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They say that a man who stares at a rock all day is a man with something on his mind. Or nothing.

– *Unknown*

UNIVERSITY OF ALBERTA

RHODOLITE DEVELOPMENT IN THE MODERN AND PLEISTOCENE OF GRAND CAYMAN

BY

DAVID JOSEPH HILLS ©

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF EARTH AND ATMOSPHERIC SCIENCES

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Rhodolite Development in the Modern and Pleistocene of Grand Cayman** submitted by **David Joseph Hills** in partial fulfillment of the requirements for the degree of **Master of Science**.

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Thursday, August 28, 1997

DEDICATION

Dedicated to my brother Sean, who showed me books on fossils when I was four. I've been a geologist since then.

ABSTRACT

The distribution and morphology of rhodolites from modern lagoons and Late Pleistocene lagoonal deposits on Grand Cayman is primarily related to hydraulic energy levels, nucleus form, and storms.

Biotic composition on modern rhodolites from South Sound and Pease Bay is determined by hydraulic energy, and varies from: the *Back-reef rhodolites*, dominated by *Hydrolithon reinboldii;* the *mid-lagoonal rhodolites*, dominated by *Neogoneolithon* sp.; and the *Near-shore nodules*, dominated by cyanobacteria with minor calcareous algae. The thickness of the cortices represents ≤ 56 years of growth.

Pleistocene rhodolites, from the Ironshore Formation at Crystal Harbour have a ~ 2 mm thick inner cortex of coralline algae, encased by a < 60 mm outer cortex of *Peyssonnelia rubra*. This has resulted from an algal colonisation succession in the absence of abrasive processes. Cortex thickness' represent ≤ 600 years of growth. This is only the second reported occurrence of Peyssonneliaceae forming rhodolites.

Differences in growth periods between modern and Pleistocene reflect the influence of storms. Storms frequently affect the modern windward lagoons, removing rhodolites, whereas the Pleistocene lagoons were protected from storms and the rhodolites remained in place over long periods.

To attain their full paleoecological potential, lagoonal rhodolites should be used in conjunction with all aspects of the facies and biota of a sequence.

ACKNOWLEDGMENTS

Unfortunately, as of yet I have been unable to collect the infinite number of chimpanzees and corresponding typewriters it would have taken to write this thesis, or any of Shakespeare's works for that matter. In this case, I have relied on my own personal use (abuse) of the English language and the editing skills of Brian Jones, so everyone else can understand it. I am greatly in debt to him for giving me the chance to do what I've done and for making this thesis what it is. This research was supported by a NSERC grant to Dr. Jones (A6090).

I'm also indebted to Doreen Haugan, George Braybrook, and Judith Enarson and other members of the departmental staff for the technical and bureaucratic support, and to the chair and other members of my committee, Dr. Brian Chatterton, Dr. Charlie Stelck and, Dr. W. G. Evans for their constructive comments.

I would like to express my gratitude to everyone at the Department of Environment on Grand Cayman, who helped our field work run smoothly and who granted the necessary permits.

Thanks to the other members of the Carbonate Group of past and present, Brent Wignall, for a wit that I aspire to and immaculate taste in velveteen art, Paul Blanchon, who's calls of 'totty' can still be heard echoing along the ESB corridors, Jason 'Tex' Montpetit, for lending me every important reprint I could have needed, and for the many discussions where we would bounce ideas to see if they should go into scientific journals or fantasy magazines. To Chun Li and his forams, Astrid Arts, whom also did some editing (now stop helping everyone else and finish already), Betsy Wilson and Dusty the cat, Jen Vézina, Bill Kalbfleisch, and Leo Piccoli.

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To my parents and family also, thanks for being so understanding with me so far away.

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CHAPTER 1
INTRODUCTION

1.1 GENERAL INTRODUCTION

Rhodolites (= rhodoliths, rhodoids or algal balls), as defined by Bosellini and Ginsburg (1971), are carbonate nodules composed predominantly of crustose coralline algae (Rhodophyta) that encrust an unattached nucleus. They have been found actively growing in a variety of non-muddy environments to depths of ~ 90 m and are common constituents in modern and ancient deposits from tropical to polar latitudes (Adey, 1973; Bosence, 1983a; Littler *et al.*, 1991). At least one or more morphological attribute of rhodolites, (*i.e.*, form, internal structure, species composition and species growth form) have been related to light (Minnery *et al.*, 1985; Martindale, 1976; Adey *et al.*, 1982), temperature (Adey, 1970b; 1973), energy (Bosellini and Ginsburg, 1971; Bosence, 1983a), grazing pressure (Steneck, 1985), space competition (Adey and Vassar, 1975), and/or substrate size (Adey, 1970a). Despite their paleoecological potential, rhodolites have rarely been used as paleoenvironmental indicators because they commonly prove difficult to interpret. For example, a change in algal composition from the inner to the outer cortex can result from a change in sea-level (*e.g.*, Toomey, 1983), interspecific competition (*e.g.*, Adey and Vassar, 1975), increase in substrate size (*e.g.*, Adey, 1970a), or transportation to a different environment (*e.g.*, Reid and Macintyre, 1988). These problems are due to the complex nature of the rhodolites and their environments, and the lack of studies of rhodolite morphology. Only with a solid understanding in all aspects of their formation, can rhodolites be used with confidence as paleoenvironmental indicators.

Objective

Rhodolites hold the potential to greatly enhance existing paleoenvironmental investigations which currently use sediment, corals, or molluscs. Rhodolites are sensitive to environmental growth conditions, they are ecologically diverse, geographically widespread, they display unique characteristics with respect to their environment, and a single specimen can be a reliable record of long periods in time.

The primary objective of this study is to *establish a model of rhodolite development in lagoons which may be used as a tool in the interpretation of ancient environments.*

No model of rhodolite development currently exists because they are generally considered too complex and sensitive to many environmental criteria (Reid and Macintyre, 1988). However, by restricting the rhodolites considered to a narrow geographic range (i.e., tropical lagoons), a number of complicating environmental influences can be considered constant, thus, simplifying the model.

The primary objective is achieved by:

- documenting modern rhodolite development in South Sound and Pease Bay on Grand Cayman and establishing the relationship between rhodolite morphology and lagoonal environments (Chapter 2);
- documenting rhodolites of the Pleistocene Ironshore Formation (Chapter 3);
- determining paleoenvironments of the Pleistocene Ironshore Formation using rhodolite morphological characteristics (Chapter 3); and,
- establishing common rhodolite characteristics throughout lagoonal environments for use in the construction of the paleoenvironmental model (Chapter 4).

Use of this rhodolite model in conjunction with other analytical techniques such as coral, bivalve, and sediment analyses will increase the sensitivity and reliability of paleoenvironmental interpretations. An environmental model based on modern rhodolite morphology may be confidently applied to fossil rhodolites as far back as the Eocene (Wray, 1977). Prior to the Eocene, knowledge of encrusting red algae is negligible due to limited studies and a poor preservational record.

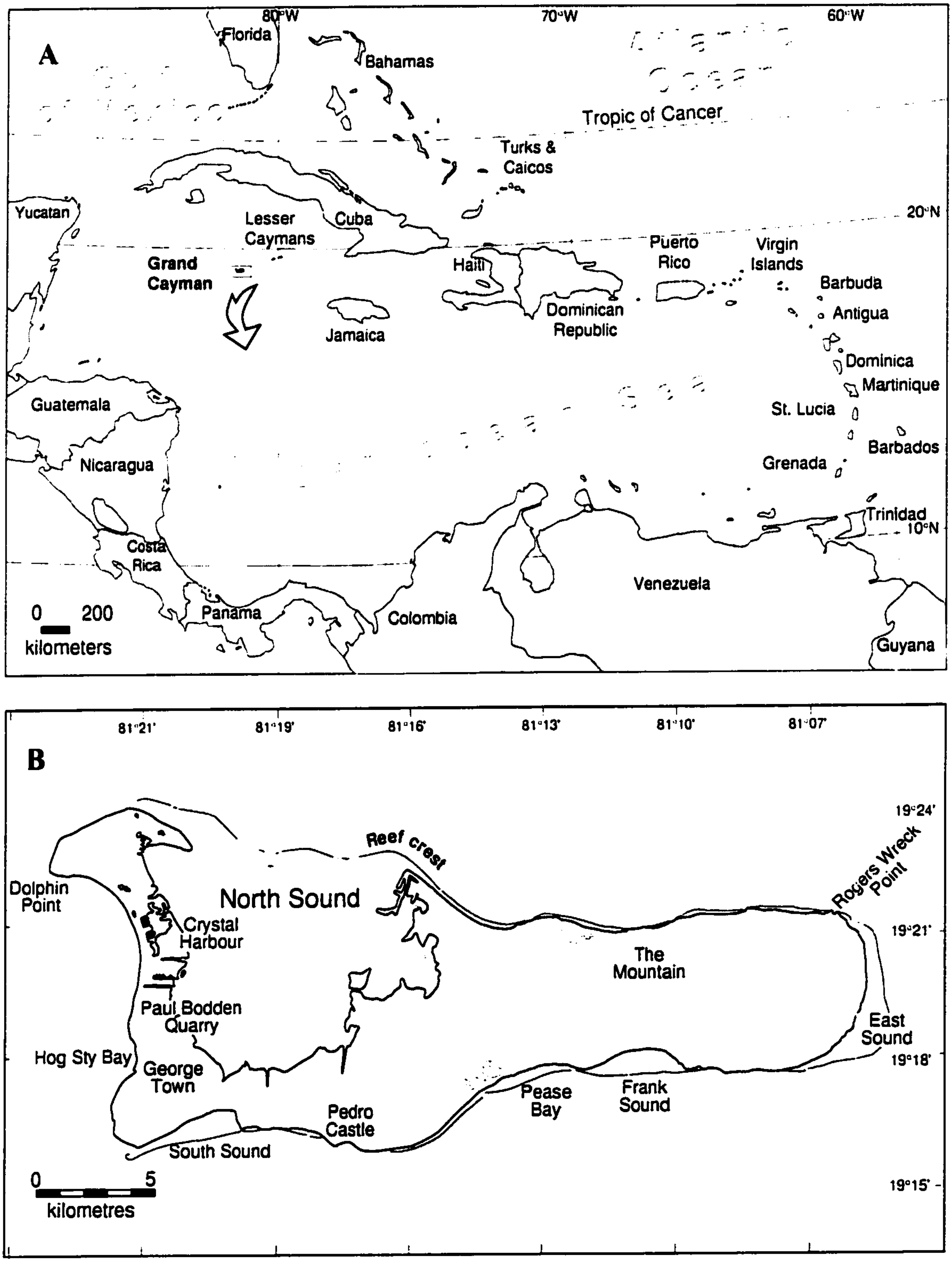


Figure 1.1A: Location map of Grand Cayman in the Caribbean Sea. **B:** Grand Cayman and localities referred to in text.

Terminology

Bosellini and Ginsburg (1971) defined the term rhodolite as "nodule and branched growths with nodule form, composed principally of coralline (Corallinaceae) algae". Although this definition includes all modern unattached red algae, it excludes one extant (Peyssonneliaceae) and two extinct superfamilies of red algae (Solenoporaceae and Gymnocodiaceae) which have been, or could potentially be found as free living nodules. As further research is likely to increase the examples of non-coralline nodules (*cf.*, Wray, 1977), it is important to establish consistent and concise terminology. To reflect the genetic similarity in form and formation, it is herein proposed that *all* crustose Rhodophyta on unattached substrates be included in the definition of 'rhodolites'. This is convenient and prevents the need for further superfluous terminology. If clarity is required, then a prefix denoting the principal component of the nodule should be included (*e.g.*, 'peyssonnelid rhodolite').

1.2 LOCATION AND SETTING OF GRAND CAYMAN

Grand Cayman is situated in the central western Caribbean, at ~ 81° 15' West and ~ 19° 20' North (Fig. 1.1). It is the largest of the Cayman Islands, 35 km long from east to west, 14 km wide in the west, 6 km wide in the east, and a surface area of 196 km^2.

Most of the island is between 0 and 3 m above sea-level (a.s.l.). The maximum elevations are at The Mountain in the north at 18 m a.s.l., and along a peripheral ridge that extends around the north, east and south coasts, at up to 11 m a.s.l. (Jones and Hunter, 1994). Brackish water mangrove swamps cover much of the central and low lying land surfaces, with dense vegetation, agricultural land and urban areas covering the rest.

A fringing reef surrounds Grand Cayman on all but its western leeward side. The reef is best developed along the southern and eastern coasts where it stretches between headlands, isolating a number of shallow lagoons. The seaward edge of the fringing reef represents the top of a pair of terraces that extend to the shelf edge. The upper terrace (0 - 10 m below sea-level), is separated from the lower terrace (12 - 40 m b.s.l.), by a scarp (10 - 20 m b.s.l.) (Blanchon and Jones, 1995). Modern coral growth at the scarp and the edge of the lower terrace have formed mid-shelf and shelf edge reefs respectively (Blanchon and Jones, 1993, 1995).

Tectonic Setting

Grand Cayman is a subaerially exposed peak of the Cayman Ridge (Fig. 1.2) that extends from Belize to the southern portion of Cuba (Fahlquist and Davies, 1971; Perfit and Heezen, 1978). The ridge is an uplifted fault block, consisting of plutonic rocks, capped by volcanic, volcaniclastic and shallow water carbonates (Perfit and Heezen, 1978; Emery and Milliman, 1980).

South of the Cayman ridge, via a 30° to 40° scarp (Fahlquist and Davies, 1971; Roberts, 1994), is the Cayman Trench. The trench is an active pull apart basin, > 4 km deep, 100 km wide and 1,400 km long (Holcombe *et al.*, 1973; Ladd *et al.*, 1990). The central quarter of the trench consists of the north/south trending Mid-Cayman Rise that marks the spreading centre. MacDonald and Holcombe (1978) interpreted magnetic anomalies to suggest at least 284 km of spreading since the Miocene, and showed a decrease in the rate of spreading from 40 ±2 mm/yr between 6 and 2.4 m.a., to 20 ±2 mm/yr since 2.4 m.a. Spreading is accommodated by a pair of left lateral transform faults, the most northern of which, the Oriente Fault, forms a 100 km wide fracture zone that incorporates Grand Cayman (Shepherd and Isaacs, 1985). Despite a relative lateral movement of 2 cm/yr across this part of the zone (Jordan, 1975), Grand Cayman is vertically stable and has been since the Late Pleistocene (Sykes *et al.*, 1982; Jones and Hunter, 1990).

