modified after PURDY et al. (2003)

3. Material and Methods

3.1 Location of Vibracores

A total of 31 cores (LANESKY et al. (1979)-type vibracorer) were taken from the three Belize atolls with a 6 m long aluminum pipe (7.5 cm diameter) and a core-catcher during March and April of 2000. To record lagoon development in several regions, the cores were taken in both marginal and interior environments of the lagoons. The lengths of cores range from 1.47 - 5.35 m. The cores penetrated Holocene sediment down to the Pleistocene limestone bedrock. Water depths range from <1 m to ~14 m bsl. To record the compaction effect, the core tubes were marked at the sediment surface. Twelve cores, four on each platform, were selected for benthic foraminifera investigations (Fig. 3.1).

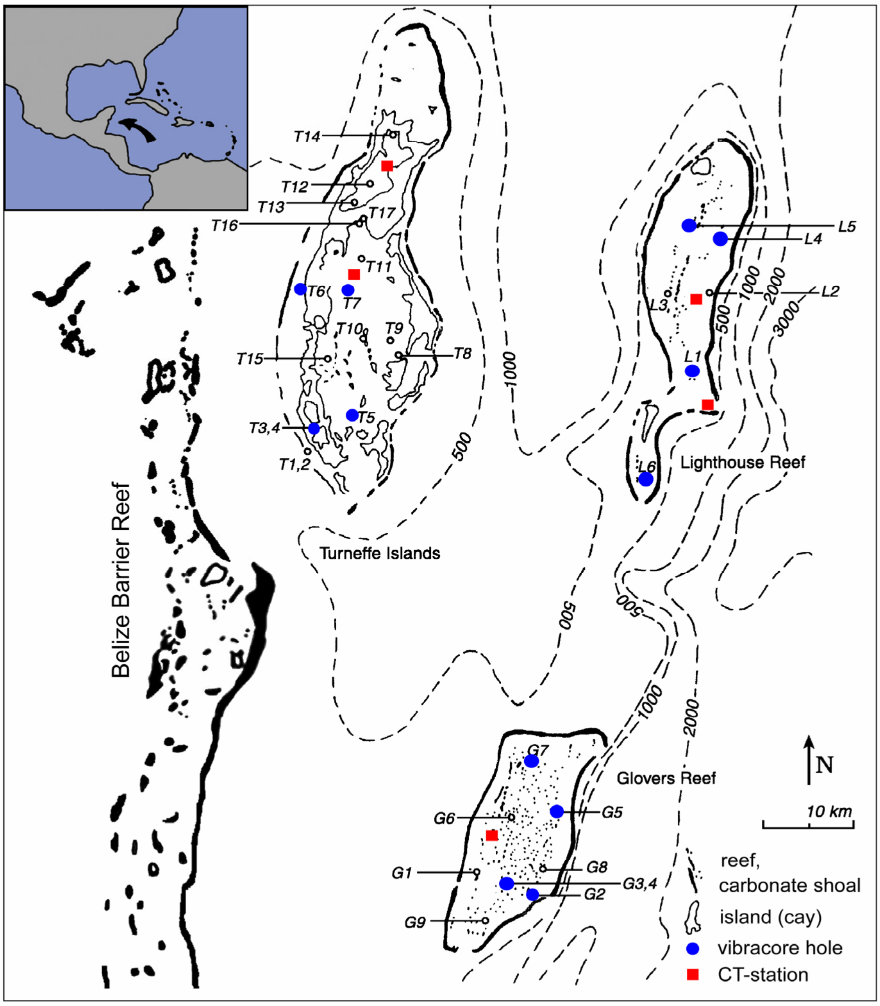


Figure 3.1:
Locations of the vibracore samples (blue dots) and the CT-stations (red dots) on the three platforms. CT-stations were used for conductivity and BW-temperature investigations on the three platforms.

3.2. Sample Collection

A total of 51 samples were investigated, 18 samples in cores from the Turneffe Islands (T4, T5, T6, T7), 16 samples from cores of the Glovers Reef (G2, G4, G5, G7) and 17 samples from cores of the Lighthouse Reef (L1, L4, L5, L6; Fig. 3.1). All selected samples were ^{14}C dated by Beta Analytic Inc., Miami, Florida. In the land-based laboratory (Frankfurt, Germany) the twelve cores were split in half and the working half was sampled at several intervals with a unit sample thickness of 5 cm. The sediment was wet-sieved, and the sand-fraction <0.125 mm was soaked in a 10% aqueous solution of hydrogen peroxide (H_2O_2) for half an hour. The sub-fraction were then sieved into three grain-size fractions >2 mm, 2 - 0.125 mm, and <0.125 mm, and dried on filter paper at 40 - 50°C. Six hundred benthic foraminifera tests were picked with small brushes from each sample, glued on micropaleontological Plummer-type slides using gelatine, and identified using monographs by LÖBLICH & TAPPAN (1988a+b), WANTLAND (1975), and BOCK et al. (1971). The total database includes 30,600 benthic foraminifera shells.

MURRAY (1991) suggested that counts of 200 to 500 specimens would provide accurate results, and that 300 specimens would provide sufficient information for most quantitative examinations.

3.2.1 Modern Sediment Composition

Each lagoon includes a characteristic sediment composition of sediment content, which was first described by STODDART (1962). Further surface sediment samples were investigated by GISCHLER & LOMANDO (1999) for grain-size analyses, which were based on the classification of DUNHAM (1962): “Wackestone” consists 21 - 40% of the <125 µm sediment fraction, “Packstone” consists 4 - 20% of this fraction, and “Grainstone” contains less than 4% of the <125 µm fraction.

GISCHLER & LOMANDO (1999) distinguished following environments on the three platforms:

(1) The reef rims on the windward and leeward sides, the patch reefs and the sand aprons of the three atolls are characterized by corals, red coralline algae and *Halimeda*-plates. Also common is the red encrusting foraminifer *Homotrema rubrum*. Grain-size analyses showed a packstone texture in the sand apron area and within the patch reefs. Reef and fore reef areas exhibit grainstone textures. The mean sediment grain size reaches ~0.65 mm, the finer sand fraction (<125 µm) obtains only abundances of 5%.

(2) The shallow lagoon areas (<5 m) of Lighthouse Reef and Glovers Reef, and the central sand apron area of Turneffe Islands are characterized by a mixed peloidal-skeletal sediment. Main materials are *Halimeda*-plates, molluscs, foraminifera and fecal pellets. Turneffe Islands shows grain sizes of mainly wackestone texture. Glovers Reef contains wackestone to packstone textures and Lighthouse Reef exhibits a mixed fraction of wackestone to grainstone texture. The sediments of this environment

consists of a fine fraction (<125 µm) up to ~23%; principal components are fecal pellets (non-skeletal grains), however they are less common in Turneffe Islands (GISCHLER 1994).

(3) The deep lagoon areas of Lighthouse Reef and Glovers Reef are characterized by molluscs, foraminifera and *Halimeda*. At the Turneffe Islands this sediment composition occurs in the northern shallow lagoon, and the western shallow and deeper lagoon. Grain-size analyses in Turneffe Islands showed a packstone texture. The sediments at Lighthouse and Glovers Reefs exhibit wackestone to packstone textures. Mean grain sizes are 0.45 mm and the fine fraction of <125 µm reaches more than 23%.

(4) The restricted northern and central lagoon of the Turneffe Islands consists of up to 50% *Halimeda*-plates, and in the channels through the eastern mangrove rim up to 90%. 24% of the sediment at this location consist of mean grain-sizes below 125 µm and is classified as a wackestone. In addition, fragments are miliolid foraminifera and organic matter. The sediment colour is dark brown to black and exhibits high average Total Organic Carbon (TOC) values of 5.6%, which reaches single TOC values of 15%. Usual TOC contents in shallow marine carbonate systems range from 0.2 - 2.5% (CREVELLA et al. 1984, EMERSON 1985). From the x-ray diffractrometry, some samples of the Turneffe Islands restricted lagoons contain high (HMC) and low (LMC) magnesium calcite and aragonite, dolomite is absent.

3.2.2 Cores Descriptions

The core succession begins with Pleistocene limestones which are covered by soil that consist of brown and greenish mudstone with plants and roots (Fig. 3.5). The soil is overlain by reddish-brown peat with roots of red and black mangroves such as *Rhizophora* and *Avicennia* respectively, and other organic materials. At all locations (Turneffe, Lighthouse and Glovers) a jump in the dates suggests that a hiatus exists between the lower peat layer and the overlying carbonate sequences. The carbonate sequences, that form the remainder of the cores, can be sub-divided into three main types of facies:

(1) Shell Beds (base); present at Lighthouse and Glovers Reefs sediments and consist of mollusc rudstones (*Laevicardium, Chione*).

(2) *Halimeda* Pack and Wackestones (~middle); dominate the Turneffe Islands sediments and consist of 30 - 80%; molluscs and foraminifera consist of <10%, and some small corals e.g. *Porites*).

(3) Mollusc Pack and Wackestones (~top); dominate the Lighthouse Reef and Glovers Reef sediments and includes molluscs from the genera *Arca, Gouldia* and *Tellina*.

Compaction averages of all cores range from 10 - 12% in the Lighthouse Reef to 18% for Glovers Reef and 33% for the Turneffe Islands (GISCHLER 2003). The relatively high compaction rates for the Turneffe Islands result from sediments, which are rich in pore water. These are the cores T4 and T6 for example, which are located in the mangroves of the leeward margin. Figure 3.2, 3.3 and 3.4 show the compaction values for all the cores.

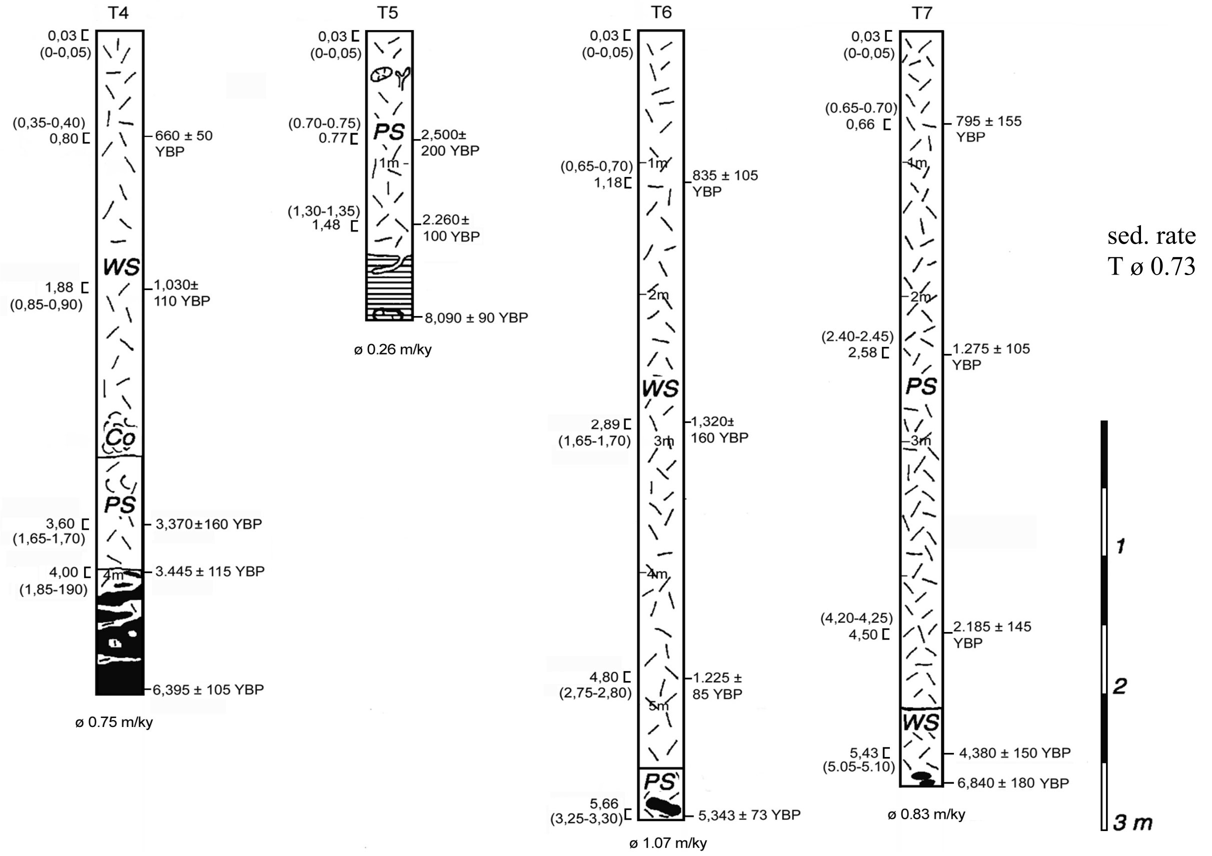


Figure 3.2: Vibracore logs for the Turneffe Islands. The cores T4, T5, T6 and T7 were selected for investigations. The cores are listed in brackets, and the true thickness of sediment samples (m) is corrected for compaction. The sediment ages for the discrete samples and the average sedimentation rates for each core are provided (base of core). An overall sedimentation rate for each location is also given (right of core description). For legend see Figure 3.4.

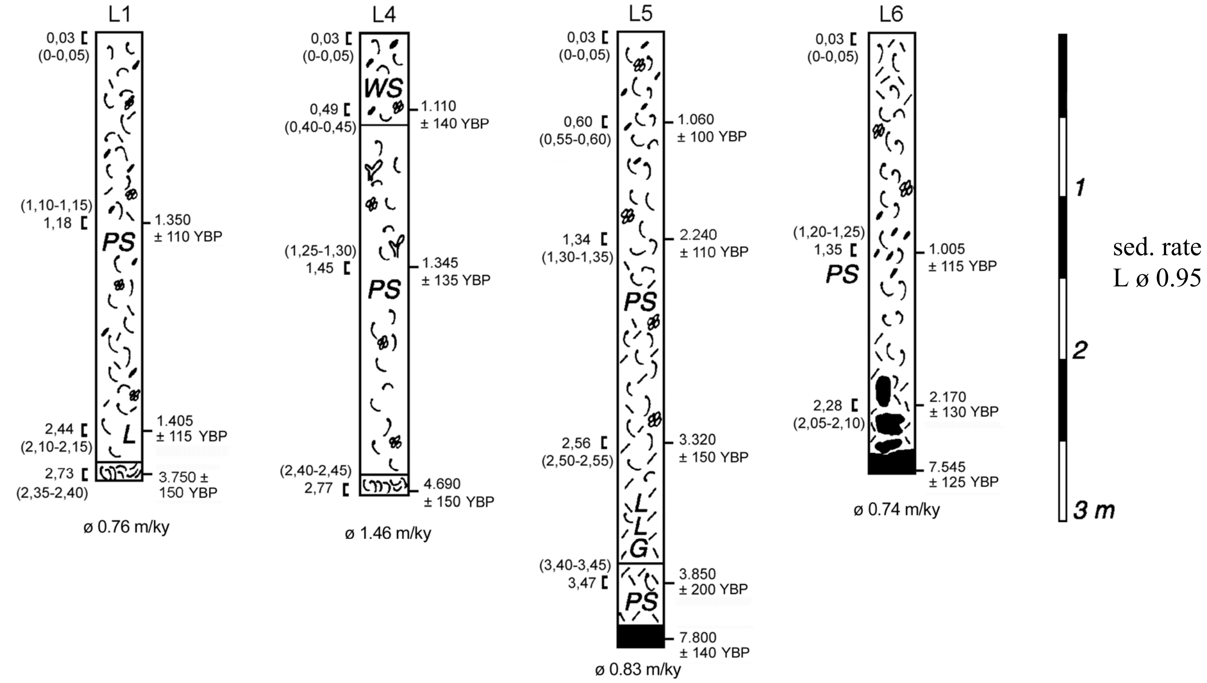


Figure 3.3: Vibracore logs for the Lighthouse Reef, with the selected cores L1, L4, L5 and L6. See Figure 3.4 for legend.

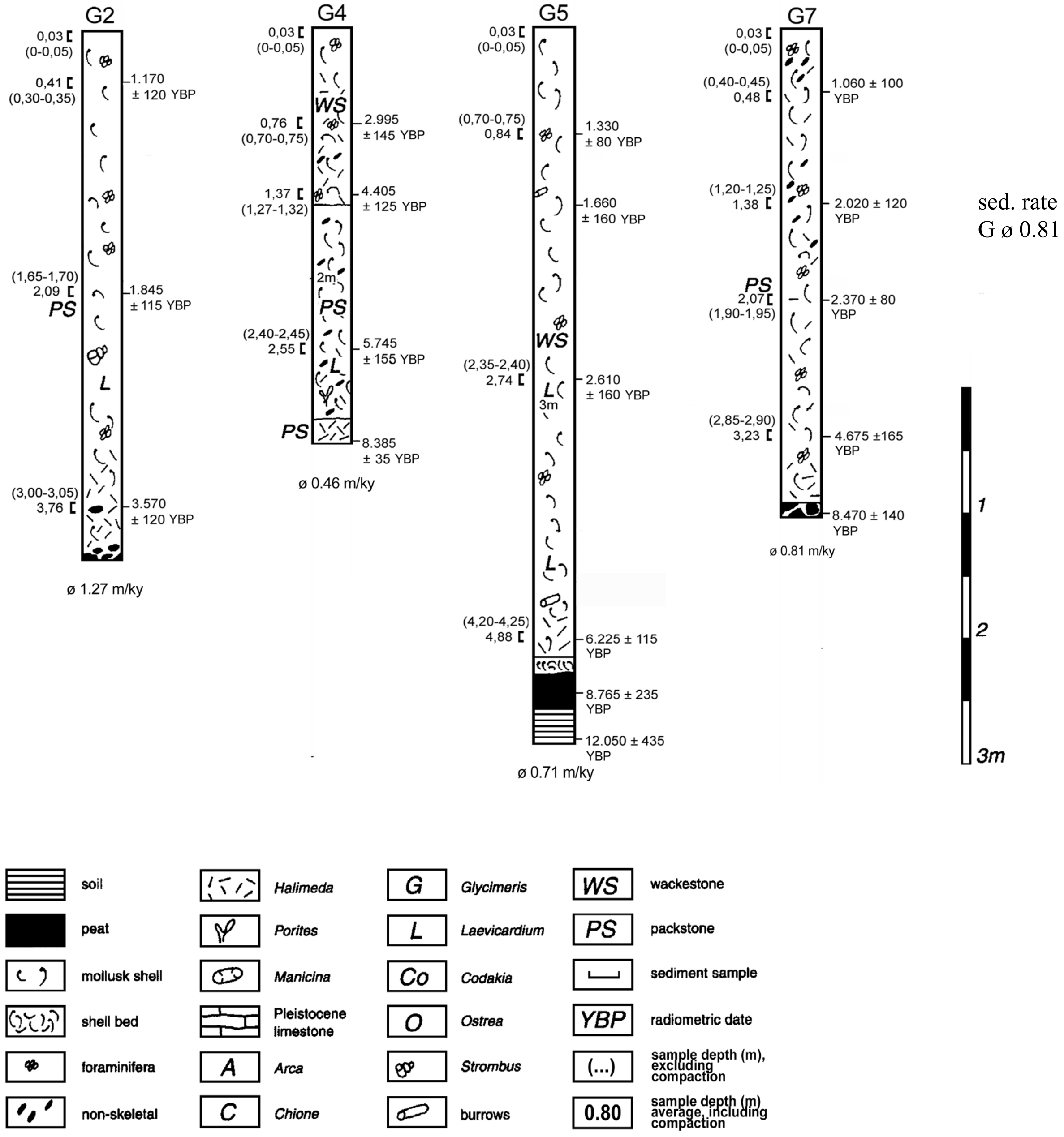
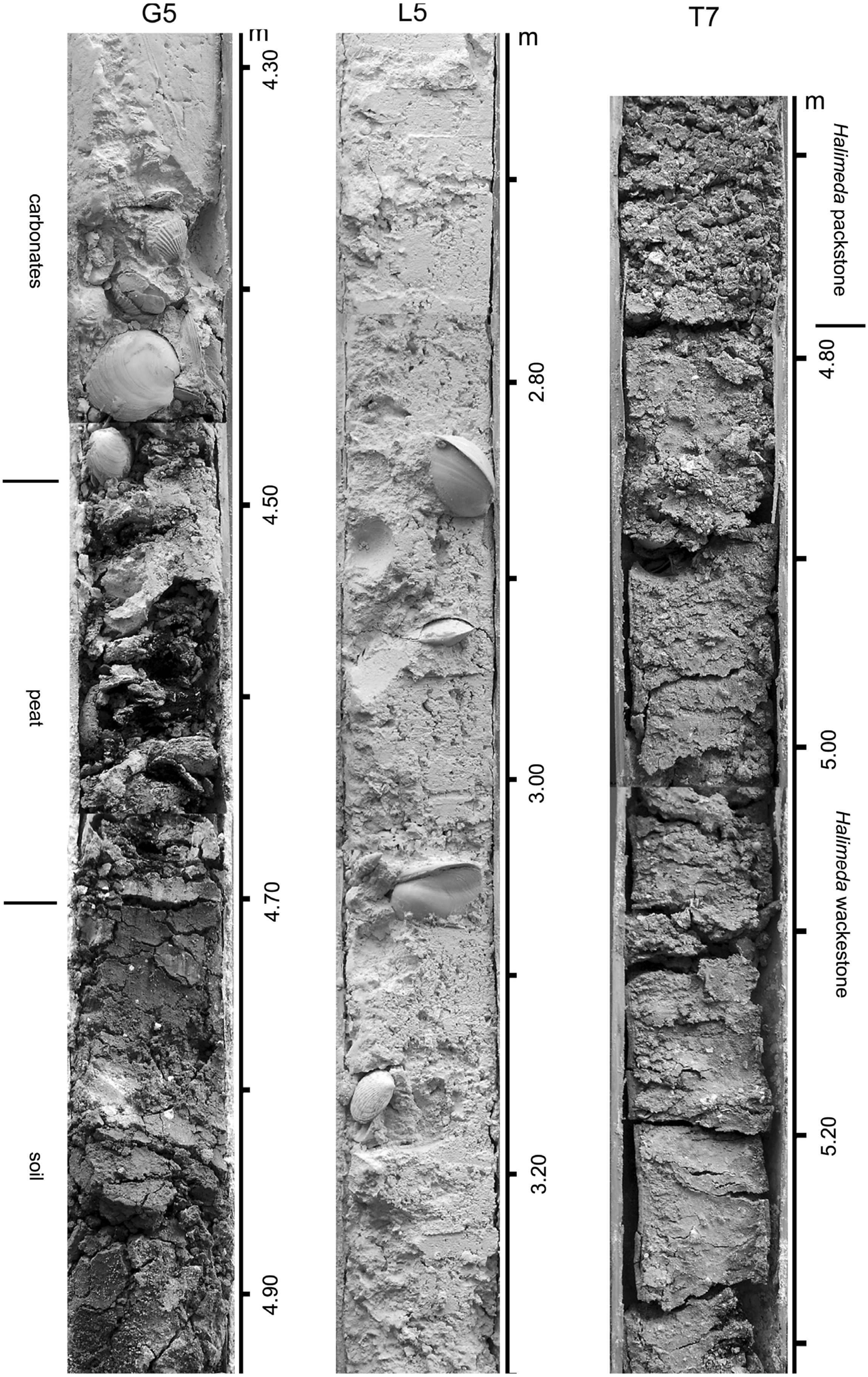


Figure 3.4:
Vibracore logs for the Glovers Reef. Selected cores at Glovers Reef are G2, G4, G5 and G7.

Figure 3.5 (next page):
Selected sections from vibracores at Glovers Reef (G5), Lighthouse Reef (L5), and the Turneffe Islands (T7); Nomenclature after DUNHAM (1962).


G5
L5
T7
m
4.30
4.50
4.70
4.90
carbonates
peat
soil
m
2.80
3.00
3.20
m
4.80
5.00
5.20
Halimeda packstone
Halimeda wackestone

3.2.3 Sampling of the Benthic Foraminifera *Archaias angulatus* for Geochemical Analysis (Micro Drill)

For the isotopic investigations one to three large individuals of *Archaias angulatus* (>2.5 mm) were picked from each sample of the Lighthouse Reef and the Glovers Reef cores. In Turneffe Islands no large and well preserved specimens of *A. angulatus* were available. The individuals were glued on glass slides with a liquid metal fluid (Fig. 3.6a). Each foraminifer was drilled with a 0.3 mm diameter dental “Micro Drill” (Fig. 3.7) along their planspiral chambers (in the direction of growth) beginning in the proloculus area (Fig. 3.6b). Ten to more than fifteen holes per test are possible depending on the size of the respective shell. One whole corresponds to more or less one month (HALLOCK et al. 1986).

For the determination of $\delta^{18}O$ and $\delta^{13}C$ values the foraminiferal cutting was weighted and placed into racks. About 50 - 120 µg of material is required for stable isotope analysis. The preparation method with phosphoric acid is described in Chapter 3.5.2. The $\delta^{18}O$ and $\delta^{13}C$ values were measured on a FINNIGAN MAT 253 at the University of Frankfurt, Germany. The standard deviation for $\delta^{13}C$ is 0.02% and for $\delta^{18}O$ it is 0.06%.

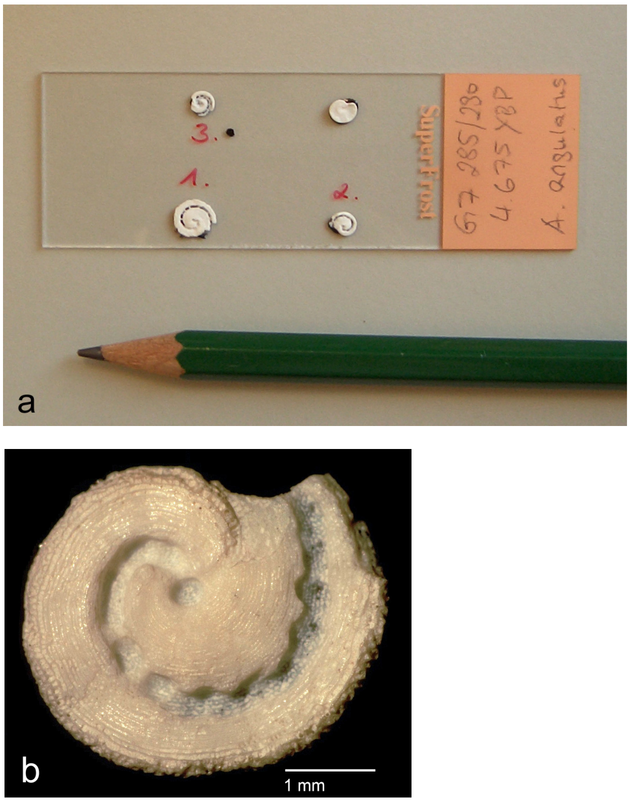


Figure 3.6a, b:
(a) *A. angulatus* glued on slides. (b) Close-up of one individual test shows evidence of drilling.

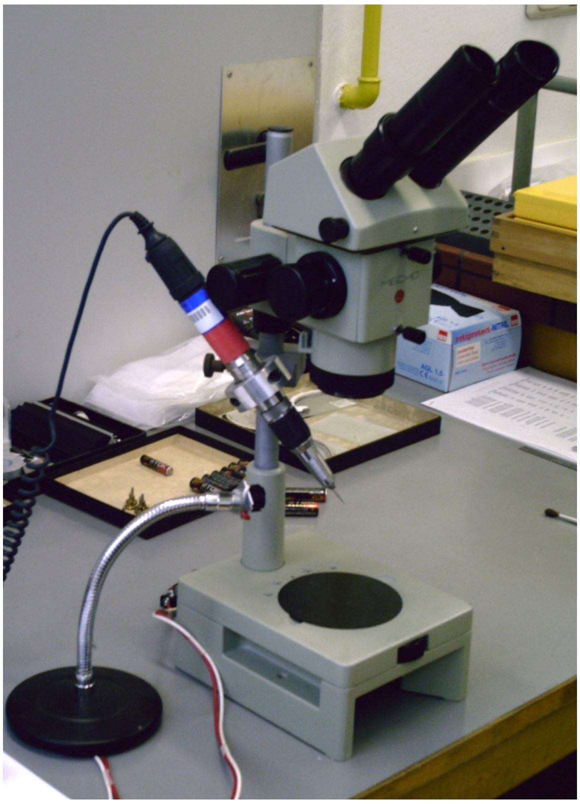


Figure 3.7:
A micro-drill was used for sampling.

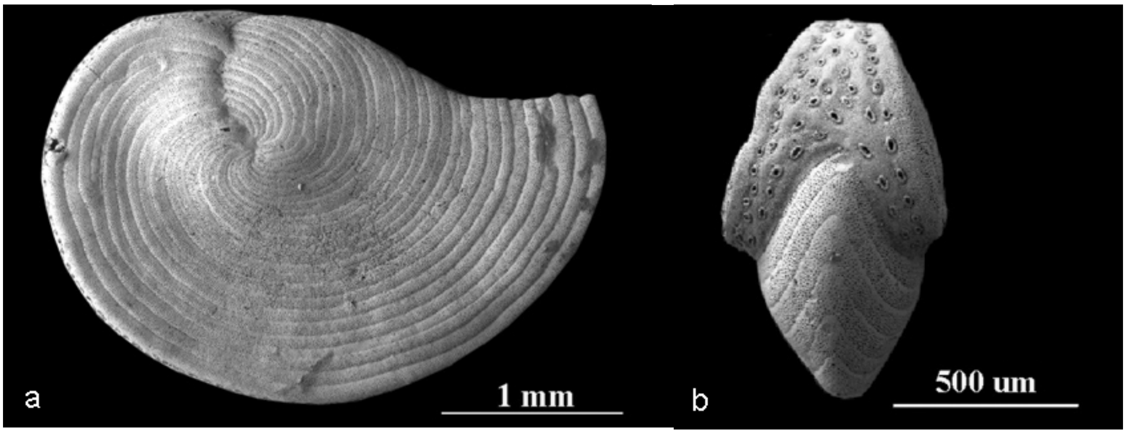


Figure 3.8:
SEM image of *Archaias angulatus* from Florida (P. Hallock: www.marine.usf.edu). (a) Dorsal (spiral) view, (b) juvenile apertural view.

3.3 SEM Documentation

All foraminifers were prepared for scanning electron microscopy (SEM) images at the University of Frankfurt, Germany (Model: CamScan S4). The specimens were glued on special SEM-racks, and sputtered with a thin layer of gold in a high vacuum sputter coater (Model: BAL-TEC MED 020). The images were summarized in plates sorted by assemblages (Appendix 5). Coloured photographs were made of the large species *Archaias angulatus* (Figs. 3.8a and b) to recognize the chambers, and of the encrusting foraminifer *Homotrema rubrum*, which is characterized by a distinct red wall (Appendix 5c).

3.4 Statistical Methods

3.4.1 Q-mode Cluster Analysis

To show characteristic taxonomic composition, a Q-mode cluster analysis, based on all species (in %) was made with the statistical program MVSP (Fig. 4.1). The cluster represents the distribution of related species in similar groups. “Pearson’s Co-efficient” and “Farthest Neighbour” produced the most significant results. The data base incorporates all foraminifera that could be assigned to their respective assemblage. Unidentifiable foraminifera were ignored.

3.4.2 Diversity, Evenness and Richness

Diversity has several aspects and may be expressed by indices. In addition to the abundance of species in different environments the diversity (H’), evenness (E) and richness (R) can be calculated.

The SHANNON-WEAVER (1949) diversity index (H’) was used to assess the environmental stability based on the proportion and the diversity of species found in each sample;

$$H' = -\sum \frac{n_i}{N} \ln\left(\frac{n_i}{N}\right)$$

Where N is equal to the total number of individuals, and n_i refers to the number of individuals of taxon i. After PATTERSON & KUMAR (2002) stable environments show H’-values between 2.5 and 3.5. Transition environments range between 1.5 and 2.5, whereas stressed environments typically show values between 0.1 and 1.5. CONNELL (1978) suggested H’-values up to 5.0 to exhibit stable environmental conditions. Low values are typically found in environments such as salt marshes, where extreme conditions limit the number of species (PATTERSON et al. 2005). This could suggest a dominance or pioneer stage after CONNELL (1978).

In addition to the diversity index, the statistical values for evenness and richness also provide significant results. Evenness (E) and richness (S) are dependent upon the number of species identified in the samples, and reflect a uniform distribution of species in an assemblage and, respectively their dominance ratios. Lower evenness values show a decreased number of species in an assemblage. The evenness is defined after PIELOU (1966):

$$E = \frac{H'}{\ln(S)}$$

H’ represents the diversity index after SHANNON & WEAVER (1949), and S is the number of taxa in the respective sample.

The richness is defined after MARGALEF (1958):

$$R = \frac{S - 1}{\ln(N)}$$

It depends on the number of taxa (S) and the total number of individuals in the corresponding sample (N).

3.4.3 Coefficient of Determination (R^2)

The coefficient of determination is the proportion of variability in a data set that is accounted for by a statistical model and is a measure of the "goodness-of-fit" of a regression line (MATTHEWS 1981). $R^2 = 1$ indicates that the fitted model explains all variability in y, while $R^2 = 0$ indicates a no linear relationship between the response variable and the regressors. An interior value such as $R^2 = 0.5$ may be interpreted as approximately 50% of the variation in the response variable. This can be expressed by the explanatory variable. The remaining 50% can be explained by the unknown variability. A statistical significance is defined by a R^2 of >0.05 and a p-value of <0.005. P-values incorporate the number of variables in the respective sample.

3.5 Radiometric Ages (^{14}C-Method)

Radiocarbon method is a radiometric dating method that uses the naturally occurring isotope ^{14}C to determine materials up to about 40.000 years BP. ^{14}C is an unstable carbon isotope. Cosmic radiation entering the earth's atmosphere produces ^{14}C, and plants take in ^{14}C as they absorb carbon dioxide. ^{14}C and ^{12}C moves up the food chain as animals eat plants. With their death the absorption of the unstable isotope ^{14}C stops, and starts to decay into ^{14}N. However, during this process ^{12}C remains stable. It takes 5,730 years for half the ^{14}C to decay to nitrogen. By measuring the proportion of ^{14}C in organic material, it is possible to determine the date of death by accelerator-based mass-spectrometric (AMS) techniques where all the ^{14}C atoms can be counted directly and by alpha counting. The standard margin of error is +/-50 years.

For the ^{14}C-dating, bulk material of the 51 samples was used and measured with the Beta Analytic Inc. in Miami, Florida. The sample quantity depended on the weight of the respective sample. For the analysis approximately 60 g sediment was required. However, the Turneffe Islands samples demanded higher quantities of material, due to the higher number of light *Halimeda* plates present in these samples. The calibrated ages (in years before present; YBP) are visible in the core illustrations (Figs. 3.4 - 3.6).

3.6 Calculation of Paleolagoon Depths

The paleo-lagoon depths (Fig. 5.4) were calculated from the diference between the sea-level curve of GISCHLER & HUDSON (2004) and the calculated water-depths of discrete samples for each core (Fig. 5.3). The sea-level curve of GISCHLER & HUDSON (2004) was based on calibrated ^{14}C dates from corals (Chapter 5.3.2 and Tab. 5.2), and the paleo-lagoon depths of the discrete samples were calculated from the addition of the corrected (for compaction) downcore sample depths with the present-day lagoon depths. The evaluated paleo-lagoon depths range from 10.97 m for the Lighthouse Reef, to 7.84 m at the Turneffe Islands. The maximum lagoon depths, of 16.38 m, were found at Glovers Reef.

3.7 Geochemical Analysis

3.7.1 Measurements of $^{18}O/^{16}O$- and $^{13}C/^{12}C$-Isotopic Variation

Stable isotope measurements were performed at the University of Frankfurt, Germany. A Thermo-FINNIGAN MAT 253 dynamic range mass spectrometer was used for oxygen and carbon isotopes. The internal standard used in the laboratory of Frankfurt is the “Carrara Marble”. The mass spectrometry is an analytical technique used to measure the mass-to-charge ratio of ions. A short description of the method is given here, detailed explanations of working processes are described by HOEFS (1997).

Shell material from the large benthic foraminifera *Archaias angulatus* consists of calcium carbonate ($CaCO_3$). The carbonate shell material is prepared using acid digestion with phosphoric acid to produce CO_2, which is then cryogenically separated on the vacuum line of the mass spectrometer. The CO_2 molecules are vaporized and ionized into electrically charged particles in the first phase of the mass spectrometry. The ions are accelerated by an electric field after which they are directed into a magnetic field. The magnetic field applies a force, which deflects the ions to different degrees depending on their mass-to-charge ratio. The magnetic field deflects the lighter ions more than the heavier ions. The detector measures the relative intensities of different masses. From this measurement, the mass-to-charge ratios of all the ions produced at the source, can be determined. The $\delta^{18}O$ and $\delta^{13}C$ variations are given as a deviation from the PDB (in ‰).

$$\delta[‰] = \frac{R_{\Pr obe} - R_{S\tan dard}}{R_{S\tan dard}} \times 1000$$

R= $^{18}O/^{16}O$ for oxygen
R= $^{13}C/^{12}C$ for carbon

The Chicago carbon dioxide standard is CO_2 produced from PDB calcium carbonate by digestion in 100% phosphoric acid (H_3PO_4) at 25°C (UREY et al. 1951). PDB is a Cretaceous belemnite, *Belemnitella americana*, from the PeeDee formation of South Carolina; the carbonate has undergone no treatment prior to the acid reaction. Before the limited PDB supply was exhausted, FRIEDMAN et al. (1982) used it to calibrate a crushed slab of white marble of unknown origin, designated as NBS-(National Bureau of Standards) standard. The IAEA (International Atomic Energy Agency) in Vienna has subsequently defined the hypothetical VPDB (considered as identical to PDB) as the reference against which all $\delta^{13}C$ measurements and carbonate $\delta^{18}O$ (after CRAIG 1957) are reported. The conversion of calcite to CO_2 follows the reaction:

$CaCO_3 + 2H^+ \rightarrow CO_2 + H_2O + Ca^{2+}$

The analytical precision is 0.06‰ for oxygen and 0.02‰ for carbon. Contamination may cause problems by organic matter incorporated within the test chambers of *A. angulatus* (EPSTEIN et al. 1953). In this case a possible reaction between organic material and phosphoric acid is CO_2 with a different isotopic composition than the derivation CO_2 of calcium carbonate. Furthermore CO_2 or other oxygen compounds which were produced during reduction of organic material could react with the carbonate. However, this error could be excluded because all organic matter was removed from the test surfaces and chambers of *A. angulatus* by chemical oxidation with H_2O_2.

3.7.2 Paleo BW-Temperature Calculations based on Oxygen Isotopes

The temperature dependent oxygen isotope effect between water and carbonate is the basis of paleotemperature reconstructions. EPSTEIN et al. (1953) and EPSTEIN & MAYEDA (1953) produced an empirical paleotemperature equation, based on isotopic analysis of molluscs with known growth temperatures:

$T\ (°C) = 16.5 - 4.3\ (\delta_c - \delta_w) + 0.14\ (\delta_c - \delta_w)^2$ EPSTEIN et al. (1953) of molluscs

Where δ_c expresses the isotopic composition of measured O^{18}/O^{16} ratios of the carbonate in per mill (‰). The δ_w represents the O^{18}/O^{16} ratio of the isotopic composition of the ambient water.

The isotopic composition of ancient seawater (δ_w) is an unknown factor. But modern $\delta^{18}O$ temperature ratios can be used for estimating ancient $\delta^{18}O$ values. The isotopic composition of seawater in the Belize platforms was measured at the University of Frankfurt, Germany and indicates $\delta^{18}O$ values between 0.8 and 1.2‰. The calculated mean value is 1.0‰ for $\delta^{18}O_{seawater}$ and was used in the paleo BW-temperature equations. The fluctuations reflect seasonal variations in the Belize area, which are affected by precipitation and evaporation (Chapter 3.7.3). Precipitation rates reach their maximum in summer. The increased input of rainwater which is isotopically lighter, leads to lighter $\delta^{18}O$ values during the summer.

Several paleotemperature equations have been proposed based on the oxygen isotopic composition of calcium carbonate. The equation of EPSTEIN et al. (1953), for calculating paleo BW-temperatures between 7 - 29.5°C, was based on oxygen isotope rates derived from the calcite shells of molluscs. The SHACKLETON (1974) equation was also valid for calcite shells of the benthic foraminifera *Uvigerina*, which was calculated for the low water temperature portion of <16.9°C, and based on inorganically precipitated calcite at temperatures of 0 - 500°C (O'NEIL et al. 1969).

$T\ (°C) = 16.9 - 4.38\ (\delta_c\text{-}\delta_w) + 0.10\ (\delta_c\text{-}\delta_w)^{\ 2}$ SHACKLETON (1974) of *Uvigerina*

Additional equations were used to assess paleo BW-temperatures based on aragonite shells of benthic foraminifera:

$T\ (°C) = 20.19 - 4.56\ (\delta^{18}O\text{-}\delta_w) + 0.19\ (\delta_c\text{-}\delta_w)$ GROSSMAN (1982) of *Hoeglundia elegans*

$T\ (°C) = 20.60 - 4.34\ (\delta_c\text{-}(\delta_w\text{-}0.2)$ GROSSMAN & KU (1986) of *H. elegans*

Aragonite shows an increase of 0.6‰ against low-magnesium calcite (LMC) of equilibrium isotopic values (TARUTANI et al. 1969) and is comparable with high magnesium calcite (HMC) values, which are typical for large miliolid benthic foraminiferal shells, such as *Archaias angulatus*. Values of 14 - 18 mole percent $MgCO_3$ for *A. angulatus*, have been reported by BLACKMON & TODD (1959) and MACINTYRE & REID (1998). For the enrichment in ^{18}O by 0.06 per mill per mol percent $MgCO_3$ (TARUTANI et al. 1969), WEFER & BERGER (1980) proposed an increase in $\delta^{18}O$ of about 0.9 per mill for large miliolid foraminifers, such as *Marginopora* and *Cyclorbiculina*. The oxygen isotope values of large benthic foraminifera are about 0.9‰ lighter (WEFER & BERGER 1980) than equilibrium values, and have to be corrected by 0.9‰ of the measured $\delta^{18}O$ values.

Considering the large number of calculations, the equations of SHACKLETON (1974) and EPSTEIN et al. (1953) show most reliable paleo BW-temperature values. The equations of GROSSMAN (1982) and GROSSMANN & KU (1986) were used for comparison.

3.7.3 Salinity Effect

A problem of calculating paleotemperatures from $\delta^{18}O$ signals is the salinity effect. One per mill salinity variation could cause a 0.5‰ change in $\delta^{18}O$ values (CRAIG & GORDON 1965). Salinity is mainly controlled by precipitation and evaporation.

High precipitation occurs in Belize during summer and autumn when weather conditions are hot and wet. This causes lighter $\delta^{18}O_{seawater}$ and could lead to a shift towards lighter $\delta^{18}O$ values (Fig. 3.9). High evaporation occurs during winter and spring when the weather is cold and dry. This causes lower salinities and heavier $\delta^{18}O_{seawater}$ values.

$\delta^{18}O_{seawater}$ at Glovers Reef was measured in August 1996 (Tab. 3.1). In March 2005 all three lagoons were measured. The $\delta^{18}O_{seawater}$ in August reflects summer conditions and shows mean values of +0.83‰ (from +0.71 to +0.98‰). Measurements in March indicate heavier mean $\delta^{18}O_{seawater}$ values of +1.19‰ (from +1.10 to +1.40‰). Average yearly $\delta^{18}O_{seawater}$ values of +1.0‰ was used for the paleo-temperature equation.

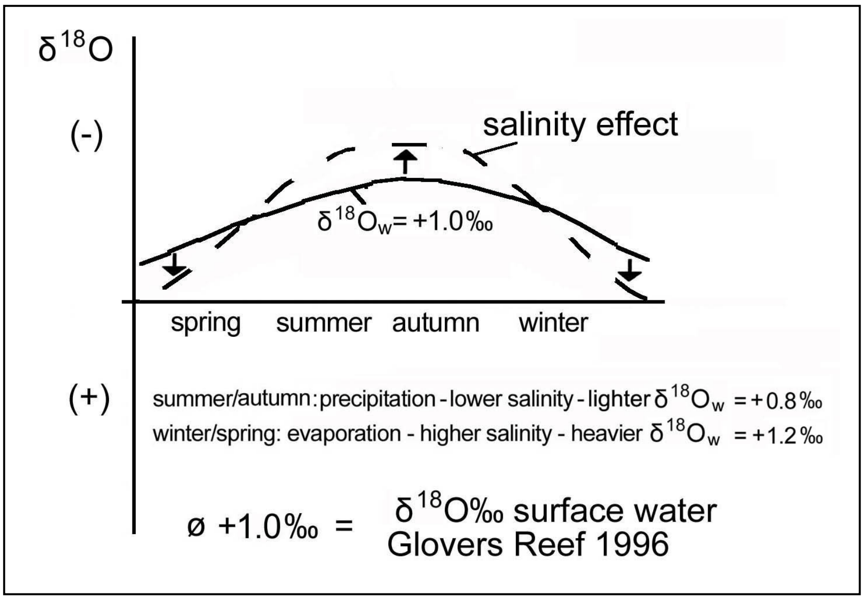


Figure 3.9:
Schematic diagram of reconstructed salinity effect. The $\delta^{18}O_{seawater}$ values of Glovers Reef could show a shift towards lighter values in summer and toward heavier values in winter times.

Aug-96		Mar-05	
sample	$\delta^{18}O$ vs VSMOW (‰)	sample	$\delta^{18}O$ vs VSMOW (‰)
G1	0.75	G1	1.10
G1	0.98	G2	1.20
G2	0.83	BBR	1.20
G2	0.71	L1	1.10
G3	0.88	L2	1.20
G3	-	L3	1.20
		T1	1.40
		T2	1.20
		T3	1.10
mean	**0.83**		**1.19**
mean all	**1.06**		

Table 3.1:
Measured isotopic compo-sition of $\delta^{18}O_{seawater}$ from August 1996 and March 2005 in the three lagoons (measurements of Gischler unpublished).

4. Results

4.1 Abundance, Occurrence and Assemblages of Benthic Foraminifera in the Lagoonal Cores

Fifty-six genera and 109 species of benthic foraminifera were identified in 51 core samples of the three lagoons. A total of 97 species and 47 genera were determined at the Turneffe Islands, 91 species and 46 genera were observed at Glovers Reef, and 77 species and 42 genera were identified at Lighthouse Reef.

The Q-mode cluster analysis of all foraminiferal species shows the characteristical taxonomic composition of the foraminiferal assemblages in each individual lagoon (Fig. 4.1). Seven samples from Glovers Reef and the Turneffe Islands form separate dendrogram entities. Further cluster analyses were performed on the 20 most common species and are shown in Figure 4.2. A total of seven benthic foraminiferal assemblages can be distinguished within the three platforms. The Turneffe Islands contains four assemblages, and Lighthouse Reef and Glovers Reef have two communities, respectively.

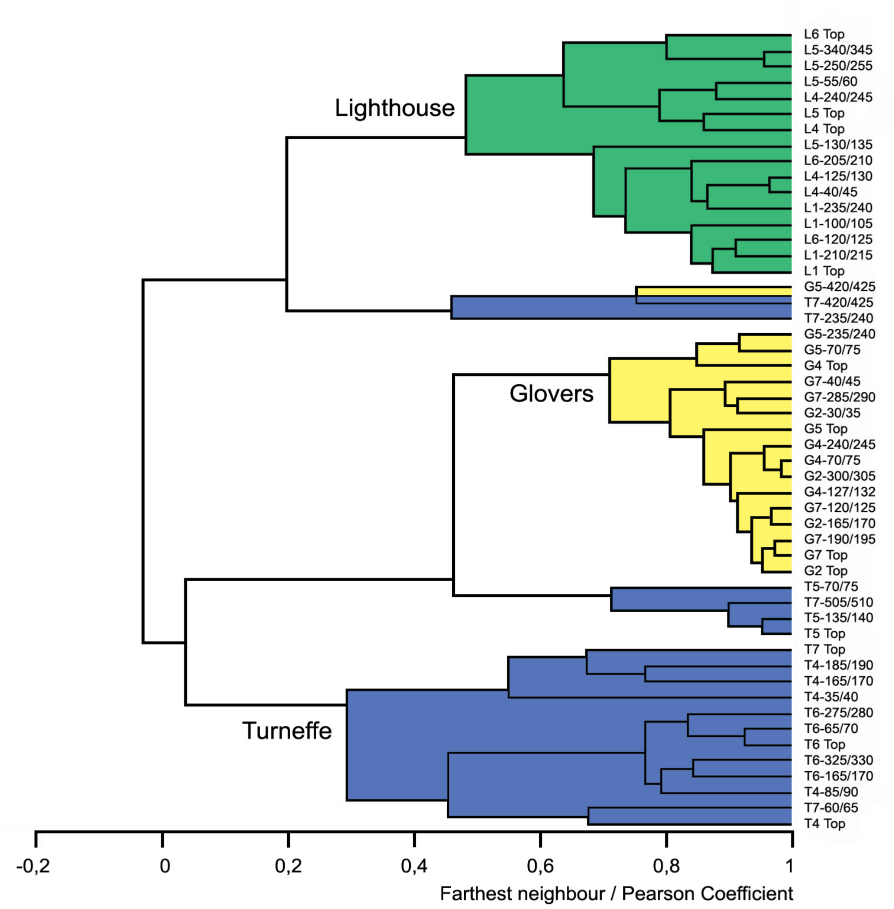


Figure 4.1:
Dendrogram of Q-mode cluster analysis based on all species shows characteristic taxonomic composition within the three lagoons. Using Farthest Neighbour and Pearson Coefficient produced the most meaningful dendrogram entities.

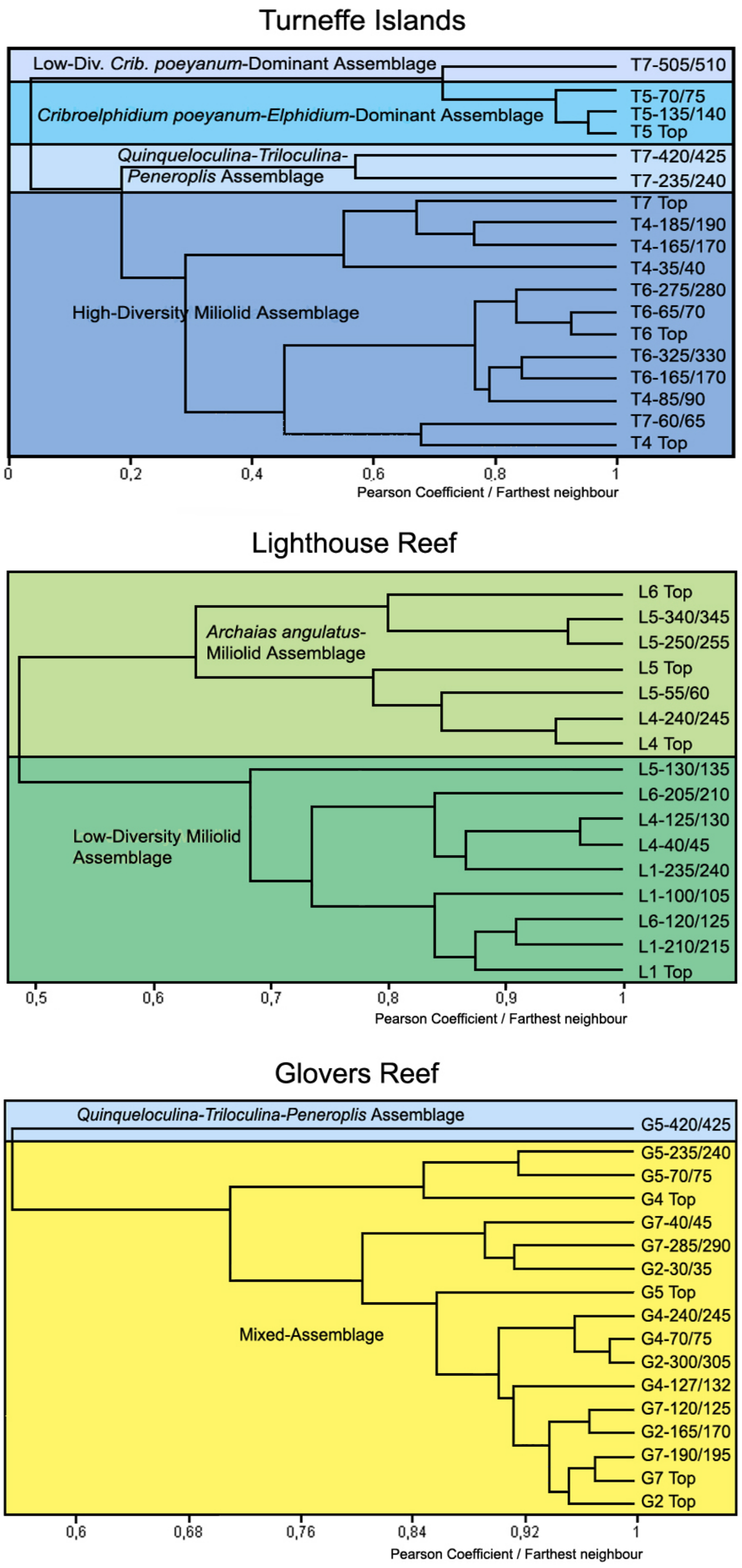


Figure 4.2:
Dendrogram of Q-mode cluster analysis for the most common species in the respective lagoonal cores. The Turneffe Islands shows four assemblages, Lighthouse Reef and Glovers Reef exhibit two communities. The dendrograms are based on the same data matrix that is used in Figure 4.1.

4.1.1 Turneffe Islands

For the Turneffe Islands, four benthic foraminifera assemblages could be identified within the four investigated cores (T4, T5, T6 and T7; Fig. 4.2).