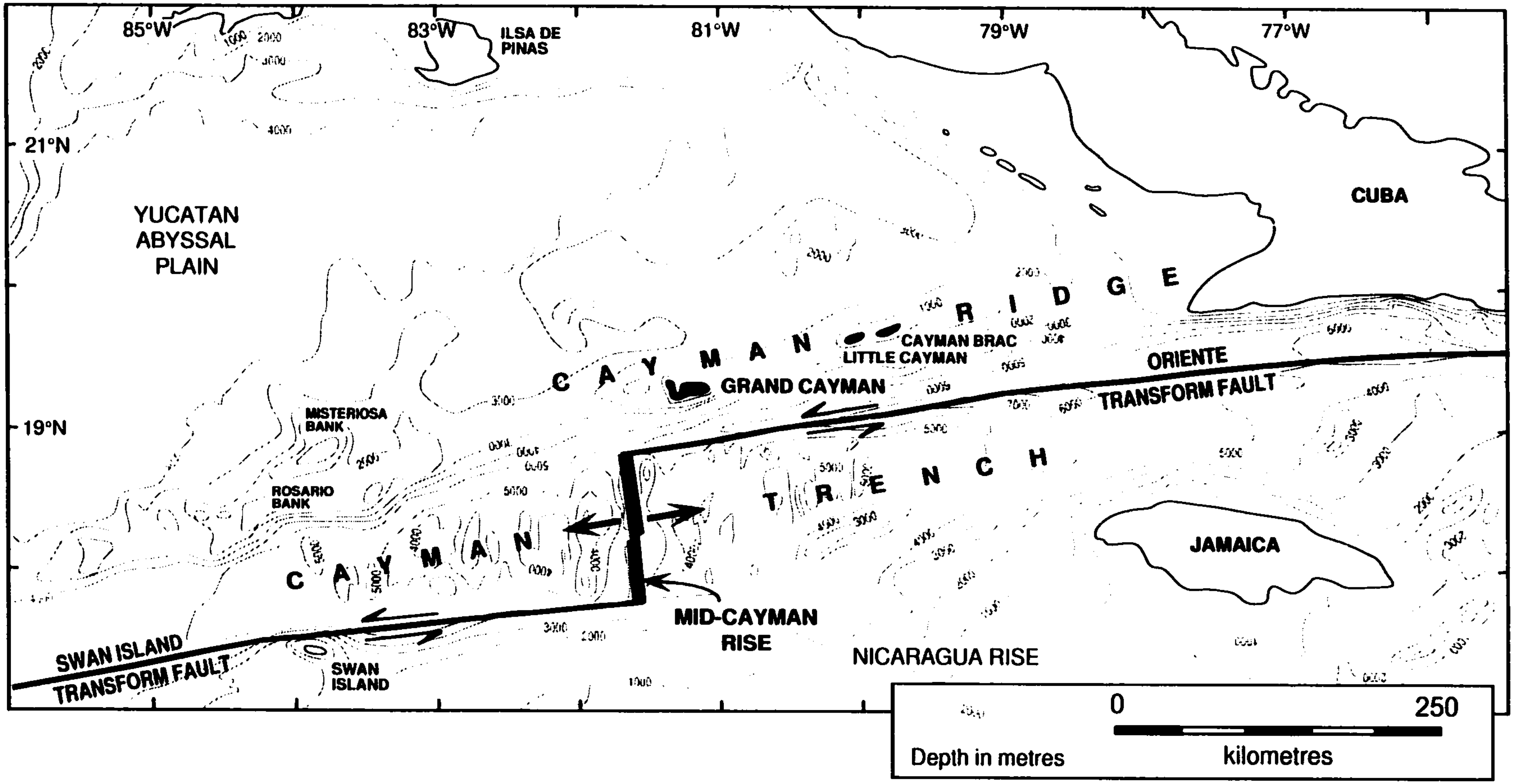
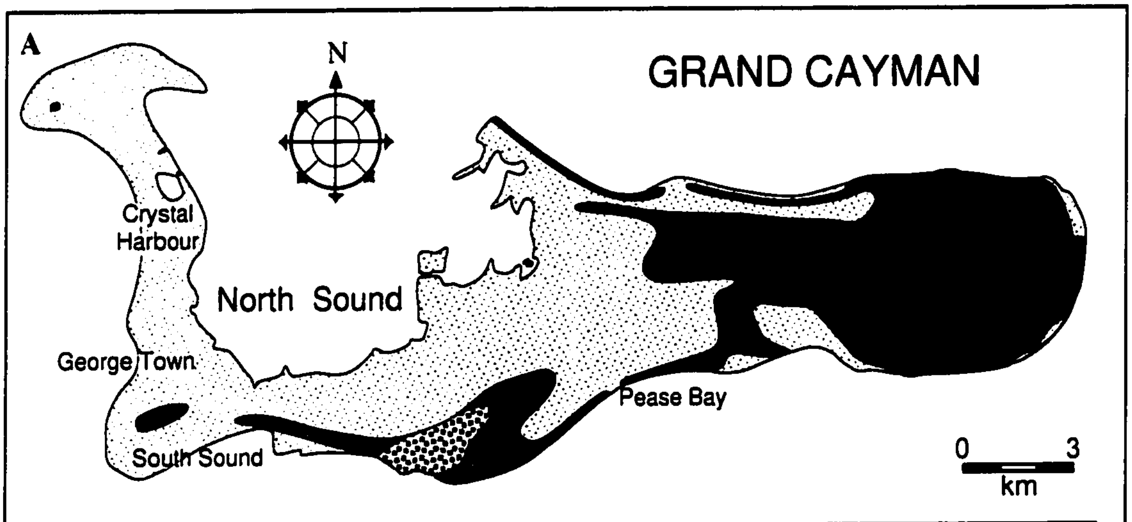


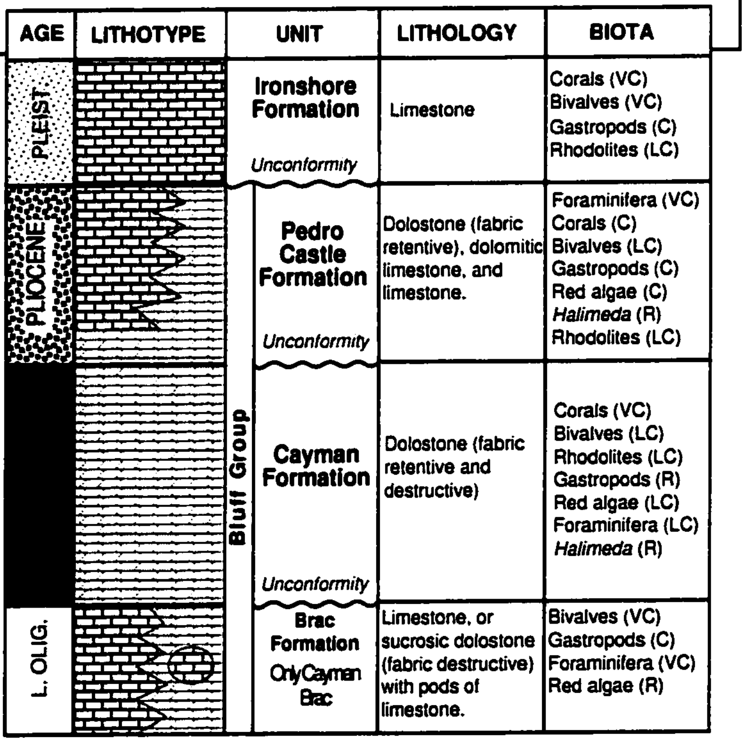
Figure 1.2: Tectonic and bathymetric setting of the central Caribbean area (adapted from Pleydell *et al.*, (1990).

Geology

Grand Cayman is formed of a central core of resistant dolostones and limestones of the Bluff Group that are unconformably surrounded and overlain by friable limestones of the Ironshore Formation (Fig. 1.3) (Matley, 1926; Rigby and Roberts, 1976; Jones and Hunter, 1989; Jones *et al.*, 1994).

The oldest formation of the Bluff Group found to date on Grand Cayman is the





AGE	LITHOTYPE	UNIT	LITHOLOGY	BIOTA
PLEIST.		**Ironshore Formation** *Unconformity*	Limestone	Corals (VC) Bivalves (VC) Gastropods (C) Rhodolites (LC)
PLIOCENE		**Pedro Castle Formation** *Unconformity*	Dolostone (fabric retentive), dolomitic limestone, and limestone.	Foraminifera (VC) Corals (C) Bivalves (LC) Gastropods (C) Red algae (C) *Halimeda* (R) Rhodolites (LC)
		Cayman Formation *Unconformity*	Dolostone (fabric retentive and destructive)	Corals (VC) Bivalves (LC) Rhodolites (LC) Gastropods (R) Red algae (LC) Foraminifera (LC) *Halimeda* (R)
L. OLIG.		**Brac Formation** Only Cayman Brac	Limestone, or sucrosic dolostone (fabric destructive) with pods of limestone.	Bivalves (VC) Gastropods (C) Foraminifera (VC) Red algae (R)

Figure 1.3: Geology of Grand Cayman.
A: Surficial geology of Grand Cayman (modified from Jones and Hunter, 1994).
B: Stratigraphy of the Cayman Islands.
VC: Very common,
C: Common, LC: Locally common, R: Rare
(modified from Jones *et al.*, 1994).

Cayman Formation (L.-M. Oligocene) composed of microcrystalline, fabric retentive dolostones with abundant and diverse fossils (Jones and Hunter, 1989; Jones *et al.*, 1994). Although the thickness of the Cayman Formation on Grand Cayman is unknown, drilling has shown that it is at least 140 m thick.

Lying disconformably on the highly karstified surface of the Cayman Formation is the Pliocene Pedro Castle Formation. The formation is composed of off-white and relatively soft rubbly weathering, fabric retentive dolostones with dolomitic limestones and limestones (Jones *et al.*, 1994). Existing parts of the formation are mostly covered by the overlying Ironshore Formation, but it does outcrop in the south of Grand Cayman, around Pedro Castle quarry (Fig. 1.3). The upper boundary is also karstified, making the formation highly variable in thickness over short distances, with a maximum thickness of 22 m (Jones *et al.*, 1994).

The Ironshore Formation (Pleistocene) outcrops around the periphery, central and western parts of Grand Cayman. This limestone is composed of mudstones, wackestones, and skeletal and ooid grainstones, and of floatstones and rudstones on coastal exposures (Jones and Hunter, 1990). The deposition of the Ironshore Formation has been, until recently, considered a simple process of a single period of deposition during the maximum sea-level of the Sangamon Highstand ~ 125,000 years ago. Much of the evidence pertaining to this came from Th/U dates of corals collected from exposures on Grand Cayman and Cayman Brac by Woodroffe *et al.* (1985). A recent study, incorporating data from 14 wells drilled at Rogers Wreck Point on the northeast coast of Grand Cayman, however, showed that the formation of that area is composed of four unconformably bound units with ages of > 400 ka BP, ~ 346 ka BP, ~ 229 ka BP and ~ 131 ka BP (Vézina, 1997). Each of these ages correlates to the last four successive interglacial highstands. Unfortunately, there is little indication of these members in the study area of Crystal Harbour, so it is assumed that the 12 m of the formation that is present, represents the uppermost units described by Vézina (1997).

CHAPTER 2

ANALYSIS OF RHODOLITES AND MICROBIALITES FROM THE STORM AFFECTED LAGOONS OF GRAND CAYMAN

2.1 INTRODUCTION

Rhodolites and microbialites have been proposed as potential paleoenvironmental indicators in fossil examples (Bosellini and Ginsburg, 1971; Bosence, 1983a; Jones and Hunter, 1991). The value of rhodolites and microbialites in paleoenvironmental interpretation ultimately relies on a broad knowledge of their diversity in modern environments, the connection between morphology and ecology, and, the environmental elements that influenced rhodolite and microbialite formation. A problem with their use in this way, is that rhodolites are sensitive to a wide variety of environmental elements that may have a similar ecological or morphological effect. By studying modern examples, it may be possible to identify the environmental factors that are most important to rhodolites, and identify factors that may be ignored under given fossil environmental conditions. As more modern examples are investigated, the utility of rhodolites and microbialites in

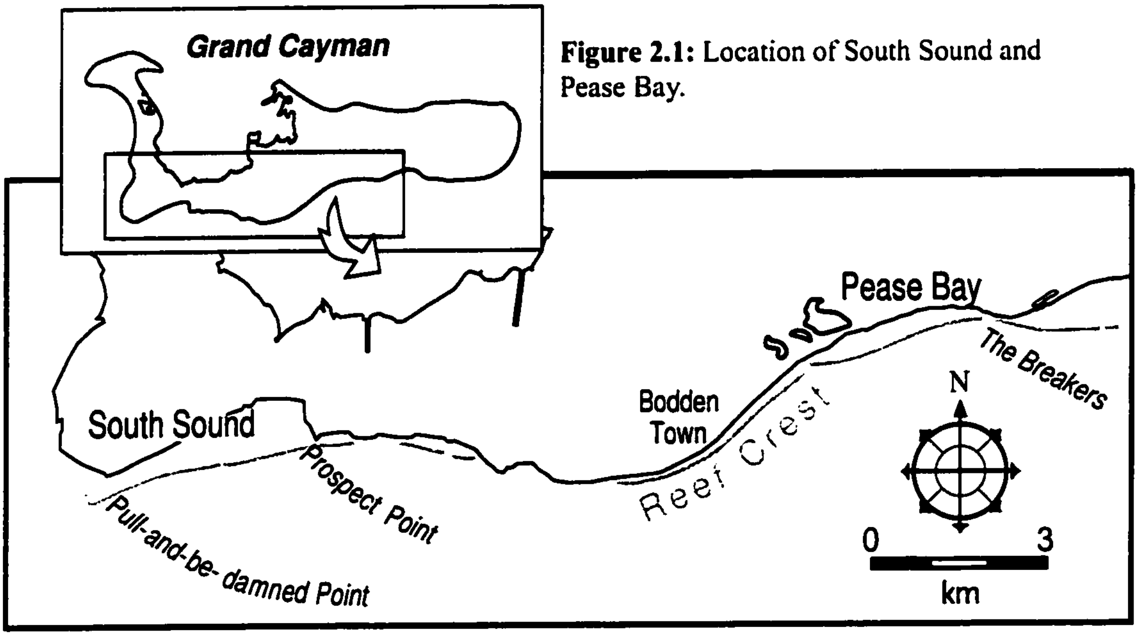


Figure 2.1: Location of South Sound and Pease Bay.

paleoenvironmental interpretations could be improved.

Lagoonal rhodolites have been previously studied by Bosellini and Ginsburg (1971) and Scoffin *et al.* (1985). Although those studies successfully illustrated the development and ecology of lagoonal rhodolites, they were conducted in sheltered lagoons that are protected from prevailing winds and storms by land barriers. This does not represent the full range of lagoonal environments in which rhodolites may develop. To broaden the database on their development, this chapter investigates the processes that led to the formation of algal nodules consisting of rhodolites and microbialites in South Sound and Pease Bay; two shallow, narrow and exposed lagoons on the southern windward coast of Grand Cayman (Fig. 2.1). The nodules vary in form and biotic composition across the lagoons, indicating a strong sensitivity to local environmental elements.

2.2 SETTING

South Sound and Pease Bay are protected from open ocean wave energy by reefs that stretch between adjacent headlands. South Sound is located on the south western coast between Pull-and-be-damned Point and Prospect Point (Fig. 2.1). It is 5.3 km long from east to west, and widens from 250 m at its western extremity to 1,000 m in the east. Pease Bay, also on the south coast, is 6 km long from Bodden Town to The Breakers. The lagoon is best developed on the eastern half of the bay where it is up to 500 m wide.

Climate

The tropical and sub-humid climate of Grand Cayman is largely controlled by the surrounding ocean (Burton, 1994). Average daily temperatures peak in July at 28.4°C and fall to 24.8°C in February. The maximum temperature recorded was 36.5°C and a minimum of 11.2°C. Open water temperature, measured at Hog Sty Bay, Georgetown, is ~ 26°C in the winter to ~ 29°C in the summer (Hog Sty Bay Water Quality Investigation, Department of Environment and Water Authority, Feb., 1991 to present).