1) The High-Diversity Miliolid Assemblage is characterized by a high dominance of the genera *Quinqueloculina* and *Triloculina* (Fig. 4.3; Appendix: Plate 1a and b), which together form 30% of this assemblage. The genus *Miliolacea* shows an abundance of approximately 6 - 18%. *Cribroelphidium poeyanum* and *Elphidium* sp. occur in frequencies of between 8 and 28%. The genera *Articulina* and *Discorbis* show frequencies of up to 16% each. *Rosalina* species occur in abundances of between 2 and 10%. Further dominant genera include *Vertebralina* (corresponding to *Cornusspiracea*), *Planorbulina*, *Peneroplis*, *Florilus atlanticus*, *Nonion despressulum* and *Tretomphalus atlanticus* show abundances of up to 10%. The genera *Bolivina* and *Ammonia* occur in minor amounts of 2 – 8%. The High-Diversity Miliolid Assemblage is characterised by a high faunal diversity (ø H'= 3.6; Fig. 4.6), high abundances (ø S= 57), and large tests (e.g. *Tretomphalus atlanticus*, *Miliolinella labiosa*, *Vertebralina cassis*).

At the Turneffe Islands, the High-Diversity Miliolid Assemblage occurs in cores T4, T6 and T7 (Fig. 4.3). Cores T4 and T6 are located in the western leeward margin of the Turneffe Islands, core T7 is positioned within the platform interior. The sediments of core T4 and T6 are completely inhabited of the High-Diversity Miliolid Assemblage during the last 5,343 years; however, in core T7 this assemblage was only present during the last 795 years.

The common genera *Quinqueloculina* and *Triloculina* show highest abundances in cores T4 and T6 from 660 to 1,320 years BP (Fig. 4.3). Older and more recent samples exhibit lower frequencies of the species mentioned above. *Cribroelphidium poeyanum* shows increasing abundances in modern (core top = modern) samples of core T4 and T6. The older sample of core T6 (at 5,343 years BP) contains higher frequencies of *Bolivina*. In core T7 the High-Diversity Miliolid Assemblage is present in the youngest samples (0 to 795 years BP). *Quinqueloculina* and *Triloculina* show an increase towards modern (core top) samples. However, the abundance of *C. poeyanum* decreases and shows higher values in older samples (795 years BP). *Articulina* sp. appears frequently in all samples of the High-Diversity Miliolid Assemblage. *Discorbis* sp. shows similar frequencies in this assemblage and consistently high abundances in core T7 during the last 795 years.

2) The *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage is dominated by the species *Cribroelphidium poeyanum* with abundances of between 25 and 35% (Fig. 4.3; Appendix: Plate 2a, b). The genus *Elphidium*, with the most common species *E. advenum, E. sagrum* and *E. discoidale*, has similar frequencies of around 20 - 35%. The remaining population contains the genera

Quinqueloculina, *Triloculina* and *Miliolacea* of up to 10%, and the genera *Planorbulinacea*, *Bolivina*, and *Amphistegina* occur with abundances of between 5 and 8%. Additional species, that occur in this *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage include *Rosalina floridana*, *Florilus atlanticus*, *Articulina* sp., *Eponides* sp. and *Cibicides* sp., which show frequencies of up to 5%. *Nonion despressulum*, shows values between 2 and 3%, and *Discorbis* sp. exhibits values of up to 3%. The *C. poeyanum-Elphidium*-Dominant Assemblage is characterized by a high number of species (ø S= 45) and a high diversity (ø H'= 2.9; Fig. 4.6).

At the Turneffe Islands, the *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage is present in core T5 during the past 2,260 years. The core T5 was drilled in the southern interior area of the platform. The genera *Planorbulinacea* (8%), *Bolivina* sp. (8%), and *Amphistegina gibbosa* (5%) occur with higher abundances in the discrete sample T5 (at 2,500 years BP). The genera *Quinqueloculina, Triloculina, Articulina, Vertebralina, Discorbis and the species Ammonia beccarii* only appear in the following sections of core T5 (top and at 2,260 years BP).

The two dominant genera of the *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage, *Cribroelphidium* and *Elphidium*, show fluctuating abundances in core T5 during the last 2,500 years BP. *Cribroelphidium poeyanum* shows slightly decreased values at 2,260 years BP and increased frequencies towards modern samples. *Elphidium* shows the opposite trend, of higher (at 2,260 years BP), and lower abundances in modern samples. *Bolivina* sp. and *Amphistegina gibbosa* developed their highest abundance 2,260 years BP and do not occur in present-day samples of core T5.

3) The Low-Diversity *Cribroelphidium poeyanum*-Dominant Assemblage is dominated by the species *Cribroelphidium poeyanum* with abundances of up to 67% (Fig. 4.3; Appendix: Plate 3). Further common species are *Ammonia beccarii* with about 14% and the genus *Quinqueloculina* with around 13%. The remaining benthic foraminiferal assemblage contains a low number of species; *Florilus atlanticus* occurs with 3%, *Elphidium* represents 1%, and *Triloculina* sp., *Miliolacea*, *Asterigerina carinata* and *Nonion despressulum* show frequencies of less than 1%. Diversity and number of species are extremely low (ø H'=1.3 and ø S= 18; Fig. 4.6).

At the Turneffe Islands, the Low-Diversity *Cribroelphidium poeyanum*-Dominant Assemblage only occurs in the oldest sample of core T7 (at 4,380 years BP; Fig. 4.3). The core T7 is located in the central interior of the Turneffe Islands. The high dominance of the species *Cribroelphidium poeyanum*, shows a high decrease towards modern samples (from 67 to 3%), whereas *Discorbis* sp., *Quinqueloculina* sp. and *Triloculina* sp. indicate increasing abundances with decreasing age in core T7.

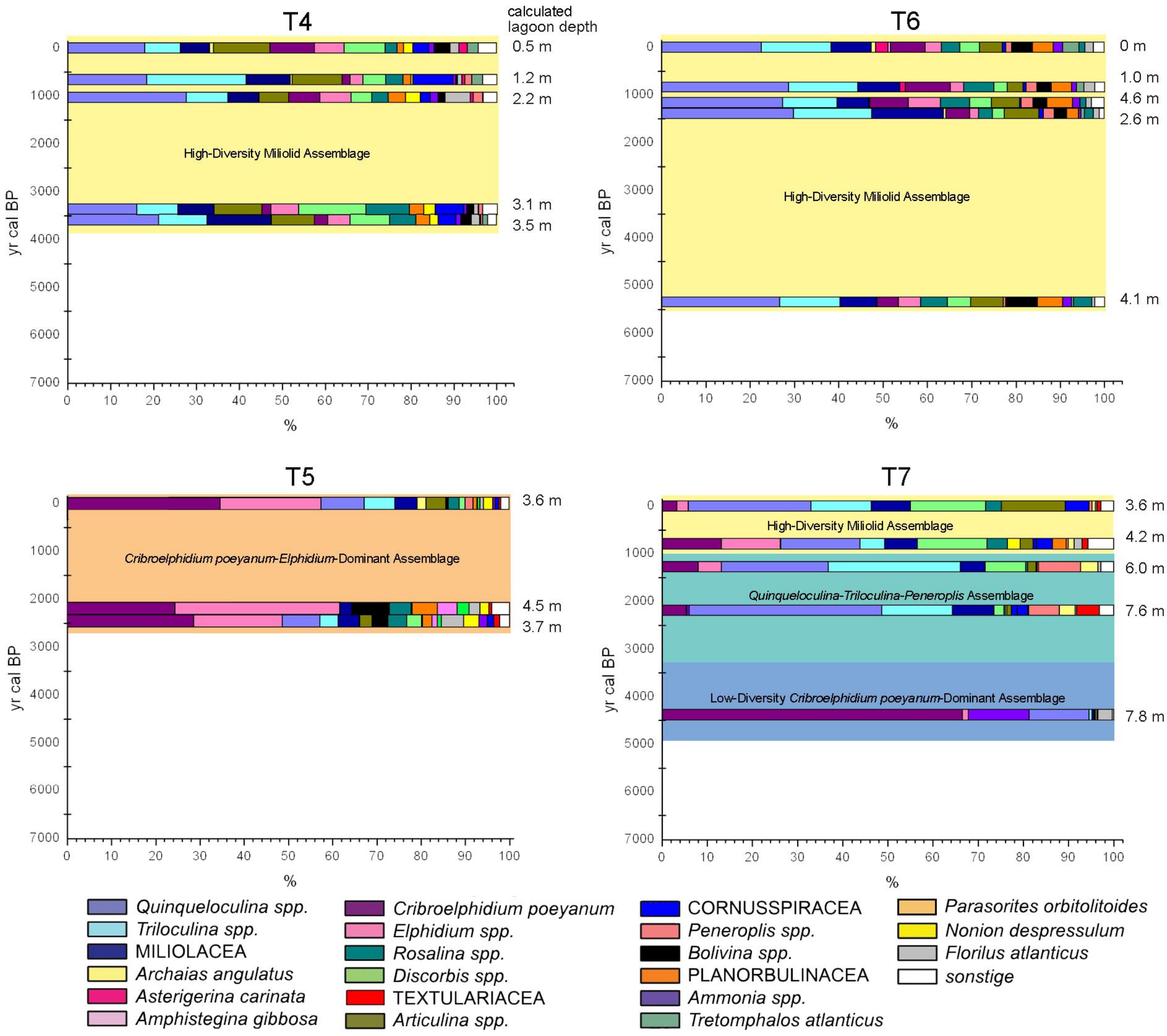


Figure 4.3:
Foraminiferal occurrence (in percent) in the cores from the Turneffe Islands. Y-axis shows the radiometric age (in years BP) of the respective core section. Cores T4 and T6 were drilled within the marginal area of the lagoon. Cores T5 and T7 are located in the interior lagoon of the Turneffe Islands. Similar assemblages are shown in the same background colours. Calculated lagoon depths are listed next to the respective samples.

4) The <u>*Quinqueloculina-Triloculina-Peneroplis* Assemblage</u> is characterized by the genus *Quinqueloculina* of between 24 – 43% and *Triloculina* shows frequencies of between 16 to 29% at the Turneffe Islands (Fig. 4.3; Appendix: Plate 4). The genera *Peneroplis, Cribroelphidium, Miliolacea*, and *Discorbis* occur in frequencies of between 2 – 9%. The species *A. angulatus* and *Textularia agglutinans* show an abundance of up to 5%. *Articulina* sp. and *Rosalina* sp. only occur in minor amounts of between 1 – 2% in samples of the Turneffe Islands. The assemblage is characterized by a moderate number of species (ø S = 39) and a high diversity index (ø H'= 3.0; Fig. 4.6).

At the Turneffe Islands, the *Quinqueloculina-Triloculina-Peneroplis* Assemblage is also present in the in the samples of core T7 (at 2,185 and 1,275 years BP; Fig. 4.3). However, this assemblage occurs additionally in core G5 of Glovers Reef (at 6,225 years BP; Fig. 4.2). Similar species occur in different frequencies in the sample of Glovers Reef; the genera *Triloculina* (of 3%), *Discorbis* (<1%) and *Textularia* (<1%) have lower frequencies at Glovers Reef, whereas *C. poeyanum* (18%) and *A. angulatus* (13%) occur in higher amounts compared to the Turneffe Islands, and the species *Tretomphalus* sp. (2%) was only observed at Glovers Reef.

Core T7, from the Turneffe Islands, contains two further assemblages (Fig. 4.3), which were already described above. The oldest sample is characterized by the (3) Low-Diversity *Cribroelphidium poeyanum*-Dominant Assemblage (at 4,380 years BP). The samples in the middle of core T7 consist of the (4) *Quinqueloculina-Triloculina-Peneroplis* Assemblage (from 1,275 - 2,185 years BP), and the youngest samples show the (1) High-Diversity Miliolid Assemblage (from 0 - 795 years BP). Within these three assemblages, the species *Quinqueloculina* sp., *Triloculina* sp. (from 13 to 27%), *Discorbis* sp. and *Articulina* sp. (from 0 to 15%) show a high increase with decreasing age, whereas the species *Cribroelphidium poeyanum* indicate decreasing abundances (from 67 to 3%) during the last 4,380 years BP in core T7 from the Turneffe Islands.

4.1.2 Lighthouse Reef

For the Lighthouse Reef, two benthic foraminifera assemblages can be recognized within the four obtained cores (L1, L4, L5 and L6; Fig. 4.2).

1) The *Archaias angulatus*-Miliolid Assemblage (Fig. 4.4; Appendix: Plate 5a, b and c) is dominated by the large benthic miliolid species *Archaias angulatus* of an abundance of up to 30%. Additional common taxa include *Quinqueloculina,* with frequencies of max. 31% and *Triloculina* of up to 19% respectively. The species *Cribroelphidium poeyanum* exhibits frequencies of 25%. The most abundant species of the family *Miliolacea* (<12%) is *Miliolinella labiosa* with an abundance of up to 5%. The genus *Textulariacea* occurs with abundances of ~12%. *Elphidium discoidale* and *Rosalin*a *candeiana* occur in frequencies of up to 8%. *Articulina*, *Planorbulina*, *Peneroplis* and *Homotrema* show frequencies of max. 5%. The species *Florilus atlanticus*, *Asterigerina carinata, Sorites marginalis* and *Tretomphalus atlanticus* occur in minor amounts of 0 - 4%. The taxa *Nonion, Parasorites, Ammonia, Discorbis, Vertebralina* and *Bolivina a*re present with frequencies of <2% in this assemblage. The *Archaias angulatus*-Miliolid Assemblage is characterized by an average diversity of ø H'= 2.9 and a moderate richness of 42 species (Fig. 4.7).

In the Lighthouse Reef, the *Archaias angulatus*-Miliolid Assemblage occurs in cores L4, L5 and L6 (Fig. 4.4). Core L4 is positioned in the deeper area of the platform and cores L5 and L6 are located in shallower platform regions. The *Archaias-angulatus* Miliolid assemblage was present in older sediment samples of Lighthouse Reef (in core L4 at 4,690 years BP, and in core L5 at 3,850 and 3,320 years BP), as well as in the younger sediments (core L4 top, L5 top and 1,060 years BP, and core L6 top). The dominant species *Archaias angulatus* indicates increasing abundances during the last 4,690 years in cores L4 and L6, whereas *Quinqueloculina* shows a constant decrease towards modern samples in the Lighthouse Reef cores L4, L5 and L6. The species *Cribroelphidium poeyanum* shows decreasing abundances in all cores, except core L5, which indicates increasing frequencies with decreasing age.

2) The <u>Low-Diversity Miliolid Assemblage</u> of the Lighthouse Reef is dominated by few miliolid species. *Quinqueloculina* shows frequencies of between 20 and 40%, and *Triloculina* 10 to 21% (Fig. 4.4; Appendix: Plate 6a and b). The species *Archaias angulatus* shows abundances of 8 - 18%, and *Cribroelphidium poeyanum* appears in frequencies of 5 - 12%. The taxon *Textulariacea* is commonly present with percentages of 1 - 11%. *Miliolinella labiosa* and *Rosalina candeiana* occur in percentages of between 3 - 8%, whereas the genera *Elphidium, Florilus, Planorbulinacea* and *Tretomphalus* show frequencies of up to 4%. The taxon *Peneroplis* appears in abundances of 1 - 7%, and *Articulina* and *Ammonia* show a frequency of 0 – 5%. Additional genera include *Homotrema*, *Discorbis*, *Sorites*, *Nonion*, *Parasorites*, *Vertebralina* and *Bolivina* of up to 2% in the Low-Diversity Miliolid Assemblage. Further characteristics of this Low-Diversity Miliolid Assemblage are represented by an average faunal diversity of ø H’= 3.3 and a richness of ø S = 48 (Fig. 4.7).

In the Lighthouse Reef, the Low-Diversity-Miliolid assemblage is present in all cores (L1, L4, L5 and L6; Fig. 4.4). Cores L1 and L4 are located in the deeper regions of the platform and cores L5 and L6 were drilled in shallower areas of Lighthouse Reef. In contrast to cores L4, L5 and L6, the total sediment sequence from core L1 consists of the Low-Diversity-Miliolid assemblage during the last 3,750 years. In cores L4, L5 and L6, the Low-Diversity-Miliolid assemblage is also present in middle core sections (from ~2,240 to ~1,005 years BP). The dominant species *Quinqueloculina* and *Triloculina* indicate decreasing abundances in core L1 during the last 3,750 years, similar to observations from the remaining cores at Lighthouse Reef (as described above). The common species *Archaias angulatus* shows increasing abundances with decreasing age in the Lighthouse Reef core L1 and show similarities to cores L4 and L6. The species *Cribroelphidium poeyanum* indicates slightly decreasing abundances in core L1 towards modern samples, which corresponds to observations of cores L4 and L6.

The (2) Low-Diversity Miliolid Assemblage shows similarities in the occurrence of species to the (1) *Archaias angulatus*-Miliolid Assemblage as described above. However, in the (2) Low-Diversity-Miliolid Assemblage, the species *Archaias angulatus* (8 - 18%) and *Cribroelphidium poeyanum* (5 – 12%) occur in lower abundances. Species of the family *Miliolacea* (*Quinqueloculina*, *Triloculina* and

Miliolinella) occur in higher frequencies, compared to the (1) *Archaias angulatus*-Miliolid Assemblage.

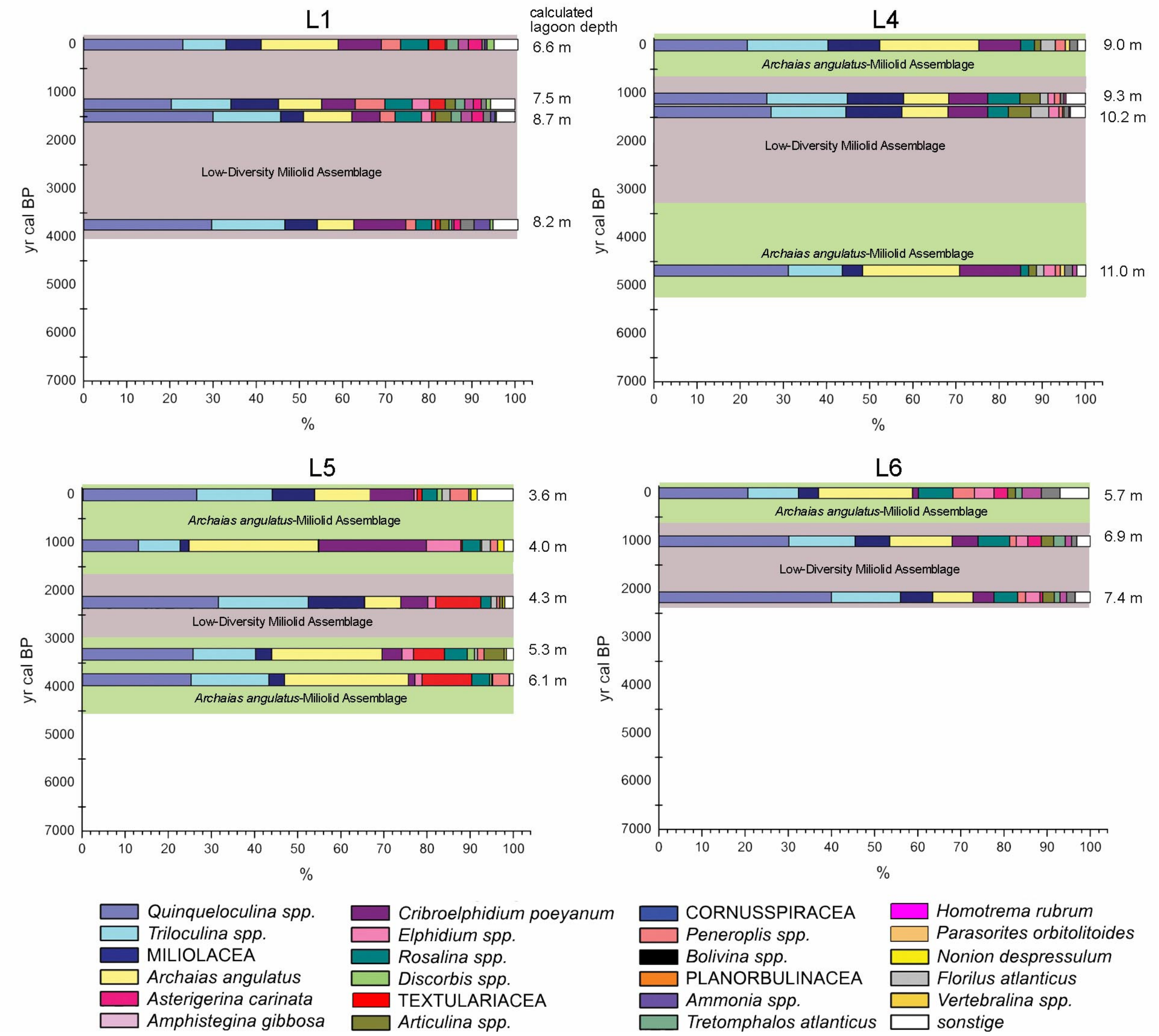


Figure 4.4:
Foraminiferal frequency in cores from the Lighthouse Reef. The cores L1 and L4 were taken from deeper areas of the platform. Cores L5 and L6 are located in shallower regions of the Lighthouse Reef. The different assemblages are shown in several colours. Calculated lagoon depths are plotted for specific samples.

4.1.3 Glovers Reef

For the Glovers Reef, two benthic foraminifera assemblages could be identified within the four obtained cores (G2, G4, G5 and G7; Fig. 4.2).

1) The Mixed-Assemblage is characterized by the genus *Quinqueloculina* and the species *Cribroelphidium poeyanum*. Both occur in high frequencies of 20 - 35% (Fig. 4.5; Appendix: Plate 7a and b). The most common species of the taxon *Quinqueloculina* are *Q. poeyana* (9%), *Q. bidentata* (10%), and *Q. lamarckiana* (9%). The taxa *Triloculina* and *Archaias* are also frequent with abundances of 5 - 13%. Further species in this assemblage are *Parasorites orbitolitoides* (1 - 8%), *Peneroplis* sp. (of up to 11%) and *Florilus atlanticus* (of up to 7%). The genera *Elphidium, Textularia*, *Miliolinella, Tretomphalus, Articulina*, *Rosalina* and *Nonion* occur in amounts of <3%. The diversity index of this Mixed-Assemblage is ø H'= 2.9. The species richness has a low average value (ø S = 39; Fig. 4.8)

At Glovers Reef, the Mixed-Assemblage occurs in all cores G2, G4, G5, and G7 during the last 5,745 years (Fig. 4.5). Core G2 is positioned in the shallow marginal area of the lagoon and cores G4, G5 and G7 are located in the deeper interior areas of the Glovers Reef.

The common species of this Mixed-Assemblage exhibit minor differences among the observed cores at Glovers Reef. Variations were only found in the occurrence of infrequent species. The genera *Articulina* and *Textulariacea* (the most common species is *Textularia agglutinans*) occur in all cores except G5 (from 2,610 to 1,330 years BP), whereas higher amounts (up to 3%) of the species *Ammonia* only occur in core G5. The species *Parasorites orbitolitoides* shows higher abundances (of 3 - 9%) in core G7.

At Glovers Reef, the common species *Cribroelphidium poeyanum* indicates decreasing abundances in cores G2 and G4, and increasing frequencies in cores G5 and G7 during the last 6,225 years. The species *Quinqueloculina* and *Triloculina* show decreasing abundances in core G5 and constant to slightly increasing amounts in the remaining cores G2, G4 and G7 with decreasing age. The common species *Archaias angulatus* indicates increasing frequencies in cores G4 and G7, and decreasing abundances in cores G2 and G5 toward modern samples.

2) The *Quinqueloculina-Triloculina-Peneroplis* Assemblage (Fig. 4.5; Appendix: Plate 4) of the Glovers Reef, was also observed at the Turneffe Islands (Chapter 4.1.1). The species *Q. candeiana* (23%), *Q. lamarckiana* (11%), *Q. seminulum* (4%), and *Q. poeyana* (3%), which belong to the genus *Quinqueloculina*, constitute the main part (of up to 48%) of this assemblage. Additional common species are *Cribroelphidium poeyanum* (17%), *Archaias angulatus* (13%), *Parasorites orbitolitoides* (5%), and *Peneroplis proteus* (4%). The genus *Triloculina* has frequencies of <4%. The taxa *Textulariacea*, *Florilus*, *Elphidium* and *Tretomphalus* occur in amounts of <2%.

In the Glovers Reef, the *Quinqueloculina-Triloculina-Peneroplis* Assemblage is only present in sample G5 (at 6,225 years BP; Fig. 4.5). Core G5 is located in the deep interior region at Glovers Reef. Differences in the species occurrence and/or frequency within the *Quinqueloculina-Triloculina-Peneroplis* Assemblage among the Turneffe Islands and Glovers Reef were observed. Compared to Glovers Reef, the species *Cribroelphidium poeyanum* (5 – 8%) and *Archaias angulatus* (~4%) occur in lower abundances in core T7 of the Turneffe Islands. The genus *Triloculina* indicates higher amounts (16 – 29%) in core T7, similar to *Textulariacea*, which occurs of up to 5% at the Turneffe Islands, compared to Glovers Reef.

Core G5 of Glovers Reef contains two assemblages: 1) The Mixed-Assemblage and the 2) *Quinqueloculina-Triloculina-Peneroplis* Assemblage. The oldest sample of core G5 shows highest values of *Quinqueloculina* (at 6,225 years BP), which decrease towards modern sample. Abundances of *C. poeyanum* remain constant from 6,225 - 2,610 years BP, increase with decreasing age (at 1,330 years BP), and decrease again in modern samples. *Elphidium* shows similar fluctuations but lower frequencies in total content. *A. angulatus* shows high abundances from 6,225 - 1,330 years BP, and decreasing abundances in modern core sections of core G5.

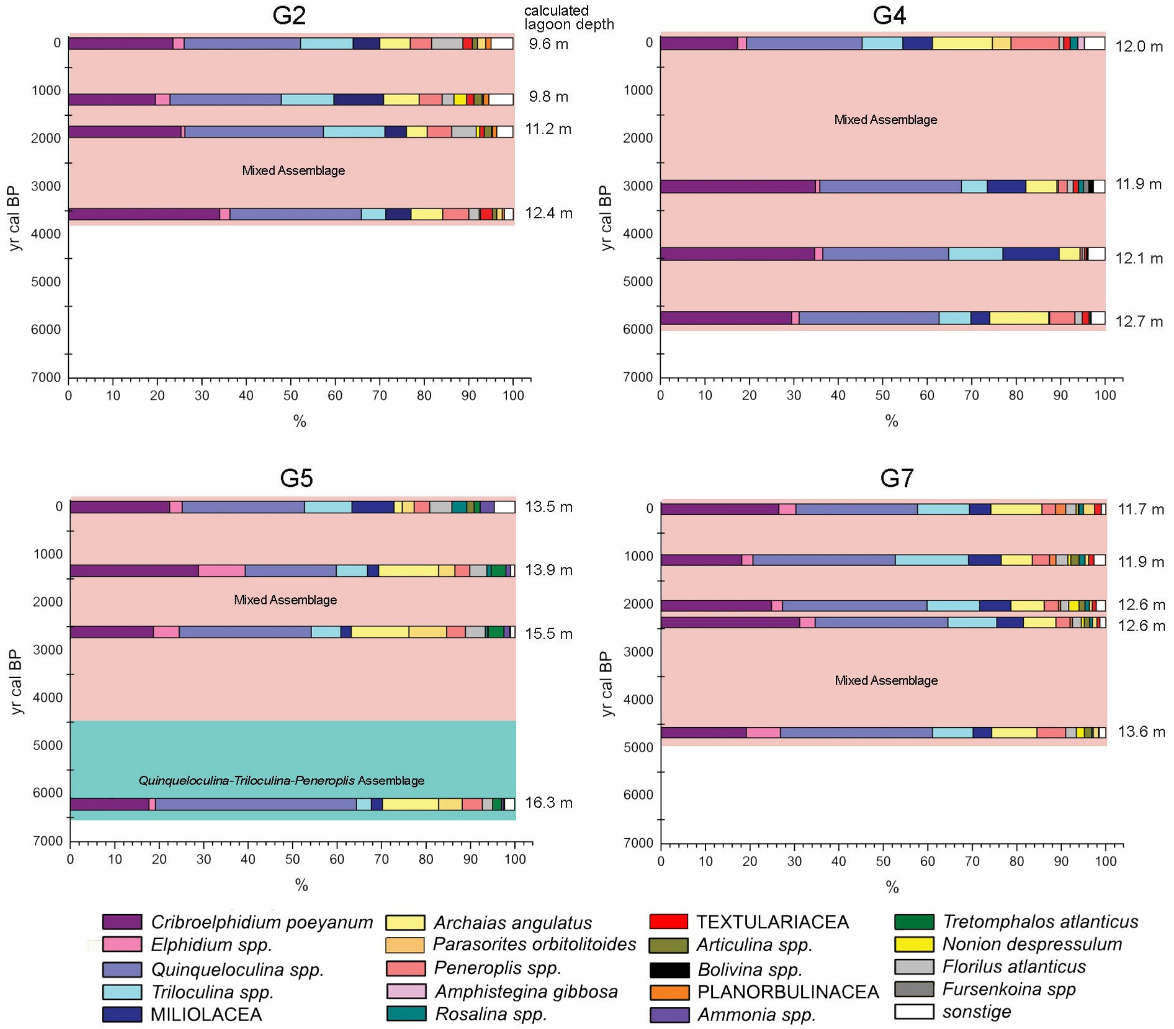


Figure 4.5:
Foraminiferal content in cores from Glovers Reef. Core G2 was drilled in the shallow marginal area of Glovers Reef. Cores G4, G5, and G7 were taken from the deeper interior areas of the lagoon. The background colours highlight individual assemblages. Calculated lagoon depths are listed behind the samples.

4.2 Diversity Development during the Holocene

4.2.1 Turneffe Islands

Compared to the other platforms, mean values of diversity and richness are highest at the Turneffe Islands. Mean evenness values are similar to Lighthouse Reef (Tab. 5.1). The diversity (H’) in the cores of the Turneffe Islands exhibits significant fluctuations, however no simple trends of increase or decrease can be observed during the last 6,000 years (Fig. 4.6). Turneffe Islands represents both lowest (core T7 H’ = 1.33; S = 19) and highest diversity values (T6 H’ = 3.79; S = 62; Appendix 3) of all three platforms. Marginal core samples (T4 and T6) show highest diversity, evenness and richness values (H’= 3.44 to 3.79; E = 0.85 to 0.92; S = 50 to 60), and a continuously high trend from 5,400 to 4,000 years BP. During the last 1,000 years, the diversity of the marginal cores (T4 and T6) exhibits slightly decreasing diversity values, a stronger decreasing richness (from 61 to 50), and constant evenness values (E = 0.85 to 0.919).

Core samples from interior lagoonal areas (T5 and T7) exhibit lower diversity, evenness and richness values (H’ = 1.33 and 3.46; E = 0.45 to 0.91; S = 19 to 57) and fluctuating diversity trends during the last 6,000 years. Core T5, which is located in the southern interior lagoon of the Turneffe Islands, shows increasing diversity values (H’ = 3.12 to 2.67) from 2,500 to 2,260 years BP, and a slight decrease towards present time (H’ = 2.85). The richness values from core T5 show a similar trend (S = 34 to 51) between 2,500 and 2,260 years BP, but the evenness values remain constant (E = 0.73 to 0.79) during this time period. Core T7 shows the following trends: Diversity and evenness exhibit strong increasing values from 4,380 to 2,185 years BP (H’ = 1.33 to 3.15; E = 0.45 to 0.84), and slightly increasing values towards present time (H’ = 3.46, E = 0.91). The richness shows a strong increase from 4,380 to 795 years BP (S = 19 to 57) and a lower number of species in modern samples (S = 49). The marginal fauna (T4 and T6) contains high abundances of miliolid species, e.g. *Quinqueloculina* and *Triloculina*, and in the interior lagoon (T5 and T7) *C. poeyanum*, *Elphidium* sp. and *Ammonia* sp. occur in high abundances.

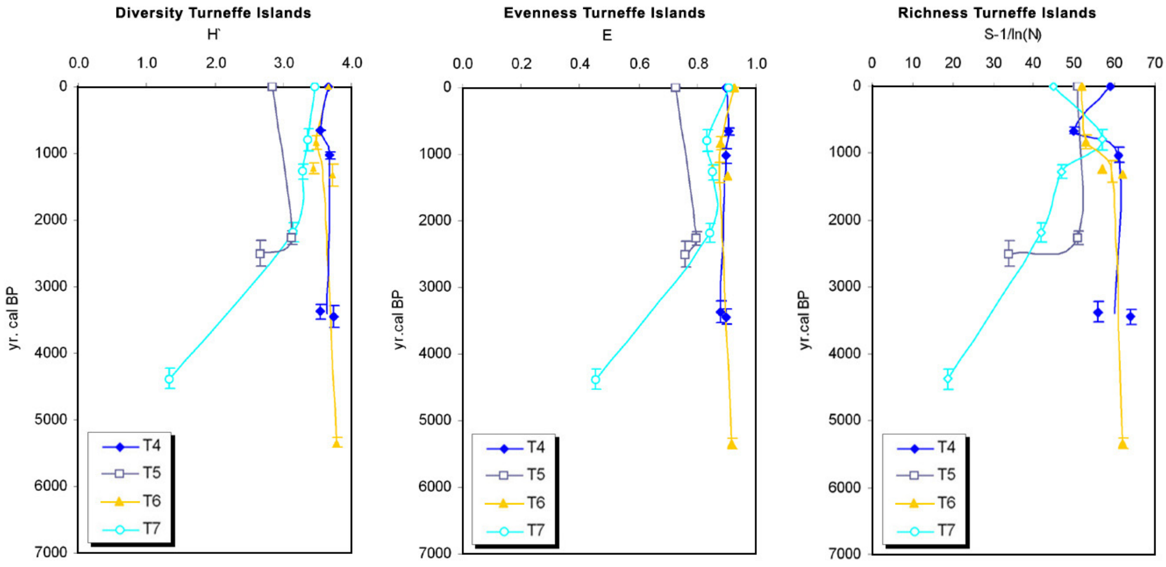


Figure 4.6:
Diversity, evenness and richness of the benthic foraminifera fauna from the respective core sections of the Turneffe Islands during the last 5,000 years. Cores T4 and T6 were taken from the marginal lagoon and cores T5 and T7 are located the interior lagoon at the Turneffe Islands.

4.2.2 Lighthouse Reef

The mean diversity, evenness, and richness values of deeper parts (cores L1 and L4) are similar to shallower parts (cores L5 and L6) at Lighthouse Reef (Tab. 5.1). Compared to the Turneffe Islands, mean values of diversity and richness are lower at Lighthouse Reef. Mean evenness values are similar to the Turneffe Islands. Miliolid genera and *A. angulatus* are the most common benthic foraminifera at Lighthouse Reef.

Core samples from L1, L4 and L6 are similarly high in diversity and evenness during the last 4,690 years (Fig. 4.7; Appendix 3). Cores L1 and L4 reach their maximum diversity values from 1,405 years BP (H' = 3.59, E = 0.87) to 1,110 years BP (H' = 3.36, 0.85). Core L6 exhibits slightly decreasing diversity values (from H' = 3.44 to 3.19), and relatively consistent evenness values (E = 0.86) during the last 2,170 years BP. The core L5 from the shallower lagoon shows lower diversity and evenness values from 3,850 (H' = 2.87; E =0.79) to 2,240 years BP (H' = 3.11, E = 0.89), increasing values from 2,240 to 1,060 years BP (H' = 2.48, E = 0.69), and again higher values in modern samples (H' = 3.41, E = 0.88). The richness values from the deeper lagoonal parts (cores L1 and L4) exhibit different trends: Core L1 shows increasing richness from 3,750 (S = 39) to 1,405 years BP (S = 62) and decreasing values from 1,405 years BP to present time (S = 44). Core L4 has constant richness values during the last 4,690 years BP (S = 44) with one exception of higher values around 1,110 years BP (S = 57). The richness values from shallower cores (L5 and L6) exhibit similar trends during the last 3,850 years. The number of species from core L5 decreases from 3,850 (S = 38) to 2,240 years BP (S = 32) and increases towards present time (S = 48). The richness from core L6 exhibits constant values (between 48 and 59 species) during the investigated time period of 2,170 years BP.

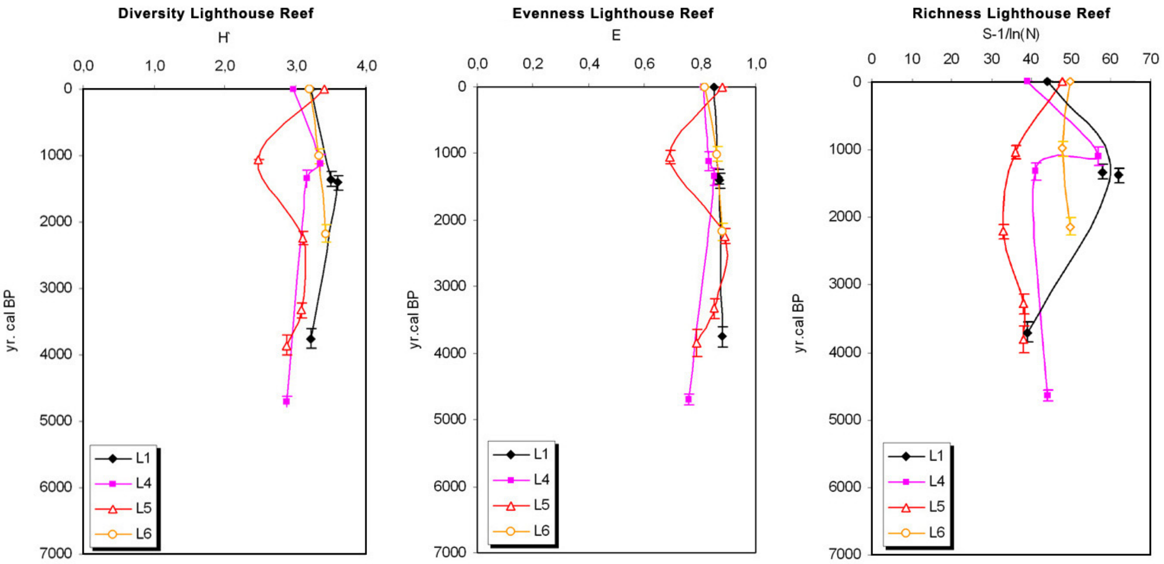


Figure 4.7:
Diversity, evenness and richness trends of the benthic foraminifera fauna from Lighthouse Reef during the last 5,000 years. Cores L1 and L4 were taken in deeper lagoonal areas and cores L5 and L6 are located in shallower parts at Lighthouse Reef.

4.2.3 Glovers Reef

Glovers Reef exhibits the lowest mean diversity, evenness, and richness values of all three platforms (Tab. 5.1). *C. poeyanum* and *A. angulatus* are the dominant species in all assemblages at Glovers Reef.

No significant differences in the foraminiferal content were observed between the shallow marginal area (core G2) and the deeper lagoon (cores G4, G5 and G7; Fig. 4.8) at Glovers Reef during the last 6,225 years. Core G2, from the shallow margin exhibits slightly increasing diversity (H' = 2.70 to 3.13) and evenness (E = 0.71 to 0.81) values during the past 3,570 years (Appendix 3). The samples from the deeper interior region at Glovers Reef (G4, G5 and G6) exhibit similar diversity and evenness values with no significant increasing or decreasing trend (G4: H' = 2.11 to 3.06, E = 0.75 to 0.80; G5: H' = 2.53 to 3.26, E = 0.76 to 0.86; G7: H' = 2.76 to 3.10, E = 0.78 to 0.85).

The richness trends are similar to the diversity trends with generally higher values at the shallow area of core G2 (S = 41 to 48). Core G5 exhibits the lowest number of species (S = 28) at 6,225 years BP and reaches maximum values in modern samples (S = 45). The richness of core G4 shows slightly increasing values from 33 to 46 species during the last 5,745 years. The richness of core G7 exhibits intermediate values of S = 38, reaches their maximum values of 40 species at 2,020 years BP and exhibits lower richness values of 36 species in modern samples.

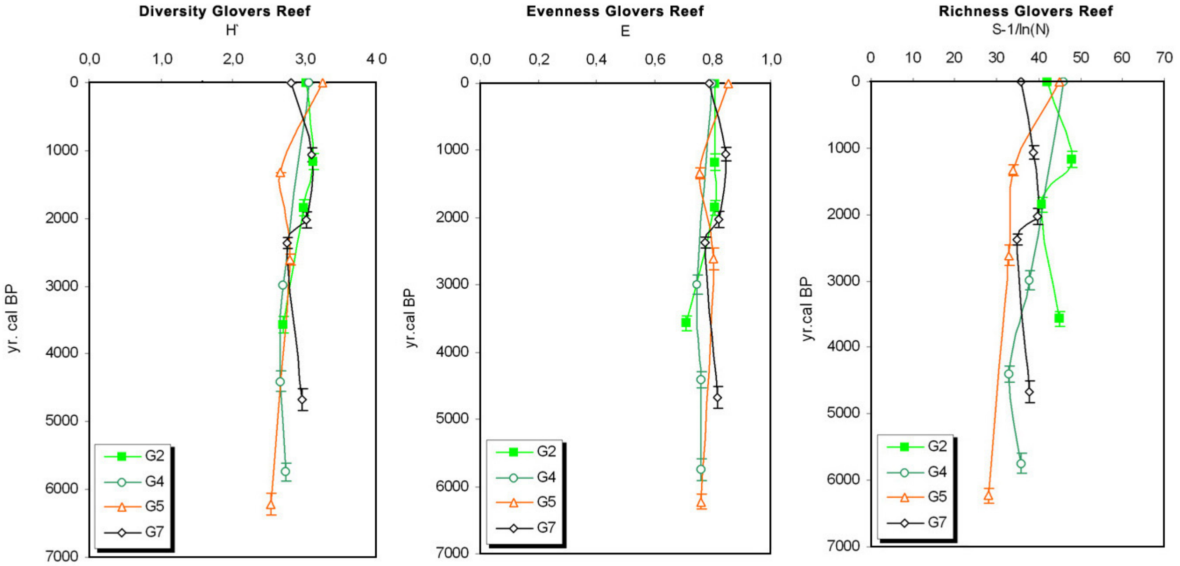


Figure 4.8:
Diversity, evenness and richness trends of the benthic foraminifera fauna from Glovers Reef cores during the last 6,000 years. Core G2 was taken in the shallower marginal area of the platform and the other cores (G4, G5 and G7) were drilled in the deeper interior region of Glovers Reef.

4.3 Stable Isotopes of δ^{18}O and δ^{13}C

Table 4.1 shows the total δ^{18}O and δ^{13}C range of single tests of the specimen *A. angulatus* in core samples at Lighthouse Reef and Glovers Reef. Specimens of *A. angulatus* at the Turneffe Islands were too small for geochemical investigations and had not been analysed. The following results are based on samples of Lighthouse and Glovers Reefs only.

In total, the minimum and maximum δ^{18}O values of *A. angulatus* range from -2.99 (L1 100) to -1.11‰ (G5 420; Tab. 4.1). The δ^{13}C values range from 3.42 (L6 Top) to 5.38‰ (L5 55). Detailed information of the δ^{18}O and δ^{13}C records from the complete data set can be found in Appendix 5.

Both lagoons only show minor differences in stable isotopes. Lighthouse Reef exhibits lighter δ^{18}O values from -2.99 (L1 100) to -1.22‰ (L5 250) ($\Delta\delta^{18}$O = -1.77‰) and Glovers Reef shows heavier δ^{18}O signals from -2.63‰ (G2 300) to -1.11 (G5 420) ($\Delta\delta^{18}$O = -1.52‰).

The δ^{13}C values at the Lighthouse Reef vary between 3.42 (L6 Top) to 5.38‰ (L5 55) with a range of 1.96‰. The δ^{13}C values at Glovers Reef are lighter and fluctuate from 3.71 (G2 300) to 5.06‰ (G7 120). The maximum range of δ^{13}C is 1.35‰.

	sample	**$\delta^{18}O$ values**		$\Delta\ \delta^{18}O$	**sample**	**$\delta^{18}O$ values**		$\Delta\ \delta^{18}O$	**sample**	**$\delta^{18}O$ values**		$\Delta\ \delta^{18}O$	**sample**	**$\delta^{18}O$ values**		$\Delta\ \delta^{18}O$
		Min.	**Max.**			**Min.**	**Max.**			**Min.**	**Max.**			**Min.**	**Max.**	
Lighthouse Reef	L1 Top	-2.62	-1.86	0.76‰	L4 Top	-2.61	-2.08	0.53‰	L5 Top	-2.20	-1.94	0.26‰	L6 Top	-2.09	-1.36	0.73‰
	L1 100	-2.99	-2.06	0.93‰	L4 40	-2.75	-1.91	0.84‰	L5 55	-2.83	-1.53	1.30‰	L6 120	-2.73	-1.89	0.84‰
	L1 210	-2.14	-1.69	0.45‰	L4 125	-2.67	-1.88	0.79‰	L5 130	-2.65	-1.99	0.66‰	L6 205	-2.25	-1.57	0.68‰
	L1 235	-2.22	-1.86	0.36‰	L4 240	-2.51	-1.55	0.96‰	L5 250	-1.52	-1.22	0.30‰				
									L5 340	-2.11	-1.30	0.81‰				
Glovers Reef	G2 Top	-2.27	-1.51	0.76‰	G4 Top	-2.08	1.59	0.49‰	G5 Top	-1.85	-1.29	0.56‰	G7 Top	-2.14	-1.58	0.58‰
	G2 30	-1.89	-1.2	0.69‰	G4 70	-2.11	-1.27	0.84‰	G5 235	-1.95	-1.40	0.55‰	G7 40	-1.75	-1.21	0.54‰
	G2165	-2.31	-1.4	0.91‰	G4 127	-2.02	-1.35	0.67‰	G5 420	-1.36	-1.11	0.25‰	G7 120	-2.39	-1.41	0.98‰
	G2 300	-2.63	-1.54	1.09‰	G4 240	-2.05	-1.18	0.87‰					G7 190	-2.45	-1.46	0.99‰
													G7 285	-2.17	-1.28	0.89‰
	sample	**$\delta^{13}C$ values**		$\Delta\ \delta^{13}C$	**sample**	**$\delta^{13}C$ values**		$\Delta\ \delta^{13}C$	**sample**	**$\delta^{13}C$ values**		$\Delta\ \delta^{13}C$	**sample**	**$\delta^{13}C$ values**		$\Delta\ \delta^{13}C$
		Min.	**Max.**			**Min.**	**Max.**			**Min.**	**Max.**			**Min.**	**Max.**	
Lighthouse Reef	L1 Top	4.10	4.76	0.66‰	L4 Top	3.64	4.53	0.89‰	L5 Top	3.99	4.68	0.69‰	L6 Top	3.42	4.00	0.58‰
	L1 100	4.05	4.93	0.88‰	L4 40	4.30	5.02	0.72‰	L5 55	4.68	5.38	0.70‰	L6 120	3.95	5.10	1.15‰
	L1 210	4.41	4.96	0.55‰	L4 125	4.26	5.21	0.95‰	L5 130	4.18	4.85	0.67‰	L6 205	4.12	4.82	0.70‰
	L1 235	4.35	4.99	0.64‰	L4 240	3.45	4.23	0.78‰	L5 250	4.24	4.59	0.35‰				
									L5 340	4.66	5.20	0.54‰				
Glovers Reef	G2 Top	4.17	5.04	0.87‰	G4 Top	4.13	4.80	0.67‰	G5 Top	3.73	4.40	0.67‰	G7 Top	4.05	4.56	0.51‰
	G2 30	4.00	5.04	1.04‰	G4 70	3.83	4.54	0.71‰	G5 70	too small *A. ang.*			G7 40	4.27	4.97	0.70‰
	G2 165	3.87	4.64	0.77‰	G4 127	3.77	4.21	0.67‰	G5 235	4.10	4.63	0.53‰	G7 120	4.33	5.06	0.73‰
	G2 300	3.71	4.57	0.86‰	G4 240	3.73	4.41	0.68‰	G5 420	4.18	4.92	0.74‰	G7 190	4.23	4.95	0.72‰
													G7 285	4.15	4.62	0.47‰

Table 4.1:
$\delta^{18}O$ and $\delta^{13}C$ maximum, minimum and range of *A. angulatus* tests from 32 samples at Lighthouse and Glovers Reefs. At the Turneffe Islands no geochemical investigations were made because no large specimens of *A. angulatus* were found in the samples.

The relationship between mean $\delta^{18}O$ and $\delta^{13}C$ values of *A. angulatus* tests from Lighthouse and Glovers Reefs show that the correlation coefficient is weak (R^2=0.0331; p>0.005; Fig. 4.9). If the p-value is greater than 0.05 the data sets are not significantly different at the 95% confidence level.

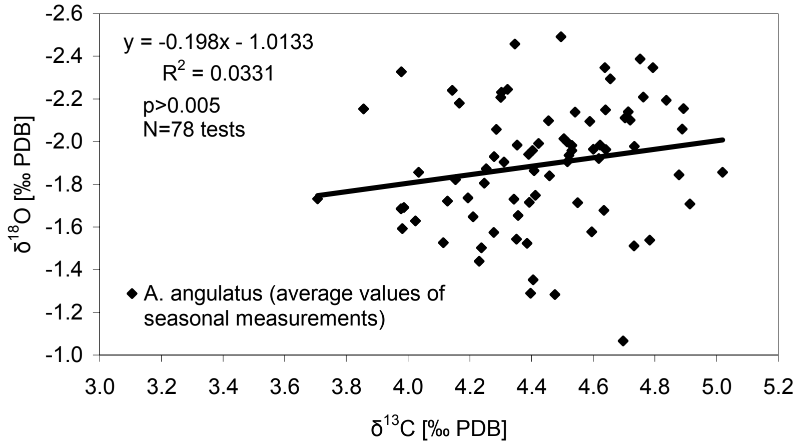


Figure 4.9:
Relationship between average values (N=78) of $\delta^{18}O$ and $\delta^{13}C$ of *A. angulatus* from Light-house Reef and Glovers Reef.

To investigate the trend of $\delta^{18}O$ and $\delta^{13}C$ during the last 6,000 years, all mean values were plotted against the calibrated age of the respective sample (Fig. 4.10). A trend of heavier oxygen values with increasing age is visible in Figure 4.10a. The decrease of approximately 0.4‰ in $\delta^{18}O$ values during the last 6,000 years corresponds to an increase of 2°C in BW-temperature (0.2‰ = 1°C) ignoring salinity effects. The correlation coefficient is statistically significant ($R^2 = 0.0833$; $p<0.0001$).

The observed average $\delta^{13}C$ values become lighter with increasing lagoonal age from 6,000 to 1,000 years BP (Fig. 4.10b), however with no significant correlation coefficient ($R^2=0.0854$; $p>0.005$). From 1,000 years BP to present day, a trend to lighter $\delta^{13}C$ values show a strong decrease of about 0.5‰.

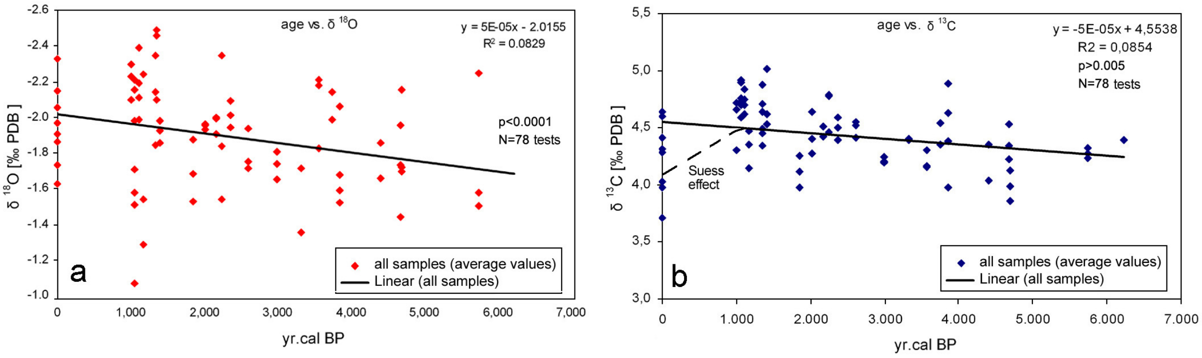


Figure 4.10:
a) Relationships of linear $\delta^{18}O$ and $\delta^{13}C$ against the calibrated sample age show heavier $\delta^{18}O$ values with increasing age, and b) a trend towards lighter $\delta^{13}C$ values with increasing age; the dashed line indicates the supposed decrease during the last 1,000 years.

The correlation between oxygen isotopes and calculated paleo-lagoon depths is weak ($R^2=0.0241$; $p>0.005$) but a general trend is visible (Fig. 4.11). The $\delta^{18}O$ values become heavier with increasing water depths (Fig. 4.11a). The $\delta^{13}C$ values become lighter with increasing calculated paleo-lagoon depths (Fig. 4.11b). However, the correlation coefficient is statistically not significant.

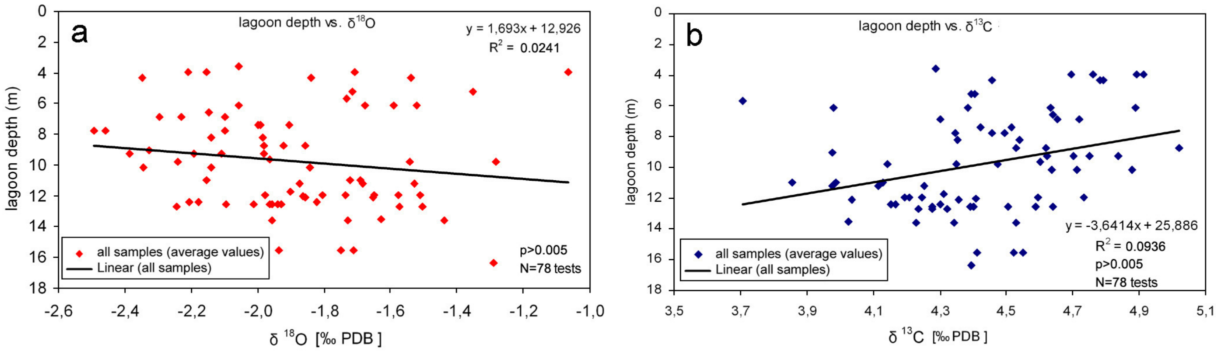


Figure 4.11:
Relationship of $\delta^{18}O$ and $\delta^{13}C$ values against paleo-lagoon depths at Lighthouse and Glovers Reefs. a) Oxygen isotope values become heavier with increasing water depths. b) Carbon isotopes show a trend to lighter values with increasing water depths.