Annual precipitation on the island ranged from 923 mm in 1986 to 2110 mm in 1979

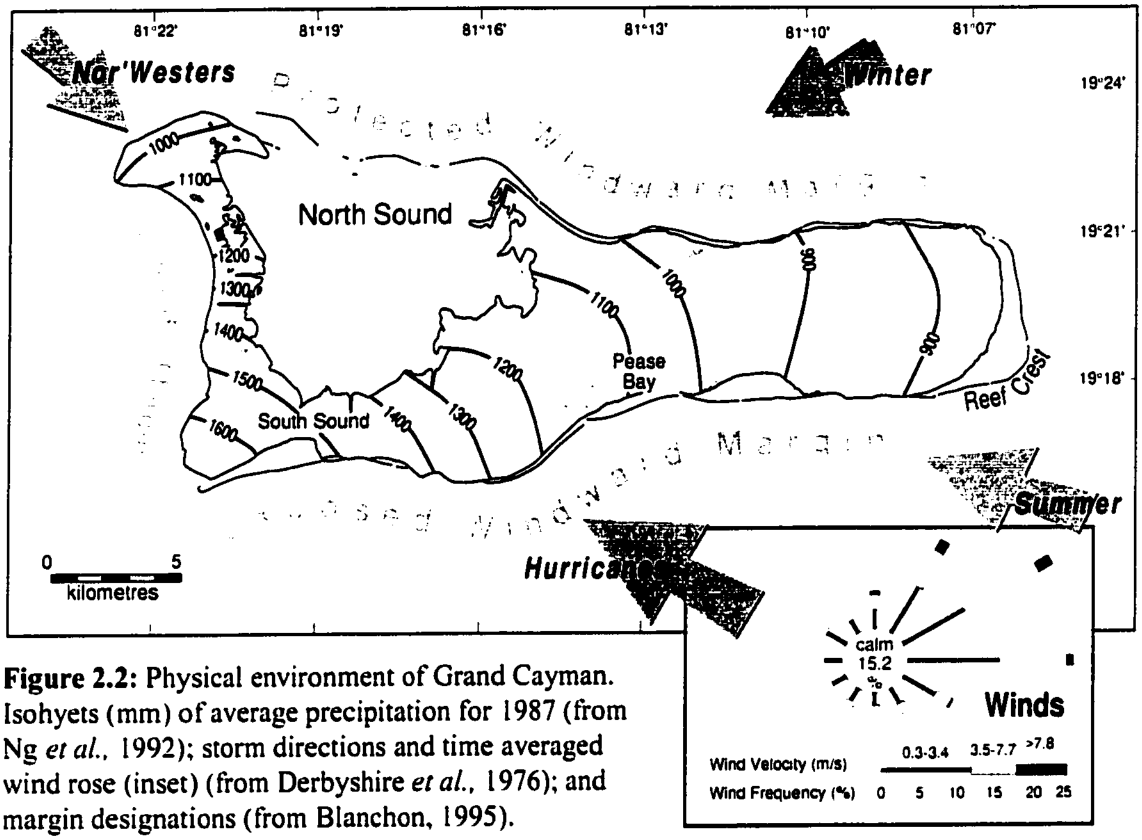


Figure 2.2: Physical environment of Grand Cayman. Isohyets (mm) of average precipitation for 1987 (from Ng *et al.*, 1992); storm directions and time averaged wind rose (inset) (from Derbyshire *et al.*, 1976); and margin designations (from Blanchon, 1995).

with a mean of 1100 mm (data from MRCU 1969-1987). The western side of the island receives 20 to 30% more rainfall than the eastern side due to clouds developing as they move west during summer months (Burton, 1994) (Fig. 2.2). The summer "wet" season lasts from May to November, with the heaviest rains usually occurring in October.

Grand Cayman is effectively shielded from much of the energetic Atlantic weather by Jamaica to the south-east, Cuba to the north and north east, and South America to the south. The dominant weather system is that of the easterly Trade Wind which blows consistently from the south east to the north east at a rate of 3 -7 m s^{-1}. Pease Bay and South Sound are on the exposed windward margin of Grand Cayman, which incorporates the southern and eastern coasts (Blanchon and Jones, 1995). A significantly longer fetch to the south east provides waves of 1.25 to 2 m high along these coasts, compared to waves of < 1.25 m high on the protected windward margin of the north coast (Darbyshire *et al.*, 1976; Blanchon and Jones, 1995). The western coast of the island is leeward

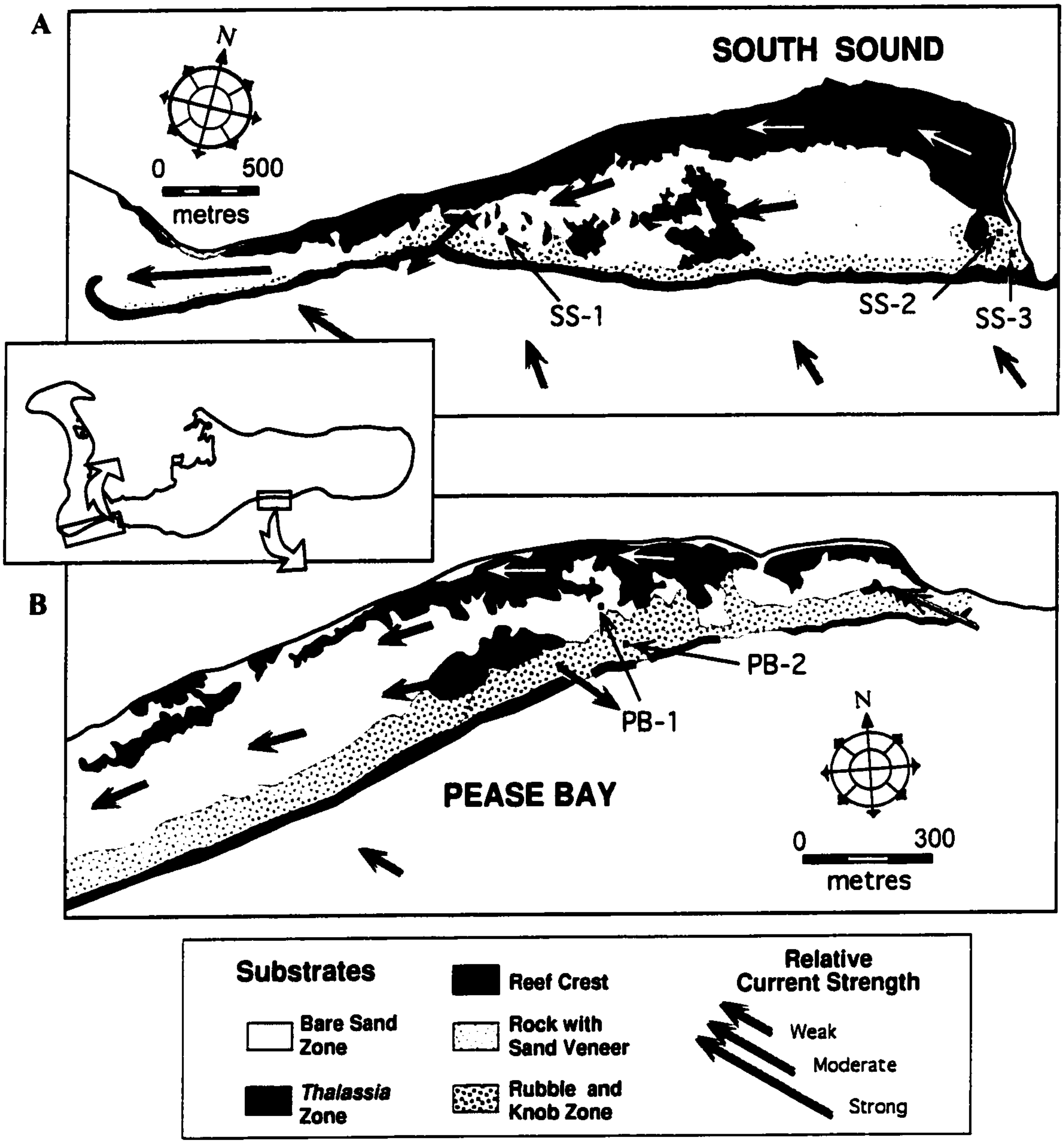


Figure 2.3: Maps of South Sound (**A**) and Pease Bay (**B**), showing substrate type, fair-weather currents and collection localities (South Sound substrate map from Li (1997), Pease Bay substrates are estimated from air photographs (1982) and Kalbfleisch and Jones (1997), current information from Rigby and Roberts (1976)).

throughout most of the year. During winter months, the climatic regime periodically reverses, as cold systems, locally known as "Nor' Westers" bring strong winds from the north west (Burton, 1994). This seasonal change in climate transforms the western coast into the windward margin, and the others to leeward.

On average, hurricanes pass over Grand Cayman once every 9.2 years and pass within 100 miles of the island every 2.5 years (Clark, 1988). Hurricane "Gilbert", in September 1988 has been the only hurricane to pass over the island since accurate wind measurements have been possible. The storm registered maximum wind gusts of 70 (± 9) $m\ s^{-1}$ and sustained wind velocities of 31 $m\ s^{-1}$ for over 10 minutes (Burton, 1994).

Hydrology of South Sound and Pease Bay

On reaching the lagoons, fair-weather waves are broken by the reef crest and lose ~ 97% of their energy (Roberts, 1981). Lagoons, therefore, are typically sedate, with waves of no more than a few centimetres high. As the wave energy is dissipated over the reef crest, it drives an oscillating current in the lagoon, with a net shoreward flow (Suhayda and Roberts, 1977) (Fig. 2.3). These currents converge in the mid-lagoon and move westward, with gradually increasing flow rates. Diurnal tides, with an average amplitude of 26 cm and maximum amplitude of 1 m (between the highest and lowest tides and excluding storm surges), also create a westward drift (Burton, 1994). At Pull-and-be-damned Point the combined westward currents may reach 45 $cm\ s^{-1}$ (Rigby and Roberts, 1976).

To date, no current measurements have been possible during severe storms. Kalbfleisch (1995), Li (1996), and Kalbfleisch and Jones (1997), however, showed from sediment and foraminiferal analyses, the effect of storms on the lagoonal sedimentology. Although fair weather currents have little effect on the lagoonal sediments, practically all erosion, reworking and deposition of sediments take place in very short periods during severe storms. At the height of these storms, sediment from the fore-reef area is dumped over the reef crest by massive waves. As the storms wane, water that has been piled up into the lagoon drains as 'mega-rip currents' which can strip areas of the lagoon to the bedrock. Between the storms, the only major process that has been recognised, is the recolonisation of the sandy sediment areas by *Thalassia* (Kalbfleisch, 1995). This may take tens of years.

Sedimentology

From the analysis of soft sediment cores, sediment sampling, and aerial photographs, Kalbfleisch (1995) and Kalbfleisch and Jones (1997) recognised three major and three minor sediment zones in Frank Sound and Pease Bay. Equivalent zones have also been established by Li (1996) in South Sound from aerial photographs (Fig. 2.3). The three major sediment zones extend parallel to the length of the lagoons and combine to form a sediment wedge from the reef crest to the shore. The zone adjacent to the reef crest is the 'Rubble and Knob Zone' which is composed predominantly of rubble sized coral fragments. Landward of this, encompassing the largest part of the lagoon is the 'Bare Sand Zone', composed of medium to fine sands. Adjacent to the shore is the '*Thalassia* and Sand Zone' where dense sea grass banks rooted in coarse to fine sands are found. Minor lagoonal sediment zones include areas stripped of sediment of the 'Bare Rock Zone', coarse beach sands along the shore called the 'Shoreline Substrates', and small coral knolls and patch reefs. These reefs and knolls, composed primarily of *Montastrea annularis* and *Siderastrea sideria*, with numerous *M. cavernosa, Diploria strigosa, Porites porites, P. astreoides,* and *Agericia agaricites,* are distributed throughout the Rubble and Knob Zone and the Bare Sand Zone (Kalbfleisch and Jones, 1997).

2.3 LOCALITIES AND METHODS

Rhodolites and microbialites were collected with a permit from the Government of the Cayman Islands. Pease Bay and South Sound were chosen as collection points because they contained numerous nodules and were easily accessible. Five localities were selected for sampling, three in South Sound (SS-1, SS-2, SS-3), and two in Pease Bay (PB-1, PB-2) (Fig. 2.3).

Locality SS-1 is ~ 100 m from the reef crest on the west side of South Sound, where the lagoon is 325 m wide. Rhodolites were found adjacent to a patch reef in channels, 2 to 3 m deep, filled with coarse sands formed of *Halimeda*, *Homotrema rubrum*, red algae, and lesser numbers of disarticulated bivalves. Well developed sediment ripples in the channel indicate a net shoreward current movement.

Localities SS-2 and SS-3 are at the eastern end of South Sound where the lagoon narrows close to the headland of Prospect Point (the *Thalassia* and Sand Zone is missing

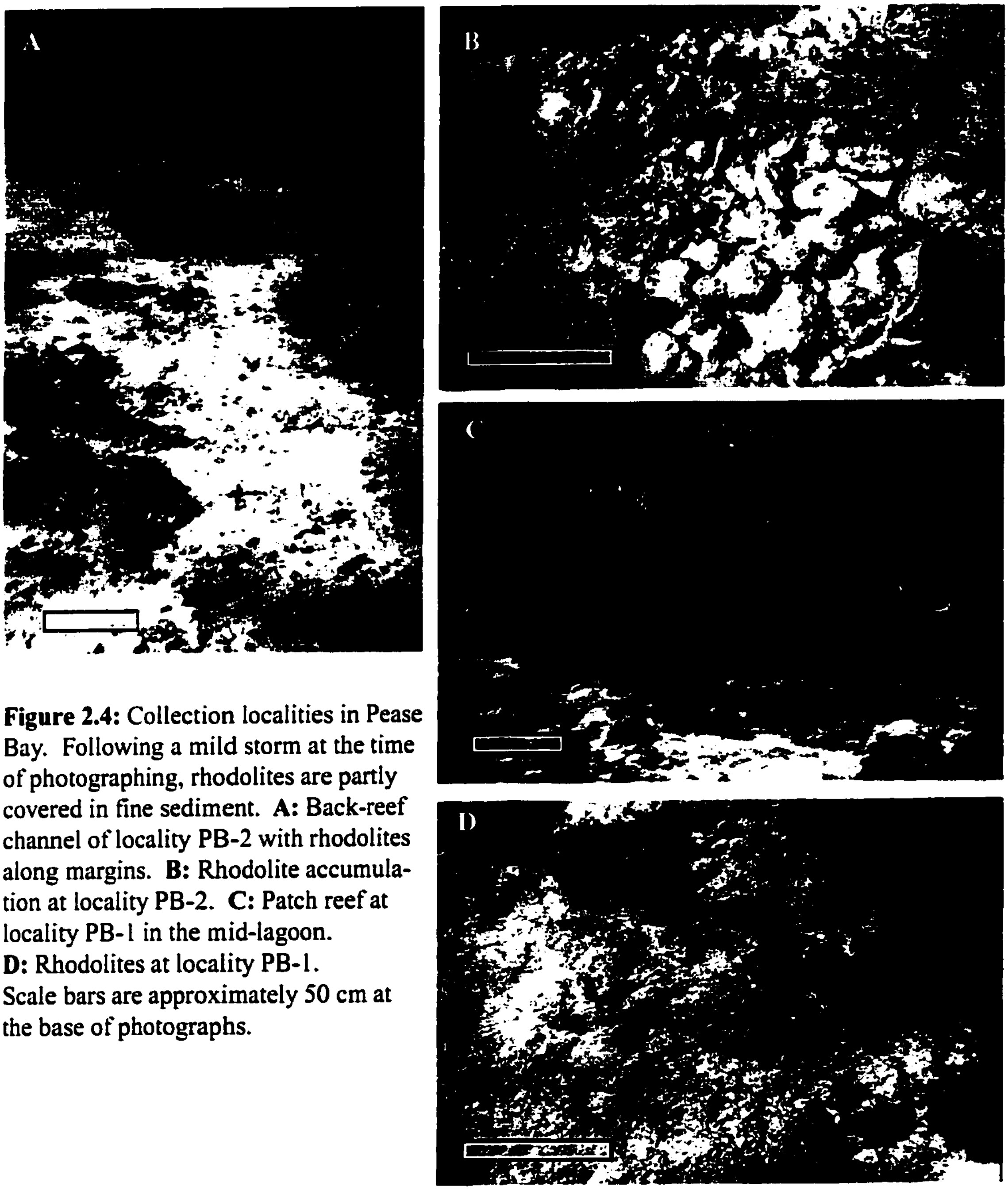


Figure 2.4: Collection localities in Pease Bay. Following a mild storm at the time of photographing, rhodolites are partly covered in fine sediment. **A:** Back-reef channel of locality PB-2 with rhodolites along margins. **B:** Rhodolite accumulation at locality PB-2. **C:** Patch reef at locality PB-1 in the mid-lagoon. **D:** Rhodolites at locality PB-1. Scale bars are approximately 50 cm at the base of photographs.

in this area, probably because the reef crest is so close to the shore). SS-2 is located ~ 6 m from the shore, where microbialites were collected at a depth of ~ 0.2 m on bare coarse sands. Locality SS-3 is south of SS-2, 30 m from the reef crest. Rhodolites were collected from this locality on bare sands at a depth of 0.5 m.