The resulting linear relationship between diversity and $\delta^{18}O$ values (Fig. 4.12a) is significant ($R^2=0.1247$; $p<0.001$; N=78). The correlation coefficient between diversity and $\delta^{13}C$ (Fig. 4.12b) is weak ($R^2=0.0352$; $p>0.005$; N=78). The $\delta^{18}O$ signals exhibit a tendency to lighter values with increasing diversity, whereas the $\delta^{13}C$ values become heavier with increasing diversity.

The comparison between stable isotopes and the respective assemblages is visible in Figure 4.13. The Low-Diversity Miliolid Assemblage exhibits a trend to lighter $\delta^{18}O$ values, as well as heavier $\delta^{13}C$ signals compared to other benthic foraminiferal assemblages from the lagoons.

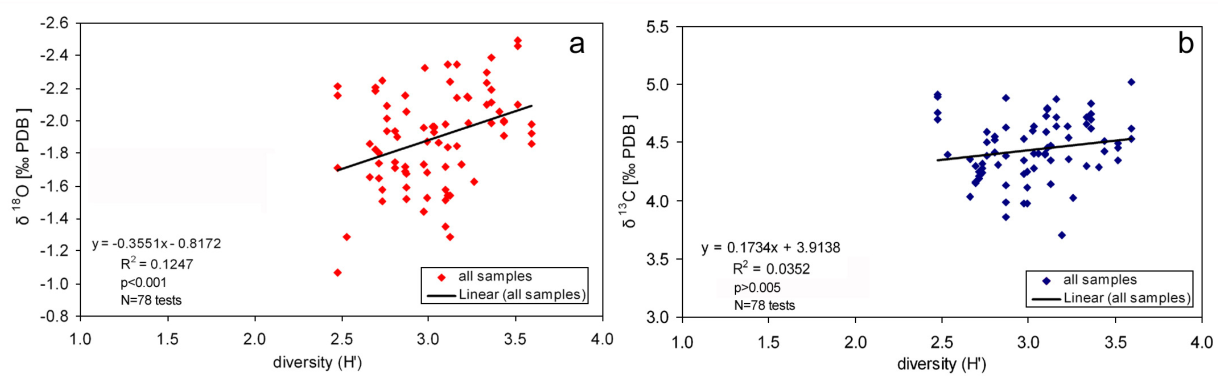


Figure 4.12:
Relationship of diversity versus $\delta^{18}O$ and $\delta^{13}C$ values from samples at Lighthouse and Glovers Reefs. a) The $\delta^{18}O$ values become lighter with increasing benthic foraminiferal diversity. b) The carbon isotopes show a trend to heavier values with increasing diversity.

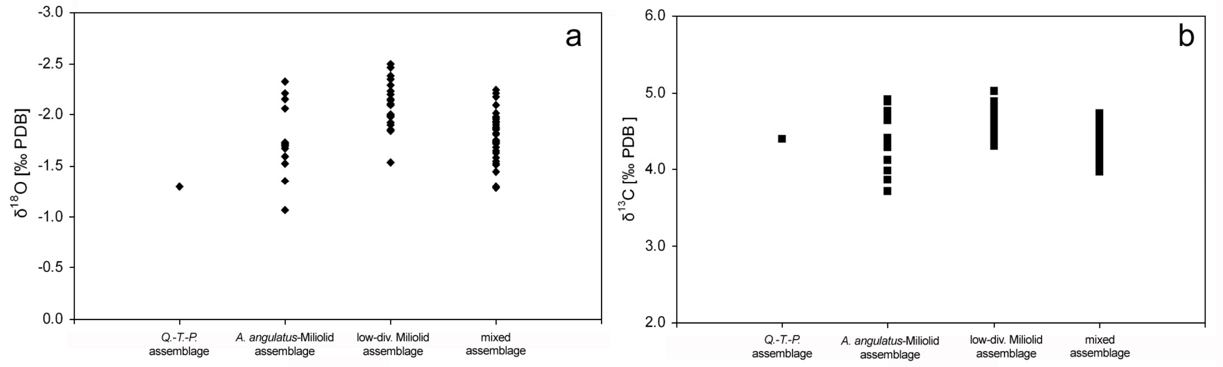


Figure 4.13:
Relationship between $\delta^{18}O$ and $\delta^{13}C$ signals against the respective benthic foraminiferal assemblages from the Lighthouse and Glovers Reefs. a) The Low-Diversity Miliolid Assemblage has slightly lighter $\delta^{18}O$ values and b) slightly heavier $\delta^{13}C$ signals compared to the *Archaias angulatus*-Miliolid and the Mixed-Assemblages. The *Quinqueloculina-Triloculina-Peneroplis* Assemblage occurs only in one sample of measured stable isotopes.

4.3.1 Seasonal Variations in Stable Isotopes of Modern Samples (Core Tops)

In order to identify seasonal BW-temperature variations, single tests of the species *A. angulatus* were measured in growth direction. Ten to 15 samples per specimen reflect approximately one year. Actual $\delta^{18}O$ signals of each test in all core tops (= modern BW-temperatures) were used for comparison of directly measured BW-temperatures of the year 2000 - 2001 (= present-day BW-temperatures; Fig. 2.3) at Lighthouse and Glovers Reefs (Fig. 4.14). These modern $\delta^{18}O$ signals (from core tops), which were measured along the growth direction of single tests exhibit values from -2.62 to -1.36‰ ($\Delta\delta^{18}O$ = 1.26‰) at Lighthouse Reef and from -2.27 to -1.29‰ ($\Delta\delta^{18}O$ = 0.98‰) at Glovers Reef (Tab. 4.1). The $\delta^{18}O$ values of single parts from these tests show, for most of the samples, fluctuations similar to present-day seasonal BW-temperature variations (Fig. 2.3). Heavier $\delta^{18}O$ values were obtained in the central (proloculus) and in the marginal areas of single tests, and lighter $\delta^{18}O$ values were measured in the middle of the tests (Fig. 4.14). Annual BW-temperatures of 2001 fluctuate by 6°C at Glovers Reef, 7°C at Lighthouse Reef and up to 10°C at the Turneffe Islands (Tab. 2.1). If 1°C BW-temperature corresponds to 0.2‰ in $\delta^{18}O$, the total range of modern oxygen isotopes indicates seasonal BW-temperature fluctuations of ~6°C (1.26‰) at Lighthouse Reef and ~5°C (0.98‰) at Glovers Reef.

The modern $\delta^{13}C$ values in single tests of *A. angulatus* range from 3.42 to 4.88‰ at Lighthouse Reef and from 3.73 to 5.04‰ at Glovers Reef (Fig. 4.14). The $\delta^{13}C$ signals of single tests from core tops are positively correlated with the $\delta^{18}O$ values. Most of the core top samples at Lighthouse and Glovers Reefs exhibit heavier $\delta^{13}C$ values in the central (proloculus) and marginal area of their tests and lighter carbon isotopes in the middle of the tests. Core L4 (sample A) shows the opposite tendency of lighter $\delta^{13}C$ values in the proloculus area, heavier values in the middle and lighter values in the margin area, and core L6 (sample A) exhibits constant carbon isotope values with increasing age of the specimens.

At Lighthouse Reef, two modern specimens (sample A and B) were measured from each core top in order to identify possible isotope fractionation. The $\delta^{18}O$ and $\delta^{13}C$ measurements of two different specimens at Lighthouse Reef show similar values as well as equal fluctuations (Fig. 4.14a). Specimens from core tops L4 and L1 exhibit lighter $\delta^{18}O$ signals (from -2.7 to -1.9‰) than specimens from core tops L6 (from -2.1 to -1.4‰). At Glovers Reef, only one specimen from each core top was analysed (Fig. 4.14b). The modern $\delta^{18}O$ signals at Glovers Reef show heavier values in core G5 (from -1.8 to -1.3‰) and lighter values in core tops of G2, G4 and G7 (from -2.3 to -1.5‰).

The $\delta^{13}C$ records of *A. angulatus* specimens at Lighthouse Reef exhibit lighter values in core L6 (3.5 to 3.9‰) and heavier values in measurements of core L4 (from 3.6 to 4.5‰) and L1 (from 4.1 to 4.9‰). At Glovers Reef, the specimens of core G5 show the lightest $\delta^{13}C$ signals (from 4.0 to 4.3‰), and cores G2, G4 and G7 exhibit heavier $\delta^{13}C$ values (from 4.1 to 5.1‰) from each core top.

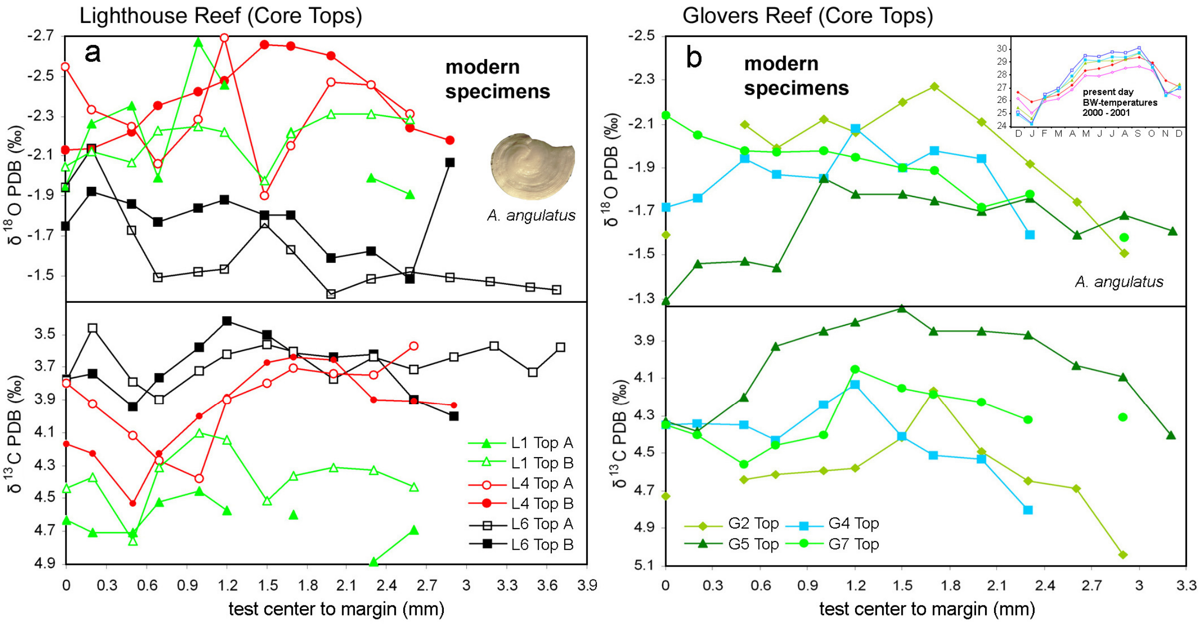


Figure 4.14:

The $\delta^{18}O$ and $\delta^{13}C$ values from single tests of *A. angulatus* (in growth direction) from modern core tops at (a) Lighthouse Reef and (b) Glovers Reef. For Lighthouse Reef, two specimens (sample A and B in L1) were used and for Glovers Reef one specimen was available for stable isotope measurements. A trend of seasonal fluctuations is visible in oxygen and carbon isotope values. For comparison, present-day BW-temperature measurements of 2001 are shown in the upper right corner and in Figure 4.15.

4.3.2 Seasonal Variations in Stable Isotopes of Fossil (Holocene) Samples

The stable isotopes of single specimens in the majority of Holocene samples show similar fluctuations like measurements in modern samples (Figs. 4.15 - 4.18). Heavier $\delta^{18}O$ signals were obtained in central and in marginal areas of *A. angulatus*. Lighter $\delta^{18}O$ records were found in the middle of the tests. During the Holocene, the $\delta^{18}O$ values at Lighthouse Reef vary between -2.99 and -1.30‰ ($\Delta\delta^{18}O$ = 1.69‰) and at Glovers Reef from -2.63 to -1.11‰, respectively ($\Delta\delta^{18}O$ = 1.52‰; Tab. 4.1). These maximum ranges in $\delta^{18}O$ of 1.69‰ at Lighthouse Reef and 1.52‰ at Glovers Reef indicate a Holocene BW-temperature range of 8.5°C at Lighthouse and 7.5°C at Glovers Reefs (1°C = 0.2‰ in $\delta^{18}O$; ignoring possible $\delta^{18}O_{seawater}$ variation).

In detail, the $\delta^{18}O$ values of single specimens exhibit the following fluctuations at Lighthouse Reef during the Holocene: Highest variations were measured in core L1 at 1,350 years BP and core L6 at 1,060 years BP with $\delta^{18}O$ ranges of 1.4 and 1.3‰ (Fig. 4.15). This range corresponds to a maximum of ~7°C in BW-temperature difference in the respective time period. The lowest fluctuations of $\delta^{18}O$ values at Lighthouse Reef show a range of 0.4‰ in core L1 at 1,405 and at 3,750 years BP. This $\delta^{18}O$ range represents a minimum of 2°C BW-temperature difference at Lighthouse Reef.

Samples at Glovers Reef show also fluctuating $\delta^{18}O$ ranges in single Holocene specimens. The highest $\delta^{18}O$ range of 1.4‰ was observed in core G2 at 3,570 years BP and a range of 1.3‰ was measured in core G4 at 5,745 years BP (Fig. 4.17). Lowest fluctuations of $\delta^{18}O$ ranges were analysed in core G5 at 6,225 years BP. However, these measurements are based on only one specimen. The calculated corresponding BW-temperature at Glovers Reef would range from 1 to 7°C during the Holocene.

The Holocene $\delta^{13}C$ values fluctuate from 3.45 to 5.38‰ at Lighthouse Reef (Fig. 4.16), and from 3.71 to 5.06‰ at Glovers Reef (Fig. 4.18; Tab. 4.1). The $\delta^{13}C$ values are positively correlated with measured $\delta^{18}O$ signals in both lagoons during the Holocene. Lighter $\delta^{13}C$ signals were observed in the test centre and in the margin, and heavier $\delta^{13}C$ values are present in the middle of the tests.

Modern $\delta^{13}C$ signals at Lighthouse Reef were described in Chapter 4.3.1 and exhibit values from 3.42 to 4.88‰. The Holocene $\delta^{13}C$ signals at Lighthouse Reef are heavier than modern $\delta^{13}C$ values from core tops. The Holocene $\delta^{13}C$ values at Glovers Reef are quite similar to those in modern samples (3.73 - 5.05‰).

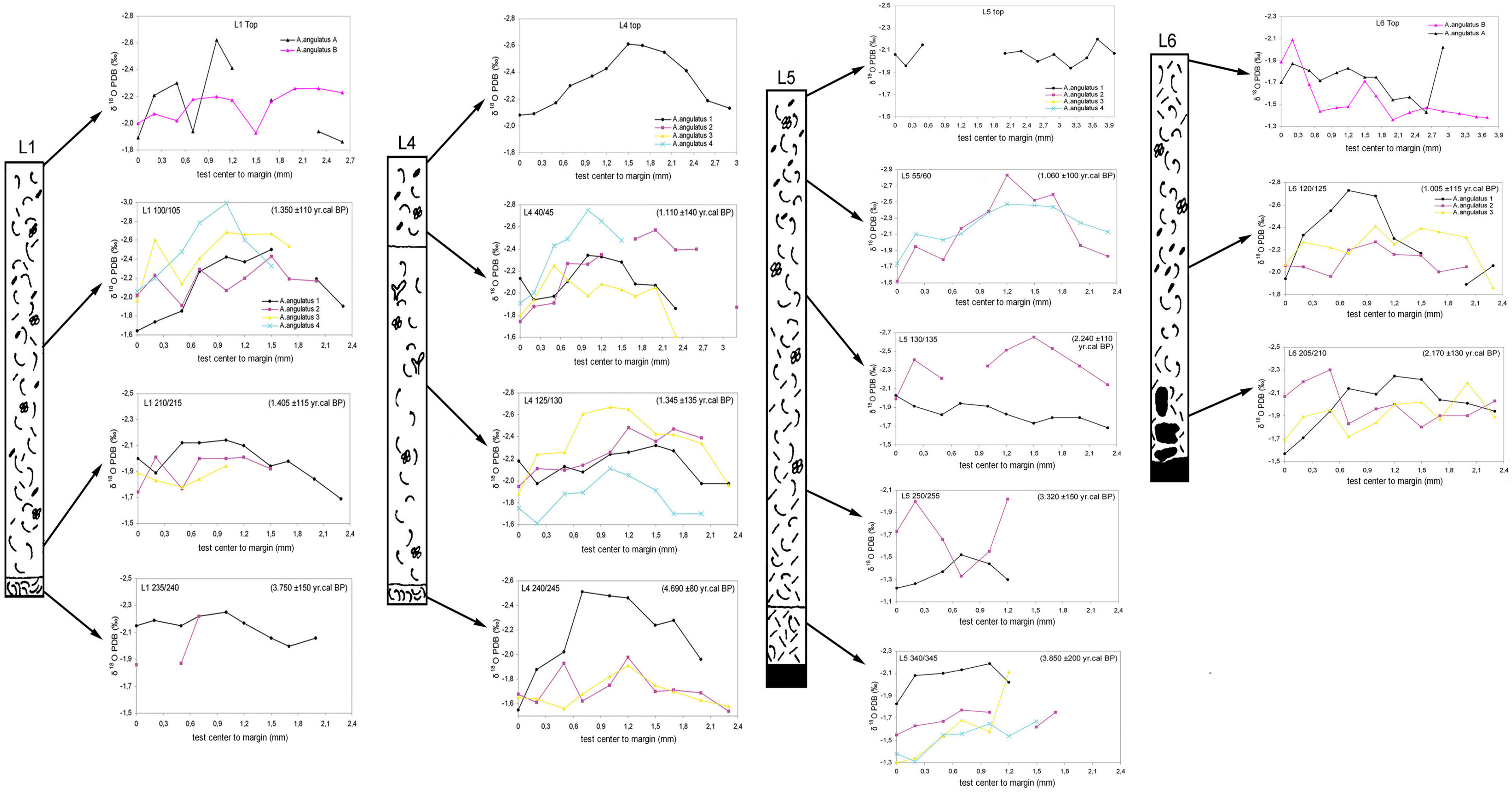


Figure 4.15:
δ^{18}O values of single *A. Angulatus* tests at Lighthouse Reef from top to bottom. Most of the specimens exhibit heavier δ^{18}O values in the center (Proloculus) and in the marginal areas of the tests. Lighter δ^{18}O values were measured in the middle of the tests. Lighter δ^{18}O records are consistent with warmer BW-temperatures and heavier values correspond to colder BW-temperatures.

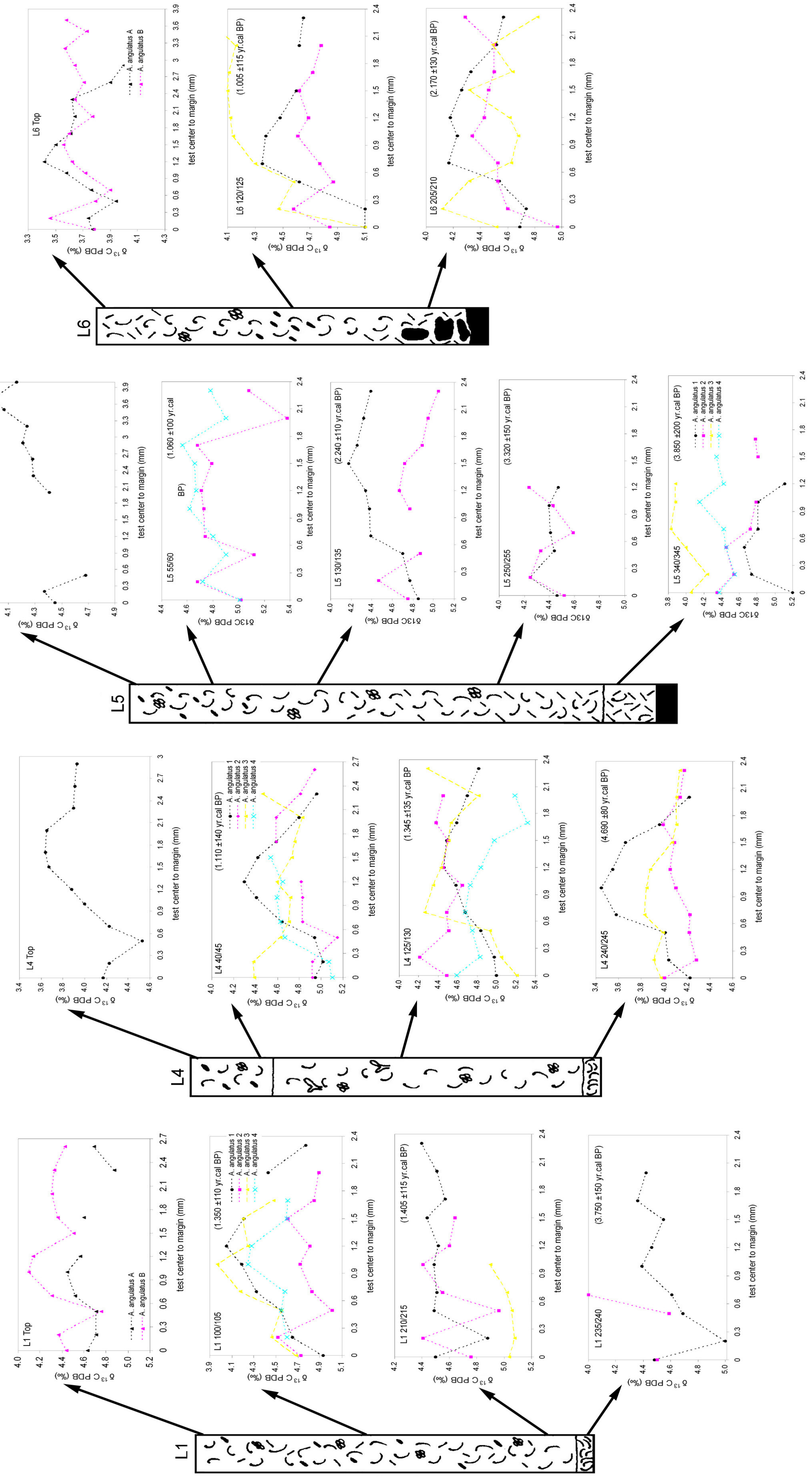


Figure 4.16:
The δ^{13}C values of single *A. angulatus* tests at Lighthouse Reef. The δ^{13}C values are positive correlated to δ^{18}O values; most samples show lighter δ^{13}C values near the test center (Proloculus), heavier carbon isotopes in the middle of the shells and lighter values again towards the margin.

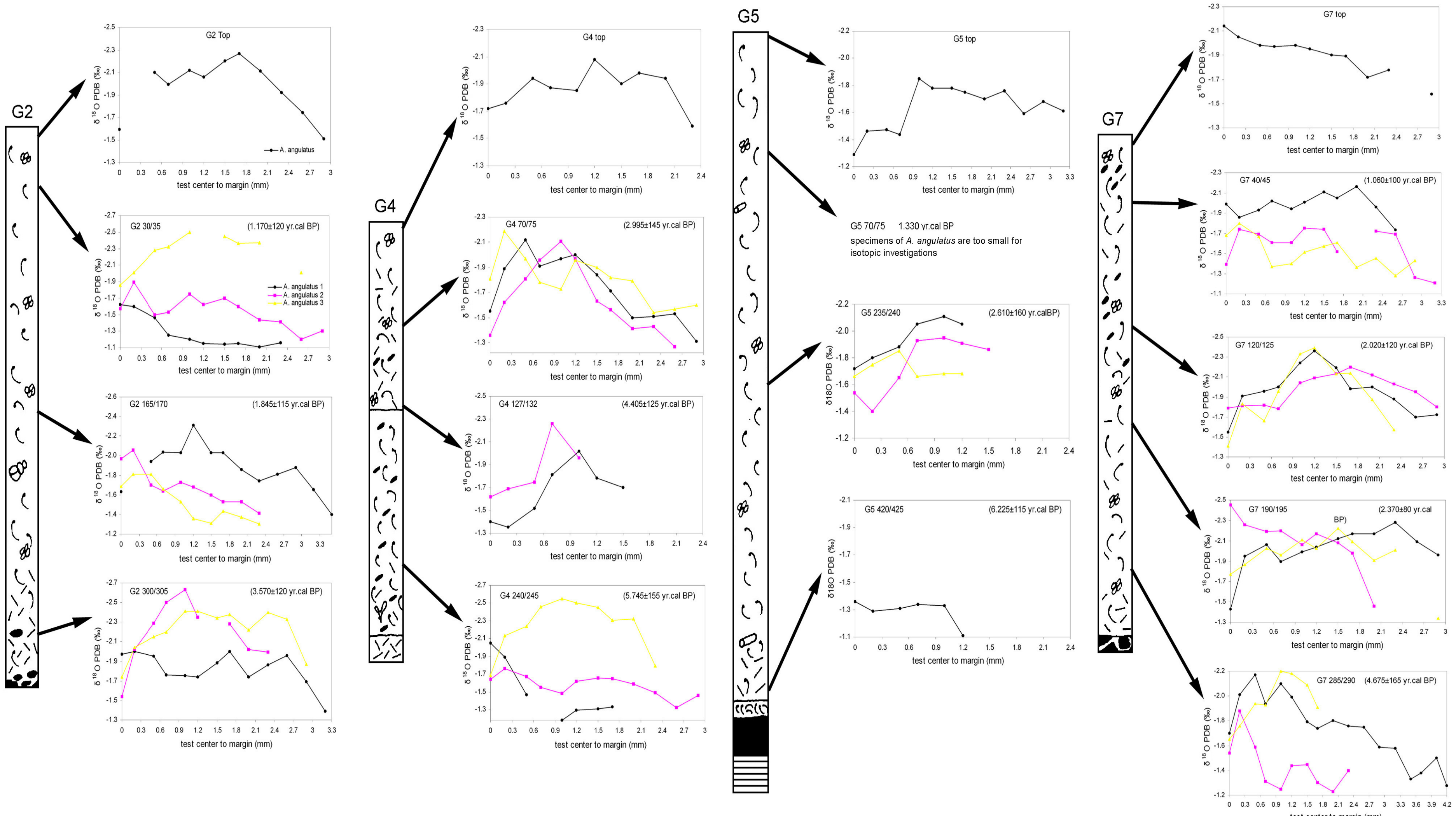


Figure 4.17:
δ^{18}O records of single *A. Angulatus* tests at Glovers Reef. A trend of heavier δ^{18}O values is visible similar to δ^{18}O measurements at Lighthouse Reef with heavier values in the central area of the tests, lighter in the middle and heavier in the margin.

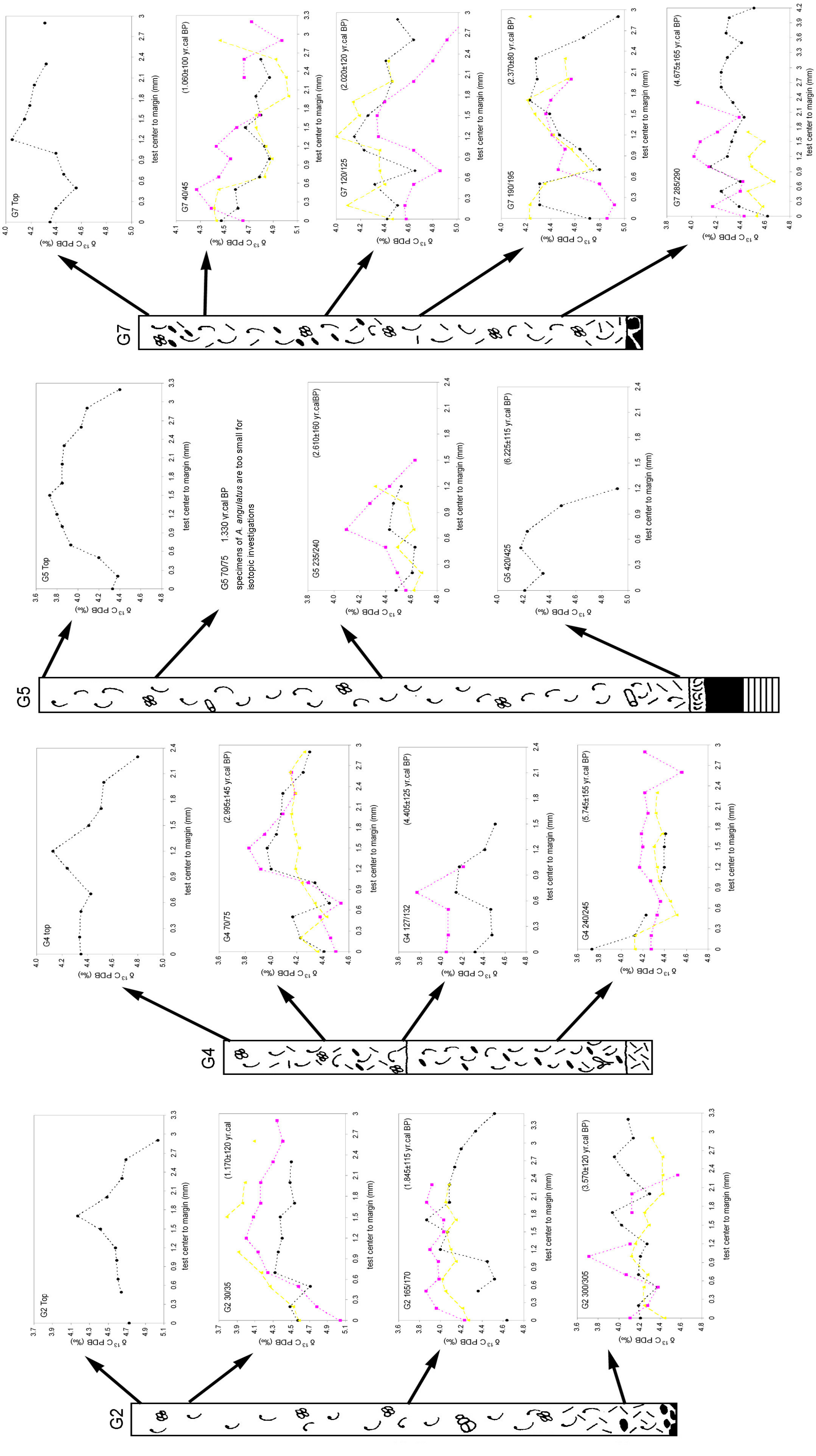


Fig. 4.18:
$\delta^{13}C$ values of single *A. angulatus* tests at Glovers Reef. The $\delta^{13}C$ values are again positive correlated to the $\delta^{18}O$ values of Glovers Reef and show similar fluctuations of heavier, lighter and again heavier values within single tests.

4.4 Calculations of Modern BW-Temperatures

The paleo BW-temperature calculations are based on four common equations of EPSTEIN et al. (1953), SHACKLETON (1974), GROSSMAN (1982), and GROSSMAN & KU (1986; Chapter 3.7.2). Mean present-day BW-temperatures of 2001 (Tab. 2.1) were compared with modern calculated BW-temperatures from $\delta^{18}O$ values from core tops (Fig. 4.14). The respective deviations and fluctuations (in °C) compared to BW-temperatures from 2001 were listed in Tables 4.2 and 4.3.

Table 4.2 shows the mean deviation between measured (from 2001) and calculated BW-temperatures (in °C). Calculated mean BW-temperatures based on equations of GROSSMANN & KU (1986) and GROSSMAN (1982) exhibit the highest deviations to measured BW-temperatures at Lighthouse and Glovers Reefs (4.4 – 6.0°C higher). Calculated BW-temperatures based on the equation of EPSTEIN (1953) show a deviation of 1.1°C to measured BW-temperatures from 2001 at Lighthouse Reef and 2.4°C at Glovers Reef. The lowest deviations of 0.7°C at Lighthouse Reef and 1.9°C at Glovers Reef derived from calculations based on the equation of SHACKLETON (1974). Thus, mean calculated BW-temperatures (after SHACKLETON 1974) reach values of 26.87°C in modern specimens of Lighthouse Reef. At Glovers Reef modern BW-temperatures exhibit values of 25.78°C.

mean Present-day BW-Temp.°C 2000 - 2001	**Top**	EPSTEIN et al. (1953) average (°C) BW-Temperature	Deviation to Present-Day Measurem. (°C)	SHACKLETON (1974) average (°C) BW-Temperature	Deviation to Present-Day Measurem.(°C)	GROSSMAN (1982) average (°C) BW-Temperature	Deviation to Present-Day Measurem. (°C)	GROSSMAN & KU (1986) average (°C) BW-Temperature	Deviation to Present-Day Measurem. (°C)
Ø 27.54	L1	26.89	-0.66	27.26	-0.28	33.95	6.41	33.40	5.86
	L4	27.77	0.23	28.13	0.58	34.73	7.19	34.17	6.63
	L5	26.43	-1.11	26.81	-0.73	33.55	6.01	33.00	5.46
	L6	24.85	-2.69	25.26	-2.28	32.13	4.59	31.59	4.05
	mean	26.48	**-1.06**	26.87	**-0.68**	33.59	**6.05**	33.04	**5.50**
Ø 27.65	G2	25.98	-1.67	26.37	-1.28	33.15	5.49	32.60	4.94
	G4	25.00	-2.66	25.89	-1.77	32.70	5.05	32.16	4.50
	G5	24.35	-3.30	24.77	-2.89	31.67	4.02	31.14	3.48
	G7	25.68	-1.97	26.08	-1.57	32.88	5.22	32.33	4.68
	mean	25.25	**-2.40**	25.78	**-1.88**	32.60	**4.95**	32.06	**4.40**

Table 4.2:
Deviation of mean measured and calculated BW-temperatures from core top sections at Lighthouse Reef and Glovers Reef. The differences are marked in bold.

Calculated BW-temperature ranges in terms of seasonal variability from Lighthouse and Glovers Reefs are listed in Table 4.3. Measured present-day BW-temperatures exhibit mean annual seasonal variations of between 25.52 - 29.04°C ($\Delta T = 3.52°C$) at Lighthouse Reef and 24.67 - 29.72 ($\Delta T = 5.05°C$) at Glovers Reef. The lowest deviation to present-day BW-temperatures variations were also found in calculations after SHACKLETON (1974). The respective deviations reach 0.35° - 2.41°C at Lighthouse and 0.08° - 3.90°C at Glovers Reefs (Tab. 4.3). BW-temperature calculations on the basis of equations of GROSSMAN (1982) and GROSSMAN & KU (1986) reach higher deviations between 3.79 - 8.13°C. The measured present-day BW-temperature range at Lighthouse Reef is $\Delta T = 3.52°C$ during the year 2000. Glovers Reef exhibits a range of $\Delta T = 5.05°C$. The calculated BW-temperature range after SHACKLETON (1974) fluctuates from $\Delta T = 1.13°$ - 3.77°C at Lighthouse Reef during one year. The calculated BW-temperature range at Glovers Reef shows lower fluctuations from $\Delta T = 2.13°$ - 3.69°C (Tab. 4.3).

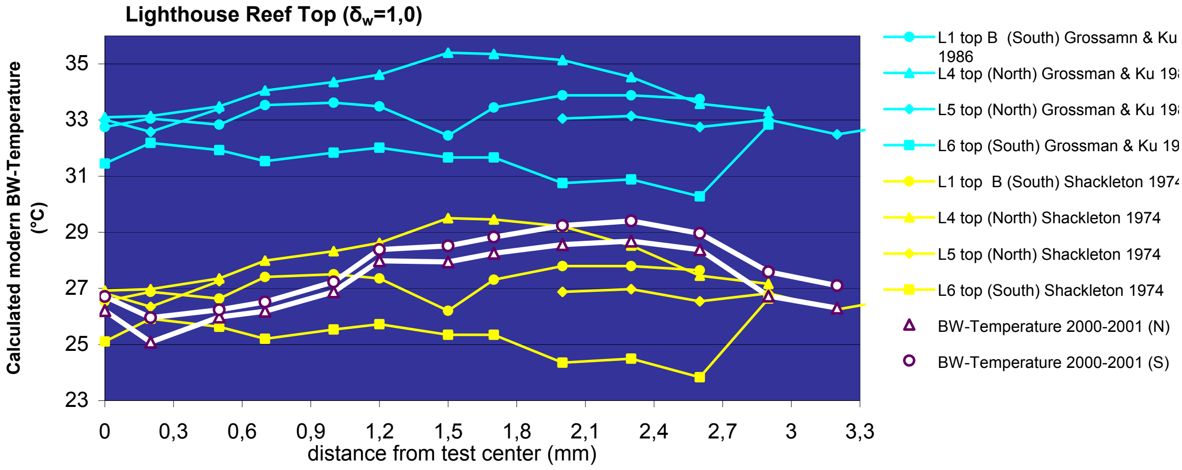
mean Present-day BW-Temp. (°C) 2000 - 2001	Top	EPSTEIN et al. (1953) BW-Temperature (°C) and (range ΔT)	deviation to CT- measure-ments (°C)	SHACKELTON (1974) BW-Temperature (°C) and (range ΔT)	deviation to CT- measure-ments (°C)	GROSSMAN 1982 BW-Temperature (°C) and (range ΔT)	deviation to CT- measure-ments (°C)	GROSSMAN & KU 1986 BW-Temperature (°C) and (range ΔT)	deviation to CT-measure-ments (°C)
25.52 - 29.04 ΔT = 3.52	L1	25.46 -29,23 3.77	0.06 - 0.19	25.86 - 29.55 3.68	0.35 - 0.51	32.69 - 36.01 3.32	7.17 - 6.96	32.14 - 35.44 3.30	6.62 - 6.40
	L4	26.53 - 29.18 2.64	1.02 -0.14	26.92 - 29.50 2.58	1.40 - 0.46	33.65 - 35.97 2.32	8.13 - 6.92	33.10 - 35.40 2.30	7.58 - 6.35
	L5	25.85 - 27.13 1.28	0.33 - 1.91	26.25 - 27.50 1.25	0.73 - 1.54	33.04 - 34.17 1.14	7.52 - 5.13	32.49 - 33.62 1.13	6.97 - 4.58
	L6	23.41 - 26.25 2.84	2.12 - 2.80	23.84 - 26.64 2.8	1.69 - 2.41	30.81 - 33.39 2.58	5.29 - 4.34	30.28 - 32.84 2.56	4.76 - 3.79
24.67 - 29.72 ΔT = 5.05	G2	23.79 - 27.48 3.69	0.88 - 2.24	24.21 - 27.84 3.63	0.46 - 1.88	31.16 - 34.48 3.32	6.49 - 4.76	30.63 - 33.92 3.30	5.96 - 4.20
	G4	23.69 - 26.05 2.36	0.98 - 3.67	24.59 - 26.92 2.34	0.08 - 2.80	31.51 - 33.65 2.14	6.84 - 3.93	30.97 - 33.10 2.13	6.30 - 3.38
	G5	22.75 - 25.42 2.67	1.92 - 4.30	23.18 - 25.82 2.64	1.49 - 3.90	30.20 - 32.64 2.45	5.53 - 2.92	29.67 - 32.10 2.43	5.00 - 2.38
	G7	24.12 - 26.83 2.72	0.55 - 2.89	24.54 - 27.21 2.67	0.13 - 2.51	31.46 - 33.91 2.45	6.79 - 4.19	30.93 - 33.34 2.43	6.26 - 3.64

Table 4.3:
Annual variabilities and ranges (ΔT) of measured and calculated BW-temperatures of modern core top samples from Lighthouse and Glovers Reefs.

The calculated seasonal BW-temperatures from modern core top specimens at Lighthouse and Glovers Reefs are illustrated in Fig. 4.19. The white lines represent the present-day BW-temperatures from 2000 - 2001 for comparison. The mean calculated isotopic composition of Belize seawater is δ_w =1.0‰ (Chapter 3.7.2). Calculated BW-temperatures from the equation of SHACKLETON (1974), marked in yellow colour, produced modern annual BW-temperatures with an maximum offset of ~0° to 5°C lower than present-day seasonal BW-temperatures. The GROSSMAN & KU (1986) equation exhibits seasonal BW-temperature variations of ~2 to 8°C higher than present-day seasonal measurements. BW-temperature reconstructions after EPSTEIN et al. (1953) and GROSSMAN (1982) are not included in Figure 4.19

At Lighthouse Reef, the reconstructed seasonal BW-temperatures from the equation of SHACKLETON (1974) correspond very well to present-day seasonal BW-temperatures of the year 2000 (Fig. 4.19a; yellow line). Especially the reconstructed BW-temperatures from core top L4 show a high similarity to measured BW-temperatures. Fluctuations during one year exhibit increasing BW-temperatures in the first six and decreasing temperatures in the last six measurements. Similar fluctuations were found in present-day seasonal BW-temperatures from 2000. The calculated BW-temperatures of GROSSMAN & KU (1986) indicate similar fluctuations, however maximum BW-temperatures of up to 35°C are not plausible as an offset of 8°C higher than measured BW-temperatures was observed (Fig. 4.19a; light blue lines).

At Glovers Reef, the calculated seasonal BW-temperatures from the equation of SHACKLETON (1974) exhibit also highest similarities to present-day seasonal measurements of 2000 (Fig. 4.19b). Reconstructed modern seasonal BW-temperatures from core tops G2, G4 and G7 fit well to the measured values. However, an offset of 2°C lower than present-day measurements in core G2 and up to 4°C in cores G4 and G7 was observed. Calculated seasonal BW-temperatures from core G5 exhibit a lower correlation to present-day measurements due to a linear decreasing BW-temperature. As expected, the reconstructed BW-temperatures from the equation of GROSSMAN & KU (1986) produced unrealistic BW-temperatures with an offset of ~2 to 7°C higher than present-day measurements from 2000.



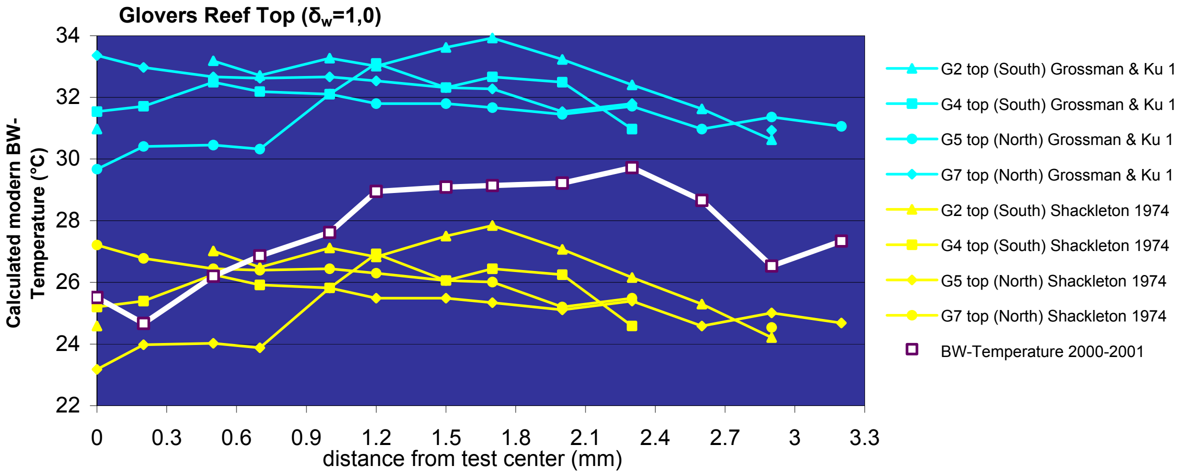


Figure 4.19:
Correlation between modern BW-temperatures from δ^{18}O values of *A. angulatus* from core tops at a) Lighthouse Reef and b) Glovers Reef. The white line exhibits measured/present-day BW-temperatures from 2000 - 2001. The yellow lines represent calculated modern BW-temperatures based on the equation of SHACKLETON (1974) and the light blue lines represent BW-temperatures of the GROSSMANN & KU (1986) equation for comparison.

4.4.1 Reconstruction of Holocene BW-Temperatures

As described above, the equation of SHACKLETON (1974) produced BW-temperatures which are within the range of present-day BW-temperatures at Lighthouse and Glovers Reefs. In fact, the same equation was used for Holocene BW-temperature reconstructions at both platforms. Holocene core samples of similar ages were summarized in time periods. Figures 4.20 and 4.21 show calculated seasonal BW-temperature fluctuations and ranges at Lighthouse and Glovers Reefs during the last 6,000 years.

In total, the BW-temperatures fluctuate from 22.86 to 31.39°C at Lighthouse Reef and from 22.90-29.60°C at Glovers Reef during the last 6,000 years. This indicates a BW-temperature range of 8.5°C at Lighthouse and 6.7°C Glovers Reefs during the Holocene.

At Lighthouse Reef, the calculated annual seasonal BW-temperatures (Fig. 4.20) fluctuate from 24.35 to 29.01°C at 4,690 years BP, and indicate similar seasonal BW-temperatures and ranges compared to present-day measurements. The investigated specimens from 3,850 - 3,750 years BP exhibit lower seasonal BW-temperature variations. Compared to former values at Lighthouse Reef, BW-temperatures are lower and range from 23.23 - 27.75°C. The lowest BW-temperatures were observed in foraminiferal tests at 3,320 years BP, with minimum values of between 22.86 - 26.64°C. The BW-temperatures from 2,240 - 2,170 years BP reached higher annual values of between 24.49 - 29.70°C. Highest BW-temperatures were observed from 1,405 - 1,345 years BP. Seasonal BW-temperature fluctuations are higher and range between 25.06 - 31.39°C. From 1,110 - 1,005 years BP, the BW-temperatures decrease slightly and exhibit similar values compared to present time (24.26 - 30.59°C).

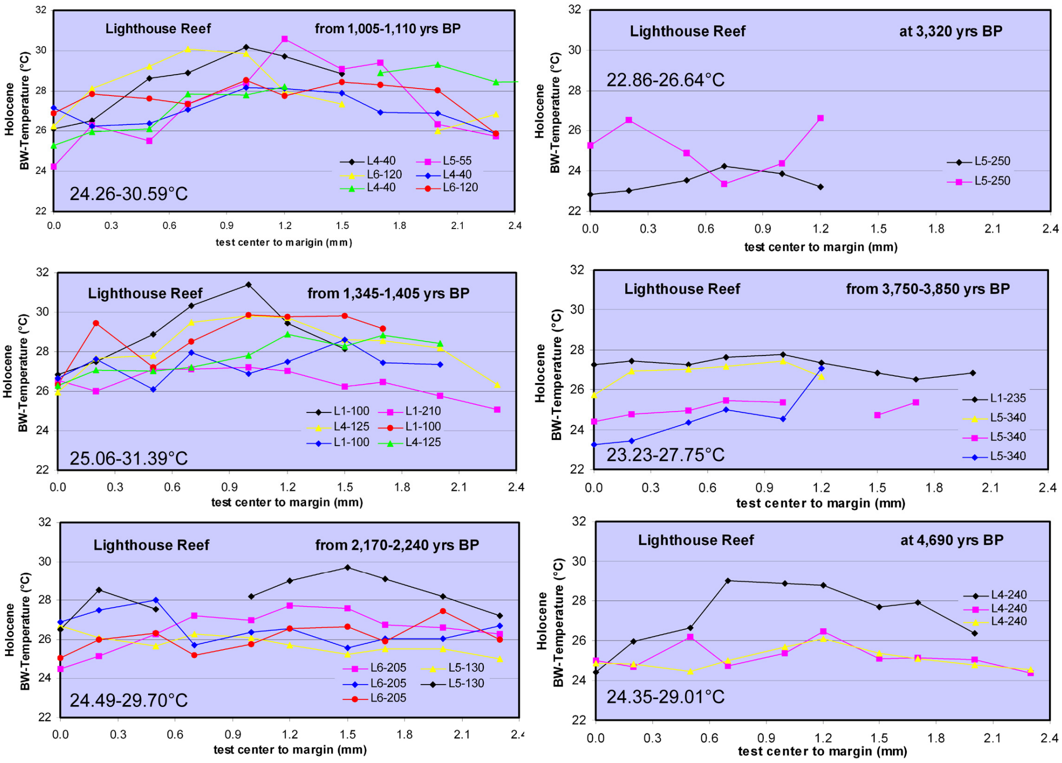


Figure 4.20:
Annual BW-temperatures at Lighthouse Reef during the Holocene. The calculated BW-temperatures are based on the equation of SHACKLETON (1974). The respective time period (from top to bottom) exhibits different BW-temperature variations and ranges during the Holocene. The time period at 3,320 years BP indicates lower BW-temperatures. Higher BW-temperatures were calculated for the following periods: 2,240-2,170, 1,405-1,345 and 1,110-1005 years BP.

At Glovers Reef, at 6,225 years BP the calculated seasonal BW-temperatures varied between 22.35 - 23.51°C, which is considerably lower compared to present-day measurements of 2000 (Fig.

4.21). However, this low range derives from only one single measured foraminifer. A high BW-temperature range from 22.67 - 29.21°C was calculated at 5,745 years BP. From 4,675 - 4,405 years BP, lower BW-temperatures of 22.90 - 27.79°C were observed in single tests, and at 3,570 years BP, highest BW-temperatures of 23.65 - 29.60°C were calculated at Glovers Reef. The lowest BW-temperatures were observed in tests at 2,995 years BP from 23.09 to 27.45°C. At 2,610 years BP, the BW-temperatures increased and reached values of 23.70 - 27.07°C. From 2,370 – 2,020 years BP, the BW-temperatures fluctuate from 23.41 to 28.72°C, and show decreasing values of 23.70 - 28.04°C at 1,845 years BP. The BW-temperatures from 1,170 - 1,060 years BP reach values of 22.76°- 28.96°C.

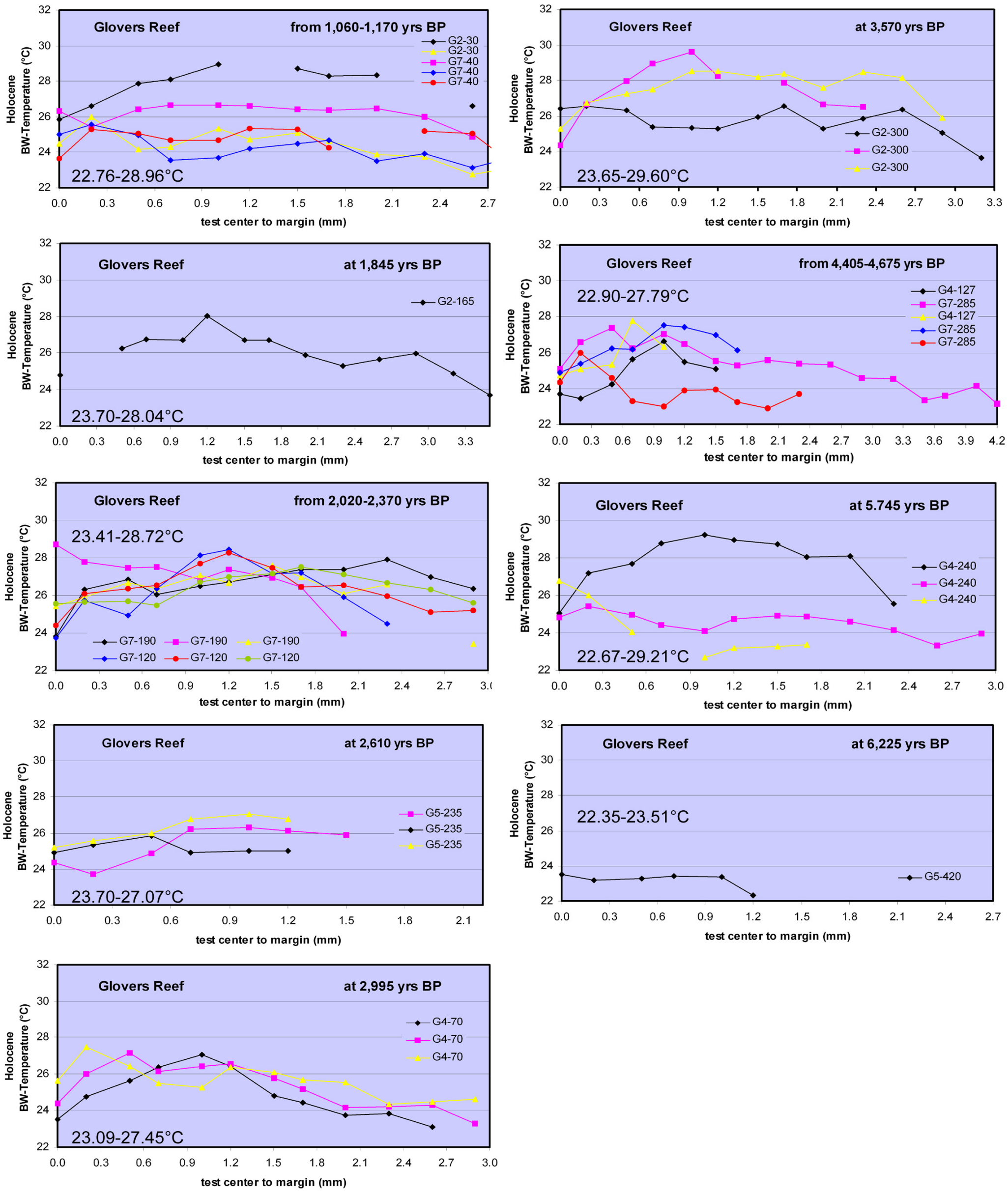


Figure 4.21:
Holocene BW-temperature fluctuations and ranges at Glovers Reef (calculated after SHACKLETON 1974). The annual range exhibits lower BW-temperatures in the following samples: 6,225, 4,675 to 4,405, 2,995 and 2,610 years BP and higher BW-temperatures at 3,570 and 2,370 years BP.

5. Discussion

5.1 Occurrence of Recent Caribbean Benthic Foraminifera

The benthic foraminiferal assemblages in the cores of Turneffe Islands, Lighthouse Reef and Glovers Reef are comparable to those observed at other Caribbean locations and on the Belize shelf (e.g. CEBULSKI 1969, WANTLAND 1975, MURRAY 1991). The most abundant foraminifera belong to the order of porcellaneous Miliolina and hyaline Rotaliina. All cores were drilled in the interiors and on the margins of the three lagoons, and therefore the expected environments are lower-energy settings. *Quinqueloculina* and *Triloculina* are abundant in the Belize carbonate platforms and are present in numerous warm shallow water environments, for example, in Florida (BANDY 1954, LYNTS 1962), in Texas (PHLEGER & LANKFORD 1957), and in Barbuda (BRASIER 1975). Both prefer normal marine to slightly hypersaline conditions (10 - 47‰) but can tolerate periods of low salinity during rainy seasons (MURRAY 1991). *Cribroelphidium poeyanum* is also abundant on the platforms, on the Belize shelf (CEBULSKI 1969, WANTLAND 1975) and around Cuba (BANDY 1964). It is characteristic of lower-energy lagoonal environments and inhabits brackish, normal marine to hypersaline environments (35 - 81‰) and is adapted to variable water temperatures (MURRAY 1991). *Elphidium discoidale*, *E. advenum* and *E. sagrum* are also common species in the three lagoons; they prefer normal marine salinities and occur in similar environments on the Gulf of Mexico and in the Caribbean Sea (MURRAY 1991). Also, well known in Recent environments and abundant in lower-energy back-reefs and lagoonal areas of Belize is *Archaias angulatus* (GISCHLER et al. 2003). The symbiont-bearing miliolid species was found in Florida (HALLOCK 1984, MARTIN 1986), in Barbuda (BRASIER 1975), and on Grand Cayman (LI & JONES 1997, LI et al. 1997, 1998). *A. angulatus* is limited to salinities between 34 - 37‰ (MURRAY 1991) and lives in very shallow water depths of <20 m (LEE et al. 1974, MARTIN 1986).

GISCHLER et al. (2003) found similarities in the recent foraminiferal distribution across the three platforms of Belize. The comparison to the recent foraminiferal fauna of investigated core tops in our study indicates several differences in species occurrence. The abundance of *A. angulatus* in all recent platform interiors was observed by GISCHLER et al. (2003). Core top investigations of our study indicate high abundances of *A. angulatus* at Lighthouse Reef and Glovers Reef but a negligible occurrence at the Turneffe Islands. The reason for this observation is possibly a change in environmental factors such as circulation or water temperature, but it can also be due to other factors such as salinity, because *A. angulatus* is very sensitive with regard to salinity fluctuations. According to GISCHLER et al. (2003) and HAUSER (2001) *Discorbis mira* and *Planorbulina* sp. occur in the lagoon habitats, in which *A. angulatus* is absent. *Discorbis mira* prefers environments of *Halimeda* shoals and channels between mangrove islands with high water energy. The occurrence of *Discorbis mira* and *Planorbulina* sp. is high in the outer channels of the Turneffe Islands. Another difference can be seen in the occurrence of *C. poeyanum*. GISCHLER et al. (2003) found the species in all recent platform interiors with lower abundances (<16%). Whereas WANTLAND (1975) described two *C. poeyanum* assemblages on the Belize shelf in which *C. poeyanum* dominates the whole population. Similar high abundances of *C. poeyanum* were found in present-day samples of Turneffe Islands in the interior restricted lagoon with fluctuating salinity.

5.1.1 Occurrence of Benthic Foraminiferal Assemblages in the Lagoons

In the Holocene cores, of the three platforms, the influence of environmental factors (lagoon age, lagoon depth, substrate, water circulation, water temperature and salinity) on diversity and distribution of foraminiferal assemblages was identified. The lagoons of the Turneffe Islands, Lighthouse Reef and Glovers Reef are different in morphology and water depths and contain different recent benthic foraminifera assemblage zonations within the lagoons, which are comparable to Holocene foraminifera. GISCHLER et al. (2003) defined four recent foraminiferal assemblages in the Belize carbonate platforms, which characterized four different environments (fore-reef, platform interior, patch reef and carbonate shoal, and high energy back reef). Two of these communities correspond to assemblages identified in this Holocene investigation; the *Quinqueloculina-Triloculina* assemblage and the *Archaias angulatus-Quinqueloculina-Triloculina* assemblage are comparable to the High-Diversity Miliolid and the *Archaias angulatus*-Miliolid Assemblages classified in this study. Both represent a lagoonal-interior community. Two further assemblages show some similarities to the High-Diversity Miliolid fauna, but the differences are sufficient to define separate communities: the Low-Diversity Miliolid and the *Quininqueloculina-Triloculina-Peneroplis* Assemblages. Both assemblages are comparable to those of WANTLAND (1975), as well as the two further assemblages of our Holocene lagoons: the *Cribroelphidium poeyanum-Elphidium*-Dominant and the Low-Diversity *C. poeyanum*-dominant Assemblages. The high-diversity *C. poeyanum* community after WANTLAND (1975), represents a marginal-marine influenced community of the Belize shelf with small water movements; and the low-diversity *C. poeyanum* assemblage indicate a restricted assemblage along the mainland coast of Belize. The Mixed Assemblage in this study corresponds to no community described before. It consists of several different populations and occurs only at Glovers Reef in deeper lagoonal areas.

All assemblages differ mainly in their species frequency and diversity, but the total composition of the species varies only slightly. Each foraminiferal community characterized a special environment.

The High-Diversity Miliolid Assemblage occurs in cores T4 and T6 of the Turneffe Islands. Both cores represent the western marginal area of the lagoon within the leeward channels. Additionally this assemblage appears in the upper units of core T7, which was drilled in the interior part of Turneffe

Islands. The common genera of this community are *Quinqueloculina* and *Triloculina*; additional taxa are *Cribroelphidium, Articulina, Discorbis* and *Planorbulina*. This assemblage inhabits shallow, marine areas on the Belize shelf, and prefers moderate to dense stands of *Thalassia* ("Turtle Grass") in poorly sorted, sandy mud (Murray 1991). Wantland (1975) found this assemblage in shallow clear water with maximum depths of 7 m. Comparing calculated lagoon depths of these core sections indicate similar shallow water depths from 0 - 4.2 m (Fig. 4.3). Murray (1991) argued, that this assemblage tolerates a wide salinity range between 10 - 47‰, and defined this community as normal-marine salinity fauna. Measured salinity at the Turneffe Islands ranges from 34.2 – 42.5‰ within one year and indicates the highest salinity range for the three platforms. The Turneffe Islands are restricted through a dense mangrove rim, which results in higher and lower freshwater influence during the rainy season. Within the channels of the Turneffe Islands, Gischler et al. (2003) found the taxa *Planorbulinacea* frequent in similar areas of recent investigations (near core T4), and described an increase of *Planorbulinacea* in the narrow channels and between the mangrove rim and reef margin with higher water movements.

The *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage occurs throughout the core T5 of the Turneffe Islands. The core was located in the interior of the southern lagoon. *C. poeyanum* and *Elphidium* sp. are the most common species in this assemblage. Other genera are *Rosalina, Articulina, Amphistegina, Bolivina* and *Ammonia*. Within this community *Quinqueloculina* and *Triloculina* occur rarely. Wantland (1975) found this community in water depths of 9 - 45 m within normal marine salinities (36‰) and bordered by mangroves in the coastal zone with a tendency to open marine conditions. Our calculated lagoon depths are slightly lower and range from 3.6 - 4.5 m. Murray (1991) called this community the *Elphidium poeyanum* assemblage, which is found on environments that range from brackish or normal marine to hypersaline (2 - 47‰), in muddy sand <12 m water depth. Rose & Lidz (1977) described an easy adaptation to fluctuations in salinity and temperature and an occurrence near the beach. According to Phleger (1960), Bandy (1964), Wallace & Schafersman (1977), and Lidz & Rose (1989) they prefer shallow water depths with low wave energy and inhabit areas with dense algae, e.g. *Halimeda* (Langer 1993). Salinity at the Turneffe Islands ranged from 34.2 - 42.5‰. Bottom water temperatures ranged from 21.7 - 31.8°C. Between this high-diversity *C. poeyanum* assemblage and the above described High-Diversity Miliolid Assemblage are differences in the species distribution. Both inhabit shallow water depths with fluctuating salinity. *Quinqueloculina* prefers normal-marine to slightly higher salinities and *C. poeyanum* lives in lower to normal-marine salinities. Restricted mangroves inhibit the exchange with surrounding seawater during periods of higher precipitation. This could lead to lower salinities in the southern lagoon of the Turneffe Islands (T5). Normal-marine salinity conditions occur because of higher water energy within the channels (T4 and T6) in which *Quinqueloculina* is more abundant.

The Low-Diversity *Cribroelphidium poeyanum*-Dominant Assemblage occurs only in core T7 in the oldest section of the restricted central lagoon of the Turneffe Islands. The population consists of two-thirds of *C. poeyanum* and additional species are *Ammonia* and some *Quinqueloculina*. WANTLAND (1975) described this community in two separate areas on the Belize shelf in similar water depths which ranged from 9 to 28 m; I) one assemblage exhibits normal-marine conditions of 34 - 36‰ with limited river influence and a restricted area between the lagoon and the open ocean, and II) the second area of this assemblage is limited by salinity, circulation and water depth, because some of the dominant taxa (*Cribroelphidium* and *Ammonia*) are abundant in extremely shallow and brackish waters. Reconstructed lagoon depths for this assemblage exhibit the highest water depths (7.8 m) for the Turneffe Islands. Circulation is generally low in the interior of the Turneffe Islands but deeper waters in this case could indicate a further decrease in circulation. This contention is supported by findings of HAUSER (2006), who found high abundances of chemosymbiont-bearing molluscs in the same sample section of core T7, and concluded lower oxygen conditions and decreased circulation. WANTLAND (1975) also described unfavourable conditions for this assemblage as indicated by the high dominance of *C. poeyanum*. The precise life modes of *C. poeyanum* are enigmatic. LANGER (1993) described *C. poeyanum* as a suspension feeder that lives clinging in mesh derived algae, and MURRAY (1991) found the same species in the sediment or at the surface. Shallow water depths are more influenced by evaporation and precipitation, so the fauna is primarily controlled by temperature and salinity, and secondarily by wave and current action (BOCK 1971).

The *Quinqueloculina-Triloculina-Peneroplis Assemblage* appears only in core T7 (from 1,000 - 2,000 years BP) at the Turneffe Islands and in one sample of G5 (at 6,000 years BP) at Glovers Reef. This assemblage shows similarities to the high-diversity Miliolid and to the Mixed Assemblages. The common species of this interior area of the lagoon are mainly *Triloculina* and *Quinqueloculina*. *Peneroplis* is more frequent than in other assemblages, and *C. poeyanum* occurs in lower proportions. However, enigmatic is the absence of the symbiont-bearing species *A. angulatus* at the Turneffe Islands, as *Peneroplis*, which is also a symbiont-bearing species and occurs in similar environments, inhabits this assemblage in high abundances. However, at Glovers Reef, *A. angulatus* reaches abundances of up to 12%. Maybe *Peneroplis* is less closely limited to specific environments than *A. angulatus*, which occurs solely in lower turbulent regimes (as described below). *Peneroplis* lives vagile, clinging on plants or hard substrate and prefers 35 - 53‰ salinity and water temperatures of 18 - 27°C (MURRAY 1991). LIDZ & ROSE (1989), CULVER (1990), TRIFFLEMAN et al. (1991) found *Peneroplis* in the leeward area of shallow platforms, and BANDY (1964), DAVIS (1964), and CEBULSKI (1969) described *Peneroplis* additionally at the higher energy reef margins. However, the high abundance of *Quinqueloculina* and *Triloculina* and the low occurrence of *C. poeyanum* indicate lower energy environments for this foraminifera assemblage. The water depths in which the *Quinqueloculina-Triloculina-Peneroplis Assemblage* occurs in the cores was calculated at 6.0 - 7.6 m at the Turneffe Islands and 16.3 m at Glovers Reef, and indicates the highest calculated lagoon depths in both platforms.

The *Archaias angulatus-Miliolid* Assemblage of Lighthouse Reef occurs in shallow, normal-marine, clear waters and prefers pure carbonate sedimentation (WANTLAND 1975). GISCHLER et al. (2003) found this assemblage on all three lagoons in the platform interior. After MARTIN (1986), CULVER (1990), MURRAY (1991), HALLOCK & PEEBLES (1993) and LI et al. (1997), *A. angulatus* is characteristic for shallow lagoons (<12 m) with low wave energy or currents. The species requires a shallow water depth because its endosymbionts are light dependent (DUGUANY & TAYLOR 1978). This corresponds to our calculated lagoon depths from 3.6 - 11 m. *A. angulatus* is also infrequent in turbulent waters because it lives, attached by its pseudopodia, on sea grass (*Thalassia testudinum*) in nearshore regions, and on sediment grains (ROSE & LIDZ 1989) and can be detached during violent storms or wave activity. The tests of *A. angulatus* are strong and resistant to abrasion and dissolution (COTTEY & HALLOCK 1988), and resist winnowing, which dominates lag assemblages (MURRAY 1991). In small living communities *A. angulatus* can inhabit the sediment and dominates this population because of its resistant tests (MARTIN & WRIGHT 1988). However, WANTLAND (1975) found another *Archaias*-influenced association on the Belize shelf, the *Archaias-Asterigerina* fauna, which forms a characteristic high turbulence population. The *Archaias angulatus*-Miliolid Assemblage is commonly accompanied by the species *Quinqueloculina* and *Triloculina* (MURRAY 1991). This observation is comparable to our investigations. Additional taxa are *C. poeyanum, Rosalina, E. discoidale*, and some *Textulariacea*. Some separated *Homotrema* fragments are also present in modern samples of core L6; the relative low number of fragments seems to be transported because in general *Homotrema* lives in high-energy and cryptic Caribbean reef- and platform-margin habitats (STREETER 1963, MURRAY 1991, GISCHLER & GINSBURG 1996), and in the windward margin of all three platforms (GISCHLER 2003). MURRAY (1991) found *D. candeianus* as an additional species in this community, but according to HAUSER (2001), *D. candeianus* occurs mainly in *Halimeda* shoals and leeward channels of the Turneffe Islands, but is absent in the *Archaias angulatus*-Miliolid Assemblage, because it is incompatible with current environment. Similar observations were found in our samples. *Discorbis* and *Archaias* do not appear together in high abundances in similar assemblages.

The Low-Diversity Miliolid Assemblage of Lighthouse Reef shows a similar foraminiferal composition as the *Archaias angulatus*-Miliolid Assemblage. In addition to common taxa, such as *Quinqueloculina*, *Triloculina*, *Rosalina*, *C. poeyanum*, *Textulariacea* and *Homotrema,* the species *A. angulatus* appears in moderate frequencies. The Low-Diversity Miliolid Assemblage of this study differs from the Low-Diversity Miliolid Assemblage of WANTLAND (1975) by the frequency of rare species, whereas the frequent species are similar in both assemblages. For example, *Discorbis,* *Heterillina cribostoma*, *T. bermudezi* and further small, smooth, unornamented tests are abundant in WANTLAND's (1975) community of living populations, whereas in our study *Discorbis* is rather inexistent in this community. However, *Rosalina* is abundant in this study and lives in similar habitats. *H. cribostoma* is also absent in our study. WANTLAND (1975) found this community in the northern part of the Belize Shelf, from Chetumal Bay to Belize City. He found this community in variable water temperatures and salinities, which are less than normal marine conditions; Hypersaline conditions are possible during the dry season because of the restricted and shallow area (<2.7 m) with often turbid water. Deposition of soft carbonate mud to sandy carbonate mud with marine-grass cover was described by the same author. Calculated lagoon depths for this study are higher and range from 4.3 - 10.2 m. *A. angulatus* is present in moderate frequencies in this assemblage and alternates with the at Lighthouse Reef, which indicates rather stable salinity conditions and a low influence of turbid waters. However, turbid conditions cannot be excluded because in general, Lighthouse Reef is exposed to high wave movements, which could deplete faunal diversity. *Rosalina* increases on coral patch reefs and decreases between patch reefs (ROSE & LIDZ 1977) and therefore can be used to indicate the existence of possible fossil patch reefs at Lighthouse Reef. Low frequencies of *Textulariacea* and *Homotrema* indicate transport of fragments from the windward breaking fore reef due to higher energy water regime.

The Mixed Assemblage of Glovers Reef is comparable to the *Cribroelphidium-Quinqueloculina* mixed fauna of WANTLAND (1975). The most common taxa are *Cribroelphidium* and *Quinqueloculina*, as well as other shoal-derived genera such as *Peneroplids, Planorbulina, Clavulina, Hauerina* and *Articulina*. However, some species of deeper lagoon areas are also present, e.g. *Elphidium, Fursenkoina, Bolivina, Florilus, Ammonia, Textularia* and *Tretomphalus*. This assemblage represents, after WANTLAND (1975), a mixture of displaced shoal fauna and endemic deeper lagoonal species. In contrast to that, in our study, *A. angulatus* appears in high abundances in this assemblage. This observation supports the contention that the assemblage in this study is also a mixture of several populations. Shoal-derived species dominate the Mixed Assemblage in this study. However, *A. angulatus* prefers lower water depths (<12 - 15 m) e.g. after HALLOCK & PEEBLES (1993). Calculated paleo-lagoon depths at Glovers Reef range from 9.6 - 15.5 m. Thus, increasing lagoon depths show increasing abundances of *A. angulatus* in some cores (e.g. G5; Fig. 4.5). *Archaias* may be transported from surrounding environments due to the high preservation of the tests.

5.2 Development of Benthic Foraminiferal Assemblages in the Holocene Cores

Assemblages are usually better indicators of the environment because species occur over several environmental zones. The distribution of different foraminiferal assemblages in the cores of the three platforms could give a first indication to possible changes in environmental conditions.

The Turneffe Islands contain different assemblages in marginal and interior areas of the lagoon (Fig. 4.3). In western marginal cores of the Turneffe Islands (T4 and T6) the High-Diversity Miliolid Assemblage occurs during the last 5,343 years. This indicates constant environmental conditions, despite the decreasing lagoon depths. The abundance of *Discorbis*, *Articulina* and *Planorbulina* could be an indication of the existence of mangroves and/or *Halimeda* shoals and leeward channels with higher water energy. *Quinqueloculina* and *Triloculina* indicate changing conditions between marine to slightly hypersaline with lower water movements. The conditions show similarities to the present-day environment in the marginal area of Turneffe Islands. The interior lagoon of the Turneffe Islands (cores T5 and T7) shows high abundances of *C. poeyanum*. Core T7 contains three different assemblages during the last 4,380 years. At 4,380 years BP the Low-Diversity *C. poeyanum* Assemblage occurs in T7. The dominance of *C. poeyanum* and *Ammonia* in this sediment indicates extreme conditions of low salinities or restricted circulation, possibly right after the Holocene inundation of the platform. Decreasing circulation due to higher water depths, which limits the seawater exchange, could be possible. From 2,185 - 1,980 years BP a *Quinqueloculina-Triloculina-Peneroplis* Assemblage inhabits the sediment and displaced *C. poeyanum*. Calculated decreasing water depths corresponds with the appearance of *Peneroplis*, which indicates increasing water circulation and slightly lower salinity conditions. During the past 1,275 years, the High-Diversity Miliolid Assemblage dominates, and also occurs in the marginal cores of the Turneffe Islands. Due to shallow lagoonal depths (4.2 - 3.6 m), high abundances of *Discorbis* and a high energy fauna, the development of channels could have been at this time. The High-Diversity *C. poeyanum* Assemblage inhabits the whole of core T5 in the open southern lagoon, during the last 2,260 years. The occurrence of *C. poeyanum* indicates lower to normal-marine conditions. However, the high abundance of *E. advenum* could be an indication of a higher water energy environment, which corresponds to the shallow calculated lagoon depths of between 3.6 to 4.5 m.

Lighthouse Reef contains two different assemblages, which occur both in deep (L1 and L4) and shallow lagoons (L5 and L6; Fig. 4.4). The calculated deeper areas of Lighthouse Reef range from 6.6 - 11 m, and the shallower areas vary from 3.6 - 7.4 m. The oldest sediment sample from 4,690 – 3,320 years BP contained the *Archaias angulatus*-Miliolid Assemblage and occurred in shallower (core L5) and deeper (core L4) areas of the lagoon. The high frequency of *Archaias* indicates lower influence from wave movements and stable saline conditions in shallow clear waters. With decreasing lagoon depths, the Low-Diversity Miliolid Assemblage inhabits the sediment and indicates higher wave-influenced water movements from 1,345 - 1,110 years BP. Some fragments of *Homotrema* and *Textulariacea* could be an indication of high energy waters. Modern samples contain the *Archaias angulatus*-Miliolid Assemblage again, which indicates stable environmental conditions in salinity and temperature, as well as lower water movement. The abundance of *Rosalina* in both environments could be an indication for the existence of patch reefs. However, these fluctuations were not found in core L1, which was located in the deeper central part of Lighthouse Reef. Solely the Low-Diversity Miliolid Assemblage occurs throughout the core L1 during the last 3,750 years. Due to higher water movements originating from wind and wave energy from the north-eastern wind direction *Homotrema* and *Textularia* fragments may occur. Core L5 shows the influence of lower water movements during the last 3,850 years, because the *Archaias angulatus*-Miliolid Assemblage occurred in highest abundances.

The oldest sample at Glovers Reef (6,225 years BP) is characterized by the *Quinqueloculina-Triloculina-Peneroplis* Assemblage and occurs only in this period (Fig. 4.5). Despite the highest lagoonal depths being calculated here, this assemblage, with abundant *Peneroplis*, indicates good water circulation. In general, this assemblage shows a higher influence from water movement than the Mixed Assemblage, which occurs from 2,610 years to the present day in the eastern deeper part of Glovers Reef. All further cores in the deeper interior and in the shallower margin areas of Glovers Reef contain the Mixed Assemblage. The composition of the benthic foraminiferal fauna during the past 5,745 years shows no significant changes and indicates stable conditions within the lagoon at Glovers Reef.

5.3 Benthic Foraminiferal Diversity and Controlling Factors

The diversity of a fauna is controlled by several environmental factors, some of which are discussed below. Investigations of modern foraminifera indicate highest species richness and diversity at Lighthouse Reef and lowest at the Turneffe Islands (GISCHLER et al. 2003). High diversity and numbers of foraminiferal species at Lighthouse Reef were explained by a high degree of circulation due to shallow water depths and high water energy regimes. Low diversity and numbers in surface samples at the Turneffe Islands were explained by restricted circulation, imposed by dense mangrove growth behind platform margins. However, calculated mean values of Holocene samples exhibit highest species richness and diversity at the Turneffe Islands and lowest values at Glovers Reef, whereas Lighthouse Reef has intermediate values (Tab. 5.1). Due to these discrepancies, the diversity of the benthic foraminiferal fauna seems to depend on additional environmental conditions:

5.3.1 Lagoonal Size

The size of the habitat is decisive for the diversity in a faunal assemblage, since larger areas usually exhibit more habitat heterogeneity than smaller areas (e.g. PRESTON 1962, MACARTHUR 1960, 1965). Classical examples of this principle are differences in the diversity of the terrestrial flora and fauna on different large islands (MACARTHUR & WILSON 1967). The area-diversity aspect of this equilibrium theory postulates that the number of species (S) is related to the surface area (A) by the equation S = CAz, where C is a constant that varies among taxa and z is an empirical constant. According to this relation, ADJEROUD et al. (2000) reported an increase in foraminifera species richness with increasing lagoon areas for macrobenthos, and BICCHI et al. (2002) described a positive correlation between the species richness and the lagoonal size in the central Tuamotu Archipelago for benthic foraminifera in French Polynesia.

This is in part similar in this study; Turneffe Island has the largest total lagoon area with approximately 225 km^2 (Tab. 5.1) and is characterized by the highest average diversity (H') (Turneffe: 3.31; Lighthouse: 3.18; Glovers: 2.88) and richness (S) values (Turneffe: 51; Lighthouse: 45; Glovers: 38). Glovers Reef (194 km^2) and Lighthouse Reef (112 km^2) have lower diversities, however, Glovers Reef exhibits the lowest values even though it is not the smallest lagoon. Average evenness values (E) show no correlation with the lagoonal size. Highest evenness values (E) can be found at the Turneffe Islands as well as at Lighthouse Reef, which has the smallest lagoon (Turneffe: 0.84; Lighthouse: 0.84). Glovers Reef has the lowest evenness values for all lagoons (Glovers: 0.79).

Lighthouse Reef and Glovers Reef exhibit one lagoonal area each. In contrast, the Turneffe Islands comprise of several lagoons (restricted through mangrove rims) with differing sizes (Fig. 5.1). The cores T5 and T7 were drilled in the interior lagoon of the Turneffe Islands, which can be divided into a larger restricted central lagoon (T7), and an open, southern lagoon (T5), with little seawater influence from the south. Both lagoons exhibit a total area of ~160 km^2 and show no sharp separation to each other. Mean diversity values of cores T5 (H'= 2.88, E = 0.76) and T7 (H' = 2.92, E = 0.78) are lower than mean values of the entire platform of Turneffe Islands (H' = 3.31), and correspond to diversity and evenness values of Glovers Reef, which represents a similar lagoon area of ~194 km^2 (e.g. G5: H' = 2.81, E = 0.79; G7: H' = 2.94, E = 0.81). The cores T4 and T6 were placed within the channels (T4), and in the leeward mangrove margin (T6) of the western part of the Turneffe Islands platform. In total they show the highest diversity, evenness, and richness values (H'= 3.64, 3.62; E = 0.90, 0.90; S = 58, 57).

The positive correlation between the species richness of macro-organisms and the area of a remote ecosystem may result from an increasing variety in the available habitats (MARTIN et al. 1995). However, this is not generally applicable to mirco-organisms such as benthic foraminifera, as described here. Benthic foraminiferal diversity appears to be less affected by the habitat size. Turneffe Islands, the largest lagoon, exhibits both the highest and the lowest species diversity (Tab. 5.1). In this study, the platforms indicate no correlation between lagoonal size and benthic foraminiferal diversity. Further abiotic factors, such as e.g. lagoonal depths, temperature or water circulation seem to have a greater influence on the benthic foraminiferal communities.

lagoon area (km^2)	core	lagoon division	diversity	evenness	richness
Turneffe Islands (225 km^2)	T4	channels	3.64	0.90	58
	T6	platform margin	3.62	0.90	57
	T5	southern lagoon (open)	2.88	0.76	45
	T7	central lagoon (restricted)	2.92	0.78	42
	mean		3.31	0.84	51
Lighthouse Reef (112 km^2)	L1	deep lagoon	3.39	0.87	51
	L4	deep lagoon	3.09	0.81	45
	L5	shallow lagoon	2.99	0.82	38
	L6	shallow lagoon	3.32	0.85	49
	mean		3.18	0.84	45
Glovers Reef (194 km^2)	G2	shallow margin	2.96	0.78	44
	G4	deep interior	2.79	0.77	38
	G5	deep interior	2.81	0.79	35
	G7	deep interior	2.94	0.81	37
	mean		2.88	0.79	38

Table 5.1:
Lagoonal area (GISCHLER 2003), lagoon divisions and mean values of diversity, evenness, and richness of benthic foraminifera in all lagoonal cores.

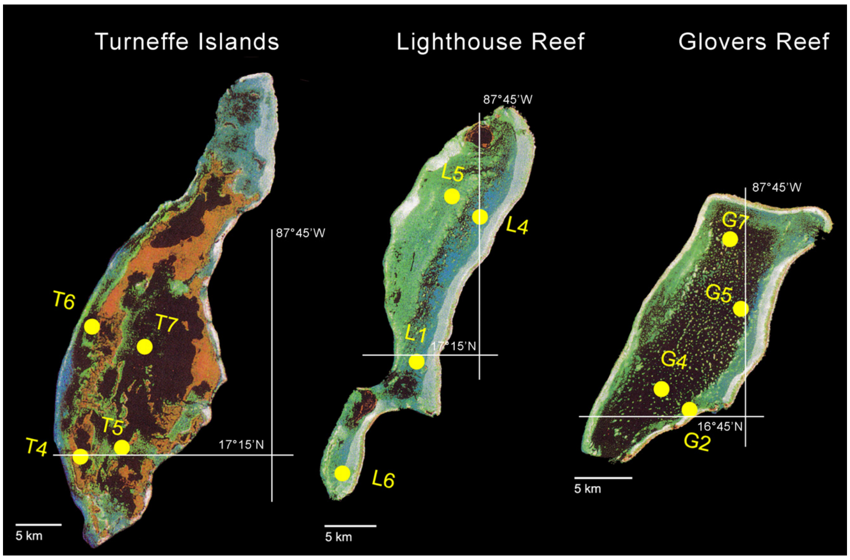


Figure 5.1:
Satellite images of the three platforms and their respective vibracore locations (yellow dots) from GISCHLER & LOMANDO (1999).

5.3.2 Lagoonal Age

The age of a habitat is also a crucial factor for the diversity development in a faunal community. Many hypotheses have been suggested to account for differences in species richness among marine benthic samples in different geographic areas (e.g. SANDERS 1968, 1969, SLOBODKIN & SANDERS 1969, GRASSLE & SANDERS 1973, CONNELL 1978, KUKERT & SMITH 1992). For example, the “Time-Stability Hypothesis” of SAUNDERS (1969) described that young and/or stressed environments will have fewer species than nonstressed and/or old environments. This hypothesis was applied for, e.g. the diversity of reef corals (LOYA 1976), diversity of copepods (COULL 1972) and invertebrate diversity on sandy beaches (DEXTER 1972). Another common hypothesis is the “Intermediate Disturbance Hypothesis” of CONNELL (1978), which suggests that highest diversity was maintained in habitats, where periodic disturbance took place (e.g. storms, bioturbation or predation); e.g. after a disturbance event opportunists colonize the habitat (Colonisation Stage) and this is followed by an increasing diversity (Diversification Stage), which could reach a maximum (Climax Stage). Without a disturbance event, diversity decreases again due to opportunists (Dominance Stage), which outcompete other taxa.

The relationship between sample ages and their respective diversity and richness values are shown in Figure 5.2. In general, an increasing diversity trend with decreasing age is visible at the three platforms, but the statistical significance is weak (R^2=0.1335; p=0.0084). Younger samples contain higher diversities than older samples. Similar trends were obtained from plots of sample ages in relation to richness values. The number of species decreases with increasing age (Fig. 4.10b), but the statistical significance is also weak (R^2=0.1116; p>0.005). The general diversity trend in the lagoons shows slightly increasing values during the last 6,000 years (Fig. 5.2). However, in comparison the single diversity trends of each lagoon are different (Figs. 4.4 – 4.8). Glovers Reef, the most ancient platform, exhibits the lowest diversity variations with a slightly increase (Fig. 4.8). Turneffe Islands, the youngest platform, reflects rather constant diversities in cores T4, T5 and T6. However, core T7 indicates a higher diversity increase (Fig. 4.6). Lighthouse Reef contains low increasing diversity values (Fig. 4.7).

Due to the different ages of the platforms (as Glovers is the oldest atoll and Turneffe is the youngest) and due to the fact, that the development of a new habitat requires a long time, the platforms are in different diversification stages. The benthic foraminiferal fauna at the Lighthouse and Glovers Reefs may be situated in a ”Diversification Stage”, because of slightly increasing diversity values during the past 6,000 years. The fauna at the Turneffe Islands is likely to be situated between a “Colonisation” (~ 4,000 years BP) and “Diversification Stage” (~2,000 – 0 years BP), due to stronger increasing diversity values in older samples.

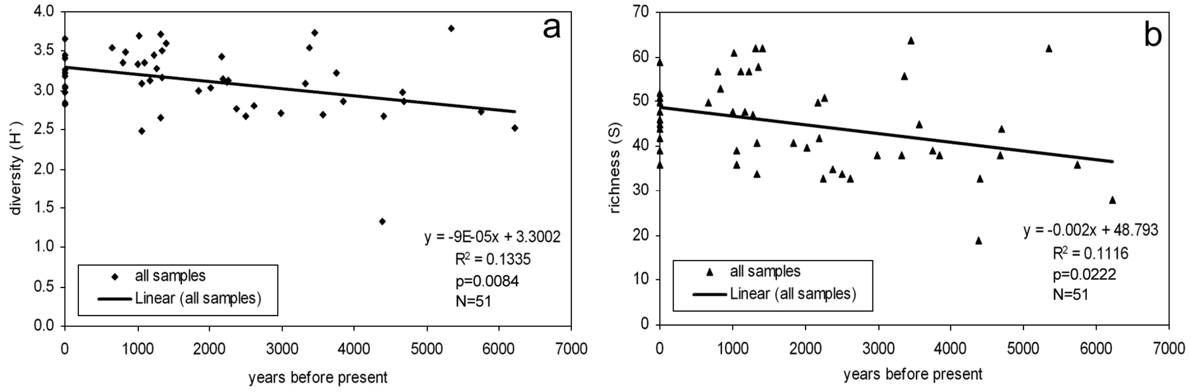


Figure 5.2:
a) Relationship of diversity (H’) and sample age. An increase of diversity during the past 6,000 years occurs in all three atolls. b) Richness (S) versus age of all samples indicate increasing number of species with decreasing age.

core	uncorrected core depth (m)	corrected for compaction (m)	age	(±)	water depth (m below present SL)	lagoon depth (m)
T4	0	0.00	0	0	0.50	0.50
	0.38	0.80	660	50	1.30	1.20
	0.88	1.88	1030	110	2.38	2.18
	1.68	3.59	3370	160	3.99	3.09
	1.88	4.00	3445	115	4.40	3.50
	2,24 (base)	4.80	6395	105	5.20	2.70
T5	0	0.00	0	0	3.60	3.60
	0.73	0.81	2500	200	4.41	3.71
	1.38	1.48	2260	100	5.08	4.48
	1,88 (base)	2.10	8090	90	5.70	-1.40
T7	0	0.00	0	0	3.60	3.60
	0.68	0.72	795	155	4.32	4.17
	2.43	2.6	1275	105	6.20	5.95
	3.68	3.94	1980	120	7.54	7.04
	4.23	4.50	2185	145	8.10	7.60
	5.08	5.44	4380	150	9.04	7.84
	5,35 (base)	5.78	6840	180	9.38	6.23
T6	0	0.00	0	0	0.00	0.00
	0.68	1.18	835	105	1.18	1.03
	1.68	2.89	1320	160	2.89	2.64
	2.78	4.80	1225	85	4.80	4.55
	3.28	5.66	2485	195	5.66	5.00
	6,50 (base)	5.70	5343	73	5.70	4.05
L1	0	0.00	0	0	6.60	6.60
	1.03	1.18	1350	110	7.78	7.48
	2.13	2.44	1405	115	9.04	8.71
	2.38	2.73	3750	150	9.33	8.23
L4	0	0.00	0	0	9.00	9.00
	0.43	0.49	1110	140	9.49	9.29
	1.28	1.45	1345	135	10.45	10.15
	2,43 (base)	2.77	4690	80	11.77	10.97
L5	0	0.00	0.0	0	3.60	3.60
	0.58	0.58	1060	100	4.18	3.98
	1.33	1.34	2240	110	4.94	4.34
	1.48	1.49	2690	60	5.09	4.39
	2.53	2.56	3320	150	6.16	5.26
	3.43	3.57	3850	200	7.17	6.12
	3,70 (base)	3.75	7800	140	7.35	1.45
L6	0	0.00	0	0	5.70	5.70
	1.23	1.35	1005	115	7.05	6.85
	2.08	2.28	2170	130	7.98	7.38
	2,46 (base)	2.70	7545	125	8.40	3.42
G2	0	0.00	0	0	9.60	9.60
	0.38	0.41	1170	120	10.01	9.81
	1.68	2.09	1845	115	11.69	11.24
	3.03	3.78	3570	120	13.38	12.40
G4	0	0.00	0	0	12.00	12.00
	0.73	0.76	2995	145	12.76	11.96
	1.3	1.37	4405	125	13.37	12.07
	2.43	2.55	5745	155	14.55	12.70
G5	0	0.00	0	0	13.50	13.50
	0.73	0.84	1330	80	14.34	13.94
	1.23	1.41	1660	160	14.91	14.51
	2.38	2.74	2610	160	16.24	15.54
	3.85	4.43	5255	215	17.93	16.23
	4.23	5.13	6225	115	18.63	16.38
	4,60 (peat)	5.30	8765	235	18.80	7.80
	4,90 (base)	5.65	12050	435	19.15	-1.00
G7	0	0.00	0	0	11.7	11.70
	0.43	0.48	1060	100	12.18	11.93
	1.23	1.38	2020	120	13.08	12.58
	1.93	2.07	2370	80	13.77	12.57
	2.88	3.23	4675	165	14.93	13.63
	3,47 (base)	3.90	8470	140	15.60	6.60

Table: 5.2:
Fluctuations of paleo-lagoon depths for the three platforms. The corrected sample depths were calculated with a correction factor for compaction (GISCHLER 2003). The paleo-water depths represent the difference between the modern water depth and the calculated corrected sample depth. The paleo-lagoon depths were calculated based on the sea-level curve for Belize (GISCHLER & HUDSON 2004) and results of the difference between sea level and sample depths for any respective time interval (see also Figure 4.11 and 4.12).

5.3.3 Water Depth

Each benthic foraminiferal assemblage tolerates a range of possible water depths. The typical shallow-water association of WANTLAND (1975) occurs in water depths of <2.7 m to 46 m on the Belize shelf. BICCHI et al. (2002) explained a positive correlation between water depths and benthic foraminiferal species richness, with an increasing variety of available biotopes. Circulation is also linked to the water depths and to the morphological relief of the lagoon. Shallow water depths and open-sea conditions are better circulated than deeper areas and enclosed water bodies. On the platforms, the correlation coefficient between depths and diversity is negative and exhibits a decreasing diversity with increasing lagoon depths.

Paleo-water depths in the study area were calculated using the sea-level curve for Belize (GISCHLER & HUDSON 2004), which is based on calibrated ages from the coral *Acropora palmata* and basal mangrove peat (Fig. 5.3). The paleo-lagoon depths represent the difference between the sea-level curve and sample depths during the time of deposition (Fig. 5.4). The lagoons were flooded successively during the Holocene transgression (GISCHLER 2003), and the upward growth of the lagoons followed the rise in sea level.

Calculated water depths increased in the early Holocene, reached its maximum values in all lagoonal platforms around 4,500 - 6,000 years BP, and continued to shallow slightly up to the present day (Fig. 5.4). The Turneffe Islands show the highest decrease in the paleo-lagoon depths (from 0.9 m in core T5 to 5 m in core T6) during the last 4,380 years; Glovers Reef indicates an intermediate paleo-lagoon decrease (from 0.7 m in G4 to 2.9 m in G5) during the past 6,225 years, and Lighthouse Reef has the lowest decrease (from 1.7 m in L6 to 2.5 m in L5) during the last 4,690 years BP (Tab. 5.2).

The calculated maximum paleo-water depths range from 7.84 m for the Turneffe Islands, to 10.97 m at Lighthouse Reef, and show the highest depths of 16.38 m at Glovers Reef (Tab. 5.2). In general, the benthic foraminiferal assemblages of the deepest lagoon (Glovers Reef), exhibit the lowest species diversity (H' = 2.88), and the Turneffe Islands exhibit the highest diversity (H' = 3.31), even though it has the shallowest lagoon. This observation contradicts the suggestion of BICCHI et al. (2002). The relationship between the benthic foraminifereal diversity and the lagoonal depths indicate a negative correlation for Turneffe Islands (R^2 = 0.1184; p>0.005; Fig. 5.5b) and Glovers Reef (R^2 = 0.2171, p>0.005; Fig. 5.5d). An increase in species richness with increasing water depths, as described by BICCHI et al. (2002) was only found at Lighthouse Reef (Fig. 5.5c), however the correlation is statistically not significant (R^2 = 0.0416; p>0.005). The negative correlation between diversity and lagoon depths, as described for Turneffe Islands and Glovers Reef, could be caused by the different light conditions between the platforms, which affect the composition of the benthic foraminiferal assemblages. At the Turneffe Islands, the dense mangrove growth, and at Glovers Reef, the fine sediment material in the water column, presumably decreases the light intensity in both deep lagoon regions. The diversity at the Turneffe Islands and Glovers Reef reaches higher values in shallower

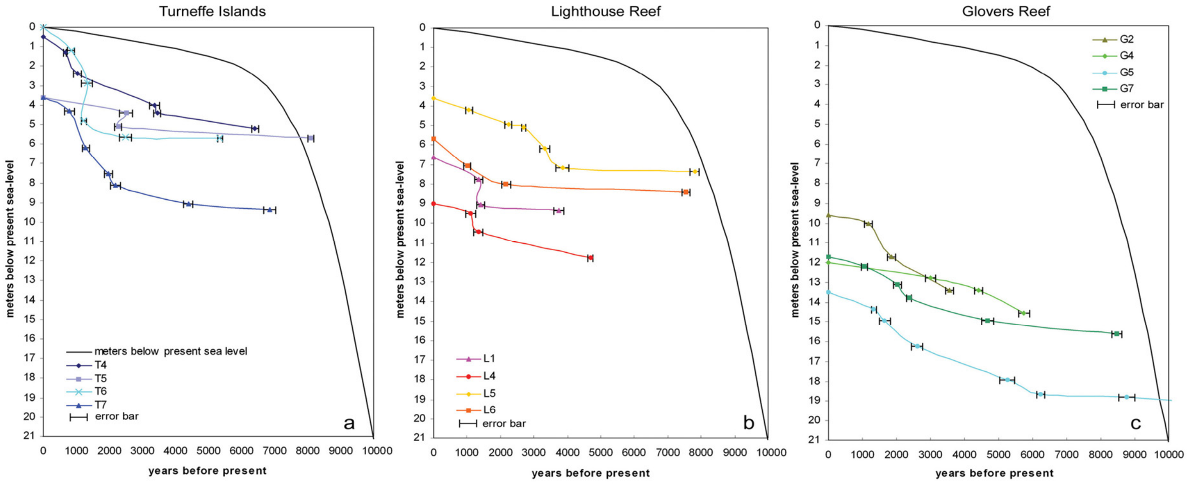


Figure 5.3:
Sea-level curve of GISCHLER & HUDSON (2004) and calculated paleo-water depths of each vibracore at the a) Turneffe Islands b) Lighthouse Reef c) Glovers Reef.

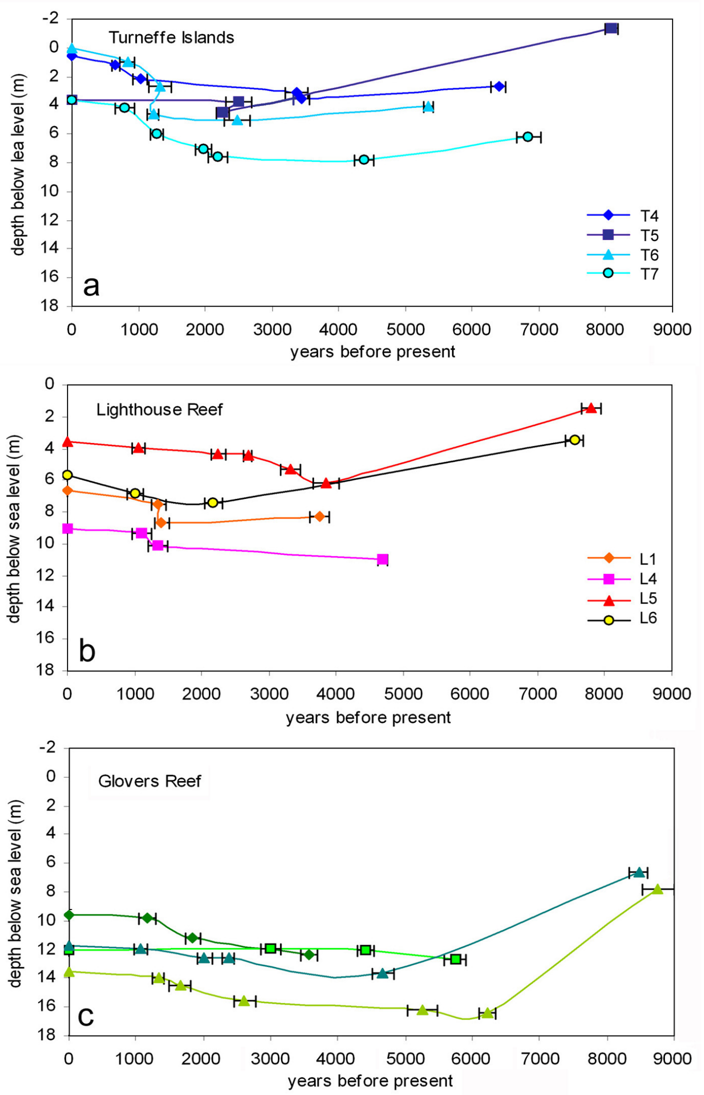


Figure 5.4:
The paleo-lagoon depths for Turneffe Islands (a), Lighthouse Reef (b), and Glovers Reef (c) represent the difference between the paleo sea-level (Fig. 5.3) and the sample depth of the respective age of deposition.

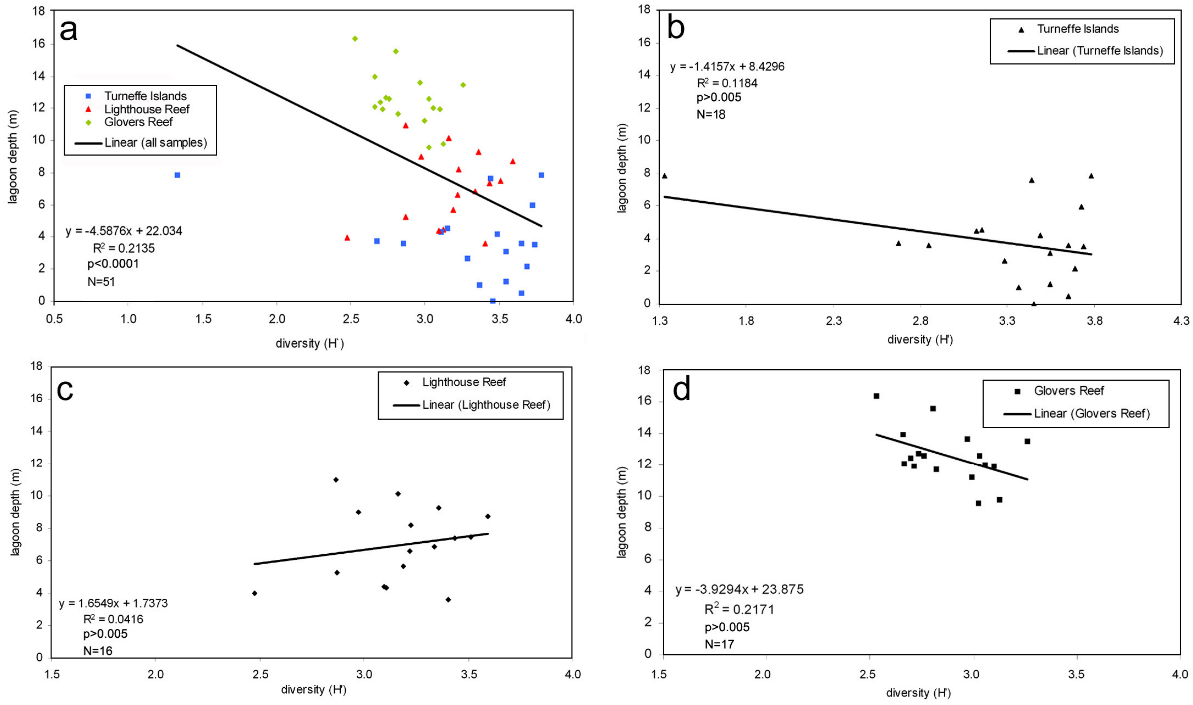


Figure 5.5:
a) Comparison of diversity (H') and lagoonal depths (m) of all samples shows a negative correlation ($R^2 = 0.3264$; $p<0.0001$). The black line indicates a diversity decrease with increasing lagoon depths. b) Diversity at the Turneffe Islands shows decreasing diversity with increasing water depths, also c) Lighthouse Reef indicates increasing diversities with increasing lagoon depths and the samples of d) Glovers Reef exhibits decreasing diversities with increasing lagoon depths.

lagoons where greater light intensity is assumed. Lighthouse Reef could reach higher species diversity despite the greater lagoon depths (of max. 11 m). Due to coarser sediment material, the water is clear and the light intensity is high. At greater lagoon depths the circulation is decreased which are optimal conditions for high diverse symbiont-bearing foraminiferal assemblages such as the *Archaias angulatus*-Miliolid Assemblage.

The investigation of the lagoon sub-divisions exhibit detailed information of the relationship between species diversity and changes of paleo-water depths during the last 6,000 years (Figs. 4.3 - 4.5). The temporal development of benthic foraminiferal assemblages seems to be partly related to changes on water depths. The marginal (cores T4, T6) and interior parts (T5, T7) of the Turneffe Islands differ in their relationship between paleo-water depths and benthic foraminiferal diversity. The shallow paleo-lagoon depths in the marginal area, fluctuate (T6) or decrease (T4) from 4.1 - 0 m during the last 5,343 years (Fig. 4.3).Despite this high decrease of the paleo-lagoon depths, the marginal part of the Turneffe Islands was inhabited only of the High-Diversity Miliolid Assemblage during the past 5,343 years. The species diversity is permanently high and fluctuates slightly in the marginal area. This observation implies an efficient adaptation potential of the species living in this highly diverse assemblage to slight environmental changes. The paleo-lagoon depths in the interior area of the Turneffe Islands remain constant (T5: 3.7 - 3.6 m) or decrease (T7: 7.8 - 3.6 m) during the last 4,380 years. Core T5 also exhibits only one assemblage (*Cribroelhidium poeyanum-Elphidium*-Dominant) with constant paleo-lagoon depths and constant species diversity during the last 2,500 years. Core T7 shows three assemblages, increasing species diversity and decreasing paleo-lagoon depths during the last 4,380 years. The highest paleo-lagoonal depth in T7 exhibits the lowest species diversity. The species diversity does not only depend on changes in water depths. This suggests that other environmental conditions have a greater influence on changes in the benthic foraminiferal diversity. Differences such as those between cores T6 and T7 support this assumption. Core T6 indicates no change in diversity but high decreasing paleo-lagoon depths. However, core T7 shows a high diversity increase with similar decreasing water depths. Further environmental conditions such as water circulation and sea-water exchange depend on water depths. Additional to the shallow water depths and the existence of possible channels in the marginal parts (T4, T6) of the Turneffe Islands, a higher water circulation than in interior areas is probable and could have produced such a highly diverse assemblage.

Lighthouse Reef is divided into deeper (cores L1, L4) and shallower parts (L5, L6; Fig. 4.4). The deeper paleo-lagoon parts indicate a decrease from 8.2 to 6.6 m (L1) and 11 to 9.0 m (L4), whereas the shallower areas decrease from 6.1 to 3.6 m (L5) and 7.4 to 5.7 m (L6) during the last 4,690 years. The paleo-lagoon depths decrease constantly to a minimum of 2.5 m in all regions at Lighthouse Reef. Despite these consistent decreasing paleo-lagoon depths, a partly related correlation between foraminiferal diversity and water depth was observed. According to BICCHI et al. (2002), in core L1, the species diversity increased with increasing water depths from 3,750 - 1,405 years BP, and core L6 indicate decreasing diversity with decreasing water depths. However, in cores L4 and L5 the species diversity increased with decreasing paleo-lagoon depths during the last 3,850 years. Lighthouse Reef contains two assemblages (*Archaias angulatus*-Miliolid Assemblage and Low-Diversity Miliolid Assemblage; Fig. 4.4). The *Archaias angulatus*-Miliolid Assemblage inhabits the lagoon of the Lighthouse Reef at its deepest and shallowest water depths (3.6 - 11 m), and the Low-Diversity Miliolid Assemblage is also present at greater and shallower depths (4.3 - 10.2 m). Both assemblages are typical for shallow lagoons, however *A. angulatus* indicates lower wave activity influenced environments (MURRAY 1991). The occurrence of the Low-Diversity Miliolid Assemblage suggests better water circulation. The occurrence of the taxa *Homotrema* and *Textulariacea* in the Low-Diversity Miliolid Assemblage could be an indication for stormy events and a transport from high-energy platform margins into the interior region. The benthic foraminiferal diversity at Lighthouse Reef seems to be also influenced by changes in water circulation and greater mixing with ambient seawater as well as changes in water depths.

Glovers Reef has shallow marginal (core G2) and deeper interior (G4, G5, G7) parts (Fig. 4.5). All regions of Glovers Reef indicate fluctuating but increasing benthic foraminiferal diversity with constantly decreasing water depths. The shallow margin (G2) exhibits decreasing paleo-lagoon depths from 12.4 to 9.6 m during the past 3,570 years. The interior part shows decreasing paleo-lagoonal depths from 12.7 to 12.0 m (G4), 16.3 to 13.5 m (G5) and 13.8 to 11.7 m (G7) during the past 6,225 years. The Mixed Assemblage occurs in all cores at Glovers Reef during the last 5,745 years. However, core G5 exhibits one additional assemblage. Only the oldest sample of Glovers Reef (at 6,225 years BP) consists of the *Quinqueloculina-Triloculina-Peneroplis* Assemblage. This assemblage occurs at the greatest lagoonal depths of 16.3 m in core G5 and indicates the lowest species diversity for Glovers Reef. This is in contradiction to the suggestion of BICCHI et al. (2002) of increasing species richness with increasing water depths. The water depths at Glovers Reef indicate a lower influence on the benthic foraminiferal diversity. The environmental conditions of the assemblages seem to be similar for greater and shallower lagoonal depths at Glovers Reef during the past 6,225 years. However, changing water circulation seems to have also a lower influence on the benthic foraminiferal assemblages, as Glovers Reef lies in the Trade Wind Belt. Despite greater water depths and a higher exchange of ambient seawater, no significant change of the benthic foraminiferal assemblages was found at Glovers Reef. For example, core G2 is positioned close to the reef margin but nevertheless, no difference in the species distribution was observed in samples of higher or lower water energy at Glovers Reef.