Localities PB-1 and PB-2 are 750 m west of The Breakers, where the lagoon is 250 m wide (Fig. 2.4). At locality PB-1, 190 m landward from the reef crest, rhodolites were collected at a depth of ~ 4 m from shallow depressions in the sediment around a patch reef. PB-2 is located at the transition between the reef crest and the back-reef where rhodolites were collected from small but dense accumulations in a sandy channel. The channel is < 2 m wide, perpendicular to the reef crest and floored with a poorly sorted coarse sand. At the time of sampling, in mid-afternoon, the floor of the channel was shaded from direct sunlight by surrounding corals and rubble.

A total of 113 rhodolites and 5 microbialites were collected from South Sound and Pease Bay (50 from SS-1, 5 from SS-2, 25 from SS-3, 26 from PB-1, and 30 from PB-2). Once collected, rhodolites were either placed in a diluted bleach mixture to remove organic material and then dried overnight, or, if surface algae displayed distinctive

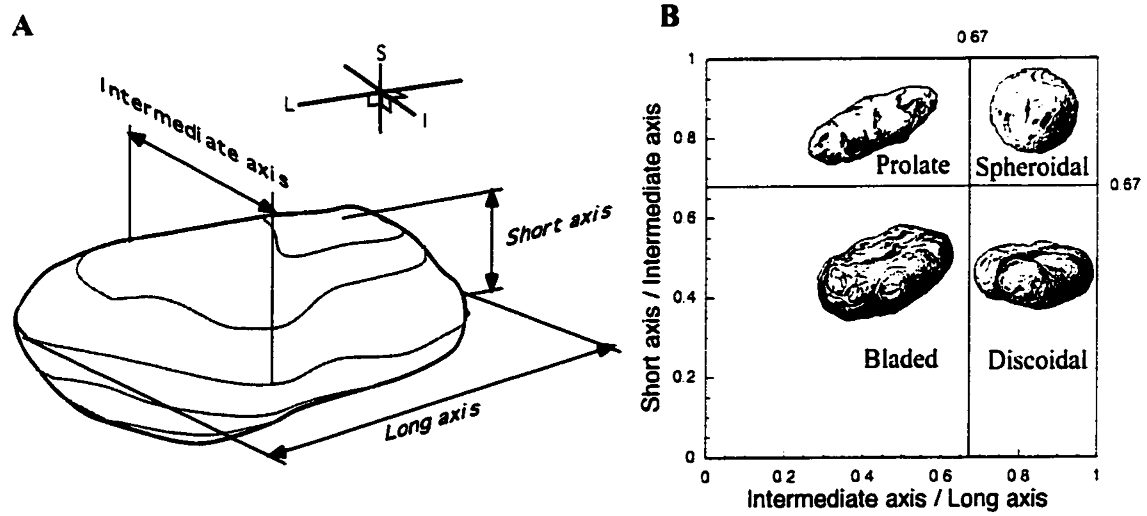


Figure 2.5: Determination of rhodolite form. **A:** Rhodolites are measured along the longest axis, and then the greatest values of the intermediate and short axis at 90° to each other. **B:** Explanation of Zingg (1935) graph and determination of shape.

colouration, they were dried without bleaching. In the laboratory, the size and shape of the nodules were calculated by measuring the greatest length (long axis), the widest (intermediate axis) and shortest (short axis) axes of the rhodolites at 90° to one another (Fig. 2.5). Rhodolite size is represented as the mean diameter which is equivalent to the sum of the long, intermediate and short axis, divided by three. Investigation of the epibiota was accomplished by direct observation, thin section analysis, and scanning electron microscope (SEM) analysis. Coralline algae have been identified from a variety of sources, including identification charts by Johnson (1961) and Wray (1977), unpublished photomicrographs from William Martindale, and the kind assistance of Yvonne Chamberlain (University of Portsmouth, UK).

2.4 RHODOLITE MORPHOLOGY

Size and Shape

The rhodolites are 1.7 to 12.1 cm long, 1.2 to 9.4 cm wide (intermediate axis), and 0.8 to 7.7 cm high (short axis). The mean diameter of the rhodolites ranges from 1.3 to 9 cm with an average of 3.9 cm (Fig. 2.6). The largest rhodolites, from locality SS-2, have an average mean diameter (AMD) of 7.6 cm. Rhodolites in the mid lagoon, which are represented by localities SS-1 and PB-1 are variable in size, with the Pease Bay rhodolites (AMD = 5.7 cm) being generally larger than those of South Sound (AMD = 3.6 cm). Most of the rhodolites from the reef crest at locality PB-2 are smaller than from elsewhere in the lagoon with an average mean diameter of 2.9 cm.

Thirty nine percent of the rhodolites are spheroidal, 35% discoidal, 20% prolate, and 6% bladed (Fig. 2.6). Although rhodolite form is typically variable at each locality, those from locality PB-2 are generally spheroidal whereas those from SS-2 and SS-3 are generally discoidal.

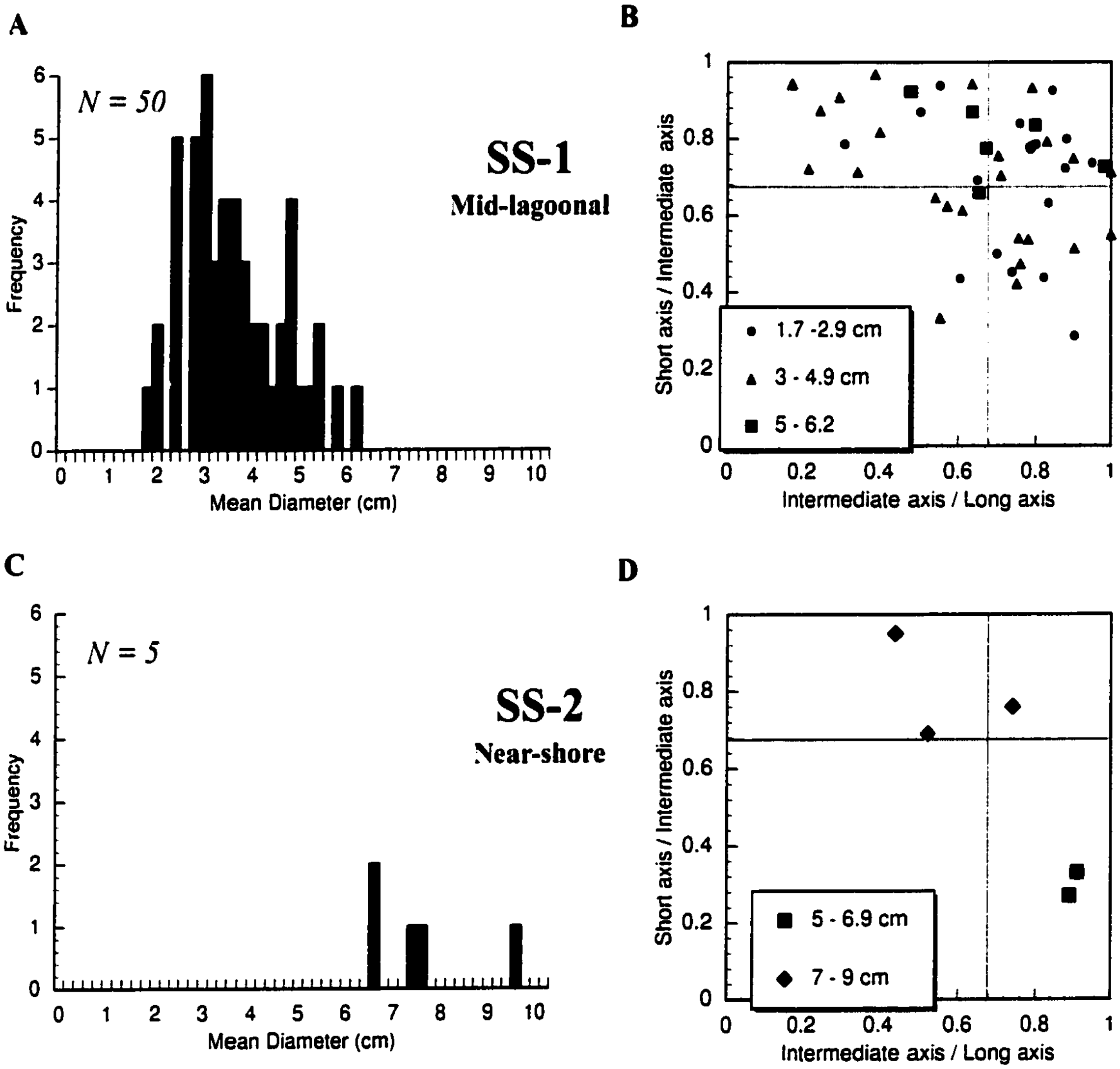
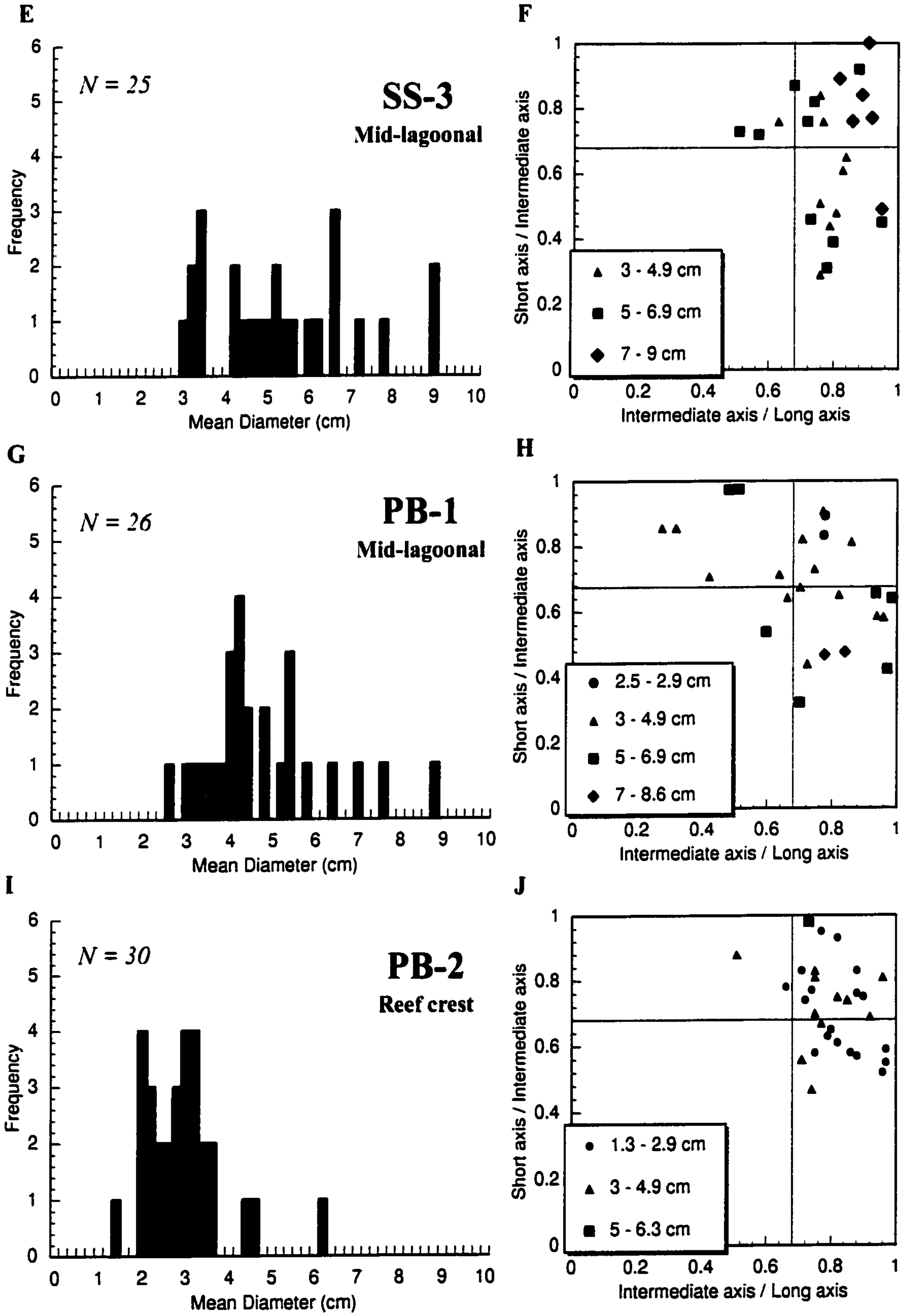


Figure 2.6 A - D, and following page E-J: Histograms and Zingg graphs of rhodolites collected at localities in South Sound (SS-1, SS-2, and SS-3) and Pease Bay (PB-1 and PB-2). Histograms represent mean diameter of rhodolites, where mean diameter = (long axis + intermediate axis + short axis) / 3. Zingg graphs represent shape distribution in relation to mean diameter. Mean diameter is divided into five arbitrary groups: 1 - 2.9 cm, 3 to 4.9 cm, 5 to 6.9 cm, and 7 to 10 cm as represented in boxes. These ranges may be truncated to the upper and lowermost mean diameters for each locality.

Nucleus Form

The nuclei typically represent from ~ 60 to 99% of the rhodolite volume because the cortices are rarely thicker than 1 cm. Rhodolites from the mid-lagoonal localities that neighbour patch reefs (SS-1 and PB-1) have nuclei dominated by fragments of branching



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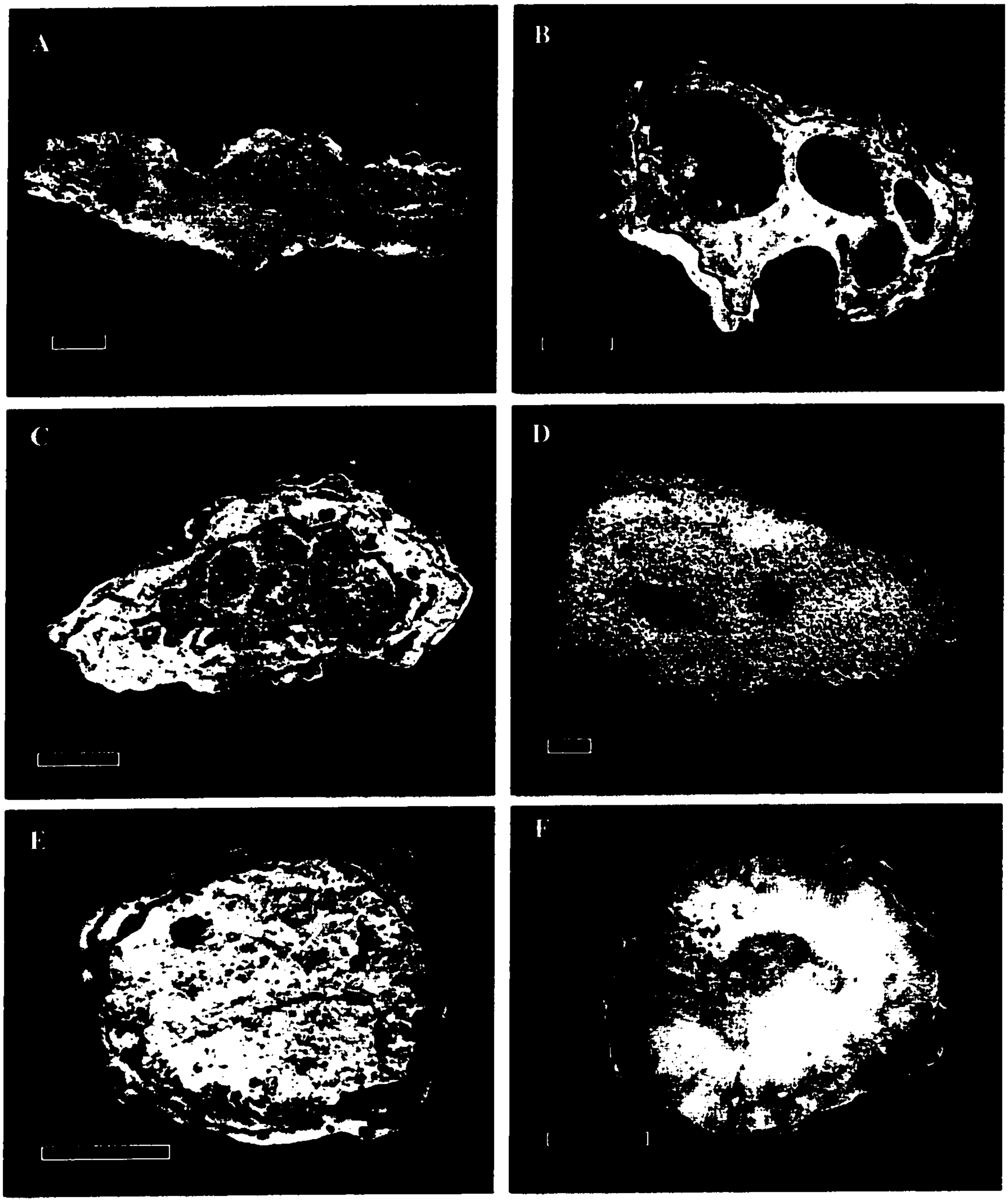

Figure 2.7: Modern rhodolite nuclei. Scale bars = 1 cm. **A:** Coral branch nucleus covered with laminar *Neogoneolithon* sp., from SS-1. **B:** Gastropod nucleus (outlined) covered with laminar *Neogoneolithon* sp., from locality SS-2. **C:** Bored coral nucleus (outlined) with foliose *Neogoneolithon* sp., and *Homotrema rubrum* cortex from locality SS-1. **D:** *Acropora palmata* fragment with thin microbialite cover, from locality SS-2. **E:** Rounded coral nucleus (outlined) with *Hydrolithon reinboldii* cortex from locality PB-2. **F:** Corallith nucleus partly covered with *Neogoneolithon* sp. and serpulid worm tubes (upper right), from locality PB-1.

corals with lightly calcified structures (Fig. 2.7A). Gastropods, bivalves and intraclasts are less common nuclei (Fig. 2.7B, C). Distinctly larger and heavier nuclei dominate rhodolites from the east end of South Sound, formed of rounded fragments of fore-reef corals, particularly *Acropora palmata* (Fig. 2.7D). Similar nuclei are found behind the reef crest at locality PB-2, however, they are much smaller and show a greater degree of rounding (Fig. 2.7D). Coralliths may also be nuclei for the rhodolites of Pease Bay (Fig 2.7E).

2.5 RHODOLITE BIOTA

The nodules are separated into three types based on their biotic composition (Fig. 2.8). As each type appears to develop in different sections of the lagoon, they are herein termed the *back-reef rhodolites* (locality PB-2), *mid-lagoonal rhodolites* (localities SS-1, SS -3, and PB-1), and *near-shore microbialites* (locality SS-2).

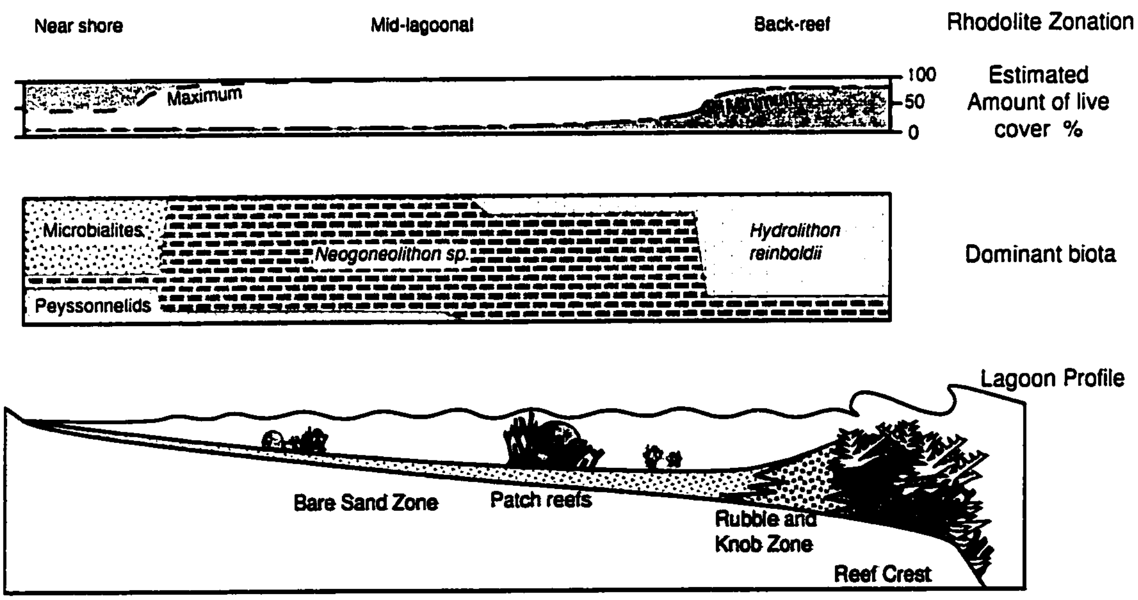

Figure 2.8: Generalised diagram of algal cover and dominant biota on the rhodolites of South Sound and Pease Bay. The vertical axis on the dominant biota chart represents the total live cover (lagoon profile modified from Kalbfleisch, 1995).

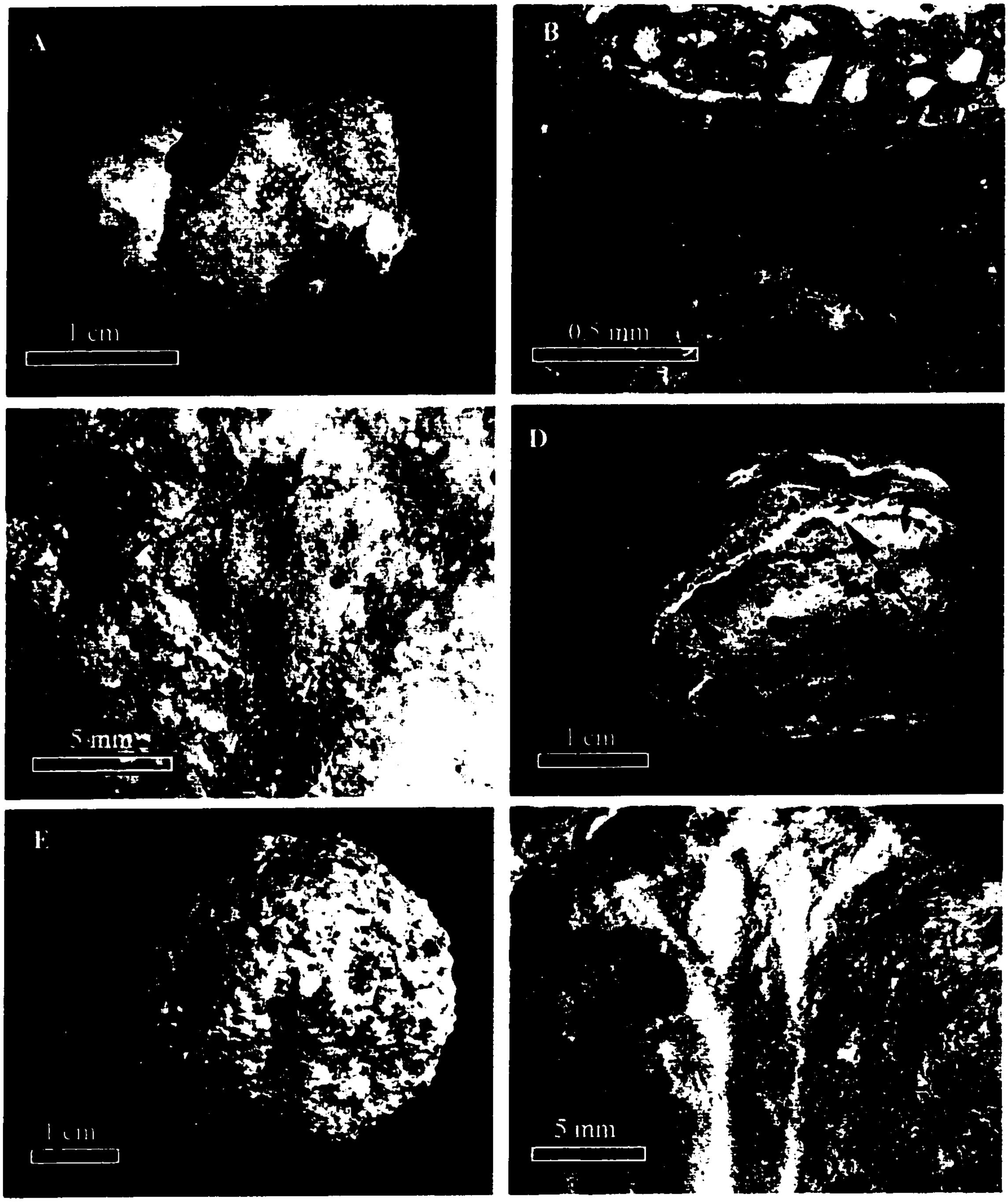

Figure 2.9: Back reef rhodolites from locality PB-2. **A:** Rhodolite encrusted with *Hydrolithon reinboldii* and *Homotrema rubrum*. **B:** Thin section photograph of *H. reinboldii* encrusted by *Carpentaria occulina*. **C:** Surface of *H. reinboldii* encrusted with *H. rubrum*. **D:** Sectioned rhodolite with corallith nucleus. Arrows mark intercalation of coralline algae between *Siderastrea sideria*. **E:** Large rhodolite encrusted by *Neogoneolithon* sp.. **F:** Parrotfish scar through *H. reinboldii*.

Back-reef Rhodolites

The back-reef rhodolites (Fig. 2.9A) are dominated by a complete living cover of *Hydrolithon reinboldii* (Fig. 2.9B), that gives the rhodolites a distinctive lilac and green colour. This alga has a laminar encrusting habit, with a smooth upper surface and a maximum thickness of ~ 4 mm. The remaining cortex is composed of *Homotrema rubrum* (Fig. 2.9C) which has a flattened form ~ 2 mm thick and ~ 4 mm in diameter. Encrusting colonies, 15 - 30 mm in diameter, of *Siderastrea sideria* are found on a few of the back reef rhodolites. Sectioning of one specimen revealed the colony is an exposed portion of a corallith which forms the nucleus (Fig. 2.9D). Banding within the corallith specimen of alternating coral and coralline algal layers indicate a switch from corallith to rhodolite has occurred on more than one occasion.

The biotic composition of the three largest of the rhodolites (mean diameter > 4 cm), is different (Fig. 2.9E). On these, *H. reinboldii* is rare and *Neogoneolithon* sp. is the dominant species, although, it rarely forms a complete cortex and much of the surface is exposed nucleus. *H. rubrum* is also present on these larger forms.

Boring organisms have removed up to 30% of the algal and nuclei skeletal structure on all sizes of rhodolites, and scars on the surface indicate fish have grazed heavily on some of the specimens (Fig. 2.9F).

Mid-lagoonal Rhodolites

Neogoneolithon sp., which is the dominant encruster of the mid-lagoonal rhodolites, forms up to 90% of the cortex. In hand sample, the species lacks colour and has a bumpy surface texture. The growth form ranges from laminar with small branches at locality SS-3 (Fig. 2.10A, B), to foliose at locality SS-1 (Fig. 2.10C, D). *H. rubrum* is the next most abundant encruster, with a branching habit, ~ 5 mm high and ~ 5 mm in diameter. *Peyssonnelia* sp., *Lithothamnium* sp., *Carpentaria utricularis*, serpulid worm tubes, cyanobacterial sheaths, boring organisms, and tunicates are minor members of the mid-

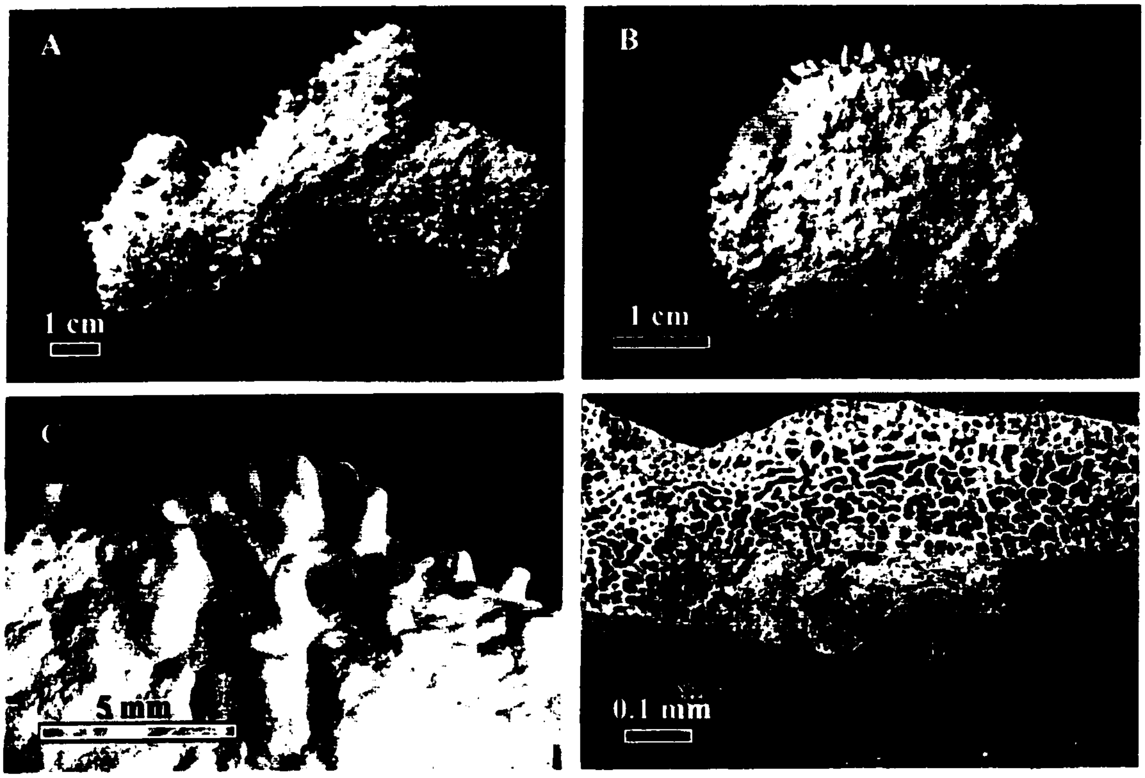

Figure 2.10: Mid-lagoonal rhodolites. **A:** *Neogoneolithon* sp. encrusting a branching coral (SS-1). **B:** Small discoidal rhodolite dominated by laminar / branching *Neogoneolithon* sp. with small coral colony (SS-1). **C:** Laminar / branching *Neogoneolithon* sp. (SS-1). **D:** SEM micrograph showing cross section of laminar *Neogoneolithon* sp. (SS-1).

lagoonal rhodolites. Laminar *H. reinboldii*, a minor constituent, is only found at locality PB-1.