5.3.4 Substrate and “Modes of Life”

Substrate is a crucial factor to characterize ecological living conditions of benthic foraminifera (e.g. HOTTINGER 1983, HALLOCK 1984, MURRAY 1991). Each lagoon shows a characteristic type of sediment content. The substrate of the Turneffe Islands has fine, darkly-stained, bottom sediment with a high abundance of *Halimeda* fragments. Sediments of the Lighthouse Reef are characterized by coarser grain sizes with generally lighter colours, and Glovers Reef consists of light-coloured sediments with finer grain sizes (Chapter 3.2.1). For the foraminiferal distribution, the relationship of sediment material, grain-size and oxygen content can be of particular importance.

Fine substrates (e.g. silt and clay) with small pore spaces usually contain abundant bacteria and are often rich in organic debris. Such substrates are attractive for thin-shelled, delicate and elongate species and support large populations. Coarser substrates (e.g. sand and gravel) with larger pore spaces contain less nutrients and smaller populations. The foraminifera, which inhabit this substrate, may be thicker-shelled, heavily ornamented and bi-convex to fusiform in shape. Foraminifera which prefer hard substrate (i.g. rock, shell, algae, seagrass) live attached with the lower surface and include discoidal, annular, flabelliform, concavo-convex, plano-convex, dendritic, irregular and thin in shape (MURRAY 1991).

Foraminifera live as encrusters, periphyton (free-living on algae or seagrass) in, or on the sediment surface. Encrusters and periphyton (epifauna) are most common in higher energy environments, whereas sediment dwellers (infauna) dominate in lower energy conditions (HALLOCK & GLENN 1986). Infaunal foraminifera live in the upper few centimeters of the sediment (BOLTOVSKOY 1966, CORLISS 1985). They become more abundant under low-oxygen conditions (e.g. BERNHARD 1989, KAIHO 1999), because epifaunal taxa are less resistant to low-oxygen stress (JORISSEN et al. 1995). MURRAY (1991) suggests, that a high number of infaunal living species indicates eutrophic conditions with low oxygen contents in the bottom waters, and a preference for muddy sediments. Epifaunal foraminifera live attached to plants, muddy to coarser sediments or hard substrate and indicate high water circulation and meso- to oligotrophic nutrient supply (JORISSEN et al. 1995).

Infaunal-dominated assemblages occur at the Turneffe Islands (70 - 85%), in water depths of 4 – 8 m, in the interior lagoons (T5 and T7, Fig. 5.6). Common infauna taxa include *Cribroelphidium poeyanum, Elphidium sagrum, Elphidium advenum, Ammonia beccarii, Cellanthus gunteri, Fursenkoina* spp., *Nonion despressulum, Bolivina* spp. and *Uvigeria* spp.

Epifaunal-dominated assemblages are present in all cores of the Lighthouse Reef with maximum values between 60 - 85%, in water depths from 2 - 12 m. The Turneffe Islands shows epifaunal dwellers from 70 - 80% in cores of the marginal area (T4 and T6), and from 70 - 85% in the interior (T7) during the last 2,000 years. Common epifauna species are, amongst others: *Archaias angulatus*, *Miliolinella labiosa, Peneroplis* spp., *Discorbis* spp., *Rosalina* spp., *Neoconorbina* spp., *Planorbulina* spp., *Homotrema* spp. and *Cibicides* spp. Glovers Reef exhibits an intermediate number of epifaunal species, ranging from 50 - 70% at water depth of 10 - 16 m, and a relative high appearance of infaunal foraminifera (from 25 - 40%) in all cores during the last 6,000 years.

Infaunal-dwelling taxa are more common in Holocene sediments of the Turneffe Islands and Glovers Reef due to their finer sediment and a lower exchange of ambient seawater. The Turneffe Islands are surrounded by a restricted mangrove rim and Glovers Reef shows the highest lagoonal depths. Highest abundances of infaunal living species were found in the southern and northern interior lagoon at the Turneffe Islands, in cores T5 and T7. Whereas in the southern lagoon (T5), continuously high values of infaunal species occur, which could indicate lower-energy environments and/or lower oxygen conditions; the northern interior lagoon of the Turneffe Islands shows a distinct decrease of infaunal dwellers since 4,380 years BP. Increasing values of epifaunal sessile species towards modern times could be an indication of higher water circulation. Similar observations were made for molluscs in cores of the Turneffe Islands (HAUSER 2006, limited to core T7). Increasing numbers of shallow endobenthic suspension feeders towards modern times indicate higher “mode of life” conditions. In the marginal areas of the Turneffe Islands, in which higher water circulation is assumed, a lower increase in infaunal species was observed within the channels (T4), whereas the western marginal lagoon (T6) shows slightly fluctuating values for infaunal species. This observation could be an indication of lower bottom-water oxygen conditions for the last 3,445 years within the channels (T4), as well as fluctuating bottom-water oxygen conditions in marginal areas (T6) at the Turneffe Islands during the past 5,345 years.

Lighthouse Reef exhibits the lowest numbers of infaunal-living species. All cores (L1, L4 and L6), excluding core L5 (northern shallower area), show a decrease in the number of infaunal species during the last 4,690 years, which suggests a greater water circulation. The abundance of infaunal dwellers in core L5 increases from 3,850 - 1,060 years BP, and decreases towards modern times. Decreasing oxygen conditions or restricted current-flow intensity could be assumed for core L5 in the shallow lagoon. HAUSER (2006) assumed restricted circulation from 3,850 - 3,320 years BP in core L5 of Lighthouse Reef, due to decreasing chemosymbiont bearing molluscs. For the timespan 2,240 to 1,060 years BP, HAUSER (2006) suggests better circulation, as indicated by the existence of deep burrowers, attached epifaunal molluscs, and the lack of free-living epifaunal dwellers.

Glovers Reef shows high numbers of infaunal dwellers, which suggests that lower water energy environments existed when compared to the Lighthouse Reef. The infaunal living species decrease slightly during the last 3,570 years in core G2 of the shallow margin. The increase of infaunal species in core G4 (deep southern area) from 5,745 - 2,995 years BP, and core G5 (deep eastern area) from 6,225 - 1,330 years BP, could be an indication of lower-oxygen conditions, due to lower energy environments. The following decrease of present-day infaunal species shows increasing oxygen conditions or greater water circulation, as well as higher values of epifaunal sessile living foraminifera. The comparison to core samples (G5) of molluscs (HAUSER 2006) shows decreasing oxygen conditions from 2,240 - 1,060 years BP, due to an increase of chemosymbiont-bearing species. In core G7 the numbers of infaunal species fluctuates slightly during the last 4,625 years BP and increases in modern samples. This observation indicates fluctuating water circulation and oxygen conditions within the northern part of Glovers Reef.

Symbiont-bearing foraminifera are limited to restricted environmental conditions (MURRAY 1991). High abundances can give an indication of very shallow clear waters, because endosymbionts depend on light intensity and a certain circulation due to their epifaunal sessile live mode (e.g. WANTLAND 1975, DUGUANY & TAYLOR 1978).

Common symbiont-bearing species at the platforms are *Archaias angulatus, Cyclorbiculina compressa, Sorites marginalis Parasorites orbitolitoides, Peneroplis proteus*, *Amphistegina gibbosa* and *Asterigerina carinata*. *Archaias angulatus* occurs in highest abundances of all symbiont-bearing foraminifera at the platforms (Fig. 5.6). The other symbiont-bearing species occur in lower frequencies. They bear various types of symbionts. *Peneroplis* lives in symbiosis with ornamented rhodophytes (red algae). *A. angulatus* includes the green alga *Chlamydomonas hedleyi* (LEE et al. 1974), *C. compressa* bears another green alga *Chlamydomonas provasoli* (LEE et al. 1979), and *P. orbitolitoides* includes dinoflagellate symbionts (PAWLOWSKI et al. 2001). Some species of the genus *Elphidium* seem to bear diatoms for photosynthetic activity, e.g. *E. williamsoni* (LOPEZ 1979).

However, species such as *E. discoidale*, *E. advenum*, *Cribroelphidium poeyanum* do not appear to sequester chloroplasts (BERNHARD & BOWSER 1999).

The abundance of symbiont-bearing foraminifera is lowest at the Turneffe Islands (0 - 15%) and highest at Lighthouse Reef (9 - 33%). Glovers Reef shows percentages of 5 - 32%. A time-dependent trend at the Turneffe Islands is observable, the abundance of symbiont-bearing foraminifera increases slightly between 4,380 - 795 years BP and decreases from 795 to present day. Despite the very shallow lagoon depths at the Turneffe Islands the abundance of symbiont-bearing foraminifera is very low. Possible explanations may be the dense cover of mangroves, which reduce the light intensity. Furthermore, the Turneffe Islands consists of fine sediments and a high nutrient supply which is in suspension in the shallow water. Fine sediment in high suspension cause further light reduction in the water column and therefore decrease the abundance of symbiont-bearing foraminifera. Furthermore, HALLOCK (2000) suggested that when nutrient supplies are high, as in the Turneffe Islands, larger tests of symbiont-bearing foraminifera become increasingly rare and smaller miliolids and rotaliids become increasingly common.

At Lighthouse Reef, the cores L1 and L6 indicate an increase of symbiont-bearing species during the last 3,750 years. Cores L4 and L5 show higher values of symbiont-bearing foraminifera in the oldest and youngest samples, and lower abundances between 1,345 - 1,110 years BP (L4), and at 2,240 years BP (L5). Shallow water depths at Lighthouse Reef and a greater mixing with the ambient seawater indicate ideal life conditions for symbiont-bearing foraminifera. Despite high water turbulence, the seawater at Lighthouse Reef is clear due to coarser grain size, which is less affected by suspension load and leads to high abundances of larger symbiont-bearing foraminifera. The slight decrease of symbiont-bearing species in cores L4 and L5 between 2,240 – 1,110 years BP could be an indication of an increased nutrient supply caused by storms or higher wave energy, as the northern part of Lighthouse Reef, in which both cores are positioned, is possibly more affected by turbulent waters compared to southern parts of the platform.

At Glovers Reef (cores G2, G4 and G7), the oldest and modern samples exhibit higher values of symbiont-bearing foraminifera, than samples of intermediate ages, which is similar to observations at Lighthouse Reef. Core G5 shows a constant decrease of symbiont-bearing species during the last 6,000 years. Despite the presence of the fine sediment and lower plant cover, high abundances of symbiontic foraminifera occur at Glovers Reef compared to the Turneffe Islands. This observation could possible be due to greater lagoon depths, which are lower influenced by suspension compared to Lighthouse Reef. The light intensity seems to be sufficient for the symbionts of the larger foraminifera in the deep lagoon at Glovers Reef.

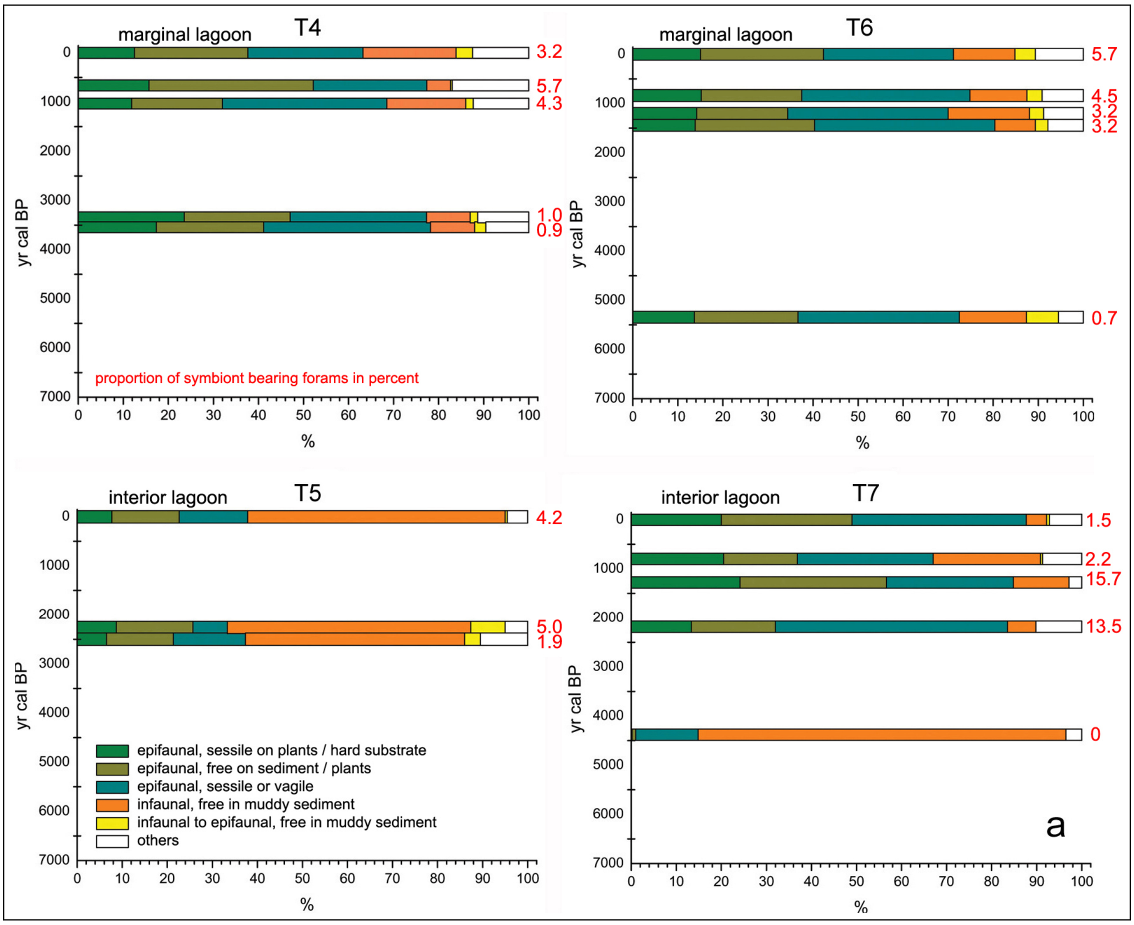


Figure 5.6:
Life modes of benthic foraminifera in (a) Turneffe Islands, (b) Lighthouse Reef, and (c) Glovers Reef. Infaunal dominated taxa prefer interior lagoons at the Turneffe Islands (T5, T7 505/510); epifaunal taxa prefer the marginal areas of the Turneffe Islands (T4, T6, T7), and all investigated areas at Lighthouse Reef. Epifaunal and infaunal benthic foraminifera Glover Reef was inhabited of both “mode of life”-types. The abundances in percentage, of symbiont-bearing foraminifera, are listed for the respective sample.

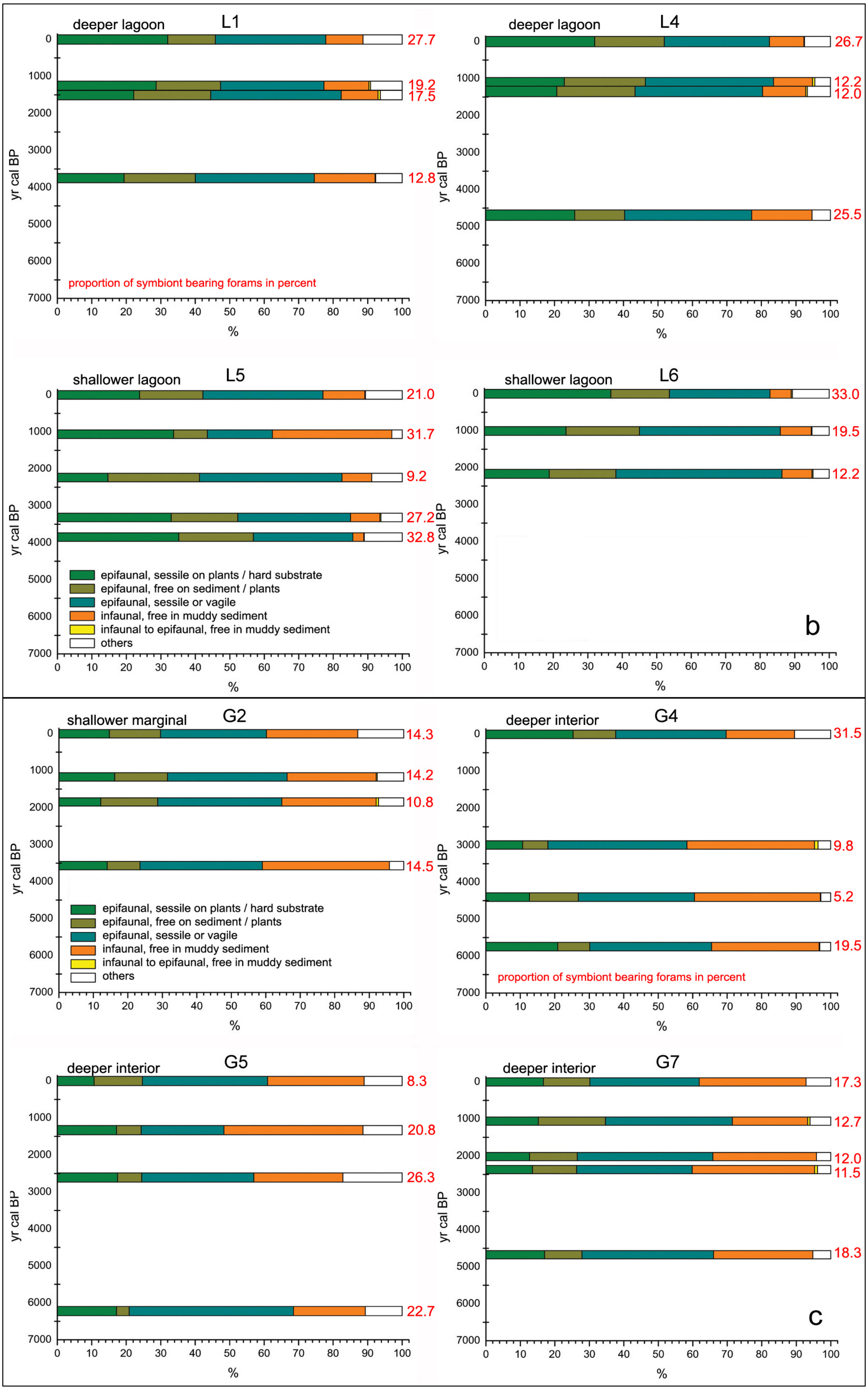


Figure 5.6 continued.

5.3.5 Sedimentation Rates and Bioturbation

The sediment accumulation of atolls is controlled by different factors which include; carbonate production within the lagoons (e.g. CHAVE et al. 1972, SCOFFIN et al. 1980), sea-level changes, topography and currents. These cause the windward sediment supply towards lagoon interior, and mud export over the leeward margins. The diversity of a habitat can be influenced by increasing sedimentation rates, also known as time-averaging (EKDALE 1977). Higher sedimentation rates could cause lower foraminiferal diversity, due to shorter residence time of infaunal or epifaunal dwellers at the sediment surface.

The Turneffe Islands exhibit the highest mean sedimentation rates for all the investigated cores (0.72 m/kyr), followed by Glovers (0.59 m/kyr) and Lighthouse Reef (0.54 m/kyr). The high sedimentation rates at the Turneffe Islands are caused by the high abundance of *Halimeda* fragments in the sediment and due to the presence of dense mangrove rims, which potentially prevent sediment export.

Sedimentation rates of individual cores were calculated from sediment thickness and samples ages (in m/kyr; Figs. 3.2 - 3.4). High sedimentation rates were observed in cores T6 (1.07), T7 (0.83), T4 (0.75), L1 (0.73), L4 (0.61), and G2 (1.05). Low values occurred in cores T5 (0.26), L5 (0.49), L6 (0.36), G4 (0.39), G5 (0.47), and G7 (0.46). However, the results reveal higher foraminiferal diversities in cores of higher sedimentation rates (Fig. 5.7). Due to the observation that core T6 exhibits the highest sedimentation rate, as well as the highest benthic foraminiferal diversity, it suggests, that the benthic foraminifera assemblages are well adapted to high sediment supply in the lagoons. Time-averaging does not appear to be of importance for diversity and abundance of benthic foraminifera.

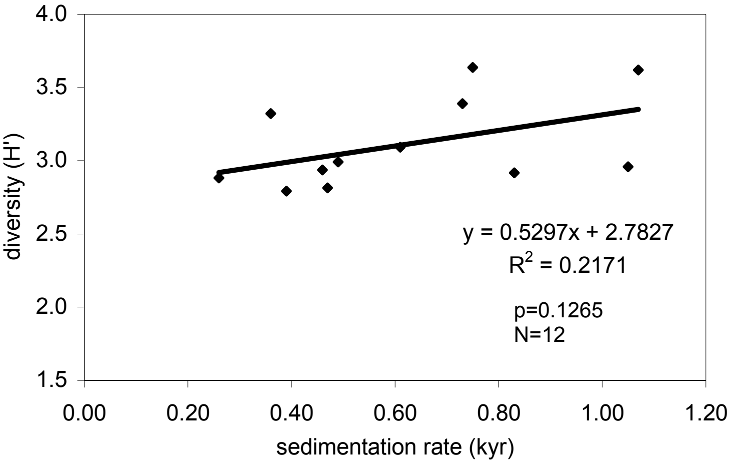


Figure 5.7:
Relationship between sedimentation rate and diversity shows a correlation of p = 0.1265, R^2 = 0.2171, N = 12. The diversity increases with increasing sedimentation rates in individual cores.

Another factor, which could modify species diversity is bioturbation. Recent burrowers are among others polychaeta, bivalves and shrimps. Burrowing organisms actively disrupt the subsurface sediment in their search for food and shelter. For example, the shrimp *Callianassa* feeds directly on the sediment, and receives nutrition from collected debris, as well as from the foraminifera and algae which live on the walls of the burrow (ABED-NAVANDI et al. 2005). *Callianassa* pumps out fine sediment from their burrows, which may be up to 2 m deep. This fine sediment goes in suspension and may be transported away by prevailing currents (ROBERTS et al. 1981) or remains as a cone on the sea floor. The coarser sediment can be stacked by *Callianassa* in chambers deep in its burrow system (TUDHOPE & SCOFFIN 1984). This results in the production of a fine grained, well sorted, surface layer above a poorly sorted, coarser sub-surface deposit. Beyond that time-averaging effect may occur due to sediment mixing. The time-averaging of the foraminiferal assemblage increases when reworking is deeper and the sedimentation rate is lower (SCOFFIN 1992). Due to increase bioturbation activity and high sedimentation rates in the lagoons off Belize, time-averaging can not be excluded. However, only two of the 51 samples exhibit a reverse chronology on the basis of radiocarbon dating (Fig. 3.2, T5 and T6). Thus, time-averaging due to bioturbation seems to have no significant influence on the benthic foraminiferal diversity in the lagoons and thus can be ignored.

5.3.6 Bottom-Water Temperature, Salinity and Photosynthetic Activity

Present-day measurements of bottom-water temperature and salinity in the three lagoons are a first approximation of the variability of both parameters in the Holocene period (GISCHLER et al. 2003). Present-day temperature and salinity values reflect highest seasonal ranges at the Turneffe Islands (21.7°-31.8°C, ΔT=10.1°C, 34.2-42.5‰, ΔS=8.0‰), lowest at Glovers Reef (23.5°-30.4°C, ΔT=6.9°C, 38.6-42.0‰, ΔS=3.4‰; Tab. 2.1) and intermediate at Lighthouse Reef (23.1°-31.3°C, ΔT=7.4°C, 37.7-41.7‰, ΔS=3.9‰). In addition to other environmental factors, modern foraminiferal assemblages seem to be dependent on bottom-water temperature where they live (Chapter 2.2). The water temperature in the lagoons is linked to the water depth and the exchange with ambient seawater. Changes in salinity of the lagoonal waters are associated with evaporation, precipitation and also ambient sea-water mixing.

The $\delta^{18}O$ and $\delta^{13}C$ values of benthic foraminifera were used to calculate Holocene water temperature trends or photosynthetic activity for the lagoons at Lighthouse and Glovers Reefs. The comparison of mean variations in $\delta^{18}O$ and $\delta^{13}C$ signals of single *A. angulatus* tests and the sample ages exhibits distinctive changes during the last 6,000 years (Fig. 4.10); Average $\delta^{18}O$ values become heavier (by 0.4‰) with increasing age (Fig. 4.10a), which corresponds to a 2°C decrease in water temperature during the last 6,000 years, ignoring salinity or evaporation effects. The decreasing paleo-water temperatures in the lagoons of Lighthouse and Glovers Reefs can be explained by increasing water depths during the last 6,000 years (Fig. 5.4). However, previously published climatic models in the Caribbean region (e.g. HODELL et al. 1991, LEYDEN et al. 1994 and HIGUERA-GUNDY et al. 1999), show a trend towards wetter conditions or higher temperatures with increasing age in the same time period.

The mean $\delta^{13}C$ values exhibit a trend towards lighter values with increasing age (Fig. 4.10b). Lighter $\delta^{13}C$ values are related to a higher rate of photosynthetic activity in symbiont-bearing organisms (EREZ 1978). Photosynthetic foraminifera in seawater are enriched in ^{12}C relative to atmospheric CO_2 because ^{12}C is incorporated into organic tissue during the photosynthetic reaction. The increase in $\delta^{13}C$ values to the present day could be interpreted by decreasing photosynthetic activity in the lagoons. From 1,000 years BP to present day, $\delta^{13}C$ decreases by 0.5‰. One possible explanation may be the dilution of atmospheric $^{14}CO_2$ concentration by large amounts of fossil-fuel derived CO_2, which is depleted in ^{13}C and does not contain any ^{14}C. This is commonly called the "Suess Effect" (SUESS 1955). During photosynthetic activity plants incorporate ^{12}C and ^{14}C; ^{13}C is depleted relative to atmosperic CO_2. After dying the carbon exchange stops and the radioactive decay depletes ^{14}C with a half-live of 5,730 years. Therefore, the carbon from fossil fuels which is returned to the atmosphere through combustion is depleted in ^{13}C and ^{14}C compared to atmospheric CO_2. The carbon composition of foraminifera shells become lighter. This so called "Anthropogenic Effect" was also found in modern coral skeletons in Belize (GISCHLER & OSCHMANN 2005), as well as in modern Caribbean sclerosponges (BÖHM et al. 1996).

The relationship between calculated paleo-lagoon depths and $\delta^{18}O$ as well as $\delta^{13}C$ signals indicates following trends: The mean $\delta^{18}O$ becomes heavier with increasing paleo-lagoon depths (Fig. 4.11a), which is comparable to other studies (BUCHARDT & HANSEN 1977, WILLIAMS et al. 1981, ZIMMERMAN et al. 1983, LANGER 1995). These authors also noted the positive correlation between $\delta^{18}O$ and depth as a result of the "vital effect"; Foraminifera in elevated light intensities exhibited a depletion of heavier isotopes. MCCONNAUGHEY (1989) and STANLEY & SWART 1995 found that photosynthetic activity has no direct effect on the ^{18}O fractionation ("kinetic effect"), but affects the $\delta^{13}C$ ("metabolic effect"). Lighter $\delta^{18}O$ are commonly used to identity warmer temperatures, whereas heavier $\delta^{18}O$ indicate cooler temperatures. In this study the $\delta^{18}O$ increases with increasing water depths, which is plausible and refers to higher temperatures in shallower water depths. Likewise, the mean $\delta^{13}C$ shows a trend to lighter values with increasing water depths (Fig. 4.11b). This can be an indication of higher photosynthetic activity in deeper lagoons. This observation is somewhat surprising as higher photosynthesis is commonly expected in shallower water depths. However, symbiont-bearing foraminifera (e.g. *A. angulatus*) occur in high abundances at the Lighthouse and Glovers Reefs compared to lower abundances at the Turneffe Islands and supports the observation for higher photosynthetic rates in deep lagoons.

The oxygen and carbon isotopes reveal differences between the diversity values. A tendency to lighter $\delta^{18}O$ and heavier $\delta^{13}C$ values with increasing species diversity was observed (Fig. 4.12).

According to this observation, a higher species diversity occurs in warmer waters, and the photosynthetic activity seems to be higher in low diversity habitats in the lagoons. Four of the seven assemblages were investigated with regard to stable isotope analyses. The Low-Diversity Miliolid Assemblage indicates slightly lighter $\delta^{18}O$ values than other communities (Fig. 4.13), and the $\delta^{13}C$ signals are slightly heavier. The difference between both $\delta^{18}O$ and $\delta^{13}C$ values compared to other assemblages is rather low and reveals mean values of approximately <0.5‰. The temperature dependence between the observed assemblages seems to be low, but could be an indication, that the Low-Diversity Miliolid Assemblage prefers warmer waters compared to the *Archaias angulatus* Miliolid, the Mixed, and the *Quinqueloculina-Triloculina-Peneroplis* Assemblages. Heavier $\delta^{13}C$ values of the Low-Diversity Miliolid Assemblage are plausible, as this assemblage contains less symbiont-bearing species which perform photosynthetic activity.

5.3.6.1 Mean BW-Temperature Trend during the Holocene Lagoons

The Holocene bottom-water temperatures of the platforms were reconstructed by mean subsampled $\delta^{18}O$ records of *A. angulatus*. High resolution reconstructions of Caribbean climate based on the $\delta^{18}O$ of ostracode shells (HODELL et al. 1991) and pollen analyses (HIGUERA-GUNDY et al. 1999) from lake Miragoane in Haiti. These autors suggested that the middle Holocene (7.0 - 3.2 kyr BP) was characterized by higher lake levels due to low ratios of evaporation to precipitation (wet times), and decreasing lake levels around 3.2 kyr BP with the onset of a drier climate (colder climate conditions) which prevailed throughout the late Holocene. CURTIS et al. (1996) suggested wet conditions from 3.3 - 1.8 kyr BP, drier conditions from 1.8 - 0.9 kyr BP and again somewhat wetter from 0.9 - 0 kyr BP based on $\delta^{18}O$ of ostracods and gastropods in sediment cores from lake Punta Laguna in Mexico. The BW-temperatures calculated from $\delta^{18}O$ values show the following climate trend at Lighthouse and Glovers Reefs during the last 6,000 years. The mean BW-temperatures calculated for both platforms indicate a different trend compared to previously observed climate models (HODELL et al. 1991, HIGUERA-GUNDY 1999). The BW-temperature trends at Lighthouse and Glovers Reefs are different to each other as well (Fig. 5.8).

At Lighthouse Reef, the BW-temperature reached lowest values, decreasing from ~25.5 to 23.5°C between 4,690 to 3,320 years BP. However, common climate models (e.g. HODELL et al. 1991, HIGUERA-GUNDY et al. 1999) evaluate a small increase in $\delta^{18}O$ values for the middle Holocene (~5,000 to 3,200 years BP) and suggest consistently high lake level, which conforms to warmer temperatures. From 3,320 to 1,345 years BP the paleo-water temperature increased to ~26 - 29°C at Lighthouse Reef and exhibits highest calculated values at 1,345 years BP, which coincides with the suggested wetter conditions of CRAIG et al. (1996) from 3,300 to 1,800 years BP. However, this observation does not agree with the suggested drying conditions of HIGUERA-GUNDY et al. (1999) from 3,200 to 1,700 years BP. From 1,110 to 1,005 years BP the temperature at Lighthouse Reef decreases slightly of between 25.5- 28.5°C. However, HODELL et al. (1991) suggested a brief period of wetter (warmer) conditions from ~1,500 to 900 years BP, which is also similar to conditions during the late Holocene in the Caribbean region (BRADBURY et al. 1981, DEEVEY et al. 1983, LEYDEN 1984, 1985, 1987 and PIPERNO et al. 1990). The calculated BW-temperatures at Lighthouse Reef from present-day formninifera, range from 25.26 - 28.13°C (Tab. 4.2), however, the bottom-water measurements from 2000 - 2001 reach BW-temperatures of between 23.1 - 31.3°C.

The BW-temperature trend at Glovers Reef differs from that observed for Lighthouse Reef. In general, more temperature fluctuations towards warmer and colder conditions were calculated, which occur in closer temperature ranges. About 6,225 years BP, lowest BW-temperatures of ~23°C were calculated for Glovers Reef. However, the data depends on one single $\delta^{18}O$ signal and might not be representative. Higher temperatures of ~24.5 - 28°C were observed 5,745 years BP, which could indicate the "Middle Holocene Climate Optimum", as described above (BRADBURY et al. 1981, DEEVEY et al. 1983, LEYDEN 1984, 1985, 1987, PIPERNO et al. 1990 and HODELL et al. 1991). Lower mean BW-temperatures of ~24 - 26.5°C occur from 4,675 to 4,405 years BP at Glovers Reef. This is comparable to the decreasing temperature trend of suggested Mid-Holocene models with high, but slightly decreasing lake levels of HODELL et al. (1991). Around 3,570 and 2,370 years BP higher mean bottom-water temperatures of between ~26 - 28°C are calculated for Glovers Reef. This fits with the wet conditions that were suggested by CRAIG et al. (1996) between 3,300 to 1,800 years BP, but do not agree with the suggested dryer and/or colder conditions of HODELL et al. (1991) and HIGUERA-GUNDY (1999). However, interruptions of lower temperatures of between ~25 to 26°C were calculated around 2,995 to 2,610 years BP from $\delta^{18}O$ signals at Glovers Reef. From 2,370 - 1,845 years BP the mean BW-temperatures at Glovers Reef decreased again and reached ~24.5 - 26°C. This is similar to dryer conditions from ~2,400 - 1,500 years BP as suggested by HODELL et al. (1991). The following period of slightly wetter conditions, as explained by the same author, is indicated by slightly higher mean BW-temperatures at Glovers Reef from 1,170 - 1.060 years BP. However, the variation of calculated BW-temperatures at Glovers Reef was very broad of between ~23 - 28°C. A slightly increasing mean BW-temperature of ~24.77 - 26.37°C (Tab. 4.2) was calculated from $\delta^{18}O$ values of present-day foraminifera. However, the bottom-water temperature measured from 2000 – 2001, range from 23.5 - 30.4°C at Glovers Reef.

In contrast to this study, proxies for indicating changes in the Caribbean climate, show a trend of warmer or wetter conditions in the mid-Holocene, and colder and drier conditions in the early Holocene HODELL et al. (1991), HIGUERA-GUNDY (1999). The different BW-temperature values and trends in both lagoons seem to reflect local climate variations during the past 6,000 years. Lighthouse Reef exhibits stronger temperature ranges within shorter time period than these observed at Glovers Reef. These observed conditions possibly had existed, due to shallower water depths at Lighthouse Reef, which are more affected by changes in water temperatures compared to deeper waters at Glovers Reef.

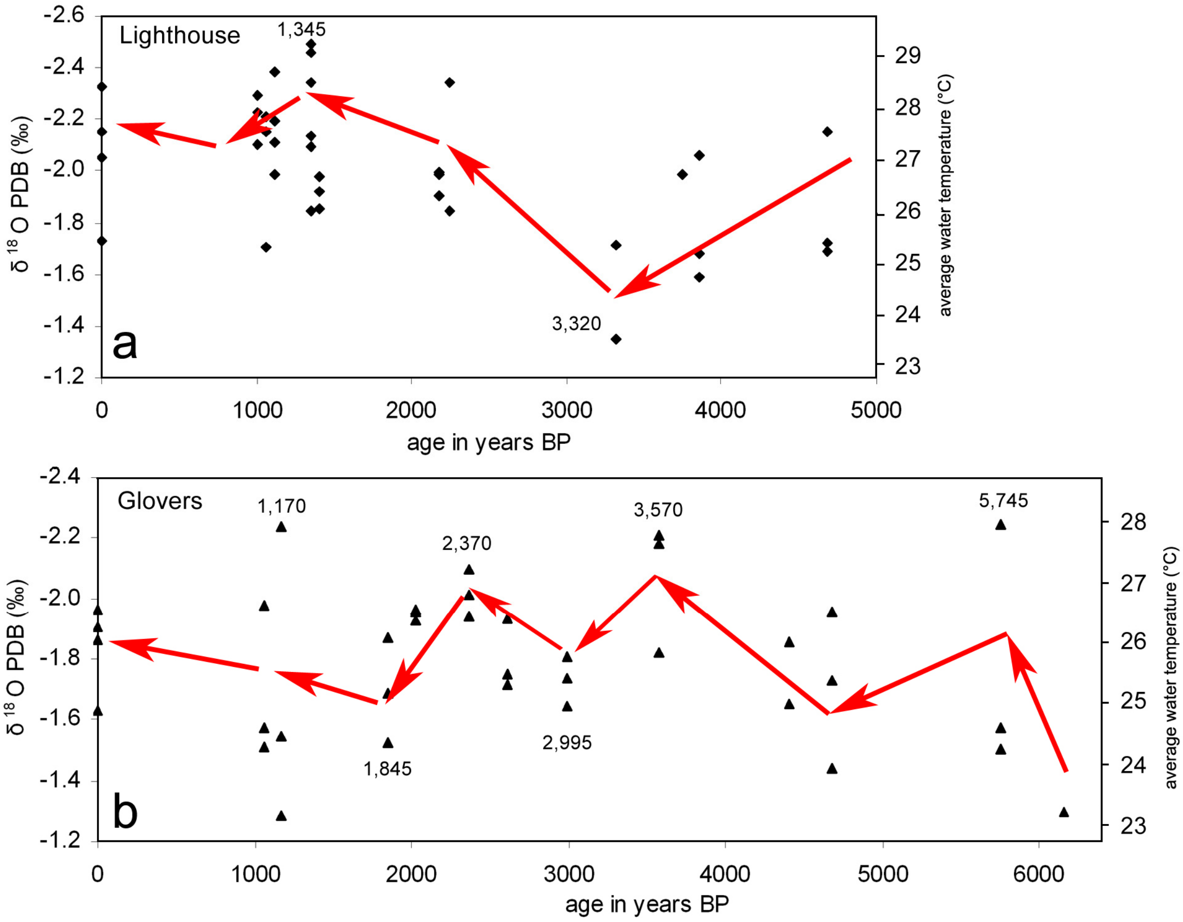


Figure 5.8:
Average δ^{18}O values for all *A. angulatus* specimens and reconstructed mean BW-temperatures (after Shackleton 1974) versus age in years BP at a) Lighthouse Reef and b) Glovers Reef. The lagoons exhibit different trends (red arrows): Lighthouse Reef exhibits decreasing temperatures from 4,690 to 3,320 years BP, and increasing water temperatures from 3,320 to 1,345 years BP. Glovers Reef shows more temperature fluctuations during the last 6,225 years; Higher temperatures were calculated at 5,745, 3,570 and 2,370 years BP. Lower temperatures were calculated at 6,225, 4,695, 2,995 and 1,845 years BP. Both lagoons show slightly increasing temperatures toward the present day.

5.3.6.2 Seasonal BW-Temperature Variations in the Holocene Lagoons

The seasonal oxygen and carbon isotopes obtained in this study indicate some comparable trends to previously published results on symbiont-bearing larger foraminifera (Wefer et al. 1981, Luz et al. 1983 and Wefer & Berger 1991). These authors suggested first seasonal variations of stable isotopes of larger miliolid foraminifera and found that the δ^{18}O values followed the annual water-temperature cycle, whereas δ^{13}C contains the life-history stages. The δ^{18}O values in this study (of *A. angulatus*) show similar seasonal fluctuations to other larger miliolid species (e.g. *M. vertebralis* and *C. compressa*). In contrast to this study, however, the observed δ^{18}O of *A. angulatus* from Wefer et al. (1981) became lighter during life, which corresponds to one to one-and-a-half year. Our seasonal or annual fluctuations in single *A. angulatus* shells reveal lighter δ^{18}O values in the middle of their tests and heavier δ^{18}O values in the proloculus and the marginal areas (Figs. 4.20 and 4.21). This observation indicates annual seasonality in terms of higher bottom-water temperatures in summer and autumn, as well as lower temperatures in spring and winter.

Our seasonal $\delta^{13}C$ values correlate positively with the $\delta^{18}O$ values (Figs. 4.16 and 4.18) and show no tendency towards lighter carbon isotopes with increasing age, as observed in all members of larger miliolids by WEFER et al. (1981). Lighter $\delta^{13}C$ values could be an indication for higher photosynthetic activity of the symbiont-bearing species, e.g. *A. angulatus*, during summer and autumn, due to higher light intensity, as compared to lower light-intensity rates during spring and winter. The $\delta^{18}O$ values seem to be independent of symbiont types and the nature of the microhabit (e.g. MCCONNAUGHEY 1989a, 1989b, STANLEY & SWART 1995 and LANGER 1995). However, the rate of $\delta^{13}C$ during calcification is much more affected by the activity of symbionts and the growth rate due to preferential removal of the lighter ^{12}C. In laboratory studies, *A. angulatus* showed a calcification rate which was two-to-three times higher in a light environment, than in a dark environment (LEE & ZUCKER 1969 and DUGUAY & TAYLOR 1978).

Compared to mean BW-temperature variations (Chapter 5.3.6.1), the seasonal BW-temperature range was used to identify annual maximum and minimum values during the Holocene. In the mid-Holocene, from 4,690 to 3,320 years BP, the calculated mean BW-temperatures, as well as annual BW-temperature ranges are low at Lighthouse Reef. The BW-temperature fluctuates from 22.86 to 29.01°C and indicates a maximum annual range of 6.15°C. In the late Holocene, higher BW-temperature of 20.51 - 31.39°C, as well as broader annual BW-temperature ranges with maximum values of 9.59°C respectively, was calculated at Lighthouse Reef. Measured annual BW-temperatures at Lighthouse Reef in the years 2000 - 2001 fluctuate from 23.1 - 31.3°C, and indicate a maximum annual range of 7.4°C.

In contrast to Lighthouse Reef, Glovers Reef exhibits lower annual BW-temperature ranges and lower BW-temperature fluctuations. In the mid-Holocene, from 6,226 - 3,570 years BP the annual ranges was 6.54°C and bottom-water temperatures reached 22.35 - 29.60°C. Temperatures in the late Holocene range from 22.35 - 28.96°C, and annual temperature ranges reached 6.61°C. Annual bottom-water temperatures from the years 2000 - 2001 vary between 23.5 - 30.4°C, and indicate a maximum annual water-temperature range of 6.9°C.

These differences in BW-temperatures also reflect the individual composition and diversity of the benthic foraminiferal assemblages at Lighthouse and Glovers Reefs. Compared to Lighthouse Reef, data from Glovers Reef indicate lower mean BW-temperature fluctuations and lower annual BW-temperature variabilities during the last 6,000 years (Fig. 5.9). Glovers Reef exhibits constantly decreasing water depths and deep water depths, which causes slightly variations in BW-temperature, salinity and water circulation in the lagoon. These small variations agree with a development of one dominant assemblage during the whole investigated time period of the last 6,000 years at Glovers Reef. Slight changes in calculated annual BW-temperatures ranges, low species diversity and the Mixed Assemblage, which characterize a mixture of displaced shoal fauna and endemic deeper lagoonal benthic foraminiferal species confirm slight environmental changes during the Holocene in the lagoon at Glovers Reef.

Higher mean BW-temperature and annual BW-temperature ranges at Lighthouse Reef fit to high abundances of the *Archaias angulatus*-Miliolid Assemblage, which prefer shallow clear waters. Lighthouse Reef indicates shallower lagoon depths with greater water circulation during the observed time period. The data indicate higher BW-temperature ranges in the last 6,000 years compared to these observed at Glovers Reef. These water-temperature fluctuations seem to have a stronger influence on the benthic foraminiferal assemblage at Lighthouse Reef compared to Glovers Reef. The benthic foraminifera would be more sensitive to environmental change, than these species at greater water depths, observed at Glovers Reef. Low-diversity assemblages occurred alternately, despite similar environmental conditions prevailing. Due to the high variability of $\delta^{18}O$ values during the past 6,000 years, annual water-temperature trends at Lighthouse and Glovers Reefs are not interpretable.

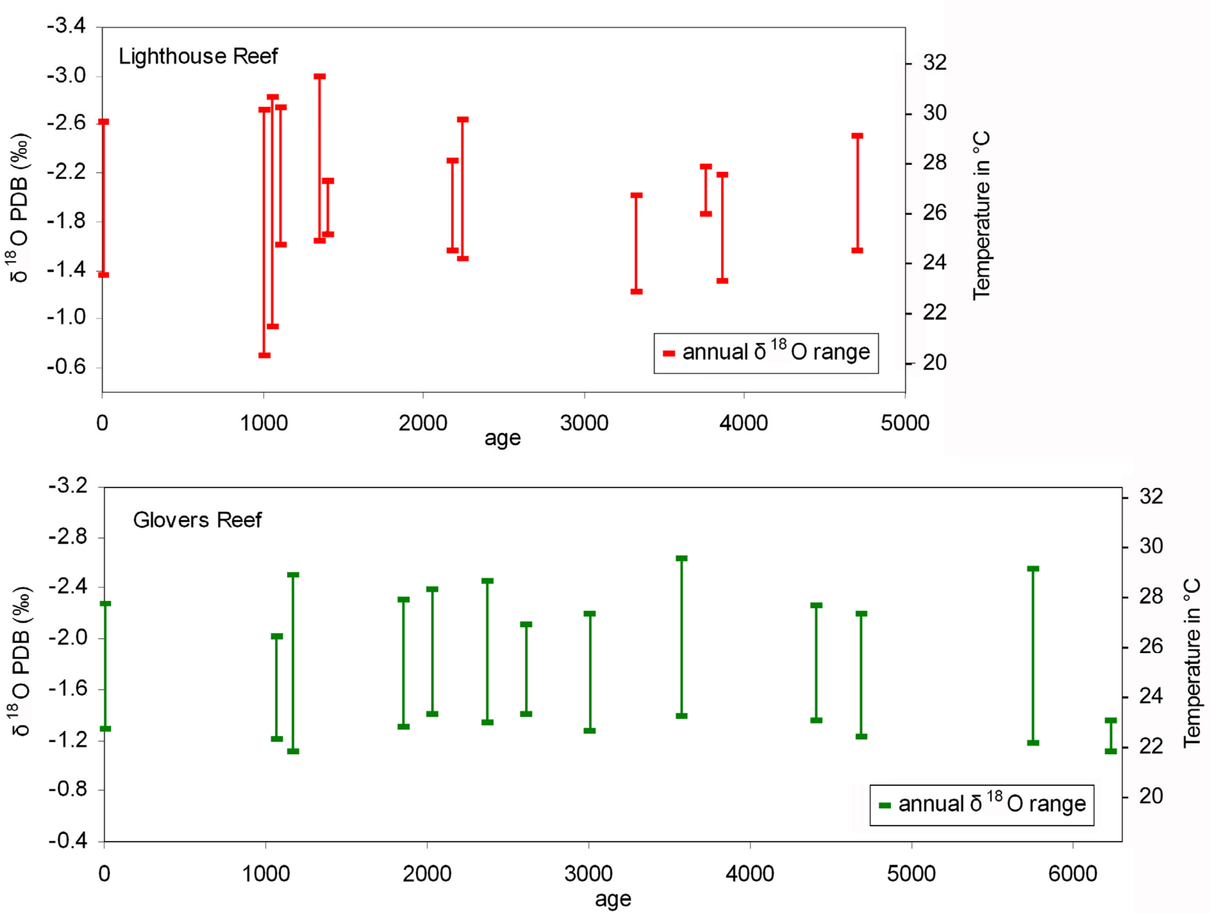


Figure 5.9:
Annual BW-temperature ranges, based on minimum and maximum values of samples during the Holocene. Lighthouse Reef indicates lower annual bottom-water-temperature ranges and lower bottom-water temperatures in the mid-Holocene, and higher annual ranges and temperatures in the late Holocene. Glover Reef shows constantly lower annual bottom-water-temperature ranges and water-temperatures values during the mid-to late Holocene.

Conclusions

Seven Holocene benthic foraminiferal assemblages could be distinguished in lagoonal vibracores from the Caribbean carbonate platforms of the Turneffe Islands, Lighthouse Reef and Glovers Reef. In the cores from the Turneffe Islands four assemblages are recognized and at Lighthouse and Glovers Reefs areas two assemblages can be defined.

In marginal areas of the Turneffe Islands (cores T4 und T6), the High-Diversity Miliolid Assemblage indicates high energy conditions and high salinity ranges which could possibly be an indication of the existence of channels. The open, southern interior lagoon (core T5) of the Turneffe Islands contains the *Cribroelphidium poeyanum-Elphidium*-Dominant Assemblage during the past 2,500 years, indicating lower water salinity and slightly higher water circulation. Three different assemblages in the central restricted lagoon (core T7) of the Turneffe Islands indicate increasing diversity towards present time; The Low-Diversity *Cribroelphidium poeyanum* Assemblage at about 4,380 years BP characterized extreme conditions of low salinity and/or restricted water circulation. The *Quinqueloculina-Triloculina-Peneroplis* and the High-Diversity Miliolid Assemblages represent increasing water circulation during the past 2,185 years. Lighthouse Reef exhibits two benthic foraminiferal assemblages, which are well adapted to both deep and shallow lagoons. The *Archaias angulatus*-Miliolid Assemblage indicates low degrees of water circulation and stable salinity. The Low-Diversity Miliolid Assemblage refers to higher wave energy. These assemblages at the Lighthouse Reef indicate changing conditions of wave activity in the lagoon during the last 6,000 years. Glovers Reef exhibits two assemblages. The Mixed Assemblage is a mixture of shoal derived and deeper lagoonal fauna and represents relatively unchanged conditions during the past 6,000 years. The *Quinqueloculina-Triloculina-Peneroplis* Assemblage occurs in the deepest lagoon and indicates higher water circulation around 6,225 years BP.

Calculated mean values of diversity and richness of the benthic foraminifera are highest at the Turneffe Islands and lowest at Glovers Reef. Single diversity trends during the Holocene are different among the three platforms. Lighthouse and Glovers Reefs exhibit constant diversity, which slightly increases towards present day. The Turneffe Islands show stronger increasing diversity towards present time. Based on biogeographic interpretations, the benthic foraminiferal fauna at Glovers and Lighthouse Reefs could be interpreted as being in a "Diversification Stage", because of slightly increasing diversity values for the time period studied. The fauna at the Turneffe Islands is possibly in a transition period between the "Colonisation" and "Diversification Stages". The benthic foraminiferal diversity and taxonomic composition of the platforms seem to be influenced by water depths, since Glovers Reef with the deepest lagoon, exhibits the lowest mean diversity and richness. The shallowest lagoon at the Turneffe Islands has the highest mean diversity. Diversity and mode of life also depend on the degree of water circulation and substrate texture. Lighthouse Reef has more epifaunal species compared to the Turneffe Islands and Glovers Reef, which is possibly an indication of higher water circulation in Lighthouse Reef during the last 6,000 years. Infaunal foraminifera are more common in finer sediments from the Turneffe Islands and Glovers Reef when compared to the Lighthouse Reef sediment. These observations correspond to a positive correlation between fine substrate and diversity at the Turneffe Islands. Age and size of the lagoons have little influence on foraminiferal diversity, as the oldest platform (Glovers Reef) does not exhibit the highest diversity and the smallest platform (Lighthouse Reef) does not show the lowest diversity.

Calculated $\delta^{18}O$ BW-temperatures correlate positively with increasing paleo-lagoon depth. Diversity and calculated BW-temperature also correlate positively. The $\delta^{13}C$ indicate higher photosynthesis activity in ancient and deeper lagoons. Calculated BW-temperatures are in the range of present-day measured BW-temperatures of the year 2000 - 2001. Based on seasonal $\delta^{18}O$ of *Archaias angulatus*, higher BW-temperatures occur during summer/autumn and lower BW-temperatures in winter/spring. Lighthouse Reef exhibits a maximum calculated annual BW-temperature range of between 20.51 - 31.39°C (ΔT = 10.88°C) during the last 6,000 years. These findings agree with present-day (year 2000 - 2001) BW-temperatures of 23.1 - 31.3°C (ΔT = 8.2°C). Seasonal maximum BW-temperatures from Glovers Reef range from 22.35 - 29.60°C (ΔT = 7.25°C) and correlate with present-day (2000 - 2001) BW-temperatures of 23.5 - 30.4°C (ΔT = 6.9°C). Glovers Reef has lower annual BW-temperature ranges during the past 6,000 years compared to Lighthouse Reef. This difference is reflected by; I) the dominance of one benthic foraminiferal assemblage in Glovers Reef, the Mixed Assemblage, II) high but constant lagoon depths during the last 6,000 years, and III) a slightly increasing foraminiferal diversity which indicates that Glovers Reef is in the "Diversification Stage" of faunal development. Higher BW-temperature fluctuations and ranges occur at Lighthouse Reef; Changing environmental conditions are reflected by; I) the occurrence of two recurring benthic foraminiferal assemblages (*Archaias angulatus* Miliolid and Low-Diversity Miliolid Assemblages), II) shallow lagoon depths during the last 6,000 years, III) high but changing water energy and IV) slightly increasing foraminiferal diversity which classifies Lighthouse Reef also in a "Diversification Stage".

In total, a 2°C BW-temperature increase was calculated for the Lighthouse and Glovers Reefs during the past 6,000 years. This temperature increase does not agree with common Holocene Climate Models (e.g. HODELL et al. 1991) for the Caribbean area. In addition, calculated BW-temperatures at the platforms rather reflect local climate variations, as the calculated BW-temperatures at Lighthouse and Glovers Reefs differ significantly between their trends and ranges.