The amount of living algae encrusting the rhodolites from the mid-lagoonal area varied from 0% on the largest specimens to 100% on the medium to smaller specimens. Many rhodolites over 6 cm in mean diameter, particularly those from locality SS-3, displayed different communities on their top and bottom surfaces when collected (Fig. 2.10E, F). The top surfaces have a thick (up to 20 mm) covering of highly foliose *Neogoneolithon* sp., with few other encrusters. The bottom surfaces consist mostly of exposed and bored nuclei, with a variety of sciaphyllic organisms including branching *H. rubrum* and serpulid worms.

Most rhodolites have been affected by intense boring prior to and during the period of

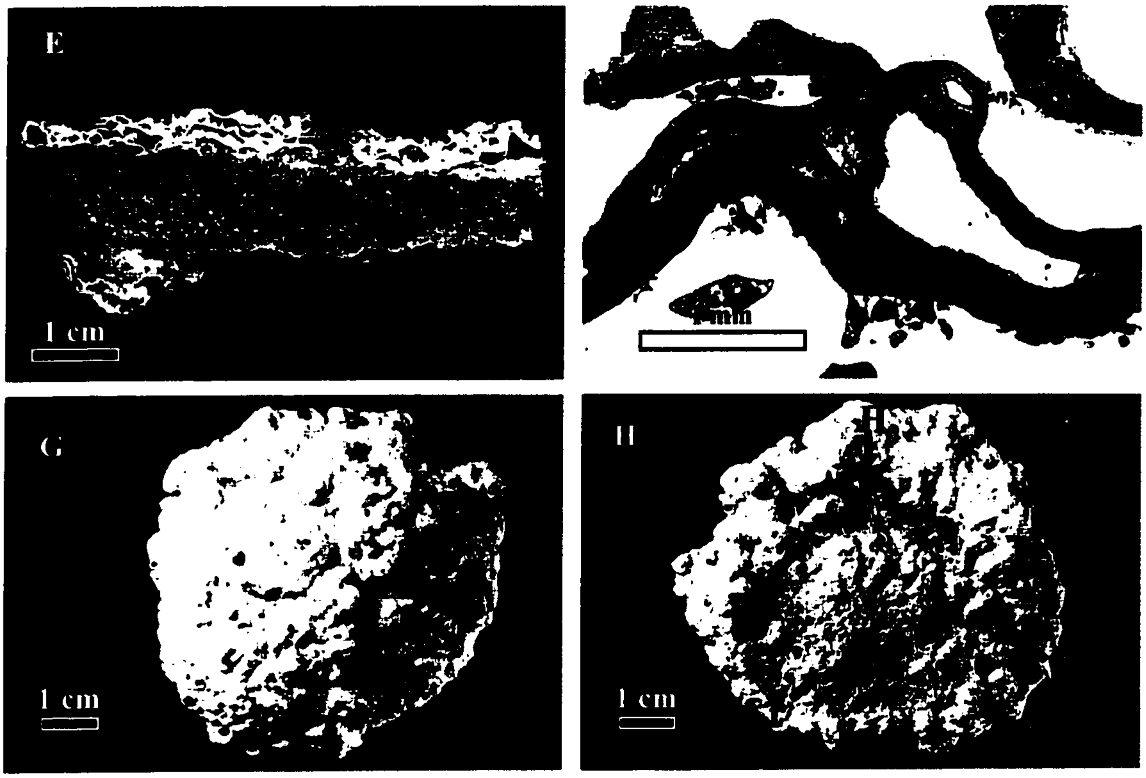

Figure 2.10 continued. E: Rhodolite with foliose *Neogoneolithon* sp. and heavily bored nucleus (SS-1). **F:** Thin section photograph of foliose *Neogoneolithon* sp. with conceptacle on upper right (SS-1). **G:** Top surface of a discoidal rhodolite with *Neogoneolithon* sp. (SS-3). **H:** Bottom surface of same rhodolite, showing scaphyllic encrusters: *Homotrema rubrum* (H), Serpulid worm tubes (S), and filamentous red algae (f).

algal encrustation. The heaviest boring is estimated at 70% removal of skeletal material, mostly from the nucleus. Boring is typically tubular, ranging from < 1 mm to ~ 10 mm in diameter. Heavy parrot fish grazing is apparent on the larger rhodolites and this probably explains why so much of the surface area on these forms is devoid of living algae.

Near-shore Microbialites

Microbialites dominate the near-shore waters. Up to three encrusting groups can be differentiated on various surfaces of the nodules. The top surface is exclusively covered in a ~ 3 mm thick cyanobacterial mat, the perimeter may be encrusted with a layer of *Neogoneolithon sp.*, and the bottom has minor amounts of *Peyssonnelia* sp. and *H. rubrum*. Boring in these nodules is the lowest of all those examined. Most borings are

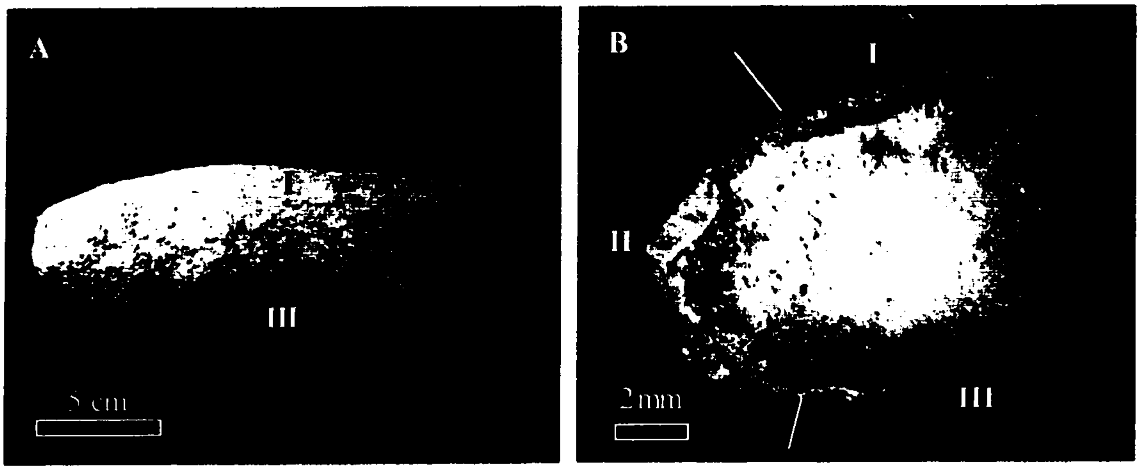

Figure 2.11: Near-shore nodules from locality SS-2. **A:** Lateral view and **B:** Lateral section through nodule with three encrusting groups: On top is a ~3 mm thick cyanobacterial mat (I); around the perimeter is a thin layer of *Neogoneolithon* sp., (II) and; on the bottom surface are a variety of sciaphyllic encrusters, including *Peyssonnelia* sp., and *Homotrema rubrum* (III).

tubular, 0.5 - 1 mm in diameter and penetrate a maximum of 5 mm into the nucleus. Parrotfish grazing is not evident.

2.6 DISCUSSION

From the analysis of these nodules, it is apparent that the particular morphological aspects of cortex thickness, rhodolite form, algal growth form, and biotic composition are sensitive to the environment in which they grow and show promise as paleoenvironmental indicators.

A feature shared by all of the rhodolites from South Sound and Pease Bay is that the thickness of the cortex never exceeds 14 mm. By comparing this thickness to typical growth rates of tropical coralline algae, 0.5 to 2 mm/year (Adey and Vassar, 1975), their age can be estimated at between 14 and 56 years. The absence of rhodolites of a greater age may imply that conditions in the lagoon prior to this period were not suitable for rhodolite growth, or that the rhodolites were periodically removed from the lagoon. Considering the control that storms have upon the sediment (*cf.*, Kalbfleisch and Jones, 1997), and their periodicity in the area (*cf.*, Clark, 1988), it is likely the latter situation is the correct one.

If transported out of the lagoon into the open sea, it is possible that these rhodolites travelled to considerable depths, because there is only a narrow shelf of a few hundred meters that separates the lagoons from the 30° shelf slopes (Roberts, 1994). Rhodolites in deep waters, which contain shallow water algal species have been discovered on a number of shelves and shelf slopes, including the Lesser Antilles shelf off Grenada (Reid and Macintyre, 1988), and the South African shelf (Seisser, 1972). The origin of these and fossil examples has been disputed. Some are believed to be *in situ*, formed during periods of lower sea level (*e.g.*, Logan *et al.*, 1969), but most studies have concluded that the rhodolites have been transported from shallower areas (*e.g.*, Minoura and Nakamori, 1982). Dates obtained from deep water rhodolites by Reid and Macintyre (1988) show they may be the result of accumulations over the last 10,000 years. An accumulation of a similar nature may exist in the waters off Grand Cayman. In a paleoenvironmental context, the value of deep water rhodolites with shallow water origins is not immediately obvious. However, they may prove of value in predicting the existence and type of local shallow water environment from which the rhodolites were transported, or, by the determination of the average cortex thickness, they may be able to establish the periodicity of the storm events that transported them.

Rhodolite form and algal growth form may be useful indicators of environmental conditions because of their sensitivity to the frequency of rhodolite turning (Bosellini and Ginsburg, 1971). In Whalebone Bay, Bermuda, Bosellini and Ginsburg (1971) noted that rhodolite and algal growth form varied for those found in sand channels, and those that were partly buried, or trapped in rocky depressions. The channel rhodolites, which were frequently turned by currents, developed an even coat of laminar coralline algae to produce a smooth and spheroidal rhodolite. The partly buried and trapped rhodolites were characterised by a bumpy surface texture and discoidal form. In South Sound and Pease Bay, different processes affect rhodolite form and algal growth. With such a thin cortex, rhodolite form is primarily controlled by nucleus form. This has led to the trends in size and shape throughout the lagoon (Fig. 2.6). In areas behind the reef crest, such as at locality PB-2, corals from the reef are broken down and abraded into relatively small and spheroidal fragments by currents. Eventually deposited into areas where abrasion is lower and coralline algae may encrust, the nuclei develop into small and spheroidal rhodolites. Coral fragments of similar origin are thrown into the lagoon during storms. Unlike those fragments deposited just behind the reef, this debris is not broken down further by wave energy, so they are typically large and discoidal. Debris such as this is the dominant nucleus supply of rhodolites from localities SS-2 and SS-3, hence they are mostly large and discoidal. Around the patch reefs, the 'background' supply of reef crest and fore-reef debris is surpassed by local material. There, molluscs and branched sections of coral produce discoidal, spheroidal and bladed rhodolites, whereas, sticks of coral produce prolate rhodolites.

The determination of what influences effect rhodolite form is therefore dependent on the type of lagoon. In protected lagoons, such as Whalebone Bay (Bosellini and Ginsburg, 1971), rhodolites are likely to develop a form that is indicative of turning frequency as the cortex thickness may mask the nucleus form. In storm affected lagoons, such as South Sound and Pease Bay, repetitive storms prevent such maturity from taking place, and rhodolite form reveals little more information than would the nucleus alone. Although this is essentially bad news as far as establishing wave and current energy in ancient storm affected lagoons, the distinction between thin and thick cortices may be used to determine if the lagoon was exposed to storm activity. To distinguish between protected and storm affected lagoons by the thickness alone will require much more detailed investigation, especially regarding other mechanisms which may lead to a thin cortex. However, compared to present methods of sediment analysis that require microscopic analysis (*e.g.*, Li, 1997) the simple sectioning of a few rhodolites may offer a 'quick and dirty' way to determine if a lagoon was affected by storms.

Unlike rhodolite growth form, algal growth form develops relatively quickly into a maturity that may indicate surrounding energy. This is evident from the variation in growth form with depth across South Sound. In deeper waters, such as at locality SS-1 (~ 2.5 m), algal growth form on the rhodolites is typically foliose, but where it is shallower, such as at locality SS-3 (~ 1 m), growth form is more laminar. The differences in form have developed through the interaction of wave energy on the sediment surface. As the lagoon shallows, as at SS-3, the amount of wave energy being absorbed by the sediment surface, and the rhodolites is greater than in deeper areas with flat bottoms.

The environmental elements that may alter epibiotic composition include temperature (Adey, 1970b), light (Adey, 1970b; Minnery *et al.*, 1985; Martindale, 1976, 1992), salinity, hydraulic energy (Adey and Vassar, 1975; Adey *et al.*, 1982), maturity of algal colony (Adey and Vassar, 1975), grazing pressure (Steneck, 1985), and substrate size (Adey, 1970a). In any single environment where encrusters are found, most of these criteria may partly influence the composition of biota. However, from the examples of South Sound and Pease Bay, identification of the dominant influence is possible by comparing the algal distribution to environmental criteria with matching variation.

From the comparison of wave and current variation and the biotic variation across the lagoon, it appears that hydraulic energy is the primary influence on algal distribution (Fig. 2.12). Observation of the lagoons has shown that hydraulic energy decreases from the reef crest to the shore in two steps. The first is due to the dissipation of currents travelling from the narrow and confined channels of the reef crest and back reef into the open lagoon. This area also represents the approximate boundary between the back-reef and mid-lagoonal communities. The second drop in energy is found at the transition from the mid-lagoon into the *Thalassia* banks, or close to the shore (when *Thalassia* is absent). There, wave energy, which has moved largely unhindered across the lagoon is absorbed by the grass or the sediment in the shallow water. This also coincides with a community boundary, the one between the mid-lagoonal rhodolites and the near-shore rhodolites (Fig. 2.12). The influence of hydraulic energy is further supported by the preferential

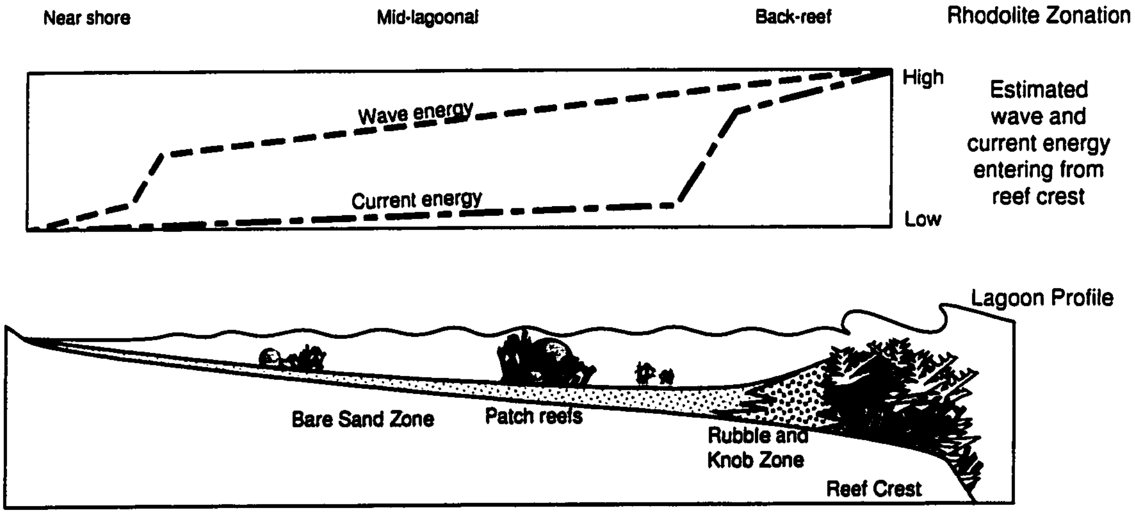

Figure 2.12: Observed variation in wave and current energy in comparison to rhodolite types across South Sound and Pease Bay lagoons (lagoon profile modified from Kalbfleisch, 1995).

distribution of particular genera throughout the lagoon and on various sizes of substrate. *Neogoneolithon* sp. for instance is found on rhodolites of all sizes in the mid-lagoon, but only on the largest rhodolites in the back-reef. Experiments by Adey (1970a) have shown that various coralline species will encrust substrates only of a certain size, which is invariably linked to the substrate's stability. Although not mentioned by Adey (1970a), hydraulic energy from currents and waves must also be considered here, as these also affect the substrate's stability. This suggests that the distribution of *Neogoneolithon* sp. is limited to substrates that are below a specific limit of stability. In the mid-lagoon, rhodolites of all sizes are well within these stable limits; however, in the back reef, smaller substrate size and higher energy prevents *Neogoneolithon* sp. growth in favour of *H. reinboldii*. The absence of *Neogoneolithon* sp. from the near-shore nodules is less related to nodule size and more to the generally low water energy. In this case, the alga was probably prevented from encrusting the upper surfaces because of the settling of fine grained sediment.

The morphology and biotic composition of rhodolites from South Sound and Pease Bay lagoons are therefore sensitive to the variation in hydraulic energy due to depth and location between the reef and the lagoon. Furthermore, the periodic effect of storms can also be recognised. If these relationships between rhodolite and environment are consistent in other modern lagoons and ancient ones, then morphology and biotic composition may allow detailed evaluation of the environment of growth in fossil examples.

2.7 SYNOPSIS

Rhodolites and microbialites from South Sound and Pease Bay on the South windward coast of Grand Cayman offer excellent analogues for the analysis of ancient storm influenced lagoonal rhodolites.

The rhodolites are characterised by a thin cortex. This is the result of a recent storm event that removed pre-existing rhodolites and initiated new rhodolite formation. As a result of the thin cortex, rhodolite shape is primarily influenced by the shape of the nucleus and not the frequency of rotation. Biotic composition of the cortex is governed principally by the hydraulic energy. This results in a pronounced variation in the biotic communities across the lagoon from those dominated by *Hydrolithon reinboldii* behind the reef crest, to *Neogoneolithon* sp. throughout the main body of the lagoon and microbialite dominated nodules close to the shoreline.

CHAPTER 3
FORM, INTERNAL STRUCTURE, ECOLOGY AND DIAGENESIS OF PEYSSONNELID RHODOLITES: AN EXAMPLE FROM GRAND CAYMAN

3.1 INTRODUCTION

Peyssonneliaceae, an aragonitic superfamily of the Phylum Rhodophyta (order: Cryptonemiales), is the only other living superfamily of red algae known apart from the more common Corallinaceae. Like the Corallinaceae (or coralline algae), the Peyssonneliaceae (or peyssonnelids) develop in marine waters within the photic zone, but are mostly restricted to its lower limits, or, in shaded regions in shallower waters (Denizot, 1968). The fossil record of the peyssonnelids extends with certainty to the Early Cretaceous (Massieux and Denizot, 1964; Johnson, 1964, 1965), but may go as far back as the Late Mississippian (Wray *et al.*, 1974; Wray, 1977). Yet, despite their long geologic range, and minor, but widespread presence in the modern marine environment, little is known about peyssonnelid habitat or ecology. This is especially true concerning their development upon unattached substrates as rhodolites, with only a single report (Buchbinder and Halley, 1985) of peyssonnelid algae dominating rhodolite growth.

This chapter describes a population of peyssonnelid dominated rhodolites of the Ironshore Formation on Grand Cayman. Excellently preserved, these rhodolites display two stages of development, initiating with an early stage of multispecific coralline growth, and a later stage of near-monospecific peyssonnelid growth. As well as investigating the unique ecology of this find, this chapter investigates the algal growth form, rhodolite form, and diagenesis with respect to the environment in which they formed. Descriptions of all encrusting algae are included, with special attention to the dominant peyssonnelid species as an aid to future identification.

3.2 LOCALITIES

There are few areas where the Ironshore Formation exceeds 2 m above sea level (Woodroffe *et al.*, 1980; Jones and Hunter, 1990), and much of the outcrop area is covered by thick mangrove vegetation. Nonetheless, over 150 localities along the coasts, in quarries, marinas and along the banks of mosquito control canals, have been examined (Jones and Hunter, 1990; Jones pers. comm.). Of these, rhodolites have been found only at Dolphin Point, on the west coast (Jones and Hunter, 1991), and Crystal Harbour (Fig. 3.1), a marina north of George Town that was under construction at the time of sampling

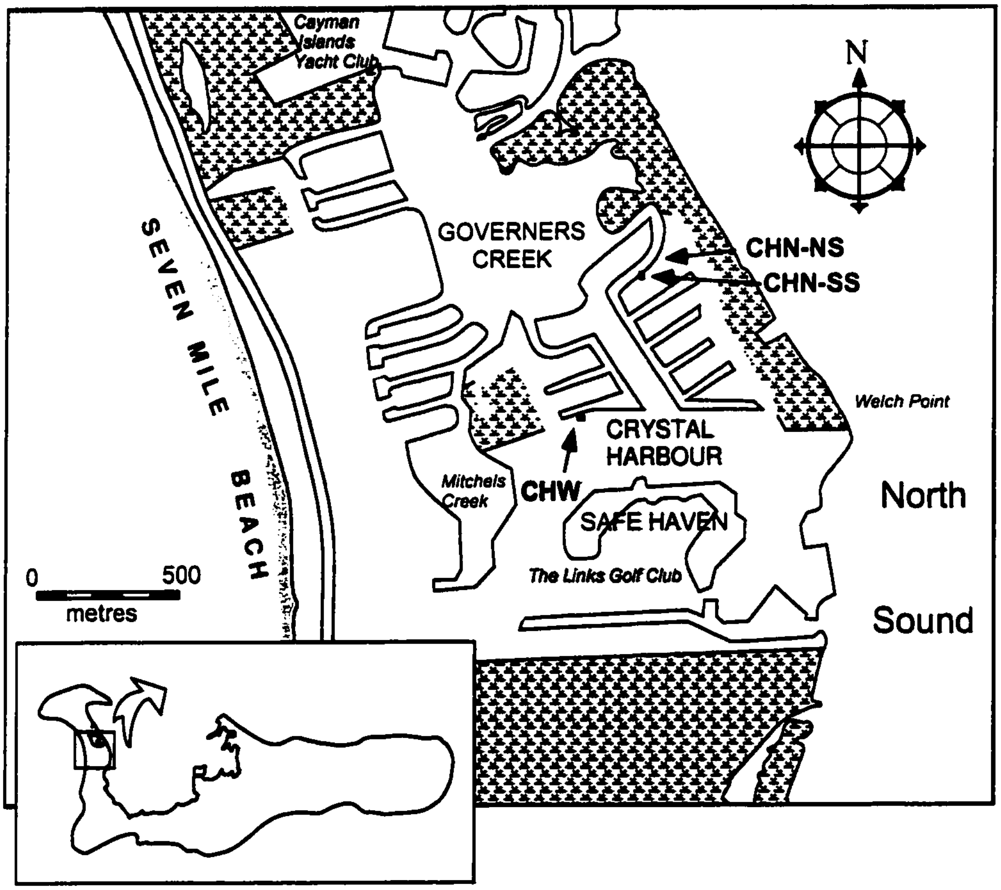

Figure 3.1: Location map of Crystal Harbour.

in 1994. This study deals only with the Crystal Harbour specimens. Channels, approximately 15 m wide, had been dredged and the material piled and levelled for construction. Rhodolites were found along the banks of these channels at three localities, one in the west, designated Crystal Harbour West (CHW), and two in the north, Crystal Harbour North-North Side (CHN-NS) and Crystal Harbour North-South Side (CHN-SS). The rhodolites were not *in situ*; however, the dense localised distribution indicated they had not been moved far from their original position.

3.3 PLEISTOCENE PALEOGEOGRAPHY AND FACIES

Throughout much of the depositional period of the Ironshore Formation (~ 125,000 ybp), sea level was ~ 6 m above present day sea-level and much of the western part of Grand Cayman was submerged (Jones and Hunter, 1990). The paleogeography of Grand Cayman at that time was dominated by a large lagoon, named the Ironshore Lagoon by Jones and Hunter (1990), that covered nearly all of the central and western parts of the island (Fig. 3.2A). The lagoon was bound to the west by a reef tract, and to the east by land which now forms the higher areas of the island. To the north and south, the lagoon was bordered by a peripheral ridge, presumed to be an erosional feature of the Cayman Formation (Jones and Hunter, 1990). The ridge is still present around a large section of the island today.

The lithofacies in the Ironshore Formation have been described in numerous studies (Table 3.1). Of these, the description and interpretation by Jones and Hunter (1990) is best suited for this investigation. They described an inter-patch reef and patch reef facies at Crystal Harbour, with a similar distribution to that described and mapped by Woodroffe *et al.* (1980) at Salt Creek (Fig. 3.2B).

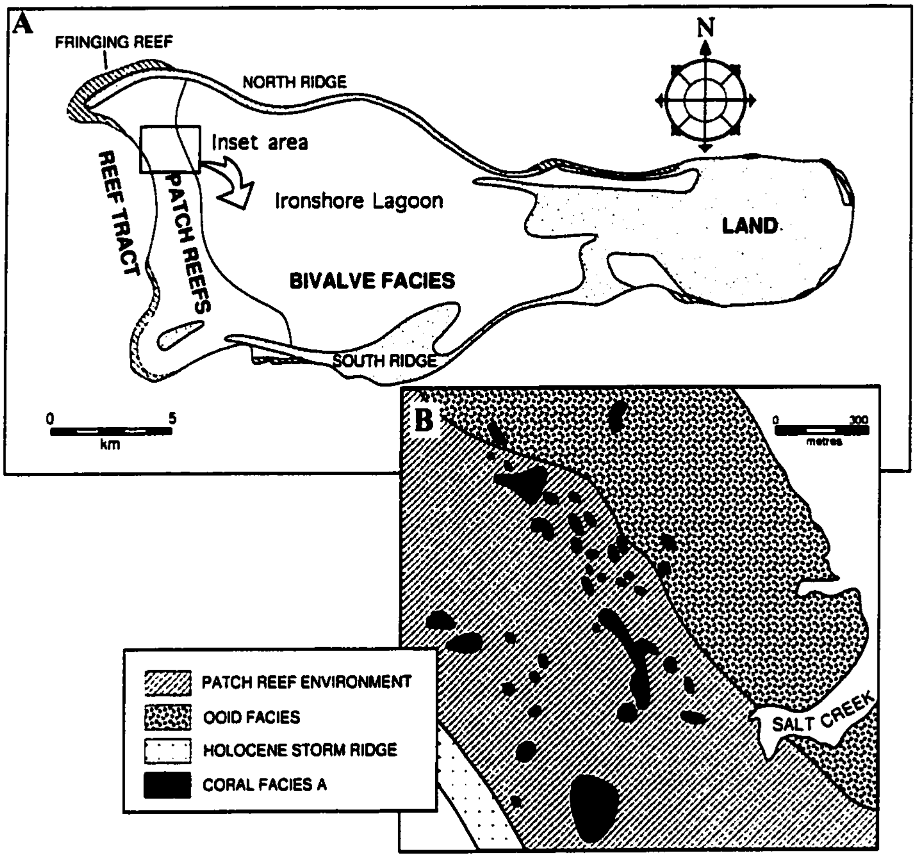

Figure 3.2. A: Ironshore paleogeography (Jones and Hunter, 1990). **B:** Facies distribution of patch reef environments at Salt Creek, north of Crystal Harbour (Woodroffe *et al.*, 1980).

Rhodolites are found in grainstones of the inter-reef ('Laminated to highly burrowed grainstones') facies (Jones and Hunter, 1990). These skeletal grainstones contain numerous gastropods and burrowing bivalves (Cerridwen, 1989; Cerridwen and Jones, 1991). Both of the Crystal Harbour North localities are adjacent to a patch reef. Patch reefs up to 200 m in diameter (Woodroffe *et al.*, 1980; Hunter and Jones, 1994), found throughout the laminated to highly burrowed grainstone facies have been named 'Coral facies A' by Jones and Hunter (1990). The patch reefs, which were influenced by currents from the west, contain a diverse coral fauna dominated by *Montastrea* and *Diploria* (Hunter, 1993). The large size and diversity of the patch reefs indicate that the environment was stable and that sedimentation and turbidity were low. Energy conditions were moderately

Brunt et. al 1973	Woodroffe et. al 1980	Jones and Goodbody 1984	Hunter and Jones 1988	Jones and Pemberton 1989	Hunter and Jones 1989a	Hunter and Jones 1989	Jones and Hunter 1990	Shourle 1993	Interpretation: Jones and Hunter, 1990
Lagoonal Facies	N/A	N/A	Bivalve Facies	N/A	Facies A	Bivalve A	Lagoonal Facies	Peneroplid-Miliolid Bivalve Wackestone/Packstone	Quiet water Setting (analogous to present day North Sound)
				N/A	Facies B	Bivalve B		Nummulitid-Bivalve Wackestone / Packstone	
								Poorly Sorted Halimeda-Bivalve Wackestone / Packstone	
								Peloidal-Bivalve Wackestone / Packstone	
	Coral Bearing Facies	N/A	Lagoonal Environment: Patch Reefs	N/A	Facies C	Coral A	Coral Facies A	Coral A Floatstone / Framestone	Patch Reefs
								Halimeda-Coral Floatstone / Framestone	
	Lagoonal Facies			N/A	Facies D	Skeletal Grainstone	Laminated to Highly Burrowed Grainstone	Poorly Sorted Skeletal Grainstone / Packstone	Inter-patch reef sediment
Reef Facies	N/A	N/A	Reef Tract	N/A	Facies E	Coral B	Coral Facies B	Coral B Floatstone / Framestone	Moderate to high Energy Reef Tract
Back-Reef Facies									
N/A	N/A	N/A		N/A	Facies F	Well Sorted Skeletal Grainstone		Well Sorted Skeletal Grainstone	
Shoal Facies	Oolitic Facies	Facies B	Ooid Facies	Facies A	Facies G	Moderately Burrowed Grainstone	Laminated to Highly Burrowed Grainstone	Moderately Burrowed Ooid Grainstone	Inter-patch reef sediment
				Facies B					
		Facies A		Facies C		Highly Burrowed		Highly Burrowed Ooid Grainstone	
		Facies C		Facies D		Unidirectional Cross-Bedded Grainstone	Unidirectional High-Angle Cross-Bedded Grainstone	Unidirectional Cross-Bedded Ooid Grainstone	Fill of lower lying areas
		N/A		Facies E		Multidirectional Cross-Bedded Grainstone	Multidirectional High-Angle Cross-Bedded Grainstone	Multidirectional Cross-Bedded Ooid Grainstone	
				Facies F		Lithoclast Rudstone	Rudstone	Lithoclast Rudstone	
				Facies G		Bioclast Floatstone		Bioclast Floatstone	
				N/A		Laminated Grainstone	Laminated To Low-Angle Cross-Bedded Grainstone	Laminated Ooid Grainstone	

Table 3.1: Previous facies designations of the Ironshore Formation.

low in the area, as indicated by a high proportion of epifaunal molluscs (Cerridwen, 1989; Cerridwen and Jones, 1991).