Zusammenfassung

Anhand von holozänen Sedimentkernen der drei Karbonatplattformen Turneffe Islands, Lighthouse Reef und Glovers Reef, vor der Küste von Belize (Zentralamerika) wurden benthische Foraminiferen-Gesellschaften untersucht. Aufgrund ihrer hohen Anpassungsfähigkeit an bestimmte Lebensräume lassen sich Rückschlüsse auf fossile Umweltbedingungen wie Lagunenalter, Lagunentiefe, Wasserzirkulation, Substrat und Bodenwassertemperatur ziehen. Sieben benthische Foraminiferen-Assoziationen konnten in den Sedimenten der drei Plattformen unterschieden werden. In den Kernen auf Turneffe Islands wurden vier benthische Foraminiferen-Gesellschaften definiert. In den Kernen von Lighthouse und Glovers Reef konnten jeweils zwei Gesellschaften unterschieden werden. Jeweils vier Kerne sind auf die drei Plattformen in den flachen- und tiefen- bzw. randlichen- und inneren Lagunenbereichen verteilt. Turneffe Islands weist in den randlichen Lagunenbereichen (Kerne T4 und T6) innerhalb der letzten 5.345 Jahre eine „High-Diversity Miliolid Gesellschaft“ auf. Ähnlich der heutigen Foraminiferenfauna, deutet diese Gesellschaft auf höhere Wasserbewegung mit höherer Salinität und auf die Existenz von Kanälen hin, die die randlichen Lagunenbereiche von Turneffe Islands durchziehen. In der südlichen Lagune (Kern T5), die teilweise einen Wasseraustausch zum umgebenden Meer zulässt, weist Turneffe Islands während der letzten 2.500 Jahre eine „*Cribroelphidium poeyanum-Elphidium*-Dominant Gesellschaft“ auf. Diese Foraminiferen Assoziation ist charakteristisch für niedrigere Salinität und leicht erhöhte Wasserzirkulation. In der zentralen inneren Lagune (Kern T7) von Turneffe Islands, die heute nur einen begrenzten Wasseraustausch mit dem umgebendem Meerwasser aufweist, entwickelten sich drei verschiedene Gesellschaften innerhalb der letzten 4.380 Jahre. Die Entwicklung dieser Assoziationen verweist auf zunehmende Artendiversität in jüngerer Zeit. Die älteste Foraminiferen-Gesellschaft, die „Low-Diversity *Cribroelphidium poeyanum* Assoziation“ weist darauf hin, dass vor 4.380 Jahren extreme Bedingungen mit niedriger Salinität und/oder eingeschränkter Wasserzirkulation in der inneren Lagune von Turneffe Islands geherrscht haben. Die „*Quinqueloculina-Triloculina-Peneroplis*“- und die „High-Diversity Miliolid Gesellschaften“ deuten auf zunehmende Wasserzirkulation in den letzten 2.185 Jahren in Turneffe Islands hin. Lighthouse Reef besitzt zwei benthische Foraminiferen-Gesellschaften, die beide an tiefere wie auch flachere Wassertiefen angepasst sind. Die „*Archaias angulatus*-Miliolid Gesellschaft“ deutet auf geringere Wasseraktivität, klares Wasser und stabile Salinität hin. Die „Low-Diversity Miliolid Gesellschaft“ verweist in Lighthouse Reef auf erhöhte Wellenenergie. Diese Foraminiferen-Gesellschaften in den Lagunen von Lighthouse Reef deuten auf wechselnde Bedingungen in der Wasseraktivität und wechselnde Diversität während der letzten 6.000 Jahre hin. In den größtenteils tiefen Lagunen von Glovers Reef kommen zwei Foraminiferen-Gesellschaften vor. Die „Mixed Gesellschaft“ ist eine Mischung aus Flachwasserfauna und Arten der tieferen Lagune und repräsentiert relativ unveränderte Bedingungen während der letzten 6.000 Jahre. Der Grad der Salinität und/oder der Wasserzirkulation kann allein durch das Vorkommen dieser

„Mixed Gesellschaft“ nicht eingeschätzt werden. Die Mischung dieser Foraminiferenfaunen lässt vermuten, dass Glovers Reef zumindest teilweise einer höheren Wasseraktivität durch umgebendes Meerwasser ausgesetzt war. Das feine Sediment am Lagunenboden von Glovers Reef deutet dagegen auf geringere Wasserbewegung bzw. Strömung am tieferen (bis zu 16 m) Lagunenboden hin. Vermutlich werden Foraminiferen aus den Randbereichen der Lagune durch die Wellenbewegung in das innere der Lagune transportiert wo sie dann in größere Tiefen absinken und sich mit der Lebendfauna vermischen. Die „*Quinqueloculina-Triloculina-Peneroplis* Gesellschaft“ kommt in der tiefsten Lagune von Glovers Reef vor und deutet auf höhere Wasserzirkulation vor etwa 6.225 Jahren.

Die höchste durchschnittliche Diversität und Artenzahl der benthischen Foraminiferen wurde auf Turneffe Islands berechnet, die niedrigste Diversität auf Glovers Reef. Die drei Plattformen zeigen unterschiedliche Diversitätstrends innerhalb der letzten 6.000 Jahre. Lighthouse Reef und Glovers Reef zeigen konstante Diversitäten mit einem leicht zunehmenden Trend in jüngeren Proben. Turneffe Islands zeigt eine stärker zunehmende Diversität innerhalb der letzen 6.000 Jahre. Aufgrund von biogeographischen Interpretationen könnte sich die Foraminiferenfauna in Glovers und Lighthouse Reef in einem „Diversifikationsstadium“ befinden, da die Diversität in dem untersuchten Zeitabschnitt nur leicht ansteigt. Die Fauna in Turneffe Islands könnte sich zwischen 4.000 und 2.000 Jahren vor heute in einem „Kolonisationsstadium“ befunden haben und in den letzten 2.000 Jahren in ein „Diversifikationsstadium“ übergegangen sein, da die Diversität später langsamer ansteigt. Die durchschnittliche Diversität und Artenzahl der Plattformen zeigt eine negative Abhängigkeit von der Wassertiefe. So weist Glovers Reef die tiefsten Lagunen und die niedrigsten Diversitäten und Artenzahlen auf, während Turneffe Islands die flachsten Lagunen und die höchsten durchschnittlichen Diversitäten zeigt. Die Abhängigkeit zwischen Diversität und Wassertiefe kann auf verschiedene Umweltfaktoren zurückgeführt werden. So sinken mit zunehmender Wassertiefe auch die Lichtintensität und die Wasserzirkulation in den Lagunen. In Turneffe Islands und Glovers Reef sinkt die Diversität mit steigender Wassertiefe vermutlich durch trüberes Wasser aufgrund von Mangrovenbewuchs in Turneffe Islands, und durch verminderte Lichteinstrahlung in größeren Wassertiefen in Glovers Reef. Im Gegensatz zu Lighthouse Reef haben die beiden anderen Lagunen zusätzlich sehr feines Sediment, denn Diversität und Lebensbedingungen der benthischen Foraminiferen hängen auch von der Substratbeschaffenheit und dem Grad der Wasserzirkulation ab. Lighthouse Reef beherbergt mehr epifaunal lebende Arten verglichen mit Turneffe Islands und Glovers Reef. Dies könnte möglicherweise ein Hinweis auf höhere Wasserzirkulation in Lighthouse Reef in den letzten 6.000 Jahren sein. Infaunal lebende Foraminiferen kommen vermehrt in feinerem Sediment auf Turneffe Islands und Glovers Reef vor und lassen auf geringere Wasserzirkulation schließen. Dies bestätigt die positive Korrelation zwischen Feinsubstrat und Diversität in Turneffe Islands. Alter und Größe der Lagunen haben einen geringeren Einfluss auf die Foraminiferen Diversität, denn die älteste Plattform (Glovers Reef) weist nicht, wie vermutet die höchsten

Diversitäten auf, und die kleinste Plattform (Lighthouse Reef) zeigt nicht, wie erwartet die niedrigste Diversität.

Symbiontentragende benthische Foraminiferen weisen ebenfalls auf wechselnde Umweltbedingungen in den Lagunen hin. Sie leben eng begrenzt in sehr flachem, klarem Wasser, das eine gute Lichtdurchflutung aufweisen muss, da ihre Endosymbionten Photosynthese betreiben. Aufgrund ihrer sessilen, epifaunalen Lebensweise bevorzugen sie eine gemäßigte Wasserzirkulation. Lighthouse Reef weist die höchste Anzahl an symbiontentragenden Foraminiferen auf, Turneffe Islands hat die geringsten Häufigkeiten. Dies ist ebenfalls durch die verschiedenen Umweltbedingungen in den drei Plattformen erklärbar. Auf Lighthouse Reef finden die symbiontentragenden Foraminiferen trotz erhöhter Wasserzirkulation durch den Austausch mit dem umgebenden Meerwasser die besten Lebensbedingungen vor. Da die Lagune geringe Wassertiefen von maximal 11 m aufweist, ist das Wasser klar und besitzt eine hohe Lichtintensität am Lagunenboden, da hier grobes Sediment vorherrscht, das weniger stark von der Suspension betroffen ist. Auf Turneffe Islands sind die Lebensbedingungen für die symbiontentragenden Foraminiferen trotz flacher Wassertiefe schlechter, denn die Lagune ist stark mit Mangroven bewachsen was die Lichtintensität reduziert. Außerdem weist Turneffe Islands ein feines Sediment und einen hohen Nährstoffanteil auf, die schon bei leichter Strömung in Suspension vorliegen und zu verminderter Lichtintensität am Lagunenboden beitragen können. Auf Glovers Reef sind symbiontentragende Foraminifern häufiger als auf Turneffe Islands, jedoch seltener als auf Lighthouse Reef anzutreffen. Die Lebensbedingungen für diese Arten sind aufgrund höherer Wassertiefen (bis zu 16 m), feinerem Sedimentmaterial und erhöhter Wasserbewebung schlechter. Jedoch scheint die Wasserzirkulation in tieferen Lagunen keine Auswirkungen auf die Suspension und damit auf die symbiontentragenden Foraminiferen zu haben. Die Lichtintensität scheint auch in tieferen Lagunen von Glovers Reef ausreichend für die Photosyntheseaktivität der symbiontentragenden benthischen Foraminiferen zu sein.

Der „Time-Averaging“ Effekt hat keine großen Auswirkungen auf die Diversität der benthischen Foraminiferen, denn die Sedimentationsraten steigen mit zunehmender Diversität in den Lagunen. Die Diversität einer Population kann durch zunehmende Sedimentationsraten negativ beeinflusst werden, und den so genannten „Time-Averaging“ Effekt hervorrufen. Höhere Sedimentationsraten können zu einer niedrigeren Diversität der benthischen Foraminifern, aufgrund der kürzeren Verweildauer von infaunalen oder epifaunalen Sedimentbewohnern am Meeresboden führen. Turneffe Islands weist trotz hoher Sedimentationsraten (0.72 m/kyr) die höchsten Diversitäten auf, Lighthouse Reef zeigt die niedrigsten (0.54 m/kyr). Generell weisen die Kerne mit höheren Sedimentationsraten auch höhere Diversitäten in der benthischen Foraminiferenfauna auf. Neben der Sedimentationsrate hat auch die Bioturbation am Lagunenboden keine signifikanten Auswirkungen auf die Diversität der benthischen Foraminiferenfauna. Lediglich in zwei der 51 Kernproben wurde eine umgekehrte Chronologie in den ^{14}C-Datierungen festgestellt. Durch bioturbate Organismen in den Lagunen wie z.B. Polychaeten, Bivalven und Krebse, (insbesondere *Callianassa* der bis zu 2 m tiefe Gänge auf seiner Nahrungssuche durch das Sediment gräbt), entsteht an der Sedimentoberfläche eine Schichtung von grobem Sediment unter feinem Material, sowie eine Mischung aus älterem und jüngerem Sediment („Time-Averaging“). Generell steigt der „Time-Averaging“ Effekt, je tiefer gegraben wurde, bzw. je mehr Material durch Bioturbation bewegt wurde und je geringer die Sedimentationsrate ist.

Der Einfluss, den die Bodenwassertemperatur in den Lagunen auf die Diversität der benthischen Foraminiferen ausübt, wurde anhand von paleo-BW-Temperaturen von δ^{18}O Werten bewertet. Die berechneten Bodenwassertemperaturen aus δ^{18}O Werten korrelieren positiv mit den zunehmenden Lagunentiefen der letzten 6.000 Jahre. Das bedeutet, dass die BW-Temperaturen in geringeren Wassertiefen in den Lagunen ansteigen. Die Diversität und die berechneten Bodenwassertemperaturen korrelieren ebenfalls positiv und entsprechen damit nicht den gängigen Interpretationen (z.B. BICCHI et al. 2002), die von steigenden Diversitäten in tieferem Wasser ausgehen. Die δ^{13}C Werte deuten auf höhere Photosyntheseaktivität in älteren und tieferen Lagunen hin. Dies ist eher überraschend, da höhere Photosyntheseaktivität normalerweise eher in flacherem Wasser zu erwarten ist, da dort die Lichtintensität am größten ist. Allerdings kommen symbiontentragende Foraminiferen, wie z.B. *Archaias angulatus* fast ausschließlich in den Lagunen von Glovers und Lighthouse Reef vor, die im Gegensatz zu Turneffe Islands tiefere Lagunen aufweisen. Dies könnte der Grund für eine negative Korrelation zwischen δ^{13}C und Diversität sein.

Die berechneten durchschnittlichen Bodenwassertemperaturen, der Lagunen von Lighthouse und Glovers Reef der letzten 6.000 Jahre, liegen im gleichen Bereich wie die gemessenen BW-Temperaturen aus dem Jahr 2000 bis 2001. Jährliche δ^{18}O Signale, die an 10 - 15 Einzelmessungen an der Großforaminifere *Archaias angulatus* durchgeführt wurden, zeigen saisonale Temperaturschwankungen, wie sie auch von WEFER et al. (1981) beobachtet wurden. Die gemessenen jährlichen δ^{18}O Werte von *Archaias angulatus*, aus dieser Studie, weisen im Sommer und Herbst höhere BW-Temperaturen auf und im Winter und Frühling niedrigere. Lighthouse Reef erreichte während der letzten 6.000 Jahre maximale jährliche BW-Temperaturen zwischen 20,51° - 31,39°C ($\Delta T = 10.88$°C). Diese Temperaturen stimmen mit gemessenen BW-Temperaturen aus dem Jahr 2000 bis 2001 von 23,1° - 31,3°C ($\Delta T = 8{,}2$°C) überein. Jährliche maximale BW-Temperaturen in Glovers Reef der letzten 6.000 Jahre liegen zwischen 22,35° - 29,60°C ($\Delta T = 7.25$°C) und korrelieren ebenfalls mit den gemessenen BW-Temperaturen aus dem Jahr 2000 bis 2001 von 23,5° - 30,4°C ($\Delta T = 6{,}9$°C). Glovers Reef weist in dem gesamten Untersuchungszeitraum geringere jährliche BW-Temperatur- und Umweltschwankungen auf als Lighthouse Reef. Dieser Unterschied zeigt sich in den Lagunen von Glovers Reef durch I) die Dominanz einer einzigen benthischen Foraminiferen Assoziation, der „Mixed Gesellschaft“, II) hohe aber konstante Lagunentiefen in den letzten 6.000 Jahren, und III) eine leicht ansteigende Diversität der benthischen Foraminiferenfauna, die andeutet dass Glovers Reef sich in der Entwicklungsphase eines „Diversifikationsstadiums“ befindet. Lighthouse Reef weist höhere BW-Temperaturfluktuationen auf. Wechselnde Umweltbedingungen und größere BW-Temperaturschwankungen werden in Lighthouse Reef widergespiegelt durch I) das Auftreten von zwei wiederkehrenden benthischen Foraminiferen-Gesellschaften („*Archaias angulatus* Miliolid“- und „Low-Diversity Miliolid Gesellschaft“), II) flache Lagunentiefen im untersuchten Zeitabschnitt, III) hohe aber wechselnde Wasserenergie in der Lagune und IV) eine leicht ansteigenden Diversität der benthischen Foraminiferenpopulation während der vergangenen 6.000 Jahre, die ebenfalls darauf hindeutet, dass sich die Foraminiferenfauna in Lighthouse Reef in einem „Diversifikationsstadium“ befindet.

Insgesamt wurde ein linearer Anstieg der BW-Temperatur von 2°C für die vergangenen 6.000 Jahre für beide Plattformen berechnet, der jedoch nicht mit den allgemeinen holozänen Klimamodellen (e.g. HODELL et al. 1991) aus dem Karibischen Raum übereinstimmt. Es ist daher wahrscheinlich, dass die berechneten BW-Temperaturen aus Lighthouse und Glovers Reef eher lokale Klimavariationen widerspiegeln, da die berechneten BW-Temperaturen sich sowohl in ihren Trends als auch in ihren Schwankungsbereichen stark voneinander unterscheiden.

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Appendix 1

Benthic Foraminiferal Content in Sedimentcores

Turneffe Islands

vibracore samples	**T4-0**	**T4-35**	**T4-85**	**T4-165**	**T4-185**	**T5-0**	**T5-70**	**T5-135**	**T6-0**	**T6-65**	**T6-165**	**T6-275**	**T6-325**	**T7-0**	**T7-60**	**T7-235**	**T7-420**	**T7-505**
percentages	%	%	%	%	%	%	%	%	%	%	%	%	%	%		%	%	%
Textularia agglutinans Defrance, 1824															0.33		2.00	
Textularia conica d´Orbigny, 1839																		
Clavulina tricarinata d`Orbigny, 1839			0.17	0.17	0.17	0.33				0.17							2.83	
Valvulina oviedoiona d`Orbigny, 1839		0.33		0.33	0.17		0.67	1.33					0.17	0.83	1.00	0.17	0.17	
Cornusspira planorbis (Schultze) var. Ammodiscus sp.	0.33		0.17		0.33				0.83	0.67	0.33	0.83			0.17			
Spiroloculina arenata Cushman, 1921	1.33	0.50	1.67	1.33	1.17				0.50		0.50	1.50	1.50	4.00	2.17		0.17	
Spiroloculina antillarum d`Orbigny, 1839			0.17		0.83	0.17			0.17	0.50	0.17					0.17	0.17	
Spirilina sp.																		
Hauerina spp.		0.17																
Hauerina compressa		0.17							0.33	0.17	0.17							
Hauerina speciosa	0.50																	
Heterillina cribostoma (Heron-Allen & Earland), 1915	0.17		0.33		0.33	0.83			0.67	0.17	0.83	1.67	0.67					
Nodobaculariella cassis d`Orbigny, 1839		0.17			0.17	0.83		1.67				0.17		0.67	3.33		2.33	
Massilina protea Parker, 1953				4.33	2.33	0.33							0.83			0.83	0.50	
MILIOLIDAE	0.33					0.17					0.17			0.67				
Quinqueloculina spp.	3.17	3.50	4.67	5.83	8.50	0.33		0.50	3.67	4.50	3.67	5.83	4.67	6.33	2.33	1.67	3.50	0.83
Quinqueloculina agglutinans d`Orbigny, 1839			0.17	0.17							0.50		0.33		0.17	0.33		
Quinqueloculina berthelotiana d`Orbigny															0.17			
Quinqueloculina bicarinata d'Orbigny,1839	0.50													0.17				
*Quinqueloculina bicornis*Walker & Jacob, 1798																		
Quinqueloculina bicostata d`Orbigny, 1839	0.33		0.17	0.33	0.33	0.17		0.33	1.00	2.00	0.67	0.17	0.33	0.50	0.33	0.50	0.50	
Quinqueloculina bidentata d`Orbigny, 1839	0.83	6.00		0.17	0.50	0.83		0.17	0.17	0.83	0.33	1.33	0.17	2.17	0.83	1.17	1.17	
Quinqueloculina bosciana d`Orbigny, 1839	1.00				0.50	1.17					0.67	0.50	0.33	0.50		0.33		
Quinqueloculina cf. *bradyana*Cushman, 1917	0.33	0.50	1.67	0.33	0.83			0.33	1.67	0.83	0.33	0.67	0.83	0.83	0.33	0.33	0.50	
Quinqueloculina candeiana d`Orbigny, 1839	1.67	0.83	1.67	1.00	2.17				2.00	4.17	6.33	5.00	4.67	0.17	0.67	2.33	16.17	5.50
Quinqueloculina crassa var. *subcuneata* Cushman, 1921								0.50							0.33	0.17		0.67
Quinqueloculina funafutiensis (=Q.tenagos)					0.17	0.83		0.50				0.33				1.17		
Quinqueloculina horrida Cushman																		
Quinqueloculina laevigata d`Orbigny, 1826	2.17	1.17	2.17	2.83	1.00				3.17	3.83	1.33	0.50	3.50	3.83	0.50	0.33	6.33	2.17
Quinqueloculina lamarckiana (d`Orbigny), 1839	1.00	0.83	2.33	0.33	0.17	3.83		1.67	1.67	1.50	2.67	2.50	2.67	3.17	2.33	5.33	9.17	2.17
Quinqueloculina poeyana d`Orbigny, 1839	4.67	5.50	10.83	3.67	5.17	1.17		2.33	7.33	10.17	7.00	9.00	6.33	4.33	5.33	4.83	4.67	0.67
*Quinqueloculina parkeri*var. *occidentalis* Cushman, 1921																		
Quinqueloculina polygona d`Orbigny, 1839	0.33	0.17	3.17	1.17	0.67	0.67			1.50	0.83	3.50	1.83	1.83	1.17	0.50		0.50	
Quinqueloculina subpoeyana Cushman, 1922	1.17		0.17	0.17	0.67				0.33			0.5	0.83	0.50	0.83	0.33	0.17	
Quinqueloculina seminulum Linnaeus, 1767			0.67		0.50	0.83		2.17			0.33	1.67	0.17	0.67	2.83	4.83		1.17
Quinqueloculina tenagos d`Orbigny, 1839																		
Quinqueloculina tricarinata d`Orbigny, 1839	0.83													2.83				
QUINQUELOCULININAE Cushman, 1917	2.50	1.67	1.83	1.50	7.17	2.00		2.17	1.50	0.83	0.33	5.17	1.00	1.50	3.50	3.33	0.67	0.50
Dentostomina bermudezi Perez Farfante																		
Miliammina fusca (H.B. Brady)																		
Sigmoilina sp.																		
Pyrgo sp.		0.33	0.33	0.17						0.50			0.17	1.00	0.17	0.17	3.83	
Pyrgo elongata (d`Orbigny), 1826			0.17	0.33							0.17		0.33		0.33			
Pyrgo denticulina	0.17	0.17			0.33						0.17	0.33			0.67	0.17	3.67	
Triloculina spp.	1.33	1.50	3.00	2.50	1.00	0.50		1.00	3.00	3.50	2.50	3.17	4.33	2.50	0.50	1.17	2.00	
Triloculina bassensis Parr, 1945	2.17	4.83	1.33	0.50	2.67	0.83		0.17	2.33	1.50	0.83	1.50	0.83	1.00	1.17	4.00	1.17	
Triloculina bermudezi Acosta, 1940		0.83	1.00	0.67	1.17	1.17		0.17	2.50	2.83	1.17	4.17	3.00	1.00		0.83	0.17	
Triloculina bicarinata (d`Orbigny), 1839	0.33	2.17	0.17	1.17	1.17				1.17	0.67	0.50	0.83	0.33		0.17	5.67	0.67	
Triloculina carinata d`Orbigny, 1839	0.50	0.83	0.17	0.17	0.83	1.33			0.17		1.00	0.33	0.33	1.50	0.67	3.00	1.17	0.17
Triloculina fitterei var. *meningoi* Acosta, 1940	0.33		0.50	0.17	0.67				0.17	0.17		0.33				0.17		
Triloculina linneiana d`Orbigny, 1839	2.50	3.17	0.67	2.00	0.67	2.83	0.17	1.83	0.83	1.17	2.17	1.50	2.17	4.17	2.17	11.17	8.00	0.50
Triloculina quadrilateralis d`Orbigny, 1839	0.33	2.67	0.33							0.17								
Triloculina sidebottomi (Martinotti), 1920	0.17	0.50				0.17		0.17			0.17	0.17		1.00	0.17	0.33	0.17	
Triloculina trigonula (Lamarck), 1804	0.67	6.67	2.50	2.33	3.17	0.17		0.83	5.67	5.67	4.00	5.67	2.67	2.17	0.67	2.83	2.33	
Miliolinella circularis (Bornemann), 1855			0.33	0.33	0.67			0.17			0.33	0.67	0.17			0.50		
Miliolinella fichtellliana (d`Orbigny), 1839									0.33	0.33	0.50	0.17	0.33	0.33				
Miliolinella labiosa (d`Orbigny), 1839	1.83	7.17	2.17	0.67	2.00	1.50		0.67	5.50	7.00	3.83	6.67	3.17	1.17	0.33	0.33	0.17	
Wiesnerella auriculata (Egger), 1893			0.17															
Articulina sp.		0.50	0.17	0.67				0.17		0.50		0.17		0.33				
Articulina lineata Brady, 1884	2.83	3.33	1.83	0.50	2.50	0.67			0.83	0.50	0.83	0.67	0.33	0.83	0.17		1.00	
Articulina mayori Cushman, 1922		0.67	0.50	3.33	1.33			0.33			1.17	0.50	1.83					
Articulina mexicana Cushman, 1921	7.50	4.33	1.83	2.83	3.17	2.33		1.00	3.67	1.67	2.17	3.83	1.67	9.33	1.17	1.00		
Articulina pacifica Cushman, 1944	2.83	2.83	2.50	3.83	3.00	1.50		1.33	0.67	1.00	2.17	2.67	3.50	3.67	1.50	0.83		0.17
Vertebralina sp.																		
Vertebralina cassis d`Orbigny, 1839	3.00	7.83	2.33	6.67	4.00	0.67		1.50	1.83	1.67	2.83	1.83	1.17	3.83	0.67	0.17	0.83	
Vertebralina atlantica	0.67	1.50			0.17	0.17			0.67	0.17		0.50		1.33	0.17		0.50	
Peneroplis sp.										0.17							0.17	
Peneroplis bradyi Cushman, 1930											0.17	1.00				0.33		
Peneroplis proteus d`Orbigny, 1839		1.67	2.00	0.5	0.50	1.67	0.17	0.17	1.33	2.00	2.00	1.33	0.33	0.67	0.50	8.50	6.33	
Peneroplis pertusus (Forskal), 1775			0.17	0.333		0.17				0.17	0.50	0.17	0.17			0.50	0.33	
Archaias angulatus (Fichtel & Moll), 1803	0.83	0.50	0.17		0.17	2.00	0.167	0.17	1.00		0.17	0.50	0.17	0.83	1.33	3.83	3.50	
Cyclorbiculina compressa d`Orbigny, 1839			0.167													1.67	1.00	
Sorites marginalis (Lamarck), 1816	0.17	2.00	1							1.00	0.33						0.17	
Parasorites orbitolitoides (Hofker),		0.17														0.17	2.00	
Dentalina sp.																		
Fursenkoina pontoni (Cushman), 1932					0.17	0.33	0.17	0.33	0.17						0.50			
Fursenkoina sp.							0.33	0.17			0.17		0.67					
Fursenkoina spinicostata (Phleger & Parker), 1951	0.50								0.17		0.33							
Bolivina sp.					0.33		2.00	0.50			0.33		0.33	0.33	0.17			
Bolivina goesi													0.17					
Bolivina pulchella (d`Orbigny)	2.83	0.17	1.33	1.00	0.83		0.50	0.67	3.33	2.67	2.17	2.50	4.50					
Bolivina strialula Cushman, 1922				0.17	0.83	0.17	0.83	1.17	0.33	0.17	0.17	0.17	0.17		0.17			
Bolivina lowmani Phleger & Parker, 1951	0.33		0.17	0.17		0.17	2.33				0.17		0.67	0.17				
Bolivina lanceolata Parker, 1954			0.17			0.17	1.17	0.17			0.33		0.17		0.17			
Bolivinita rhomboidales (Millet), 1899	0.50	0.17		0.33	0.33		0.83	1.00	0.83	0.50		0.17	1.17	0.17				
Rectobolivina advena (Cushman), 1922							0.17											

Turneffe Islands	**T4-0**	**T4-35**	**T4-85**	**T4-165**	**T4-185**	**T5-0**	**T5-70**	**T5-135**	**T6-0**	**T6-65**	**T6-165**	**T6-275**	**T6-325**	**T7-0**	**T7-60**	**T7-235**	**T7-420**	**T7-505**
Reusella atlantica Cushman, 1947	0.33	0.17					0.17		0.50	0.50	0.50	0.33	0.33					
Uvigerina sp.					0.17													
Trifarina bella (Phleger & Parker), 1951	0.67						0.167		0.83									
Discorbis sp.	7.00	2.00	2.50	5.83	3.50	0.67		2.17	2.00	1.50	4.17	1.00	2.67	8.00	8.00	1.33	0.17	
Discorbis mira Cushman, 1922	2.50	3.33	2.33	9.83	5.67	0.67		1.17	2.50	1.50	0.83	1.67	2.67	8.67	7.50	7.67	2.00	0.17
Eponides antillarum (d`Orbigny), 1839	0.33		0.33	0.50	0.17	0.50	2.00	1.00						0.83	1.33	0.17		
Eponides sp.			0.50	0.33			0.67				0.33		0.17					
Rosalina sp.	1.67	3.17	2.17	6.17	1.67	2.50	2.50	2.33	2.50	5.17	3.67	1.17	3.00	2.50	1.33		0.33	0.17
Rosalina candeiana d´Orbigny, 1839		0.83	0.50	1.33	0.83		0.83	0.33		0.67	1.50	0.50	1.00		1.00	0.17		
Rosalina floridana (Cushman), 1922	1.17		1.17	2.667	3.67		1.67	1.67	1.67	1.00	1.33	1.50	2.00	1.00	2.17	0.33		
Neoconorbina sp.											0.50		0.50					
Neoconorbina orbicularis (Terquem), 1876	0.33	0.33	0.5		0.83		2.67	0.17	1.50	1.50	0.17	0.33	0.50		0.83		0.17	
Valvulineria cf. V. araucana (d`Orbigny)						0.17												
Siphonina pulchra Cushman, 1919				0.17		0.17	0.17	0.17					0.17		1.17			
Cancris sagra (d`Orbigny), 1839	0.17	0.17	0.50	0.50	0.50		1.67	0.50	0.50	0.17			0.17	0.17	1.50			
Asterigerina carinata d`Orbigny, 1839	2.00	0.67	0.67	0.17	0.17	0.17	0.17	0.33	2.83	1.17		0.17						
Ammonia beccarii (Linné), 1772	1.33	0.67	1.83	0.67	1.17	0.50	0.17	1.83	2.17	1.17	1.67	0.50	2.00		0.17		0.50	13.50
Ammonia sp.																		
Elphidium sp.								1.50	0.17									
Elphidium advenum (Cushman), 1922	1.33	0.67	2.33	2.17	1.83	3.17	10.50	5.83	2.50	1.67	1.50	0.83	1.83	1.33	5.83	0.83		
Elphidium sagrum (d`Orbigny), 1839	5.00	1.17	1.00	2.50	2.00	2.17	5.83	4.17	1.00	0.67	2.17	0.67	0.83	1.00	4.50	3.17	0.17	0.33
Elphidium discoidale (d´Orbigny), 1839	0.50	1.17	2.33	1.33	1.00	11.67	17.50	7.83		0.17	2.00	0.50	1.50	0.17	2.67	1.17		0.17
Cribroelphidium poeyanum (d`Orbigny), 1839	10.33	1.83	7.33	2.00	3.17	34.50	24.50	28.67	7.83	10.17	8.67	5.33	4.83	3.33	13.17	8.00	5.33	66.50
Cellanthus gunteri (Cole), 1931	0.17		1.50	0.50	0.33	5.83	3.33	0.67		0.50	1.67		0.83					0.83
Cibicides sp.		0.67	0.33	0.33		0.33	3.00		0.67	0.67			1.33	0.33				
Cibicides lobatulus (Walker & Jacob), 1798				0.33	0.50	0.17	0.50	0.67				0.33	0.50		0.67			
Cibicides mayori				0.50			0.67	0.50										
Cibicides cf. rugosa Phleger & Parker, 1951				0.17			0.67											
Planulina sp.									0.17									
Amphistegina gibbosa d`Orbigny, 1839	0.17	0.17	0.17			0.17	4.5	1.17	0.50						0.33	0.67		
Gypsina planta																		
Planorbulina sp.																		
Planorbulina acervalis Brady, 1884			1.33	0.33	1.00		0.83	0.33		0.17	0.83		0.33		1.17	0.33		
Planorbulina mediterranensis d`Orbigny, 1826					0.17	0.17		0.33		0.17	0.17				0.17			
Cymbaloporetta squammosa (d`Orbigny), 1826	1.17	0.83	1.83	1.67	0.67	0.17		0.17		0.17	2		1.33		0.17			
Tretomphalos atlanticus Cushman, 1934	2.50	2.50	0.17		1.17	0.17		0.33	3.67	1.67	0.33	0.83	0.50	0.17	0.17			0.17
Homotrema rubrum (Lamarck), 1816																		
Nonion despressulum (Walker & Jacob)	2.17	0.50	3.50	2.67	2.00	2.17	2.00	3.50	1.33		1.33	2.00	4.17		2.83		0.33	0.33
Florilus atlanticus (Cushman), 1947	2.00	1.00	5.83	1	2.00	0.83	2.50	5.00	1.83	2.50	1.17	1.33	0.67	0.33	1.67	0.67	0.33	3.17
Trichohyalos aguayoi (Bermudez)	0.67			0.33	0.17						0.17	0.17						
Globigerinoides sp.	0.17		0.17										0.17					
Globigerinoides ruber(d`Orbigny), 1939									0.17									
Globorotalia cultrata(d`Orbigny), 1926																		
others	0.83	0.17		1.00	0.17	0.17	1.33	0.33	0.17	0.33	0.17	0.17	0.33		0.17			0.17

Lighthouse Reef

vibracore samples	**L1-0**	**L1-100**	**L1-210**	**L1-235**	**L4-0**	**L4-40**	**L4-125**	**L4-240**	**L5-0**	**L5-55**	**L5-130**	**L5-250**	**L5-340**	**L6-0**	**L6-120**	**L6-205**
percentages	%	%	%	%	%	%	%	%	**%**	**%**	**%**	**%**	**%**	**%**	**%**	%
Textularia agglutinans Defrance, 1824	0.17	0.33	0.17													
Textularia conica d´Orbigny, 1839			0.17							0	5	3	4			
Clavulina tricarinata d`Orbigny, 1839	0.17	0.67			0.17				0.50		1	2	1	0.17		
Valvulina oviedoiona d`Orbigny, 1839	3.50	2.67	0.50	1.17					0.67	0	5	2	7			
Cornusspira planorbis (Schultze) var.Ammodiscus sp.	0.83			0.33		0.33	0.17		1.33		0			1	0	0.33
Spiroloculina arenata Cushman, 1921																
Spiroloculina antillarum d`Orbigny, 1839	0.50	0.17	0.17			0.17			0.50					0		
Spirilina sp.			0.33													
Hauerina spp.																
Hauerina compressa	0.50				0.33				0.17				0.17	0	0	0.17
Hauerina speciosa														1		
Heterillina cribostoma (Heron-Allen & Earland), 1915			0.33	0.17		0.17	0.17	0.17	0.33		0	0	0.17			
Nodobaculariella cassis d`Orbigny, 1839			0.33				0.33		0.50		0					
Massilina protea Parker, 1953	0.17	0.17								0						
MILIOLIDAE	0.17				0.50				0.67							
Quinqueloculina spp.	4.00	2.00	2.83	6.83	2.50	6.83	7.17	5.17	5.67	2	4	1	0.50	7	6	7.67
Quinqueloculina agglutinans d`Orbigny, 1839	2.00	0.83	2.50		1.50	1.00	0.33	1.00	0.33			1	0.50	1	1	2.17
Quinqueloculina berthelotiana d`Orbigny																
Quinqueloculina bicarinata d'Orbigny,1839		0.33								0						0.33
*Quinqueloculina bicornis*Walker & Jacob, 1798			3.00			0.50	2.33	0.50				0			1	0.50
Quinqueloculina bicostata d`Orbigny, 1839	1.83	3.33	1.67	1.50	2.00	4.00	3.83	2.17	4.00	4	8	2	1.33	1	4	2.67
Quinqueloculina bidentata d`Orbigny, 1839	4.83	2.83	5.17	3.67	3.00	2.17	1.67	5.67	1.00	1	8	6	5.50	3	4	5.00
Quinqueloculina bosciana d`Orbigny, 1839	0.33		0.67		0.83	0.50	0.33	1.33	4.50	0		0			1	1.17
Quinqueloculina cf. *bradyana*Cushman, 1917	4.00	1.17	1.50	2.17	0.33	0.83	0.33	0.33	2.50	1	2	3	1.17	2	1	0.83
Quinqueloculina candeiana d`Orbigny, 1839		0.17														0.17
Quinqueloculina crassa var. *subcuneata* Cushman, 1921		0.83	0.50			0.17					0	4	3.83	0		
Quinqueloculina funafutiensis d`Orbigny, 1839					0.17			0.17	0.33	0		2	2.33		1	1.00
Quinqueloculina horrida Cushman, 1921			0.17					0.17								
Quinqueloculina laevigata d`Orbigny, 1826	0.83	0.17	1.33	1.67	1.00	1.33	1.67	0.67	2.50	0	1	0		1	1	0.67
Quinqueloculina lamarckiana (d`Orbigny), 1839	2.67	2.67	2.50	4.00	0.67			1.00	2.50	2	2	3	6.00	2	2	4.33
Quinqueloculina poeyana d`Orbigny, 1839	2.33	5.00	6.33	9.83	8.50	7.83	9.33	12.50	1.83	2	6	2	1.83	4	8	8.50
*Quinqueloculina parkeri*var. *occidentalis* Cushman, 1921									0.17							
Quinqueloculina polygona d`Orbigny, 1839	0.17				1.00	0.67		0.17	0.17		2	1	0.33	1	1	0.17
Quinqueloculina subpoeyana Cushman, 1922						0.17									2	1.83
Quinqueloculina seminulum Linnaeus, 1767		0.83	1.50		0.17	0.17		0.33	0.83	0		1				3.00
Quinqueloculina tenagos d`Orbigny, 1839		0.17												1		
Quinqueloculina tricarinata d`Orbigny, 1839																
QUINQUELOCULININAE Cushman, 1917	1.83	3.17	1.50	1.17	5.17	2.83	5.17	3.67	3.83	2	7	2	1.33		3	2.33
Dentostomina bermudezi Perez Farfante													1.83			
Miliammina fusca (Brady)							0.17									
Sigmoilina sp.																
Pyrgo sp.	0.17		0.33			0.33					1				0	0.33
Pyrgo elongata (d`Orbigny), 1826								0.17						0		
Pyrgo denticulina						0.17										
Triloculina spp.	0.67		1.33	2.50	2.50	3.33	4.83	2.83	2.67	0	1	2	0.67	2	2	3.67
Triloculina bassensis Parr, 1945	5.50	3.33	6.50	6.00	8.17	7.17	7.67	5.17	6.00	6	9	5	4.00	4	6	4.33
Triloculina bermudezi Acosta, 1940	0.50	1.33	0.67	1.00	0.67	3.00	2.17	0.67	2.67	2	1	1	0.67	1	1	1.00
Triloculina bicarinata (d`Orbigny), 1839	0.83	1.00	0.50		0.50	0.33		0.17		1	6	3	5.00		1	0.17
Triloculina carinata d`Orbigny, 1839	0.50	0.67	0.17	1.50	0.17	0.33	0.17		0.67	1		1	3.00	1	0	0.33
Triloculina fitterei var. *meningoi* Acosta, 1940		0.50	1.00	1.00	1.17	1.33	1.00	1.67	0.33	0					2	1.17
Triloculina linneiana d`Orbigny, 1839	1.00	5.33	4.50	3.00	0.67	0.67	0.33	0.67	0.83	1	1	2	3.17	3	2	4.50
Triloculina quadrilateralis d`Orbigny, 1839					0.17											
Triloculina sidebottomi (Martinotti), 1920	0.17		0.17	0.50	1.50	0.50	0.17		0.50			0	0.33			
Triloculina trigonula (Lamarck), 1804	0.83	1.67	0.83	1.50	3.17	2.00	1.00	1.33	3.83	0	4	3	1.17	1	2	0.83
Miliolinella circularis (Bornemann), 1855		1.00	0.67		1.00	1.00	0.83		1.17							
Miliolinella fichtellliana (d`Orbigny), 1839		0.33				0.50									0	0.17
Miliolinella labiosa (d`Orbigny), 1839	4.83	6.17	2.33	6.17	5.00	7.83	6.83	0.67	3.17	0	5	4	2.00	4	4	4.50
Wiesnerella auriculata (Egger), 1893																
Articulina sp.			0.50	0.33	0.67	1.67	1.17							1	1	1.33
Articulina lineata Brady, 1884	0.17	0.50	0.83	0.17	0.83	2.17	3.33	1.33			1	0	0.17	1	1	1.00
Articulina mayori Cushman, 1922	0.17	0.50		0.50		0.17			0.17					0		
Articulina mexicana Cushman, 1921		1.17	1.50	0.83		0.50	0.17	0.33	0.33		0					0.17
Articulina pacifica Cushman, 1944		0.17	0.83	0.17		0.17	0.50	0.17						1	0	0.17
Vertebralina sp.																
Vertebralina cassis d`Orbigny, 1839			0.17						1.00							
Vertebralina atlantica			0.17						0.17							
Peneroplis sp.																
Peneroplis bradyi Cushman, 1930		0.83	0.33							1					0	
Peneroplis proteus d`Orbigny, 1839	4.33	5.83	3.00	2.33	2.00	1.33	0.83	1.17	3.00	1	1	2	3.67	5	1	1.83
Peneroplis pertusus (Forskal), 1775	0.17	0.17	0.17		0.33				1.33				0.17	0		
Archaias angulatus (Fichtel & Moll), 1803	17.83	10.00	11.17	8.50	23.00	10.50	10.67	22.50	13.00	30	9	26	28.83	22	15	9.33
Cyclorbiculina compressa d`Orbigny, 1839			0.17		0.17	0.17		0.67						0		
Sorites marginalis (Lamarck), 1816	1.17	0.17			0.17				2.83					1	0	
Parasorites orbitolitoides (Hofker),	1.00			0.33	1.00		0.33	1.00	0.83				0.17	2	0	0.33
Dentalina sp.		0.17														
Fursenkoina pontoni (Cushman), 1932																
Fursenkoina sp.												0				
Fursenkoina spinicostata (Phleger & Parker), 1951																
Bolivina sp.														0	0	
Bolivina goesi																
Bolivina pulchella (D'Orbigny) var. *primitiva* Cushman, 1930		0.33	0.50	0.17	0.17	0.17	0.33		0.17			0	0.17			0.17
Bolivina strialula Cushman, 1922																
Bolivina lowmani Phleger & Parker, 1951		0.17				0.17	0.17									
Bolivina lanceolata Parker, 1954																
Bolivinita rhomboidales (Millet)			0.17			0.17								0		0.17
Rectobolivina advena (Cushman), 1922																

Lighthouse Reef	**L1-0**	**L1-100**	**L1-210**	**L1-235**	**L4-0**	**L4-40**	**L4-125**	**L4-240**	**L5-0**	**L5-55**	**L5-130**	**L5-250**	**L5-340**	**L6-0**	**L6-120**	**L6-205**
Reusella atlantica Cushman, 1947																
Uvigerina sp.						0.17										
Trifarina bella (Phleger & Parker), 1951		0.17	0.17			0.17										
Discorbis sp.	0.33	1.00		0.67				0.17	0.17	0		2	0.17	0	1	0.17
Discorbis mira Cushman, 1922	1.33		0.33						1.00	0			0.33		0	
Eponides antillarum (d`Orbigny), 1839																
Eponides sp.																
Rosalina sp.	1.33	2.33	1.50	3.50	3.17	1.83	1.33	0.50	2.17	2	2	2	0.50	8	0	3.00
Rosalina candeiana d´Orbigny, 1839	5.00	3.67	4.00			4.67	2.33	1.33	0.83	1	0	4	3.33		7	2.00
Rosalina floridana (Cushman), 1922		0.33	0.67	0.17		1.00	1.17		0.50	2			0.33		0	0.50
Neoconorbina sp.																
Neoconorbina orbicularis (Terquem), 1876	0.17	0.50	1.00	1.17	0.33	0.83	1.17	0.17	1.00	1	0			1	1	1.00
Valvulineria cf. V. araucana (d`Orbigny)																
Siphonina pulchra Cushman, 1919			0.67											0		
Cancris sagra (d`Orbigny), 1839																
Asterigerina carinata d`Orbigny, 1839	3.17	1.83	2.67	1.50		0.17	0.17	0.17						3	3	0.67
Ammonia beccarii (Linné), 1772	0.50		1.00	3.67		0.17	0.67	0.50				1				
Ammonia sp.																
Elphidium sp.						0.33										
Elphidium advenum (Cushman), 1922	0.17								0.33					0		
Elphidium sagrum (d`Orbigny), 1839		0.17		0.17									0.33			
Elphidium discoidale (d´Orbigny),		3.83	1.67	0.67		1.00	2.33	2.50	0.33	7	2	3	1.33	4	3	3.33
Cribroelphidium poeyanum (d`Orbigny), 1839	10.00	7.83	6.50	12.00	9.67	9.00	9.17	14.17	10.33	25	6	5	1.50	1	6	4.83
Cellanthus gunteri (Cole), 1931			0.67			0.17		0.17		1						
Cibicides sp.														0		
Cibicides lobatulus (Walker & Jacob), 1798										0				0	0	0.33
Cibicides mayori																
Cibicides cf. rugosa Phleger & Parker, 1951		0.50	0.17												0	
Planulina sp.						0.17										
Amphistegina gibbosa d`Orbigny, 1839		0.33		0.17										0		
Gypsina planta		0.50	0.17			0.17		0.17							0	0.67
Planorbulina sp.																
Planorbulina acervalis Brady, 1884	0.50	0.17	0.17			0.17		0.17						0		
Planorbulina mediterranensis d`Orbigny, 1826														0		
Cymbaloporetta squammosa (d`Orbigny), 1826		0.50	0.33	2.00	1.50	0.67		0.17	0.50	0	1			3	0	0.67
Tretomphalos atlanticus Cushman, 1934	2.67	2.17	2.33	0.67	0.67	0.67	1.33	1.50		1	1	1	0.50	2	3	1.67
Homotrema rubrum (Lamarck), 1816	2.33	2.00	2.50	0.50		0.50	0.33	1.00						5	2	1.50
Nonion despressulum (Walker & Jacob)	0.33	1.00	0.67	1.17	0.33	0.50	0.17	0.17	1.50	2	1	1		1	0	0.50
Florilus atlanticus (Cushman), 1947	1.00	1.00	0.67	3.00	3.33	1.83	4.17	1.67	1.83	2	1	1	0.17	1	1	0.67
Trichohyalos aguayoi (Bermudez)																
Globigerinoides sp.		0.33														
Globigerinoides ruber(d`Orbigny), 1939		0.33				0.17								0		
Globorotalia cultrata(d`Orbigny), 1926						0.17	0.17								0	0.17
others	0.50	0.67	0.50		0.17	0.17										

Glovers Reef

vibracore samples	**G2-0**	**G2-30**	**G2-165**	**G2-300**	**G4-0**	**G4-70**	**G4-127**	**G4-240**	**G5-0**	**G5-70**	**G5-235**	**G5-420**	**G7-0**	**G7-40**	**G7-120**	**G7-190**	**G7-285**
percentages	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
Textularia agglutinans Defrance, 1824	1.83	1.50	1.00	2.50	1.00	1.17	0.50	1.50	0.17		0.17	0.17	1.50	1.00	0.67	0.67	
Textularia conica d´Orbigny, 1839				0.17													
Clavulina tricarinata d`Orbigny, 1839	0.17				0.33												
Valvulina oviedoiona d`Orbigny, 1839	0.17	0.17			0.17									0.17	0.17		0.17
Cornusspira planorbis (Schultze) var.Ammodiscus sp.	0.67	0.67	0.17		0.67	0.33	1.17	0.17	1.00								
Spiroloculina arenata Cushman, 1921					0.17		0.33										0.17
Spiroloculina antillarum d`Orbigny, 1839		0.17	0.17	0.17					0.17								
Spirilina sp.						0.17											
Hauerina spp.																	
Hauerina compressa																0.17	
Hauerina speciosa	0.17				0.33				0.50								
Heterillina cribostoma (Heron-Allen & Earland), 1915					1.67	0.17										0.33	
Nodobaculariella cassis d`Orbigny, 1839							0.17										
Massilina protea Parker, 1953	0.17	0.33	0.17	0.17	0.17												
MILIOLIDAE	0.00				0.33				0.67								
Quinqueloculina spp.	3.50	1.67	2.17	0.50	4.50	3.33	3.83	2.33	2.50	0.50	0.50	1.00	3.50	5.67	3.83	3.00	2.00
Quinqueloculina agglutinans d`Orbigny, 1839		2.33	4.00	4.83		5.83		4.00	1.00	0.67	0.17	0.17	0.83		4.33		0.83
Quinqueloculina berthelotiana d`Orbigny																	
Quinqueloculina bicarinata d'Orbigny,1839		1.17	1.17	0.33		2.00		1.17	0.50	0.17		0.33		0.83			
*Quinqueloculina bicornis*Walker & Jacob, 1798																	
Quinqueloculina bicostata d`Orbigny, 1839	3.83				0.83	0.83	3.33		1.00	1.17	1.33	0.50	0.50	5.83	1.83	2.67	1.17
Quinqueloculina bidentata d`Orbigny, 1839	5.00	8.67	6.00	8.50	3.17	6.33	8.17	5.83	2.00	0.50	1.00	0.17	7.33	6.67	5.17	6.17	9.67
*Quinqueloculina bosciana d`Orbigny, 1839* d`Orbigny, 1839					0.50				2.33				0.50				
Quinqueloculina cf. *bradyana* Cushman, 1917	0.33	0.50	0.83	1.83	1.83	1.67	2.67	1.00		0.17	0.50		1.00	1.67	1.67	0.67	0.67
Quinqueloculina candeiana d`Orbigny, 1839	0.33	2.33	2.33	2.50	1.50	2.17	1.50	4.83	3.67	2.33	7.00	23.00	0.17	0.17	0.67	0.50	2.67
Quinqueloculina crassa var. *subcuneata* Cushman, 1921	0.17									3.33	1.33	1.83			0.33	0.17	0.33
Quinqueloculina funafutiensis d`Orbigny, 1839								0.17					0.33				
Quinqueloculina horrida Cushman																	
Quinqueloculina laevigata d`Orbigny, 1826	1.33	0.83	0.17	0.83	2.17	0.83	1.67	1.00	2.83	0.33	0.67		0.83	1.50	0.50	2.17	1.00
Quinqueloculina lamarckiana (d`Orbigny), 1839	3.17	2.17	4.33	3.50	8.83	4.50	2.50	5.50	1.67	6.17	9.50	10.83	5.17	4.17	2.50	4.50	6.33
Quinqueloculina poeyana d`Orbigny, 1839	7.17	3.17	5.83	5.50	1.50	2.33	2.83	4.83	8.00	3.00	6.50	3.17	5.83	5.00	6.67	8.67	6.83
*Quinqueloculina parkeri*var. *occidentalis* Cushman, 1921																	
Quinqueloculina polygona d`Orbigny, 1839	1.33	1.83	3.17	0.83	0.50	1.00	1.33	0.33	0.50	0.50	0.33	0.17	0.67	0.50	2.17	1.33	
Quinqueloculina subpoeyana Cushman, 1922			1.33	0.33		1.00	0.50	0.33		0.50	0.17	0.17			1.83		
Quinqueloculina seminulum Linnaeus, 1767					0.67				1.50	1.17	0.83	3.83	0.67		1.00		2.50
Quinqueloculina tenagos d`Orbigny, 1839																	
Quinqueloculina tricarinata d`Orbigny, 1839																	
QUINQUELOCULININAE Cushman, 1917	3.17	9.00	4.00	5.17	3.67	7.33	4.67	3.50	4.67	2.50	2.17	2.50	3.33	3.33	5.67	3.00	3.50
Dentostomina bermudezi Perez Farfante																	
Miliammina fusca (Brady)																	
Sigmoilina sp.		0.17															
Pyrgo sp.	0.33				0.17		0.17	0.17						0.17			
Pyrgo elongata (d`Orbigny), 1826	0.00																0.17
Pyrgo denticulina	0.00																
Triloculina spp.	0.67	1.83	0.33		2.67	1.50	1.50	0.83	2.67			0.17	1.00	1.67	1.17	1.00	
Triloculina bassensis Parr, 1945	4.50	6.17	7.17	3.33	4.17	2.33	3.67	2.17	2.67	3.83	3.83	1.33	5.83	8.50	5.67	4.00	5.33
Triloculina bermudezi Acosta, 1940		1.17	0.17	0.17		0.50	0.83	0.83	0.67	0.33						0.50	
Triloculina bicarinata (d`Orbigny), 1839	2.00	0.50	1.17	0.67		0.33	3.17	1.33	0.33	0.33	0.33	0.17	0.67	1.33	1.33	0.50	0.67
Triloculina carinata d`Orbigny, 1839		0.50	1.00	0.17	1.00	0.17		0.17		0.17		0.33	1.33	0.17	0.67	0.17	0.33
Triloculina fitterei var. *meningoi* Acosta, 1940	0.50	0.50							0.50					1.00	0.17	0.67	
Triloculina linneiana d`Orbigny, 1839	1.50	1.17	2.00	0.67	0.83	0.67	2.33		1.00	2.17	1.33	1.33	2.00	2.00	2.00	2.33	1.50
Triloculina quadrilateralis d`Orbigny, 1839																	
Triloculina sidebottomi (Martinotti), 1920					0.17												
Triloculina trigonula (Lamarck), 1804	2.67		2.00	0.50	0.33	0.33	0.67	1.83	2.83	0.17	1.00		0.83	1.83	0.83	1.83	1.33
Miliolinella circularis (Bornemann), 1855																	
Miliolinella fichtellliana (d`Orbigny), 1839				0.17	0.17		0.50										
Miliolinella labiosa (d`Orbigny), 1839	2.17	1.67	0.50			1.17	7.00	0.67	3.50		0.17		1.50	3.83	1.33	2.50	0.33
Wiesnerella auriculata (Egger), 1893																	
Articulina sp.				0.17											0.83		
Articulina lineata Brady, 1884	0.67	0.83	0.83	0.17				0.17	0.50					1.67	0.17	1.00	0.33
Articulina mayori Cushman, 1922			0.17	0.17	0.17				0.67				0.17		0.33	0.17	0.17
Articulina mexicana Cushman, 1921			0.33			0.17	1.17		0.50					0.17			0.33
Articulina pacifica Cushman, 1944	0.50	1.00	0.33	0.50	0.17	0.17	0.33	0.50			0.17						0.83
Vertebralina sp.																	
Vertebralina cassis d`Orbigny, 1839	0.33	0.17		0.17	0.17		0.67						0.17				
Vertebralina atlantica d`Orbigny, 1839																	
Peneroplis sp.			0.17														
Peneroplis bradyi Cushman, 1930		1.33	2.50	2.50		0.50		3.33		0.67	2.17	1.00			1.67		2.67
Peneroplis proteus d`Orbigny, 1839	4.50	3.67	2.83	3.17	10.00	1.33	0.50	2.33	2.33	2.67	2.00	3.50	3.00	3.83	1.50	3.00	3.83
Peneroplis pertusus (Forskal), 1775	0.33	0.17		0.17	0.83	0.17			1.17							0.17	
Archaias angulatus (Fichtel & Moll), 1803	6.83	8.00	4.67	7.17	13.50	7.00	4.67	13.33	1.83	13.50	13.00	12.67	11.50	7.00	7.50	7.33	10.17
Cyclorbiculina compressa d`Orbigny, 1839	0.33	0.33	0.50	0.17	0.17	0.50		0.33	0.17	0.17	0.50		0.17	0.50	0.67		0.50
Sorites marginalis (Lamarck), 1816	0.50	0.17			1.33				0.17					0.50			
Parasorites orbitolitoides (Hofker),	1.83	0.33	0.17	1.17	4.17	0.33		0.17	2.67	3.67	8.50	5.33	2.50	0.83	0.67	1.00	1.17
Dentalina sp.																	
Fursenkoina pontoni (Cushman), 1932			0.33			1.17									0.17		
Fursenkoina sp.																	
Fursenkoina spinicostata (Phleger & Parker), 1951	0.17												0.17	0.33		0.17	
Bolivina sp.			0.50			0.17	0.17										
Bolivina goesi																	
Bolivina pulchella (d`Orbigny)		0.33	0.17			0.67								0.67		0.83	
Bolivina strialula Cushman, 1922								0.17									
Bolivina lowmani Phleger & Parker, 1951						0.17											
Bolivina lanceolata Parker, 1954																	
Bolivinita rhomboidales (Millet)																	
Rectobolivina advena (Cushman), 1922																	

Glovers Reef	**G2-0**	**G2-30**	**G2-165**	**G2-300**	**G4-0**	**G4-70**	**G4-127**	**G4-240**	**G5-0**	**G5-70**	**G5-235**	**G5-420**	**G7-0**	**G7-40**	**G7-120**	**G7-190**	**G7-285**
Reusella atlantica Cushman, 1947																	
Uvigerina sp.																	
Trifarina bella (Phleger & Parker), 1951																	
Discorbis sp.		0.17						0.33		0.17					0.17		
Discorbis mira Cushman, 1922			0.33	0.17				0.50	0.33								
Eponides antillarum (d`Orbigny), 1839															0.17		
Eponides sp.																	
Rosalina sp.	1.00				1.50		0.17		3.00	0.67	0.17		1.00	0.83		0.67	
Rosalina candeiana d´Orbigny, 1839		0.50	0.33	0.17	0.17	0.83			0.17	0.33				0.50	0.83		0.17
Rosalina floridana (Cushman), 1922		0.33	0.17	0.50		0.33		0.33	0.17		0.33				0.17		0.17
Neoconorbina sp.																	
Neoconorbina orbicularis (Terquem), 1876	0.33	0.50	1.00	0.33	0.33	0.33		0.33	0.83	0.17			0.50	0.17	0.50	0.50	
Valvulineria cf. V. araucana (d`Orbigny), 1839																	
Siphonina pulchra Cushman, 1919		0.17															
Cancris sagra (d`Orbigny), 1839														0.17			
Asterigerina carinata d`Orbigny, 1839										0.17			0.17				
Ammonia beccarii (Linné), 1772	0.33	0.17		0.33	0.50				0.83	1.00	1.33	0.50		0.17	0.17		0.17
Ammonia sp.									2.33								
Elphidium sp.	0.17	0.17															
Elphidium advenum (Cushman), 1922				0.17	0.33				1.50								
Elphidium sagrum (d`Orbigny), 1839	0.33			0.50			0.17										
Elphidium discoidale (d´Orbigny), 1839	2.00	3.17	0.83	1.67	1.67	1.00	1.67	0.50	1.33	9.00	5.17	1.50	3.83	2.50	2.50	3.50	3.17
Cribroelphidium poeyanum (d`Orbigny), 1839	23.50	19.50	25.33	34.00	17.33	34.83	34.67	29.50	22.33	28.83	18.67	17.67	26.50	18.17	24.83	31.17	19.17
Cellanthus gunteri (Cole), 1931								1.17		1.50	0.67						4.50
Cibicides sp.																	
Cibicides lobatulus (Walker & Jacob), 1798				0.17							0.17						
Cibicides mayori																	
Cibicides cf. rugosa Phleger & Parker, 1951																	
Planulina sp.																	
Amphistegina gibbosa d`Orbigny, 1839		0.17		0.17	1.50						0.17	0.17					
Gypsina planta																	
Planorbulina sp.																	
Planorbulina acervalis Brady, 1884	0.33				0.17				0.17					0.33			
Planorbulina mediterranensis d`Orbigny, 1826 (größer)					0.17												
Cymbaloporetta squammosa (d`Orbigny), 1826	0.50	0.67										1.00	1.83	1.00			
Tretomphalos atlanticus Cushman, 1934	1.33	1.00	1.00	0.33	0.33	0.67	0.33	0.67	1.33	3.33	3.50	2.00	0.17	0.33	0.83	0.33	0.83
Homotrema rubrum (Lamarck), 1816		0.33							0.50				0.17				
Nonion despressulum (Walker & Jacob)		2.83	0.83	0.33	0.33				1.17			1.17	0.50	0.67	2.33	0.67	1.83
Florilus atlanticus (Cushman), 1947	7.00	2.67	5.50	2.33	1.00	1.33	0.50	1.67	5.00	3.83	4.50	2.33	2.33	2.67	1.83	2.00	2.33
Trichohyalos aguayoi (Bermudez)																	
Globigerinoides sp.									0.17								
Globigerinoides ruber(d`Orbigny), 1939																	
Globorotalia cultrata(d`Orbigny), 1926																	
others	0.33	1.17			0.17	0.33		0.17		0.33	0.17						0.17

Appendix 2

Occurrence of benthic foraminiferal assemblages in the respective core section

assemblage	**core section**	**diversity (H`)**	**eveness (E`)**	**richness (S)**
Low-Diversity *C. poeyanum*-dominant	T7-505/510	1,330	0,452	18,844
C. poeyanum-Elphidium-dominant	T5 Top	2,852	0,725	50,844
	T5-70/75	2,674	0,758	33,844
	T5-135/140	3,122	0,794	50,844
Quinquel.-Trilocul.-Peneroplis	T7-235/240	3,286	0,853	46,844
	T7-420/425	3,152	0,843	41,844
	G5-420/425	2,531	0,759	27,844
High-Diversity Miliolid	T4 Top	3,653	0,896	58,844
	T4-35/40	3,549	0,907	49,844
	T4-85/90	3,688	0,897	60,844
	T4-165/170	3,549	0,882	55,844
	T4-185/190	3,741	0,899	63,844
	T6 Top	3,652	0,924	51,844
	T6-65/70	3,490	0,879	52,844
	T6-165/170	3,725	0,902	61,844
	T6-275/280	3,443	0,852	56,844
	T6-325/330	3,785	0,917	61,844
	T7 Top	3,456	0,908	44,844
	T7-60/65	3,365	0,832	56,844
Archaias angulatus-Miliolid	L4 Top	2,975	0,812	38,844
	L4-240/245	2,868	0,758	43,844
	L5 Top	3,405	0,880	47,844
	L5-55/60	2,475	0,691	35,844
	L5-250/255	3,094	0,851	37,844
	L5-340/345	2,871	0,789	37,844
	L6 Top	3,191	0,816	49,844
Low-Diversity Miliolid	L1 Top	3,222	0,852	43,844
	L1-100/105	3,513	0,865	57,844
	L1-210/215	3,592	0,870	61,844
	L1-235/240	3,227	0,881	38,844
	L4-40/45	3,360	0,831	56,844
	L4-125/130	3,163	0,852	40,844
	L5-130/135	3,108	0,889	32,844
	L6-120/125	3,337	0,862	47,844
	L6-205/210	3,436	0,878	49,844
Mixed Assemblage	G2 Top	3,024	0,809	41,844
	G2-30/35	3,125	0,807	47,844
	G2-165/170	2,994	0,806	40,844
	G2-300/305	2,697	0,708	44,844
	G4 Top	3,058	0,799	45,844
	G4-70/75	2,714	0,746	37,844
	G4-127/132	2,664	0,762	32,844
	G4-240/245	2,734	0,763	35,844
	G5 Top	3,258	0,856	44,844
	G5-70/75	2,661	0,755	33,844
	G5-235/240	2,806	0,802	32,844
	G7 Top	2,821	0,787	35,844
	G7-40/45	3,099	0,846	38,844
	G7-120/125	3,029	0,821	39,844
	G7-190/195	2,762	0,777	34,844
	G7-285/290	2,969	0,816	37,844

Appendix 3

Average diversity, evenness, richness and age of each core section

Turneffe Islands

Sample	H`	E	S	age	error (±)
T4 Top	3,653	0,896	58,844	0	0
T4 30/35	3,549	0,907	49,844	660	50
T4 85-90	3,688	0,897	60,844	1030	110
T4 165-170	3,549	0,882	55,844	3370	160
T4-185/190	3,741	0,899	63,844	3445	115
T5 Top	2,852	0,725	50,844	0	0
T5 70-75	2,674	0,758	33,844	2500	200
T5 135/140	3,122	0,794	50,844	2260	100
T6 Top	3,652	0,924	51,844	0	0
T6 65/70	3,490	0,879	52,844	835	105
T6-165-170	3,725	0,902	61,844	1320	160
T6-275/280	3,443	0,852	56,844	1225	85
T6 325-330	3,785	0,917	61,844	5343	73
T7 Top	3,456	0,908	44,844	0	0
T7 60/65	3,365	0,832	56,844	795	155
T7 235-240	3,286	0,853	46,844	1275	105
T7 420/425	3,152	0,843	41,844	2185	145
T7 505-510	1,330	0,452	18,844	4380	150

Lighthouse Reef

Sample	H`	E	S	age	error (±)
L1 Top	3,222	0,852	43,844	0	0
L1 100/105	3,513	0,865	57,844	1350	110
L1 210/215	3,592	0,870	61,844	1405	115
L1 235/240 (base)	3,227	0,881	38,844	3750	150
L4 Top	2,975	0,812	38,844	0	0
L4 40/45	3,360	0,831	56,844	1110	140
L4 125/130	3,163	0,852	40,844	1345	135
L4 240/245	2,868	0,758	43,844	4690	80
L5 Top	3,405	0,880	47,844	0	0
L5 55/60	2,475	0,691	35,844	1060	100
L5 130/135	3,108	0,889	32,844	2240	110
L5 250/255	3,094	0,851	37,844	3320	150
L5 340/345	2,871	0,789	37,844	3850	200
L6 Top	3,191	0,816	49,844	0	0
L6 120/125	3,337	0,862	47,844	1005	115
L6 205/210	3,436	0,878	49,844	2170	130

Glovers Reef

Sample	H`	E	S	age	error (±)
G2 Top	3,024	0,809	41,844	0	0
G2-30/35	3,125	0,807	47,844	1170	120
G2-165/170	2,994	0,806	40,844	1845	115
G2-300/305	2,697	0,708	44,844	3570	120
G4 Top	3,058	0,799	45,844	0	0
G4-70/75	2,714	0,746	37,844	2995	145
G4-127/132	2,664	0,762	32,844	4405	125
G4-240/245	2,734	0,763	35,844	5745	155
G5 Top	3,258	0,856	44,844	0	0
G5-70/75	2,661	0,755	33,844	1330	80
G5-235/240	2,806	0,802	32,844	2610	160
G5-420/425	2,531	0,759	27,844	6225	115
G7 Top	2,821	0,787	35,844	0	0
G7 40/45	3,099	0,846	38,844	1060	100
G7-120/125	3,029	0,821	39,844	2020	120
G7 190/195	2,762	0,777	34,844	2370	80
G7-285/290	2,969	0,816	37,844	4675	165

H`= Diversity; E= Evenness; S= Richness

Appendix 4

Summary of “Modes of Life”

Mode of Life	T4 Top	T4-35/40	T4-85/90	T4-165/170	T4-185/190	T5 Top	T5-70/75	T5-135/140	T6 Top
epifaunal, sessil on plants / hard substrat	12,50	15,67	11,83	23,50	17,33	7,67	8,67	6,50	15,00
epifaunal, free on sediment / plants	25,16	36,50	20,17	23,50	23,83	15,00	17,00	14,83	27,33
epifaunal, sessil or vagil	25,55	25,17	36,50	30,33	37,00	15,17	7,67	16,00	28,83
infaunal to epifaunal, free in muddy sed.	3,66	0,33	1,67	1,67	2,50	1,33	10,17	8,50	6,33
infaunal, free in muddy sediment	20,67	5,33	17,50	9,67	9,83	57,17	54,00	48,67	13,67
others	12,46	17,00	12,33	11,33	9,51	3,66	2,49	5,50	8,84
	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

Mode of Life	T6-65/70	T6 - 165/170	T6-275/280	T6-325/330	T7 Top	T7-60/65	T7-235/240	T7-420/425	T7-505/510
epifaunal, sessil on plants / hard substrat	15,17	14,17	13,83	13,66	20,00	20,50	24,16	13,33	0,17
epifaunal, free on sediment / plants	22,33	20,17	26,50	23,00	29,00	16,33	32,50	18,67	0,83
epifaunal, sessil or vagil	37,33	35,67	40,00	35,83	38,67	30,17	28,17	51,50	13,83
infaunal to epifaunal, free in muddy sed.	5,83	4,34	4,16	7,84	1,00	2,17	0,67	0,33	3,17
infaunal, free in muddy sediment	12,67	18,00	9,00	14,84	4,50	23,83	12,33	6,33	81,67
others	6,67	7,65	6,51	4,83	6,83	7,00	2,17	9,84	0,33
	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

Mode of Life	L1 top	L1-100/105	L1-210/215	L1-235/240	L4 Top	L4-40/45	L4-125/130	L4-240/245	L5 Top
epifaunal, sessil on plants / hard substrat	32,00	28,66	22,17	19,33	31,67	22,83	20,66	25,84	23,83
epifaunal, free on sediment / plants	13,84	18,67	22,34	20,67	20,16	23,50	22,68	14,50	18,34
epifaunal, sessil or vagil	32,00	30,00	37,83	34,50	30,50	37,17	36,99	36,83	34,83
infaunal to epifaunal, free in muddy sed.	0,00	0,50	0,67	0,17	0,17	0,67	0,5	0,00	0,17
infaunal, free in muddy sediment	10,83	13,00	10,66	17,66	10,00	11,33	12,51	17,50	12,17
others	11,33	9,17	6,33	7,67	7,50	4,50	6,66	5,33	10,66
	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

Mode of Life	L5-55/60	L5-130/135	L5-250/255	L5-340/345	L6 Top	L6-120/125	L6-205/210	G2 Top	G2-30/35
epifaunal, sessil on plants / hard substrat	33,67	14,67	33,00	35,17	36,66	23,67	18,83	14,67	16,17
epifaunal, free on sediment / plants	9,83	26,50	19,33	21,67	17,00	21,33	19,33	14,83	15,33
epifaunal, sessil or vagil	18,83	41,33	32,67	28,83	29,17	40,83	48,17	30,67	34,67
infaunal to epifaunal, free in muddy sed.	0,00	0,00	0,33	0,17	0,33	0,17	0,33	0,00	0,33
infaunal, free in muddy sediment	34,67	8,67	8,50	3,16	6,17	9,00	8,67	26,50	25,83
others	3,00	8,83	6,17	11,00	10,67	5,00	4,67	13,33	7,67
	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

Mode of Life	G2-165/170	G2-300/305	G4 Top	G4-70/75	G4-127/132	G4-240/245	G5 Top	G5-70/75	G5-235/240
epifaunal, sessil on plants / hard substrat	12,17	14,00	25,33	10,67	12,67	20,83	10,67	17,17	17,50
epifaunal, free on sediment / plants	16,50	9,50	12,34	7,33	14,17	9,33	14,00	7,16	7,00
epifaunal, sessil or vagil	36,00	35,50	32,00	40,33	33,67	35,33	36,33	24,00	32,50
infaunal to epifaunal, free in muddy sed.	0,67	0,00	0,00	1,00	0,17	0,17	0,00	0,00	0,00
infaunal, free in muddy sediment	27,33	36,83	19,83	37,00	36,50	31,17	28,00	40,34	25,83
others	7,33	4,17	10,50	3,67	2,82	3,17	11,00	11,33	17,17
	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

Mode of Life	G5-420/425	G7 Top	G7-40/45	G7-120/125	G7-190/195	G7-285/290
epifaunal, sessil on plants / hard substrat	17,17	16,67	15,17	12,67	13,50	17,00
epifaunal, free on sediment / plants	3,67	13,50	19,50	13,84	12,83	10,83
epifaunal, sessil or vagil	47,67	31,67	36,83	39,33	33,50	38,17
infaunal to epifaunal, free in muddy sed.	0,00	0,00	0,67	0,00	0,83	0,00
infaunal, free in muddy sediment	20,82	31,00	21,83	30,00	35,50	28,83
others	10,67	7,16	6,00	4,16	3,84	5,17
	100,00	100,00	100,00	100,00	100,00	100,00

Appendix 5

Complete Dataset of $\delta^{18}O$ and $\delta^{13}C$ Values

Lighthouse Reef

sample		
L1/A-1 recent	**d 13C**	**d 18O**
1	4.63	-1.89
2	4.71	-2.21
3	4.71	-2.30
4	4.52	-1.94
5	4.45	-2.62
6	4.57	-2.41
7		
8	4.60	-2.17
9		
10	4.88	-1.94
11	4.69	-1.86
L1/B-1 recent	**d 13C**	**d 18O**
1	4.44	-2.00
2	4.37	-2.07
3	4.76	-2.02
4	4.31	-2.18
5	4.10	-2.20
6	4.14	-2.17
7	4.51	-1.93
8	4.36	-2.16
9	4.31	-2.26
10	4.33	-2.26
11	4.43	-2.23
L1 100/105-1	**d 13C**	**d 18O**
1	4.93	-1.64
2	4.65	-1.74
3	4.55	-1.85
4	4.32	-2.27
5	4.19	-2.42
6	4.05	-2.37
7	4.21	-2.50
8		
9	4.43	-2.19
10	4.77	-1.90
L1 100/105-2	**d 13C**	**d 18O**
1	4.73	-2.02
2	4.52	-2.23
3	5.01	-1.91
4	4.83	-2.29
5	4.72	-2.07
6	4.81	-2.20
7	4.61	-2.43
8	4.85	-2.19
9	4.89	-2.17
L1 100/105-3	**d 13C**	**d 18O**
1	4.68	-1.96
2	4.46	-2.60
3	4.55	-2.14
4	4.18	-2.41
5	3.97	-2.68
6	4.25	-2.66
7	4.20	-2.67
8	4.48	-2.54
L1 100/105-4	**d 13C**	**d 18O**
1	4.60	-2.06
2	4.55	-2.20
3	4.58	-2.48
4	4.25	-2.78
5	4.28	-2.99
6	4.60	-2.60
7	4.61	-2.33
L1 210/215-1	**d 13C**	**d 18O**
1	4.50	-2.00
2	4.88	-1.89
3	4.49	-2.12
4	4.51	-2.12
5	4.49	-2.14
6	4.52	-2.10
7	4.44	-1.94
8	4.57	-1.98
9	4.51	-1.84
10	4.40	-1.69
L1 210/215-2	**d 13C**	**d 18O**
1	4.76	-1.74
2	4.41	-2.01
3	4.96	-1.77
4	4.55	-2.00
5	4.41	-2.00
6	4.60	-2.01
7	4.64	-1.92
L1 210/215-3	**d 13C**	**d 18O**
1	5.04	-1.89
2	5.08	-1.83
3	5.06	-1.78
4	5.02	-1.84
5	4.90	-1.94

sample		
L1 235/240-1	**d 13C**	**d 18O**
1	4.47	-2.15
2	4.99	-2.19
3	4.68	-2.15
4	4.60	-2.22
5	4.38	-2.25
6	4.45	-2.17
7	4.54	-2.06
8	4.35	-2.00
9	4.41	-2.06
L1 235/240-2	**d 13C**	**d 18O**
1	4.49	-1.86
2		
3	4.58	-1.87
4	3.99	-2.22
L4/A-1 recent	**d 13C**	**d 18O**
1	4.17	-2.08
2	4.23	-2.09
3	4.53	-2.17
4	4.23	-2.3
5	4	-2.37
6	3.88	-2.43
7	3.67	-2.61
8	3.64	-2.6
9	3.65	-2.55
10	3.9	-2.41
11	3.91	-2.19
12	3.93	-2.13
L4/B-1 recent	**d 13C**	**d 18O**
1	3.80	-2.50
2	3.92	-2.28
3	4.12	-2.20
4	4.27	-2.01
5	4.38	-2.23
6	3.90	-2.64
7	3.80	-1.85
8	3.70	-2.10
9	3.74	-2.42
10	3.75	-2.41
11	3.57	-2.26
L4 40/45-1	**d 13C**	**d 18O**
1	4.95	-2.13
2	5.02	-1.94
3	4.94	-1.97
4	4.64	-2.11
5	4.41	-2.34
6	4.30	-2.33
7	4.42	-2.28
8	4.59	-2.08
9	4.80	-2.07
10	4.96	-1.86
L4 40/45-2	**d 13C**	**d 18O**
1	4.92	-1.74
2	4.92	-1.88
3	5.15	-1.91
4	4.83	-2.27
5	4.83	-2.26
6	4.82	-2.35
7		
8	4.59	-2.49
9	4.59	-2.57
10	4.81	-2.39
11	4.94	-2.40
12		
13	4.81	-1.87
L4 40/45-3	**d 13C**	**d 18O**
1	4.39	-1.80
2	4.38	-1.94
3	4.63	-2.25
4	4.71	-2.12
5	4.72	-1.98
6	4.60	-2.08
7	4.73	-2.03
8	4.76	-1.97
9	4.83	-2.05
10	4.47	-1.61
L4 40/45-4	**d 13C**	**d 18O**
1	5.10	-1.91
2	5.07	-2.00
3	4.67	-2.43
4	4.63	-2.49
5	4.60	-2.75
6	4.65	-2.65
7	4.54	-2.48

sample		
L4 125/130-1	**d 13C**	**d 18O**
1	5.00	-2.18
2	4.98	-1.97
3	4.84	-2.13
4	4.68	-2.08
5	4.58	-2.24
6	4.46	-2.26
7	4.49	-2.32
8	4.59	-2.27
9	4.70	-1.97
10	4.82	-1.97
L4 125/130-2	**d 13C**	**d 18O**
1	4.49	-1.95
2	4.21	-2.11
3	4.51	-2.10
4	4.49	-2.14
5	4.65	-2.26
6	4.45	-2.48
7	4.50	-2.36
8	4.38	-2.47
9	4.45	-2.39
10		
11	4.60	-2.26
L4 125/130-3	**d 13C**	**d 18O**
1	5.21	-1.88
2	5.05	-2.24
3	4.93	-2.26
4	4.26	-2.61
5	4.35	-2.67
6	4.43	-2.65
7	4.51	-2.43
8	4.53	-2.42
9	4.82	-2.34
10	4.29	-1.96
L4 125/130-4	d 13C	d 18O
1	4.59	-1.75
2	4.83	-1.61
3	4.75	-1.88
4	4.68	-1.89
5	4.73	-2.11
6	4.84	-2.05
7	4.98	-1.91
8	5.32	-1.70
9	5.19	-1.70
L4 240/245-1	**d 13C**	**d 18O**
1	4.23	-1.55
2	4.04	-1.88
3	4.01	-2.02
4	3.58	-2.51
5	3.45	-2.48
6	3.55	-2.46
7	3.66	-2.24
8	3.96	-2.28
9	4.22	-1.96
L4 240/245-2	**d 13C**	**d 18O**
1	4.00	-1.68
2	4.28	-1.61
3	4.22	-1.93
4	4.23	-1.62
5	4.10	-1.75
6	4.05	-1.98
7	4.09	-1.70
8	3.99	-1.71
9	4.14	-1.69
10	4.18	-1.54
L4 240/245-3	**d 13C**	**d 18O**
1	3.97	-1.65
2	3.91	-1.64
3	3.99	-1.56
4	3.83	-1.68
5	3.85	-1.82
6	3.88	-1.91
7	4.07	-1.75
8	4.11	-1.70
9	4.11	-1.63
10	4.14	-1.58

Lighthouse Reef

sample			sample			sample		
L5-1 recent	**d 13C**	**d 18O**	**L5 250/255-1**	**d 13C**	**d 18O**	**L6 120/125-2**	**d 13C**	**d 18O**
1	4.45	-2.06	1	4.46	-1.22	1	4.84	-2.06
2	4.37	-1.96	2	4.25	-1.26	2	4.58	-2.05
3	4.68	-2.15	3	4.44	-1.37	3	4.87	-1.96
4			4	4.41	-1.52	4	4.77	-2.20
5			5	4.40	-1.44	5	4.61	-2.27
6			6	4.47	-1.30	6	4.69	-2.16
7			**L5 250/255-2**	**d 13C**	**d 18O**	7	4.62	-2.15
8			1	4.52	-1.73	8	4.72	-2.00
9	4.41	-2.07	2	4.25	-2.00	9	4.78	-2.05
10	4.29	-2.09	3	4.33	-1.66	**L6 120/125-3**	**d 13C**	**d 18O**
11	4.28	-2	4	4.59	-1.33	1	5.10	-2.07
12	4.21	-2.06	5	4.43	-1.55	2	4.47	-2.27
13	4.24	-1.94	6	4.24	-2.02	3	4.58	-2.22
14	4.07	-2.03	**L5 340/345-1**	**d 13C**	**d 18O**	4	4.30	-2.17
15	3.99	-2.2	1	5.20	-1.83	5	4.14	-2.41
16	4.16	-2.07	2	4.74	-2.08	6	4.12	-2.25
L5 55/60-1	**d 13C**	**d 18O**	3	4.66	-2.10	7	4.10	-2.39
1	4.93	-1.74	4	4.81	-2.13	8	4.11	-2.36
2	5.18	-1.83	5	4.81	-2.19	9	4.16	-2.31
3	4.84	-1.76	6	5.11	-2.02	10	3.95	-1.86
4	4.76	-1.68	**L5 340/345-2**	**d 13C**	**d 18O**	**L6 205/210-1**	**d 13C**	**d 18O**
5	4.86	-1.53	1	4.35	-1.55	1	4.69	-1.57
L5 55/60-2	**d 13C**	**d 18O**	2	4.54	-1.63	2	4.74	-1.71
1	5.02	-1.52	3	4.45	-1.67	3	4.54	-1.94
2	4.68	-1.95	4	4.72	-1.77	4	4.17	-2.14
3	5.12	-1.79	5	4.79	-1.75	5	4.23	-2.09
4	4.74	-2.17	6			6	4.18	-2.25
5	4.73	-2.38	7	4.81	-1.62	7	4.26	-2.22
6	4.71	-2.83	8	4.78	-1.75	8	4.33	-2.04
7	4.79	-2.52	**L5 340/345-3**	**d 13C**	**d 18O**	9	4.52	-2.01
8	4.68	-2.59	1	4.06	-1.30	10	4.57	-1.94
9	5.38	-1.96	2	4.24	-1.34	**L6 205/210-2**	**d 13C**	**d 18O**
10	5.08	-1.83	3	4.00	-1.54	1	4.97	-2.07
L5 55/60-3	**d 13C**	**d 18O**	4	3.83	-1.68	2	4.60	-2.20
1	4.50	-1.21	5	3.88	-1.58	3	4.53	-2.30
2	4.62	-1.40	6	3.88	-2.11	4	4.53	-1.83
3	4.70	-1.29	**L5 340/345-4**	**d 13C**	**d 18O**	5	4.34	-1.96
4	4.55	-1.21	1	4.37	-1.38	6	4.43	-2.00
5	4.55	-1.04	2	4.55	-1.31	7	4.46	-1.80
6	4.65	-0.94	3	4.45	-1.55	8	4.50	-1.90
7	4.82	-0.86	4	4.42	-1.56	9	4.50	-1.90
8	5.12	-0.71	5	4.15	-1.65	10	4.29	-2.03
9	4.76	-0.94	6	4.42	-1.54	**L6 205/210-3**	**d 13C**	**d 18O**
L5 55/60-4	**d 13C**	**d 18O**	7	4.34	-1.67	1	4.52	-1.69
1	5.01	-1.74	**L6/A-1 recent**	**d 13C**	**d 18O**	2	4.12	-1.89
2	4.72	-2.10	1	3.77	-1.70	3	4.32	-1.95
3	4.90	-2.03	2	3.74	-1.87	4	4.63	-1.72
4	4.80	-2.11	3	3.94	-1.81	5	4.68	-1.84
5	4.62	-2.37	4	3.76	-1.72	6	4.62	-2.00
6	4.67	-2.47	5	3.58	-1.79	7	4.32	-2.02
7	4.66	-2.46	6	3.42	-1.83	8	4.64	-1.87
8	4.56	-2.44	7	3.50	-1.75	9	4.49	-2.19
9	4.90	-2.24	8	3.61	-1.75	10	4.82	-1.89
10	4.78	-2.13	9	3.64	-1.54			
L5 130/135-1	**d 13C**	**d 18O**	10	3.62	-1.57			
1	4.85	-2.03	11	3.90	-1.43			
2	4.77	-1.91	12	4.00	-2.02			
3	4.70	-1.82	**L6/B-2 recent**	**d 13C**	**d 18O**			
4	4.39	-1.94	1	3.78	-1.89			
5	4.38	-1.91	2	3.46	-2.09			
6	4.34	-1.83	3	3.79	-1.68			
7	4.18	-1.73	4	3.90	-1.44			
8	4.26	-1.79	5	3.72	-1.47			
9	4.32	-1.79	6	3.62	-1.48			
10	4.39	-1.68	7	3.56	-1.71			
L5 130/135-2	**d 13C**	**d 18O**	8	3.60	-1.58			
1	4.75	-1.99	9	3.77	-1.36			
2	4.47	-2.41	10	3.64	-1.43			
3	4.87	-2.21	11	3.71	-1.47			
4			12	3.64	-1.44			
5	4.77	-2.34	13	3.57	-1.42			
6	4.67	-2.51	14	3.73	-1.39			
7	4.72	-2.65	15	3.58	-1.38			
8	4.89	-2.53	**L6 120/125-1**	**d 13C**	**d 18O**			
9	4.95	-2.34	1	5.10	-1.94			
10	5.05	-2.14	2	5.10	-2.33			
L5 130/135-3	**d 13C**	**d 18O**	3	4.62	-2.55			
1	4.81	-1.54	4	4.35	-2.73			
2	4.70	-1.52	5	4.38	-2.68			
3	4.74	-1.57	6	4.48	-2.30			
4	4.71	-1.56	7	4.60	-2.17			
5	4.79	-1.57	8					
6	4.95	-1.50	9	4.62	-1.89			
7	4.78	-1.51	10	4.65	-2.06			

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sample		
G2-1 recent	**d 13C**	**d 18O**
1	4.73	-1.59
2		
3	4.64	-2.10
4	4.61	-1.99
5	4.59	-2.12
6	4.58	-2.06
7	4.42	-2.20
8	4.17	-2.27
9	4.49	-2.11
10	4.65	-1.92
11	4.69	-1.74
12	5.04	-1.51
G2 30/35-1	**d 13C**	**d 18O**
1	4.57	-1.62
2	4.49	-1.60
3	4.71	-1.46
4	4.32	-1.25
5	4.36	-1.20
6	4.40	-1.15
7	4.38	-1.14
8	4.54	-1.15
9	4.49	-1.11
10	4.50	-1.16
G2 30/35-2	**d 13C**	**d 18O**
1	5.04	-1.57
2	4.78	-1.89
3	4.58	-1.50
4	4.24	-1.53
5	4.13	-1.75
6	4.00	-1.62
7	4.08	-1.70
8	4.16	-1.60
9	4.16	-1.44
10	4.30	-1.41
11	4.41	-1.20
12	4.34	-1.30
G2 30/35-3	**d 13C**	**d 18O**
1	4.59	-1.86
2	4.52	-2.01
3	4.26	-2.28
4	4.17	-2.32
5	3.92	-2.5
6		
7	3.79	-2.45
8	3.96	-2.36
9	3.99	-2.37
10		
11	4.09	-2.01
G2 165/170-1	**d 13C**	**d 18O**
1	4.64	-1.63
2		
3	4.36	-1.94
4	4.52	-2.04
5	4.45	-2.03
6	4.00	-2.31
7	4.07	-2.03
8	3.87	-2.03
9	4.09	-1.86
10	4.09	-1.74
11	4.14	-1.81
12	4.20	-1.88
13	4.34	-1.65
14	4.52	-1.40
G2 165/170-2	**d 13C**	**d 18O**
1	4.23	-1.97
2	3.96	-2.06
3	3.86	-1.70
4	3.99	-1.64
5	3.98	-1.73
6	3.90	-1.68
7	4.03	-1.60
8	4.03	-1.53
9	3.87	-1.53
10	3.92	-1.41
G2 165/170-3	**d 13C**	**d 18O**
1	4.27	-1.69
2	4.21	-1.81
3	4.05	-1.81
4	4.02	-1.66
5	4.15	-1.53
6	4.10	-1.36
7	4.06	-1.31
8	4.15	-1.43
9	4.05	-1.37
10	4.08	-1.30
11	4.64	-1.40

sample		
G2 300/305-1	**d 13C**	**d 18O**
1	4.21	-1.97
2	4.19	-2.00
3	4.37	-1.95
4	4.19	-1.76
5	4.21	-1.75
6	4.27	-1.74
7	4.03	-1.88
8	3.94	-2.00
9	4.30	-1.74
10	4.09	-1.86
11	3.96	-1.96
12	4.14	-1.69
13	4.09	-1.39
G2 300/305-2	**d 13C**	**d 18O**
1	4.11	-1.54
2	4.28	-2.02
3	4.38	-2.29
4	4.07	-2.50
5	3.71	-2.63
6	4.11	-2.35
7		
8	4.13	-2.28
9	4.13	-2.02
10	4.57	-1.99
G2 300/305-3	**d 13C**	**d 18O**
1	4.44	-1.74
2	4.25	-2.04
3	4.24	-2.15
4	4.28	-2.20
5	4.12	-2.41
6	4.16	-2.41
7	4.29	-2.34
8	4.25	-2.38
9	4.42	-2.22
10	4.42	-2.40
11	4.42	-2.33
12	4.32	-1.87
G4-1 recent	**d 13C**	**d 18O**
1	4.35	-1.72
2	4.34	-1.76
3	4.35	-1.94
4	4.43	-1.87
5	4.24	-1.85
6	4.13	-2.08
7	4.41	-1.90
8	4.51	-1.98
9	4.53	-1.94
10	4.80	-1.59
G4 70/75-1	d 13C	d 18O
1	4.41	-1.55
2	4.23	-1.89
3	4.17	-2.12
4	4.45	-1.91
5	4.34	-1.97
6	4.00	-2.00
7	3.97	-1.84
8	4.04	-1.71
9	4.08	-1.50
10	4.09	-1.51
11	4.25	-1.53
12	4.30	-1.31
G4 70/75-2	**d 13C**	**d 18O**
1	4.50	-1.36
2	4.46	-1.62
3	4.38	-1.81
4	4.54	-1.96
5	4.29	-2.11
6	3.92	-1.97
7	3.83	-1.63
8	3.95	-1.56
9	4.09	-1.41
10	4.19	-1.43
11	4.16	-1.27
G4 70/75-3	**d 13C**	**d 18O**
1	4.36	-1.81
2	4.23	-2.19
3	4.43	-1.97
4	4.34	-1.78
5	4.24	-1.73
6	4.19	-1.96
7	4.22	-1.90
8	4.19	-1.82
9	4.16	-1.79
10	4.19	-1.54
11	4.15	-1.57
12	4.26	-1.60

sample		
G4 127/132-1	**d 13C**	**d 18O**
1	4.32	-1.40
2	4.48	-1.35
3	4.47	-1.52
4	4.14	-1.81
5	4.17	-2.02
6	4.41	-1.78
7	4.51	-1.70
G4 127/132-2	**d 13C**	**d 18O**
1	4.05	-1.62
2	4.07	-1.69
3	4.07	-1.75
4	3.77	-2.26
5	4.21	-1.96
G4 240/245-1	**d 13C**	**d 18O**
1	3.73	-2.05
2	4.13	-1.89
3	4.23	-1.47
4		
5	4.36	-1.18
6	4.40	-1.29
7	4.40	-1.31
8	4.41	-1.33
G4 240/245-2	**d 13C**	**d 18O**
1	4.28	-1.64
2	4.28	-1.76
3	4.33	-1.67
4	4.36	-1.55
5	4.27	-1.48
6	4.17	-1.62
7	4.20	-1.66
8	4.19	-1.65
9	4.25	-1.59
10	4.22	-1.49
11	4.56	-1.32
12	4.22	-1.46
G4 240/245-3	**d 13C**	**d 18O**
1	4.13	-1.69
2	4.13	-2.13
3	4.51	-2.24
4	4.45	-2.46
5	4.35	-2.55
6	4.33	-2.50
7	4.30	-2.45
8	4.38	-2.31
9	4.32	-2.32
10	4.33	-1.79
G5-1 recent	**d 13C**	**d 18O**
1	4.33	-1.29
2	4.38	-1.46
3	4.20	-1.47
4	3.93	-1.44
5	3.85	-1.85
6	3.80	-1.78
7	3.73	-1.78
8	3.85	-1.75
9	3.85	-1.70
10	3.87	-1.76
11	4.03	-1.59
12	4.09	-1.68
13	4.40	-1.61
G5 235/240-1	**d 13C**	**d 18O**
1	4.48	-1.72
2	4.61	-1.80
3	4.63	-1.88
4	4.43	-2.05
5	4.46	-2.11
6	4.52	-2.05
G5 235/240-2	**d 13C**	**d 18O**
1	4.56	-1.54
2	4.49	-1.40
3	4.40	-1.65
4	4.10	-1.93
5	4.28	-1.95
6	4.43	-1.91
7	4.63	-1.86
G5 235/240-3	**d 13C**	**d 18O**
1	4.62	-1.66
2	4.68	-1.75
3	4.49	-1.85
4	4.62	-1.66
5	4.57	-1.68
6	4.32	-1.68

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sample		
G5 420/425-1	**d 13C**	**d 18O**
1	4.21	-1.36
2	4.35	-1.29
3	4.18	-1.31
4	4.23	-1.34
5	4.49	-1.33
6	4.92	-1.11
G7-1 recent	**d 13C**	**d 18O**
1	4.35	-2.14
2	4.40	-2.05
3	4.56	-1.98
4	4.46	-1.97
5	4.40	-1.98
6	4.05	-1.95
7	4.15	-1.90
8	4.19	-1.89
9	4.23	-1.72
10	4.32	-1.78
11		
12	4.31	-1.58
G7 40/45-1	**d 13C**	**d 18O**
1	4.47	-1.99
2	4.61	-1.86
3	4.59	-1.93
4	4.79	-2.02
5	4.87	-1.94
6	4.83	-2.01
7	4.67	-2.11
8	4.80	-2.05
9	4.76	-2.16
10	4.87	-1.96
11	4.80	-1.73
G7 40/45-2	**d 13C**	**d 18O**
1	4.65	-1.39
2	4.39	-1.74
3	4.27	-1.69
4	4.45	-1.61
5	4.55	-1.61
6	4.43	-1.75
7	4.60	-1.74
8	4.79	-1.52
9		
10	4.66	-1.72
11	4.66	-1.69
12	4.97	-1.26
13	4.72	-1.21
G7 40/45-3	**d 13C**	**d 18O**
1	4.43	-1.68
2	4.41	-1.80
3	4.45	-1.67
4	4.83	-1.37
5	4.89	-1.40
6	4.84	-1.51
7	4.76	-1.57
8	4.76	-1.61
9	5.03	-1.36
10	5.01	-1.45
11	4.92	-1.28
12	4.46	-1.43
G7 120/125-	**d 13C**	**d 18O**
1	4.41	-1.55
2	4.50	-1.91
3	4.31	-1.96
4	4.64	-2.00
5	4.22	-2.24
6	4.14	-2.36
7	4.25	-2.19
8	4.39	-1.98
9	4.45	-2.00
10	4.40	-1.88
11	4.63	-1.70
12	4.50	-1.72
G7 120/125-2	d 13C	d 18O
1	4.57	-1.79
2	4.56	-1.81
3	4.63	-1.82
4	4.85	-1.78
5	4.63	-2.04
6	4.34	-2.09
7	4.33	-2.13
8	4.39	-2.20
9	4.63	-2.12
10	4.79	-2.03
11	4.91	-1.95
12	5.06	-1.80
sample		
G7 120/125-3	**d 13C**	**d 18O**
1	4.45	-1.41
2	4.08	-1.83
3	4.39	-1.66
4	4.35	-1.96
5	4.35	-2.33
6	3.99	-2.39
7	4.18	-2.13
8	4.13	-2.14
9	4.45	-1.87
10	4.42	-1.57
G7 190/195-1	**d 13C**	**d 18O**
1	4.72	-1.43
2	4.31	-1.95
3	4.31	-2.06
4	4.80	-1.90
5	4.64	-1.99
6	4.47	-2.04
7	4.39	-2.12
8	4.23	-2.17
9	4.29	-2.17
10	4.28	-2.28
11	4.67	-2.09
12	4.95	-1.96
G7 190/195-2	**d 13C**	**d 18O**
1	4.86	-2.45
2	4.92	-2.26
3	4.80	-2.19
4	4.46	-2.2
5	4.52	-2.06
6	4.41	-2.17
7	4.36	-2.08
8	4.40	-1.98
9	4.57	-1.46
G7 190/195-3	**d 13C**	**d 18O**
1	4.23	-1.77
2	4.23	-1.87
3	4.35	-2.03
4	4.73	-1.96
5	4.57	-2.11
6	4.42	-2.03
7	4.27	-2.22
8	4.21	-2.09
9	4.54	-1.91
10	4.52	-2.01
11		
12	4.23	-1.34
G7 285/290-1	**d 13C**	**d 18O**
1	4.62	-1.70
2	4.39	-2.01
3	4.24	-2.17
4	4.40	-1.94
5	4.15	-2.10
6	4.29	-1.99
7	4.33	-1.79
8	4.36	-1.74
9	4.43	-1.80
10	4.34	-1.76
11	4.24	-1.75
12	4.24	-1.59
13	4.29	-1.58
14	4.41	-1.33
15	4.28	-1.38
16	4.31	-1.50
17	4.51	-1.28
G7 285/290-2	d 13C	d 18O
1	4.43	-1.54
2	4.17	-1.88
3	4.40	-1.59
4	4.42	-1.31
5	4.14	-1.25
6	4.02	-1.44
7	4.07	-1.45
8	4.21	-1.30
9	4.39	-1.23
10	4.05	-1.40
G7 285/290-3	d 13C	d 18O
1	4.53	-1.65
2	4.58	-1.76
3	4.46	-1.94
4	4.67	-1.93
5	4.49	-2.20
6	4.47	-2.18
7	4.59	-2.09
8	4.46	-1.91

Appendix 6

Plates

Plate 1a

High-Diversity Miliolid Assemblage

Fig. 1	*Quinqueloculina poeyana* d`Orbigny, 1839
Fig. 2	*Quinqueloculina candeiana* d`Orbigny, 1839
Fig. 3	*Triloculina bermudezi* Acosta, 1940
Fig. 4	*Articulina mexicana* Cushman, 1921
Figs. 5a, b	*Discorbis mira* Cushman, 1922 Fig. 5a: ventral view (apertural) Fig. 5b: spiral view (dorsal)
Fig. 6	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Fig. 7	*Elphidium discoidale* (d´Orbigny), 1839
Fig. 8	*Rosalina floridana* (Cushman), 1922
Fig. 9	*Elphidium advenum* (Cushman), 1922
Fig. 10	*Elphidium sagrum* (d`Orbigny), 1839
Fig. 11	*Bolivina strialula* Cushman, 1922
Fig. 12	*Planorbulina acervalis* Brady, 1884
Fig. 13	*Vertebralina cassis* d`Orbigny, 1839
Fig. 14	*Vertebralina atlantica* (Cushman & Hanzawa), 1937
Fig. 15	*Bolivina pulchella* (d`Orbigny) var. *primitiva* Cushman, 1930

Plate 1a

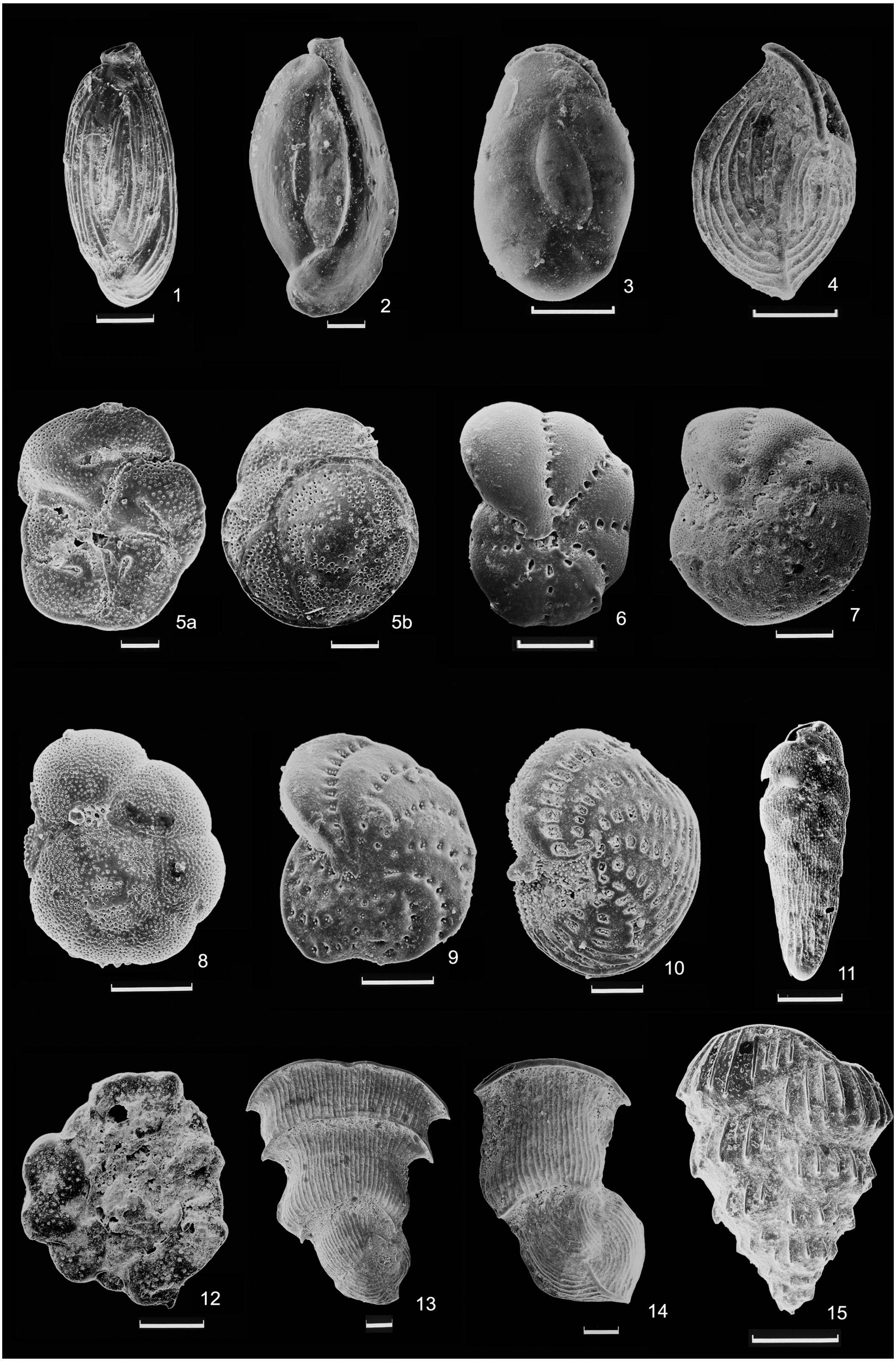
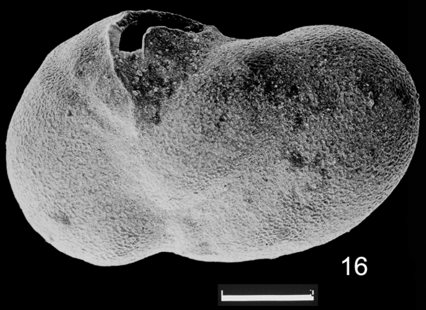


Plate 1b

High-Diversity Miliolid Assemblage

Fig. 16	*Miliolinella labiosa* (d`Orbigny), 1839
Fig. 17	*Miliolinella circularis* (Bornemann), 1855
Fig. 18	*Nonion despressulum* (Walker & Jacob) var. *matagordanum* Kornfeld, 1931
Fig. 19	*Quinqueloculina laevigata* d`Orbigny, 1826
Fig. 20	*Heterillina cribostoma* (Heron-Allen & Earland), 1915
Fig. 21	*Triloculina linneiana* var. *comis* Bandy, 1956
Fig. 22	*Valvulina oviedoiona* d`Orbigny, 1839
Fig. 23	*Triloculina carinata* d`Orbigny, 1839
Fig. 24	*Articulina lineata* Brady, 1884
Fig. 25	*Spiroloculina arenata* Cushman, 1921
Fig. 26	*Miliolinella fichtellliana* (d`Orbigny), 1839
Fig. 27	*Cibicides lobatulus* (Walker & Jacob), 1798
Fig. 28	*Ammonia beccarii* (Linné), 1772

Plate 1b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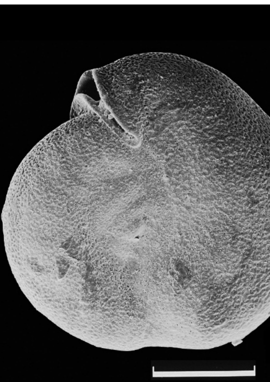
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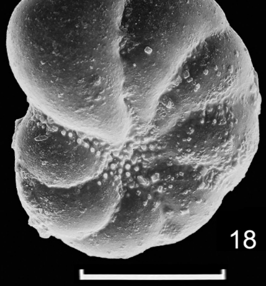
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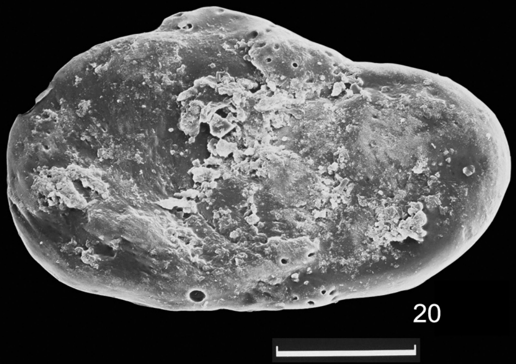
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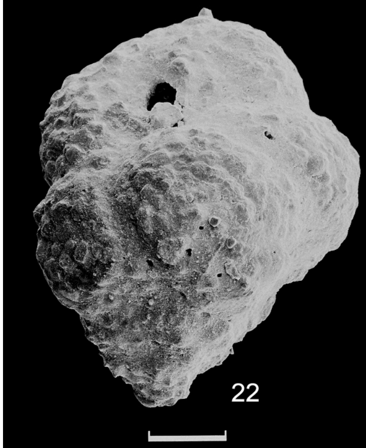
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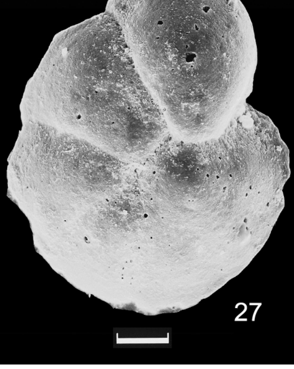
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Plate 2a

Cribroelphidium poeyanum-Elphidium-Dominant Assemblage

Fig. 1	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Fig. 2	*Elphidium advenum* (Cushman), 1922
Fig. 3	*Elphidium sagrum* (d`Orbigny), 1839
Fig. 4	*Elphidium discoidale* (d´Orbigny), 1839
Fig. 5	*Cellanthus gunteri* (Cole), 1931
Fig.6	*Florilus atlanticus* (Cushman), 1947
Fig. 7	*Nonion despressulum* (Walker & Jacob) var. *matagordanum* Kornfeld, 1931
Figs. 8a, b	*Amphistegina gibbosa* d`Orbigny, 1839 Fig. 8a: ventral view (apertural) Fig. 8b: spiral view (dorsal)
Fig. 9	*Rosalina floridana* (Cushman), 1922
Figs. 10a, b, c	*Cibicides lobatulus* (Walker & Jacob), 1798 Fig. 10a: spiral view (dorsal) Fig. 10b: ventral view (apertural) Fig. 11c: side view

Plate 2a


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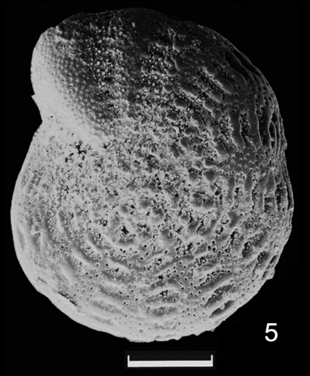
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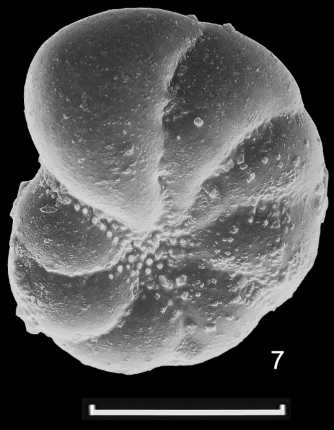
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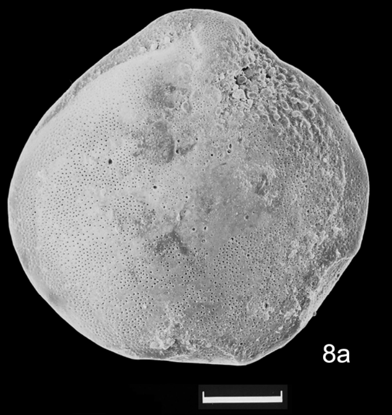
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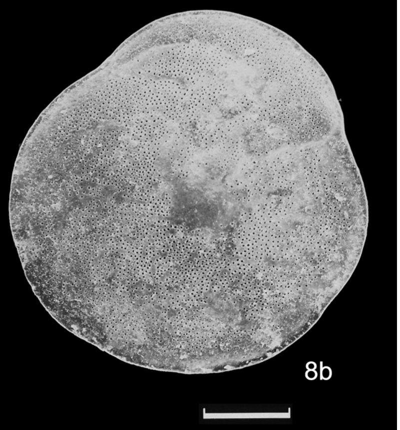
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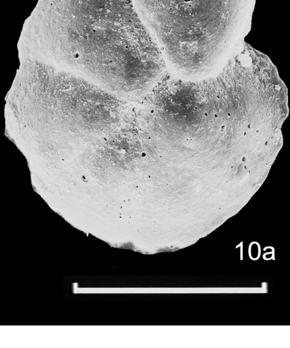
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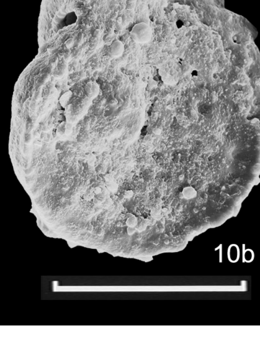
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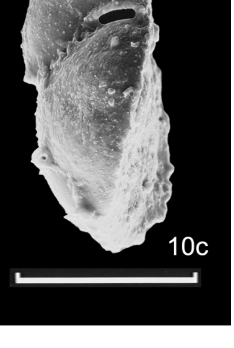
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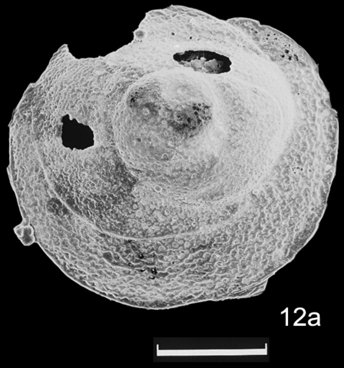
Plate 2b

Cribroelphidium poeyanum-Elphidium-Dominant Assemblage

Fig. 11	*Quinqueloculina poeyana* d`Orbigny, 1839
Figs. 12a, b	*Neoconorbina orbicularis* (Terquem), 1876
Figs. 13a, b	*Eponides antillarum* (d`Orbigny), 1839
Fig. 14	*Ammonia beccarii* (Linné), 1772
Fig. 15	*Vertebralina cassis* d`Orbigny, 1839
Fig. 16	*Triloculina linneiana* var. *comis* Bandy, 1956
Fig. 17	*Bolivina lowmani* Phleger & Parker, 1951
Fig. 18	*Bolivina strialula* Cushman, 1922
Fig. 19	*Bolivinita rhomboidales* (Millet), 1899
Fig. 20	*Bolivina lanceolata* Parker, 1954

Plate 2b

11



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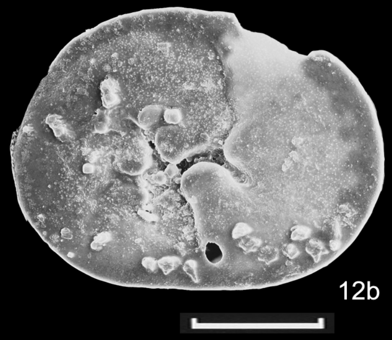

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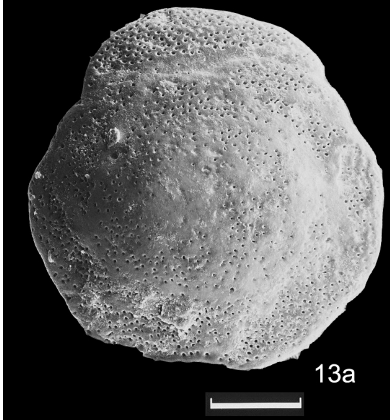

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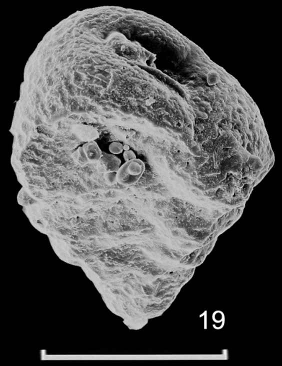

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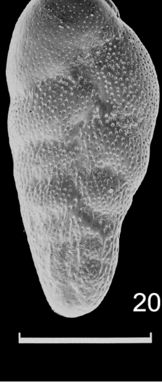

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Plate 3

Low-Diversity *Cribroelphidium poeyanum*-Dominant Assemblage

Figs. 1a-c	*Cribroelphidium poeyanum* (d`Orbigny), 1839
	Fig. 1a: side view
	Fig. 1b: apertural view
	Fig. 1c: side view
	Fig. 1d: apertural view
Figs. 2a, b	*Florilus atlanticus* (Cushman), 1947
	Fig. 2a: spiral view (dorsal)
	Fig. 2b: ventral view (apertural)
Fig. 3	*Florilus atlanticus* (Cushman), 1947
Figs. 4a, b, c	*Quinqueloculina candeiana* d`Orbigny, 1839
	Fig. 4a: 4-chamber side
	Fig. 4b: 3-chamber side
	Fig. 4c: aperture
Fig. 5	*Cellanthus gunteri* (Cole), 1931
Figs. 6a, b, c	*Quinqueloculina laevigata* d`Orbigny, 1826
	Fig. 6a: 4-chamber side
	Fig. 6b: 3-chamber side
	Fig. 6c: aperture
Fig. 7	*Quinqueloculina lamarckiana* (d`Orbigny), 1839

Plate 3

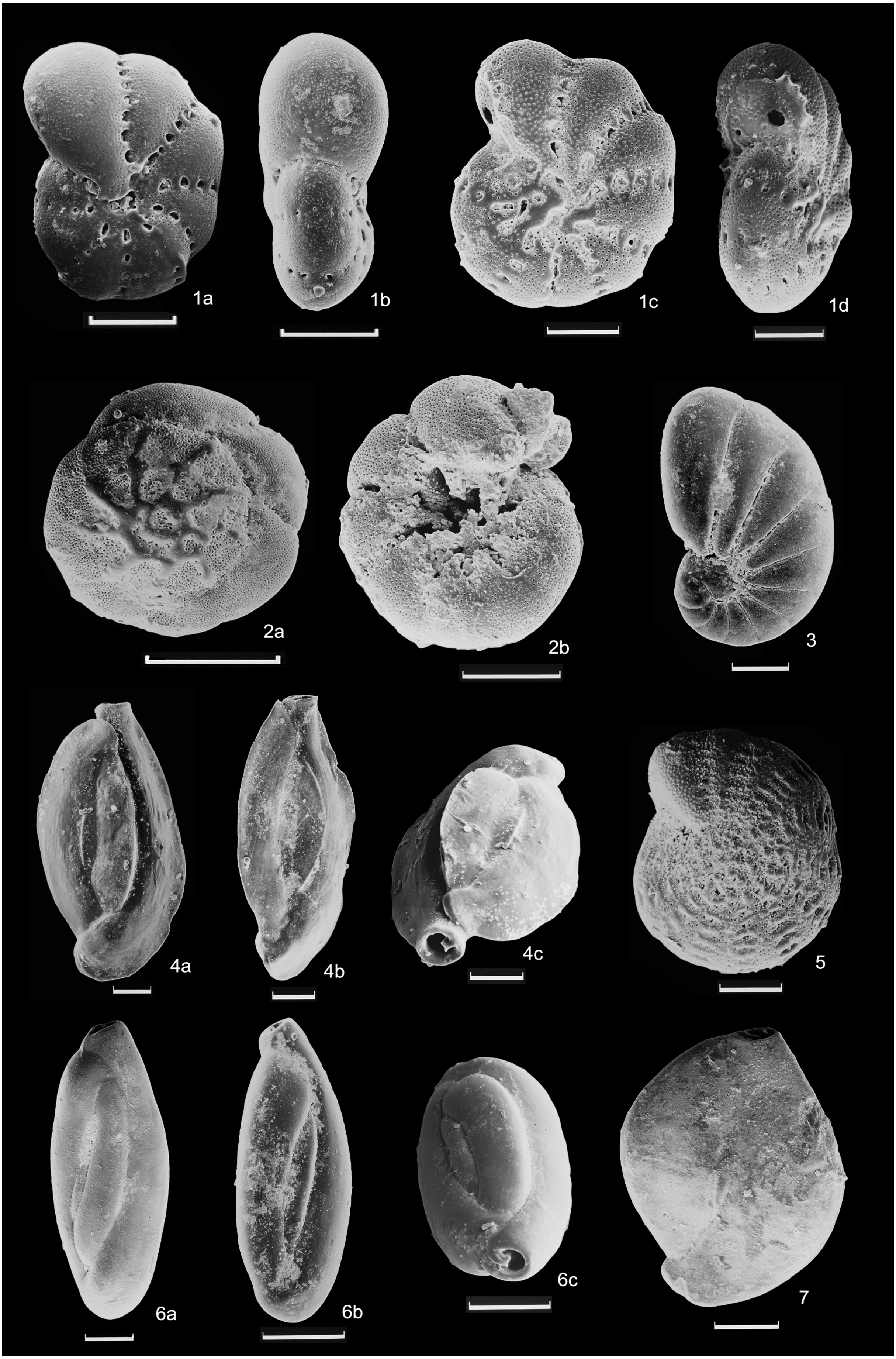

Plate 4

Quinqueloculina-Triloculina-Peneroplis Assemblage

Fig. 1	*Triloculina linneiana* var. *comis* Bandy, 1956
Fig. 2	*Quinqueloculina lamarckiana* (d`Orbigny), 1839
Fig. 3	*Quinqueloculina candeiana* d`Orbigny, 1839
Fig. 4	*Peneroplis proteus* d`Orbigny, 1839
Fig. 5	*Triloculina bicarinata* (d`Orbigny), 1839
Fig. 6	*Quinqueloculina poeyana* d`Orbigny, 1839
Fig. 7	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Fig. 8	*Triloculina bassensis* Parr, 1945
Fig. 9	*Discorbis mira* Cushman, 1922
Fig. 10	*Archaias angulatus* (Fichtel & Moll), 1803
Fig. 11	*Amphistegina gibbosa* d`Orbigny, 1839
Fig. 12	*Clavulina tricarinata* d`Orbigny, 1839
Fig. 13	*Peneroplis pertusus* (Forskal), 1775
Fig. 14	*Pyrgo denticulata* (Brady), 1884
Fig. 15	*Nodobaculariella cassis* d`Orbigny, 1839

Plate 4


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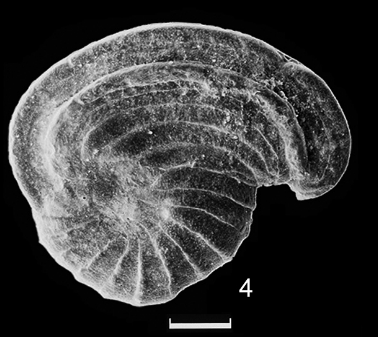
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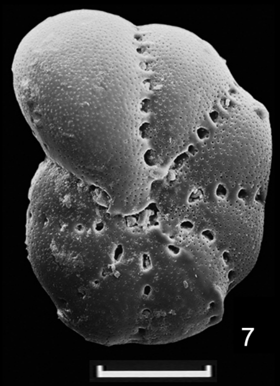
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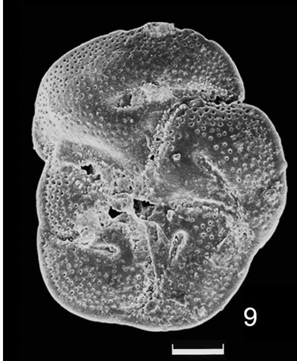
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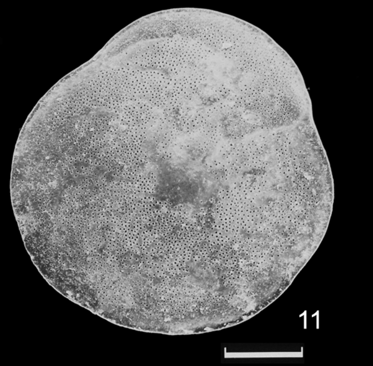
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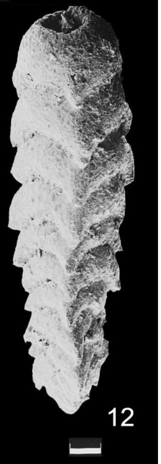
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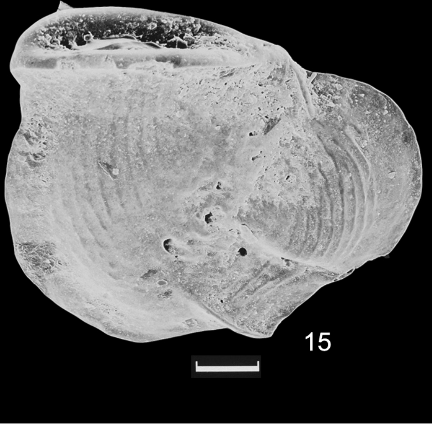
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Plate 5a

Archaias angulatus-Miliolid Assemblage

Fig. 1	*Archaias angulatus* (Fichtel & Moll), 1803
Fig. 2	*Parasorites orbitolitoides* (Hofker)
Fig. 3	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Figs. 4a, b, c	*Triloculina bassensis* Parr, 1945 Fig. 4a: 3-chamber side Fig. 4b: 2-chamber side Fig. 4c: aperture
Fig. 5	*Florilus atlanticus* (Cushman), 1947
Figs. 6a, b,c	*Quinqueloculina bicostata* d`Orbigny, 1839 Fig. 6a: 4-chamber side Fig. 6b: 3-chamber side Fig. 6c: aperture
Figs. 7a, b, c	*Triloculina bermudezi* Acosta, 1940 Fig. 7a: 3-chamber side Fig. 7b: 2-chamber side Fig. 7c: aperture
Figs. 8a, b	*Quinqueloculina poeyana* d`Orbigny, 1839 Fig. 8a: 4-chamber side Fig. 8b: 3-chamber side

Plate 5a

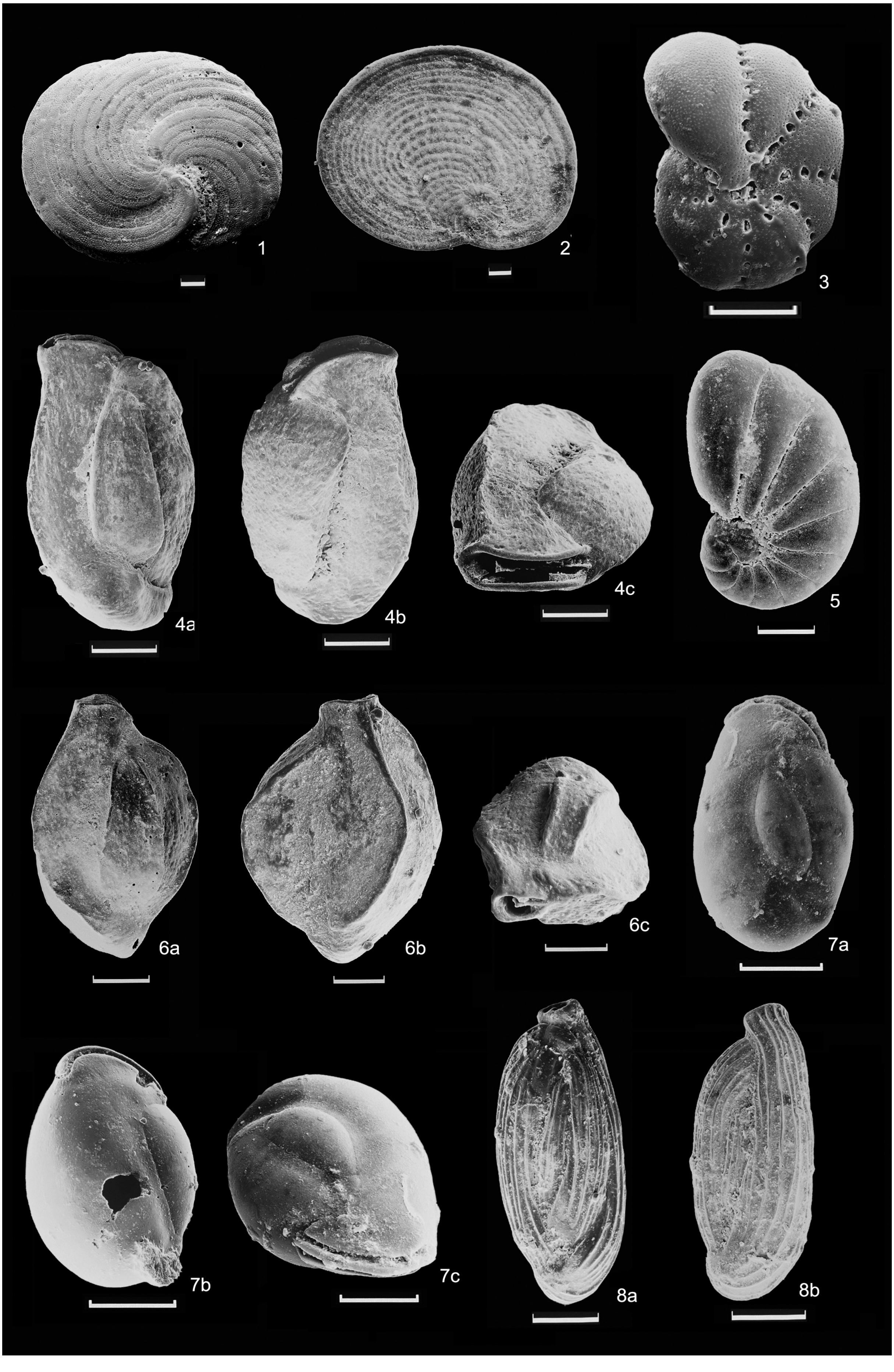
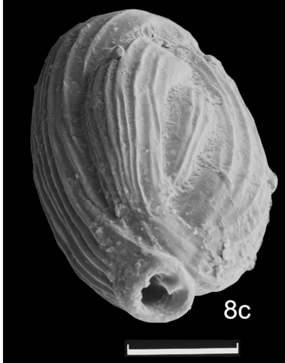


Plate 5b

Archaias angulatus-Miliolid Assemblage

Fig. 8c	*Quinqueloculina poeyana* d`Orbigny, 1839 Fig. 8c: aperture
Figs. 9a, b, c	*Triloculina trigonula* (Lamarck), 1804 Fig. 9a: 3-chamber side Fig. 9b: 2-chamber side Fig. 9c: aperture
Figs. 10a, b, c	*Quinqueloculina* cf. *bradyana* Cushman, 1917 Fig. 10a: 4-chamber side Fig. 10b: 3-chamber side Fig. 10c: aperture
Figs. 11a, b, c	*Triloculina linneiana* var. *comis* Bandy, 1956 Fig. 11a: 2-chamber side Fig. 11b: 3-chamber side Fig. 11c: aperture
Figs. 12a, b	*Triloculina linneiana* d`Orbigny, 1839 Fig. 12a: 3-chamber side Fig. 12b: aperture
Fig. 13	*Miliolinella labiosa* (d`Orbigny), 1839
Figs. 14a, b, c	*Quinqueloculina bosciana* d`Orbigny, 1839 Fig. 14a: 4-chamber side Fig. 14b: 3-chamber side Fig. 14c: aperture

Plate 5b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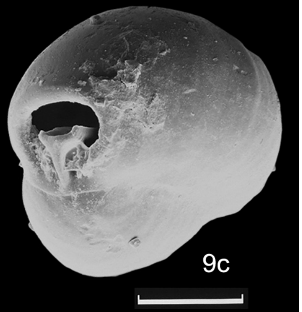
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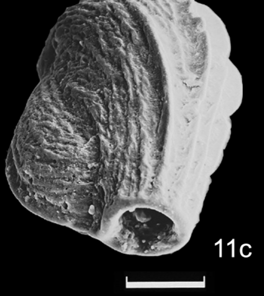
11a


11b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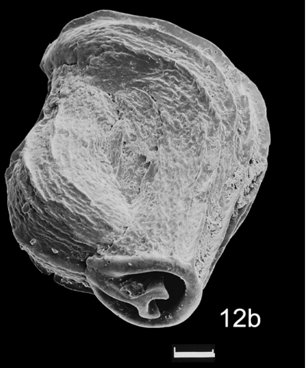
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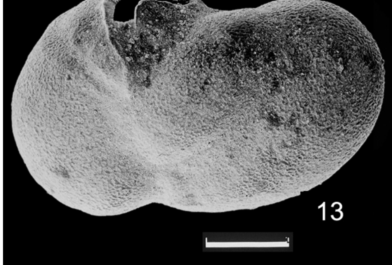
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14a


14b


14c

Plate 5c

Archaias angulatus-Miliolid Assemblage

Fig. 15	*Cornusspira planorbis* Schultze var. *Ammodiscus* sp.
Figs. 16a, b	*Cymbaloporetta squammosa* (d`Orbigny), 1826 Fig. 16a: doral view Fig. 16b: ventral view
Fig. 17	*Clavulina tricarinata* d`Orbigny, 1839
Fig. 18	*Cellanthus gunteri* (Cole), 1931
Fig. 19	*Peneroplis pertusus* (Forskal), 1775
Fig. 20	*Peneroplis proteus* d`Orbigny, 1839
Fig. 21	*Rosalina candeiana* d´Orbigny, 1839
Fig. 22	*Textularia conica* d´Orbigny, 1839
Fig. 23	*Triloculina fitterei* var. *meningoi* Acosta, 1940
Figs. 24a, b	*Triloculina sidebottomi* (Martinotti), 1920 Fig. 24a: 3-chamber side Fig. 24b: aperture
Fig. 25	*Homotrema rubrum* (Lamarck), 1816

Plate 5c


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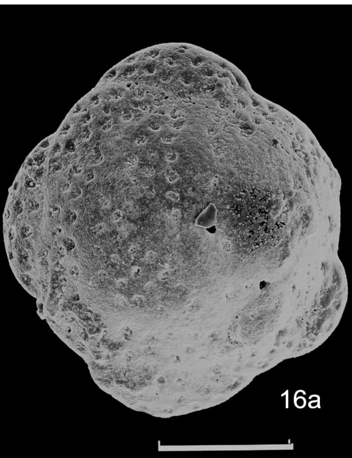
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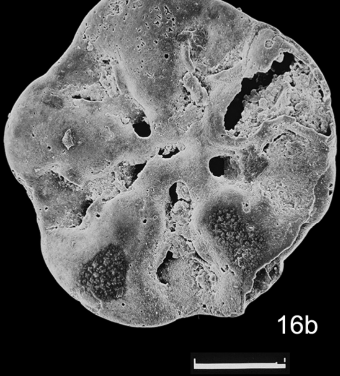
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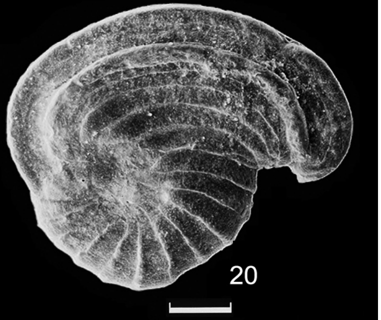
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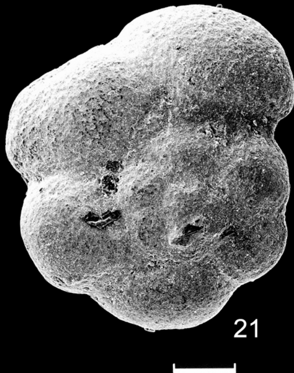
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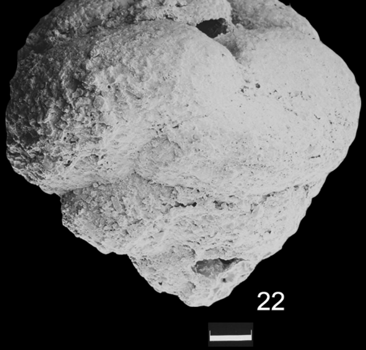
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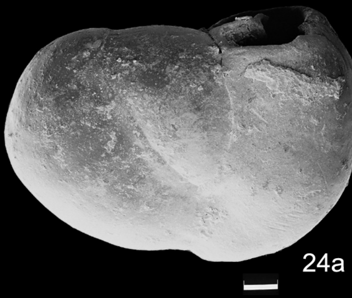
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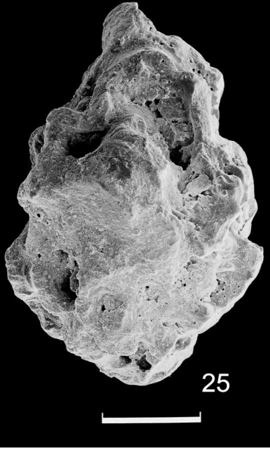
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Plate 6a

Lower-Diversity Miliolid Assemblage

Fig. 1	*Quinqueloculina poeyana* d`Orbigny, 1839
Fig. 2	*Archaias angulatus* (Fichtel & Moll), 1803
Fig. 3	*Miliolinella labiosa* (d`Orbigny), 1839
Fig. 4	*Triloculina fitterei* var. *meningoi* Acosta, 1940
Fig. 5	*Quinqueloculina poeyana* d`Orbigny, 1839
Fig. 6	*Triloculina bermudezi* Acosta, 1940
Fig. 7	*Triloculina bassensis* Parr, 1945
Fig. 8	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Figs. 9a, b	*Heterillina cribostoma* (Heron-Allen & Earland), 1915 Fig. 9a: side view Fig. 9b: aperture
Fig. 10	*Articulina lineata* Brady, 1884
Fig. 11	*Cellanthus gunteri* (Cole), 1931
Fig. 12	*Quinqueloculina bicostata* d`Orbigny, 1839
Fig. 13	*Clavulina tricarinata* d`Orbigny, 1839
Fig. 14	*Miliolinella circularis* (Bornemann), 1855

Plate 6a

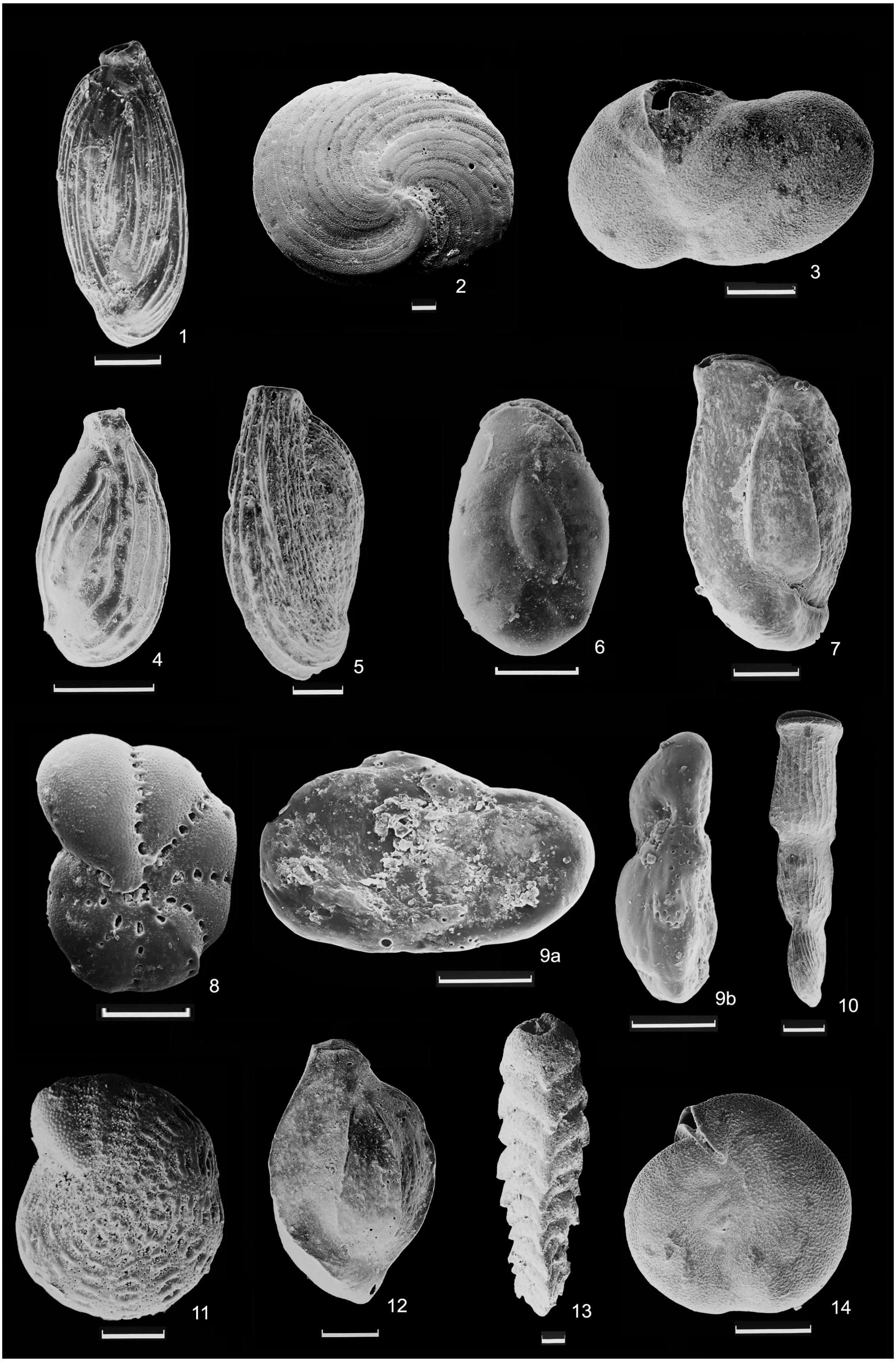
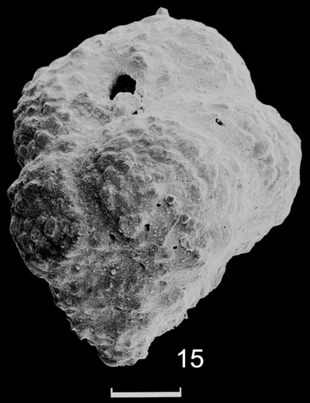


Plate 6b

Lower-Diversity Miliolid Assemblage

Fig. 15	*Valvulina oviedoiona* d`Orbigny, 1839
Fig. 16	*Elphidium discoidale* (d´Orbigny),
Fig. 17	*Rosalina candeiana* d´Orbigny, 1839
Fig. 18	*Quinqueloculina bidentata* d`Orbigny, 1839
Fig. 19	*Quinqueloculina lamarckiana* (d`Orbigny), 1839
Fig. 20	*Quinqueloculina laevigata* d`Orbigny, 1826
Fig. 21	*Tretomphalos atlanticus* Cushman, 1934
Fig. 22	*Articulina mexicana* Cushman, 1921
Fig. 23	*Florilus atlanticus* (Cushman), 1947
Fig. 24	*Homotrema rubrum* (Lamarck), 1816
Fig. 25	*Quinqueloculina crassa* var. *subcuneata* Cushman, 1921
Fig. 26	*Asterigerina carinata* d`Orbigny, 1839
Fig. 27	*Neoconorbina orbicularis* (Terquem), 1876
Fig. 28	*Ammonia beccarii* (Linné), 1772

Plate 6b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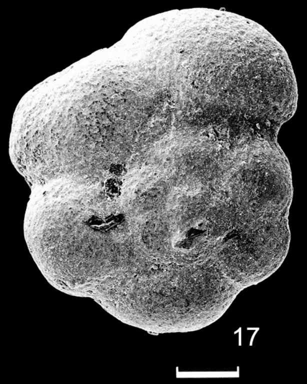
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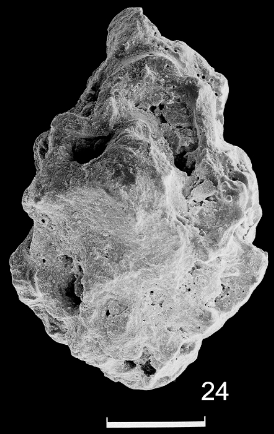
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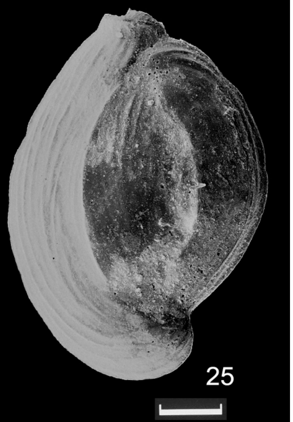
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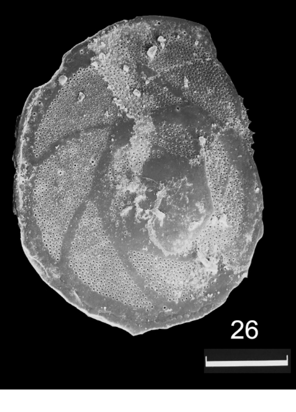
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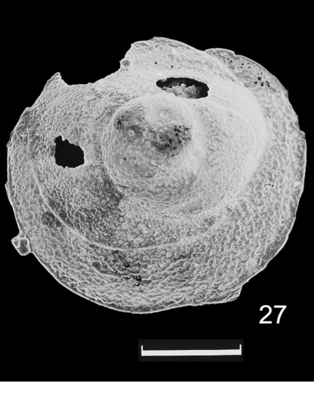
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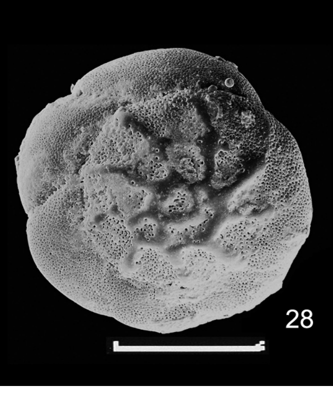
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Plate 7a

Mixed Assemblage

Fig. 1	*Cribroelphidium poeyanum* (d`Orbigny), 1839
Fig. 2	*Quinqueloculina candeiana* d`Orbigny, 1839
Fig. 3	*Quinqueloculina lamarckiana* (d`Orbigny), 1839
Fig. 4	*Quinqueloculina poeyana* d`Orbigny, 1839
Fig. 5	*Archaias angulatus* (Fichtel & Moll), 1803
Fig. 6	*Triloculina bassensis* Parr, 1945
Fig. 7	*Quinqueloculina laevigata* d`Orbigny, 1826
Fig. 8	*Quinqueloculina polygona* d`Orbigny, 1839
Fig. 9	*Triloculina bermudezi* Acosta, 1940
Fig. 10	*Peneroplis proteus* d`Orbigny, 1839
Fig. 11	*Florilus atlanticus* (Cushman), 1947
Fig. 12	*Fursenkoina pontoni* (Cushman), 1932
Fig. 13	*Parasorites orbitolitoides* (Hofker),
Fig. 14	*Quinqueloculina bidentata* d`Orbigny, 1839
Fig. 15	*Miliolinella labiosa* (d`Orbigny), 1839

Plate 7a

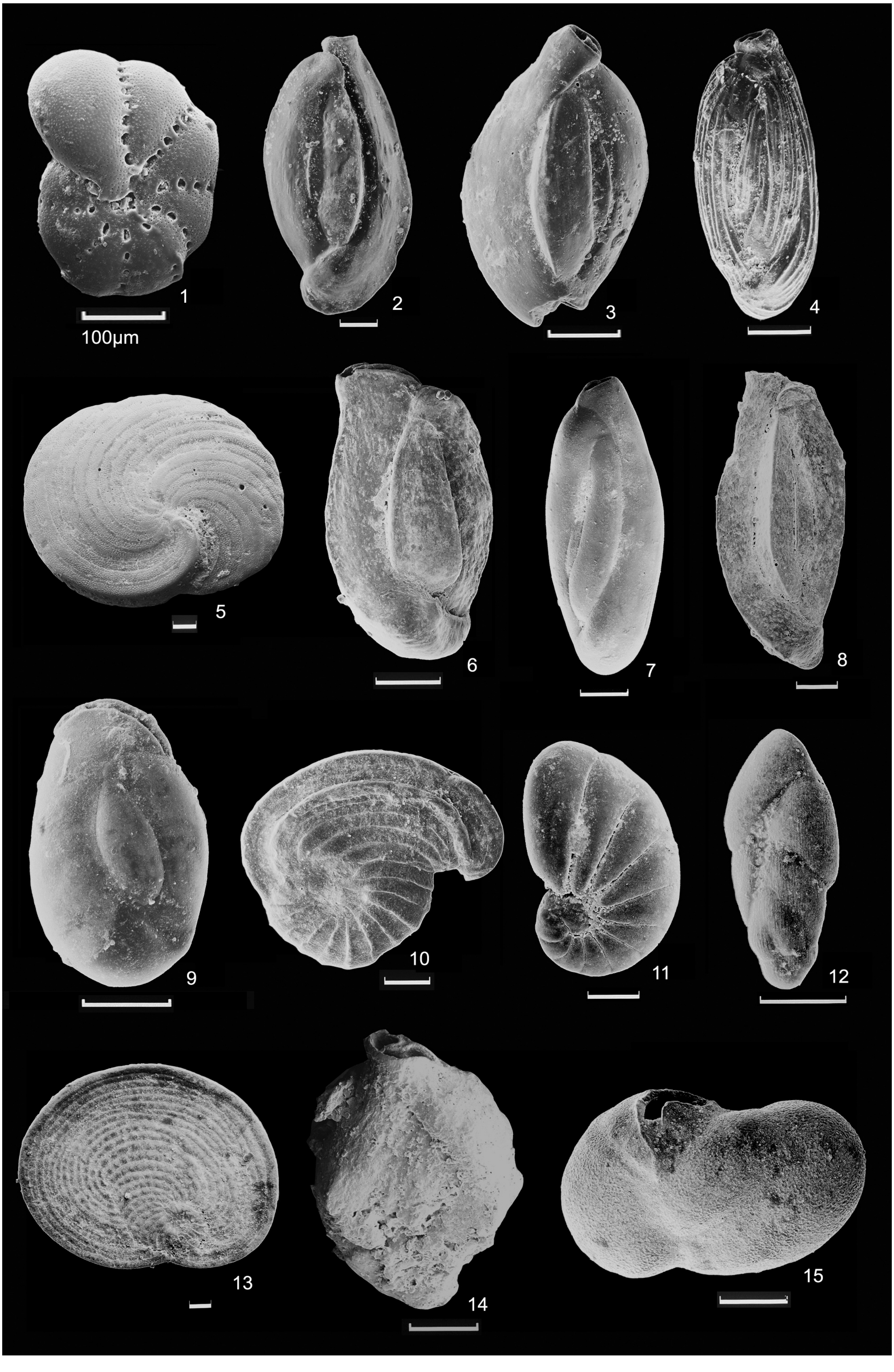
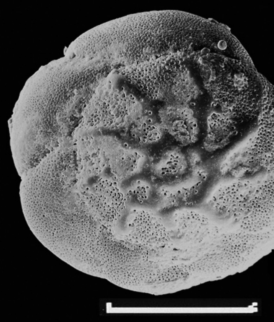


Plate 7b

Mixed Assemblage

Fig. 16	*Ammonia beccarii* (Linné), 1772
Fig. 17	*Tretomphalos atlanticus* Cushman, 1934
Fig. 18	*Elphidium discoidale* (d´Orbigny),
Fig. 19	*Triloculina trigonula* (Lamarck), 1804
Fig. 20	*Bolivina pulchella* (d`Orbigny) var. *primitiva* Cushman, 1930
Fig. 21	*Textularia agglutinans* Defrance, 1824
Fig. 22	*Cyclorbiculina compressa* d`Orbigny, 1839
Figs. 23a, b	*Amphistegina gibbosa* d`Orbigny, 1839 Fig. 23a: ventral view (apertural) Fig. 23b: spiral view (dorsal)
Fig. 24	*Heterillina cribostoma* (Heron-Allen & Earland), 1915
Figs. 25a, b	*Rosalina floridana* (Cushman), 1922 Fig. 25a: spiral view (dorsal) Fig. 25b: ventral view (apertural)

Plate 7b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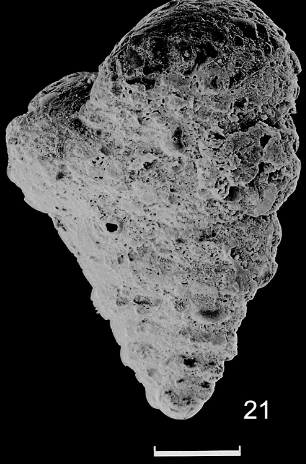
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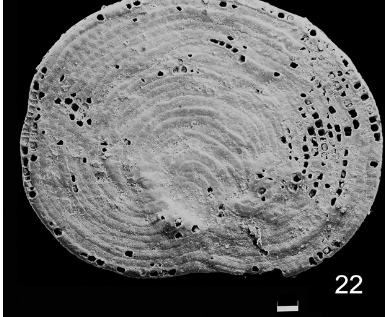
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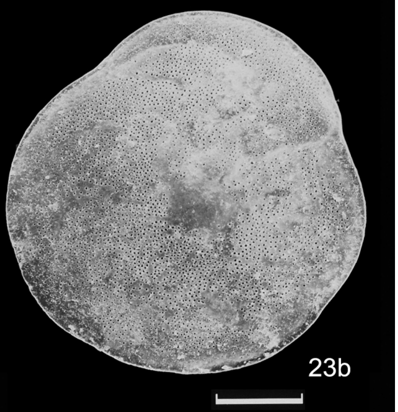
23a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25a


25b

Appendix 7

Taxonomy

ORDER: *TEXTULARIIDA* Fursenko, 1858

Suborder: *TEXTULRIINA* Delage & Hérouard, 1896

- Superfamily: *Ammodiscaceae* Reuss, 1862
  - Family: *AMMODISCIDAE* Reuss, 1862
    - Subfamily: *Ammodiscinae* Reuss, 1862
      - Genus: *Ammodiscus* Reuss, 1862
- Superfamily: *Textulariacea* Ehrenberg, 1838
  - Family: *TEXTULARIIDAE* Ehrenberg, 1838
    - Subfamily: *Textulariinae* Ehrenberg, 1838
      - Genus: *Textularia* Defrance, 1824
        - Species: *T. agglutinans* D´Orbigny, 1839
        - Species: *T. conica* D´Orbigny, 1839
  - Family: *VALVULINIDAE* Berthelin, 1880
    - Subfamily: *Valvulininae* Berthelin, 1880
        - Species: *Valvulina oviedoina* D´Orbigny, 1839
      - Genus: *Clavulina* D’Orbigny, 1826
        - Species: *C. tricarinata* D’Orbigny, 1839

Suborder: *SPIRILLINA* Hohenegger & Piller, 1975

  - Family: *SPIRILLINIDAE* Reuss und Fritsch, 1861
      - Genus: *Spirillina* Ehrenberg, 1861

ORDER: *MILIOLIDA* Calkins, 1909

Suborder: *MILIOLINA* Delage & Hérouard, 1896

- Superfamily: *Cornuspiracea* Schulze, 1854
  - Family: *FISCHERINIDAE* Millett, 1898
    - Subfamily: *Nodobaculariellinae* Borgdanovich, 1981
      - Genus: *Vertebralina* D’Orbigny, 1826
        - Species: *V. cassis* D’Orbigny, 1839
        - Species: *V. atlantica* D’Orbigny, 1839
      - Genus: *Nodobaculariella* D’Orbigny, 1839
        - Species: *N. cassis* D’Orbigny, 1839
- Superfamily: *Miliolacea* Ehrenberg, 1839
  - Family: *SPIROLOCULINIDAE* Wiesner, 1920
    - Subfamily: *Spiroloculininae* Wiesner, 1920
      - Genus: *Spiroloculina* D´Orbigny, 1826
        - Species: *S. antillarum* D´Orbigny, 1839
        - Species: *S. arenata* Cushman, 1921
  - Family: *HAUERINIDAE* Schwager, 1876
    - Subfamily: *Hauerininae* Schwager, 1876

  - Genus: *Hauerina* D´Orbigny, 1839
    - Species: *H. comressa* D’Orbigny, 1839
    - Species: *H. speziosa* (Karrer), 1868
  - Genus: *Massilina* Schlumberger, 1893
    - Species: *M. protea* Parker, 1953
- Subfamily: *Quinqueloculininae* Cushman, 1917
  - Genus: *Quinqueloculina* D´Orbigny, 1826
    - Species: *Q. agglutinans* D´Orbigny, 1839
    - Species: *Q berthelotiana* D´Orbigny, 1839
    - Species: *Q bicarinata* D´Orbigny, 1839
    - Species: *Q bicornis* Walker & Jacob, 1798
    - Species: *Q biconstata* D´Orbigny, 1839
    - Species: *Q brayana* Cushman, 1917
    - Species: *Q. bidentata* D´Orbigny, 1839
    - Species: *Q candeiana* D´Orbigny, 1839
    - Species: *Q crassa* Cushman, 1921
    - Species: *Q funafutiensis* D´Orbigny, 1839
    - Species: *Q horrida* Cushman, 1921
    - Species: *Q. laevigata* D´Orbigny, 1826
    - Species: *Q lamarckiana* (D´Orbigny), 1839
    - Species: *Q parkeri* Cushman, 1921
    - Species: *Q. poeyana* D´Orbigny, 1839
    - Species: *Q. polygona* D´Orbigny, 1839
    - Species: *Q seminulum* Linnaeus, 1767
    - Species: *Q. subpoeyana* Cushman, 1922
    - Species: *Q. tricarinata* D´Orbigny, 1839
- Subfamily: *Miliolinellinae* Vella, 1957
  - Genus: *Miliolinella* Wiesner, 1931
    - Species: *M. circularis* (Bornemann), 1855
    - Species: *M. labiosa* (D´Orbigny), 1839
    - Species: *M. labiosa* (D´Orbigny), 1839
  - Genus: *Pyrgo* Defrance, 1824
    - Species: *P. elongata* (D´Orbigny), 1826
    - Species: *P. denticulina* (D´Orbigny), 1826
  - Genus: *Triloculina* D´Orbigny, 1839
    - Species: *T. bassensis* Parr, 1945
    - Species: *T. bermudezi* Acosta, 1940
    - Species: *T. bicarinata* D´Orbigny, 1839
    - Species: *T. carinata* D´Orbigny, 1839
    - Species: *T. fitterei* var. *meningoi* Acosta, 1940
    - Species: *T. linneiana* D´Orbigny, 1839
    - Species: *T. trigonula* (Lamarck), 1804

- Species: *T. quadrilateralis* D´Orbigny, 1839
- Species: *T. sidebottomi* (Martinotti), 1920

Subfamily: *Tuninellinae* Rhumbler, 1906

- Genus: *Speciesiculina* D´Orbigny, 1826
  - Species: *A. lineata* Brady, 1884
  - Species: *A. mayori* Cushman, 1922
  - Species: *A. mexicana* Cushman, 1921
  - Species: *A. pazifica* Cushman, 1944

Superfamily: *Soritacea* Ehrenberg, 1839

Family: *PENEROPLIDAE* Schultze, 1854

- Genus: *Peneroplis* de Montfort, 1808
  - Species: *P. pertusus* (Forscål), 1775
  - Species: *P. proteus* D'Orbigny, 1839
  - Species: *P. bradyi* Cushman, 1930

Family: *SORITIDAE* Ehrenberg, 1839

Subfamily: *Archaiasinae* Cushman, 1927

- Genus: *Archaias* de Montfort, 1808
  - Species: *A. angulatus* (Fichtel & Moll), 1798
- Genus: *Cyclorbiculina* A. Silvestri, 1937
  - Species: *C. compressa* (D'Orbigny), 1839
- Genus: *Parasorites* Seiglie & Rivera, 1977
  - Species: *P. orbitolitoides* (Hofker), 1930

Subfamily: *Soritinae* Ehrenberg, 1838

- Genus: *Sorites* Ehrenberg, 1839
  - Species: *S. marginalis* Lamarck, 1816

ORDER: *ROTALIIDA* Fursenko, 1958

Suborder: *ROTALIINA* Delage & Hérouard, 1896

Superfamily: *Bolivinacea* Glaessner, 1937

Family: *BOLIVINITIDAE* Cushman, 1927

- Genus: *Bolivina* D'Orbigny, 1839
  - Species: *B. lanceolata* Parker, 1951
  - Species: *B. lowmani* Phleger & Parker, 1951
  - Species: *B. pulchella* (D'Orbigny) var. *primitiva* Cushman, 1930
  - Species: *B. striatula* Cushman, 1922
  - Species: *R. advena* (Cushman), 1922

Superfamily: *Buliminacea* Jones, 1875

Family: *UVIGERINIDAE* Haeckel, 1894

- Genus: *Trifarina* Cushman, 1923
  - Species: *T. bella* (Phleger & Berger), 1951

  - Family: *EPONIDINAE* Hofker, 1951
    - Subfamily: *Eponidinae* Hofker, 1951
      - Genus: *Eponides* de Montfort, 1808
        - Species: *E. antillarum* D’Orbigny, 1839
  - Family: *DISCORBIDAE* Ehrenberg, 1838
    - Subfamily: *Discorbinae* Galloway, 1933
      - Genus: *Discorbis* Lamarck, 1804
        - Species: *D. mira* Cushman, 1922
      - Family: *ROSALINIDAE* Reiss, 1963
    - Subfamily: *Rosalininae* Reiss, 1963
      - Genus: *Neoconcorbina* Hofker, 1951
        - Species: *N. orbicularis* (Terquem), 1876
      - Genus: *Rosalina* D’Orbigny, 1826
        - Species: *R. candeiana* d´Orbigny, 1839
        - Species: *Rosalina floridana* (Cushman), 1922
- Superfamily: *Siphoninacea* Cushman, 1927
  - Family: *SIPHONINIDAE* Cushman, 1927
      - Genus: *Siphonina* Reuss, 1850
        - Species: *S. pulchra* Cushman, 1919
  - Family: *PLANULINIDAE* Bermudez, 1952
      - Genus: *Planulina* D’Orbigny, 1839
  - Family: *CIBICIDAE* Cushman, 1927
      - Genus: *Cibicides* de Montfort, 1808
        - Species: *C. lobatulus* (Walker & Jacob), 1798
        - Species: *C. mayori* (Walker & Jacob), 1798
  - Family: *PLANORBULINIDAE* Bermudez, 1952
    - Subfamily: *Planorbulininae* Schwager, 1877
      - Genus: *Planorbulina* D’Orbigny, 1826
        - Species: *Planorbulina acervalis* Brady, 1884
        - Species: *Planorbulina mediterranensis* D’Orbigny, 1826
  - Family: *CYMBALOPORIDAE* Cushman, 1927
    - Subfamily: *Cymbaloporinae* Cushman, 1927
      - Genus: *Cymbaloporetta* Cushman, 1928
        - Species: *C. squammosa* D’Orbigny, 1826
  - Family: *HOMOTREMATIDAE* Cushman, 1927
      - Genus: *Homotrema* Hickson, 1911
        - Species: *H. rubrum* (Lamarck), 1916
- Superfamily: *Asterigerinacea* D’Orbigny, 1839
  - Family: *ASTERIGERINIDAE* D’Orbigny, 1839
      - Genus: *Asterigerina* D’Orbigny, 1839
        - Species: *A. carinata* D’Orbigny, 1839
  - Family: *Amphisteginidae* Cushman, 1927

Genus: *Amphistegina* D'Orbigny, 1826
Species: *A. gibbosa* D'Orbigny, 1839
Superfamily: *Nonionacea* Schultze, 1854
Family: *NONIONIDAE* Schultze, 1854
Genus: *Nonion* de Montfort, 1808
Species: *N. despressulum* (Walker & Jacob), 1931
Genus: *Florilus* de Montfort, 1808
Species: *F. atlanticus* (Cushman), 1947
Superfamily: *Rotaliacea* Ehrenberg, 1839
Family: *ROTALIIDAE* Ehrenberg, 1839
Subfamily: *Ammoniinae* Saidova, 1981
Genus: *Ammonia* Brünich, 1772
Species: *A. beccarii* (Linné), 1758
Family: *ELPHIDIIDAE* Galloway, 1933
Genus: *Criboelphidium* Cushman & Brönnimann, 1948
Species: *C. poeyanum* (D'Orbigny), 1839
Genus: *Elphidium* de Montfort, 1808
Species: *E. advenum* (Cushman), 1930
E. discoidale (D'Orbigny), 1930
E. sagrum (D'Orbigny), 1930

Suborder: *GLOBIGERININA* Delage & Hérouard, 1896

Superfamily: *Globigerinacea* Carpenter, Parker & Jones, 1862
Family: *GLOBIGERINIDAE* Carpenter, Praker & Jones, 1862
Subfamily: *Globigerininae* Carpenter, Praker & Jones, 1862
Genus: *Globigerinoides* Cushman, 1927
Species: *G. ruber* D'Orbigny, 1839
Genus: *Globigerinella* Cushman, 1927
Genus: *Globigerina* D'Orbigny, 1826
Superfamily: *Globorotaliacea* Cushman, 1927
Family: *GLOBOROTALIIDAE* Cushman, 1927
Genus: *Globorotalia* (D'Orbigny), 1826
Species: *G. cultrata* D'Orbigny, 1839

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