The maximum possible water depth at Crystal Harbour during the Late Pleistocene was 13.8 m. This represents the thickness of the Ironshore Formation in the area, and the maximum extent of sea-level elevation in the Late Pleistocene (Shourie, 1993; Wignal, 1996)

3.4 RHODOLITE AND ALGAL GROWTH FORM

Size and Shape

One Hundred and fifty six rhodolites were collected from the three localities at Crystal Harbour. Measurements of the long, intermediate, and short axes, (at 90° to each other) were taken for 126 whole rhodolites. The rhodolites are 2.5 to 13.7 cm long, 2.5 to 8.8 cm wide (intermediate axis) and 1.9 to 6.3 cm high (short axis). The mean diameter (long + intermediate + short / 3) of the rhodolites is 2.4 cm to 8.5 cm. The largest rhodolites came from CHN-SS with 20% of the rhodolites having a mean diameter > 7.5 cm (Fig. 3.3, 3.4). Seventy five percent of the Crystal Harbour rhodolites are spheroidal, 16% discoidal, 8% prolate and < 1% bladed. Rhodolites from CHN-NS are dominantly spheroidal, whereas rhodolites from CHN-SS and the CHW are prolate, spheroidal, and discoidal. Many of the discoidal rhodolites display shallow depressions on one or two surfaces. The thickness of the cortex is up to 60 mm on the largest rhodolites.

Nuclei of the rhodolites are fragmented branching corals (predominantly *Siderastrea radians* and *Porites porites*) and bivalve shells in approximately equal proportions. Nuclei are 15 to 30 mm in diameter for branching coral fragments and 20 to 60 mm long for bivalves. The nuclei at the CHN localities are similar in composition to the biota that

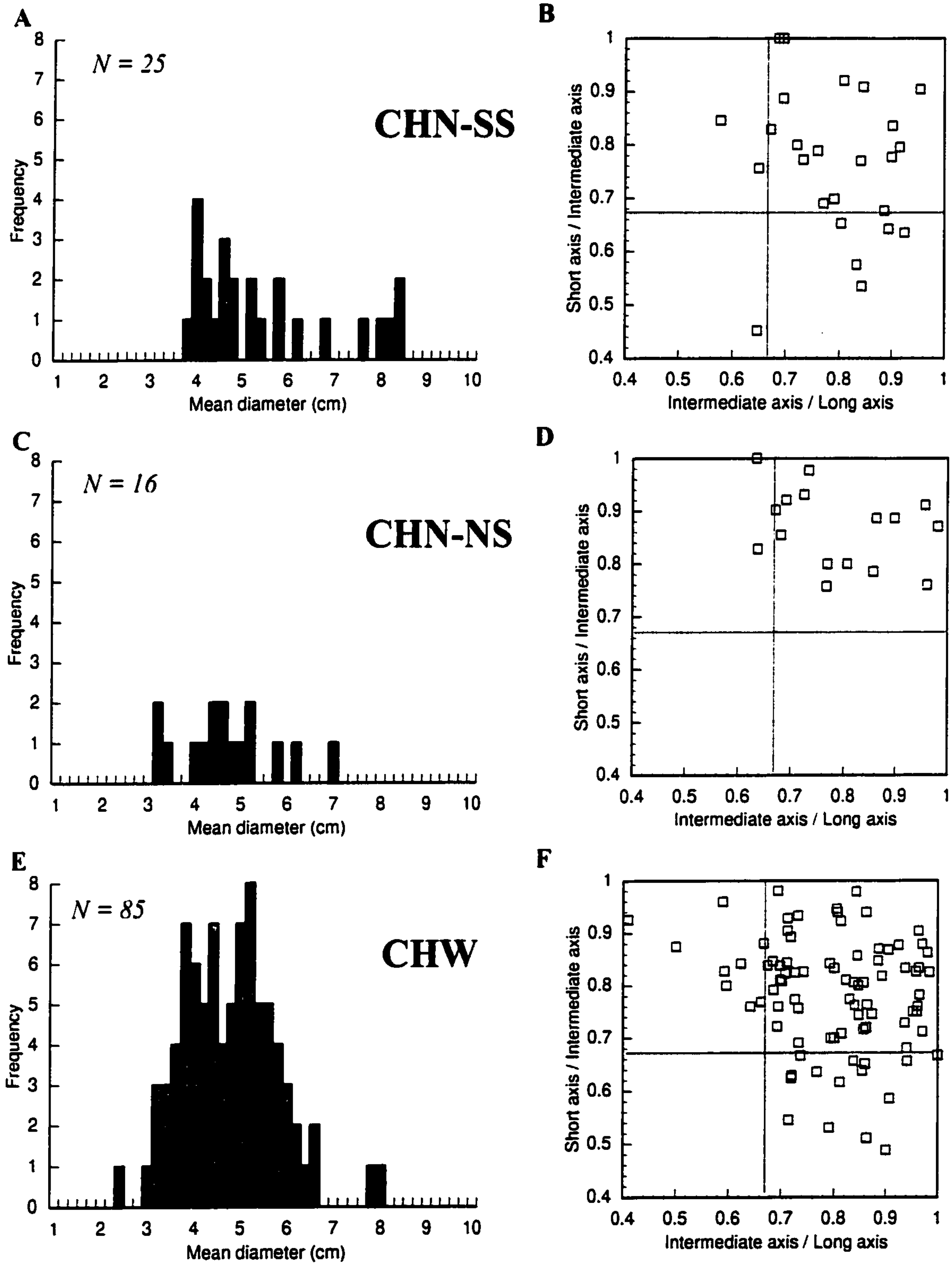

Figure 3.3: Size and shape of rhodolites from CHN-SS, CNH-NS and CHW. Histograms (A, C, E) represent mean diameter of rhodolites, where mean diameter = (long axis + intermediate axis + short axis) / 3. Zingg graphs (B, D, F) represent shape distribution (for explanation of Zingg graph see Figure 2.5).

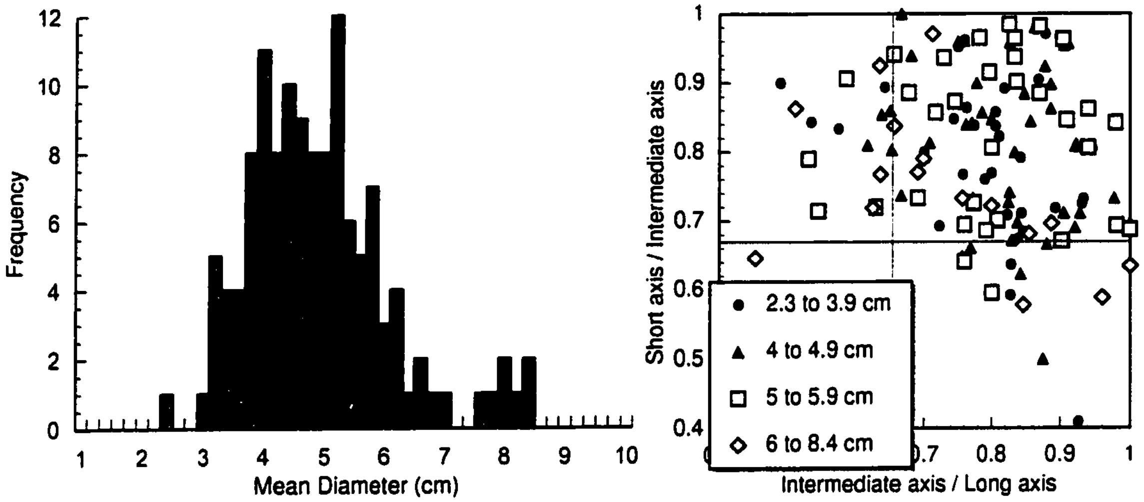

Figure 3.4: Frequency distribution of mean diameter, and shape distribution of Crystal Harbour rhodolites. Histograms represent mean diameter of rhodolites, where mean diameter = (long axis + intermediate axis + short axis) / 3. Zingg graphs represent shape distribution in relation to mean diameter. Mean diameter is subdivided into four arbitrary groups as represented in box.

were found on the adjacent patch reef, indicating a local origin. As the nuclei from locality CHW are of similar composition to those of CHN it is presumed that this locality may also have been adjacent to a patch reef, that was not evident from the collection site.

The surface form of the rhodolites ranges from smooth, to bumpy with irregular globular protrusions typically ~ 3 cm high and ~ 6 cm in diameter (Fig. 3.5). Sectioning through these types reveals that they are produced by the different algal growth forms of *Peyssonnelia rubra*, the dominant encruster. The algal growth form of this species is essentially massive, varying from massive laminar, to massive columnar. Rhodolites with smooth surfaces are dominated by laminar growth. Bumpy rhodolites, however, are formed by growth as separate mounds that increase in diameter throughout development. This form is intermediate between laminar and columnar and is herein termed 'globular'. Bumpy rhodolites may also, in rare cases, be formed by columnar algal growth. Algal layers develop as separate columns, typically 1 to 2 cm wide and rarely more than 1.5 cm

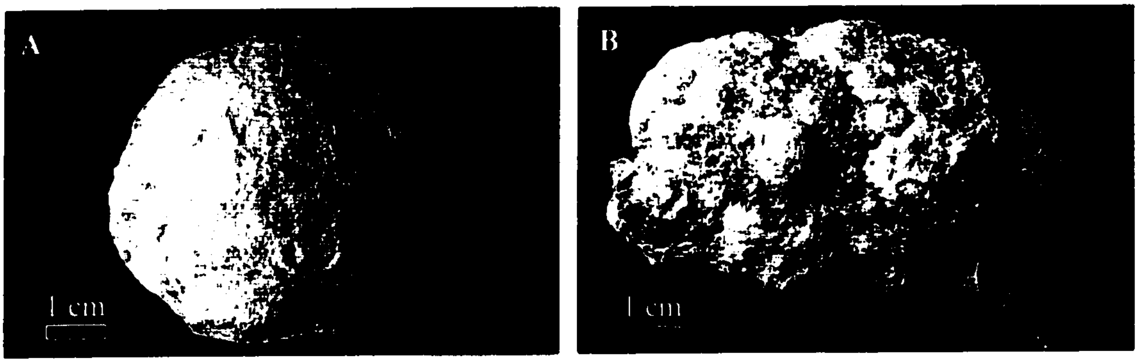

Figure 3.5 A: Spheroidal rhodolite with a smooth surface, a product of laminar algal growth. **B:** Tabular rhodolite with uneven 'globular' surface from columnar/globular algal growth.

high.

Influences on Rhodolite Shape and Algal Growth Form

The first investigation into the use of rhodolite shape and algal growth form as paleoenvironmental tools was by Bosellini and Ginsburg (1971). They concluded that wave energy had the greatest influence, because it controlled the rate that the rhodolites were turned. In areas of high energy, they stated, rhodolites are turned more frequently and develop an even coating of laminar algae to form a spheroidal shape. In low energy conditions, uneven growth results in a knobbly rhodolite, with an irregular shape. Unfortunately, other processes may also modify rhodolite shape, and need to be considered when investigating paleoenvironments. These other processes are of two types: those that modify shape through other methods of turning, such as the disturbance from grazing fish (Glynn, 1974); and those that concern the ability of an alga to evenly colonise a rhodolite without turning. The latter has been investigated by Scoffin *et al.* (1985). Their investigation of modern rhodolites on the shifting sandy substrates showed that a complete living algal envelope could be maintained for a number of months without being turned. Although it is impossible to determine if either biological disturbance, or wave energy turned the rhodolites, it is possible to determine if the encrusting algae required turning to grow a complete envelope. To do this, individual algal layers may be traced on sectioned rhodolites to ascertain how continuous they are. It may be presumed that if the algae grew around the whole rhodolite at once, as implied by Scoffin *et al.* (1985), then individual algal layers would also be traceable around most of the rhodolite. This was not found to be the case with the Crystal Harbour rhodolites. There, individual algal layers appear to have grown only on a single hemisphere of the rhodolites at one time (Fig. 3.6). Furthermore, this analysis shows that the alga grew only when a surface was facing up.

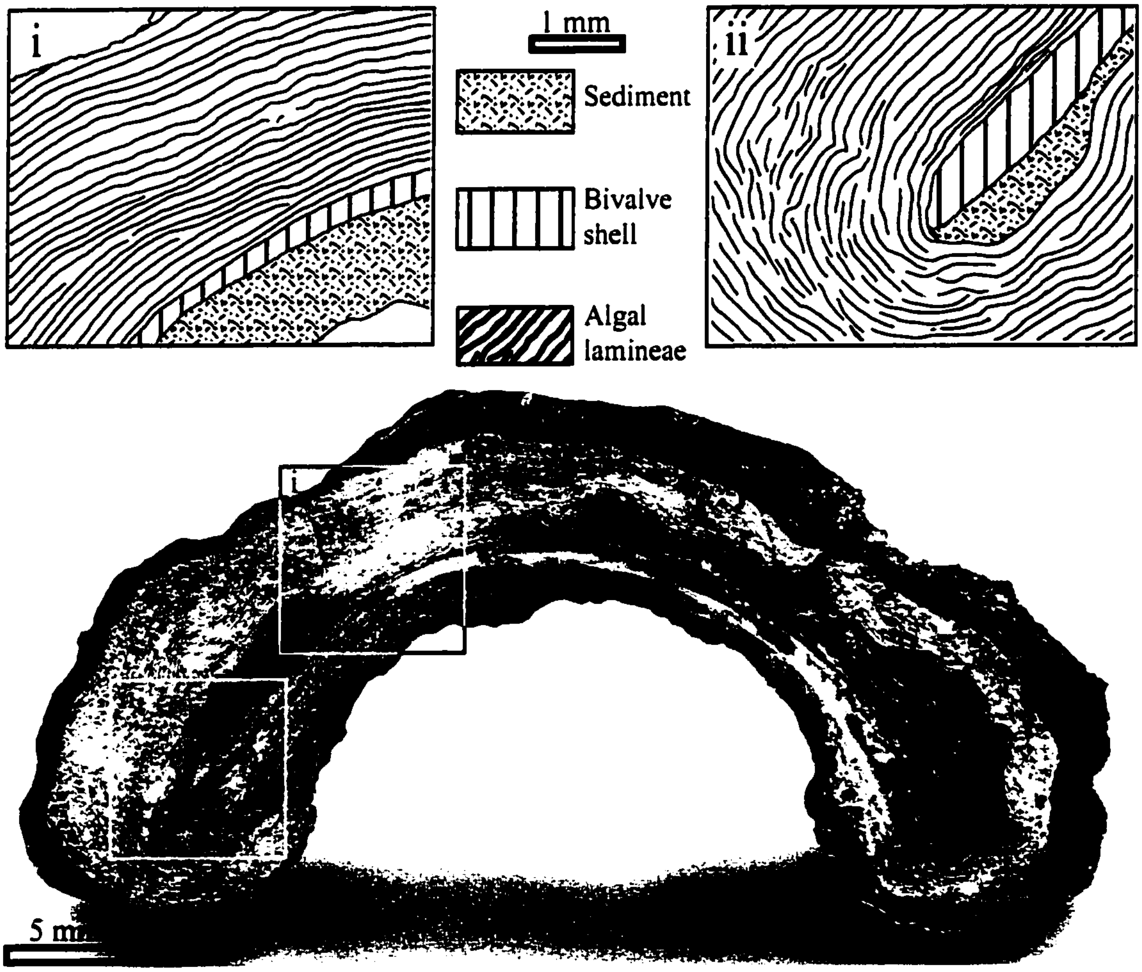

Figure 3.6: Lateral extension of algae in response to position on rhodolite. Individual layers of algae are continuous on the top surface (**i**) but are discontinuous around the perimeter (**ii**).

This is evident from the continuity of the layers throughout each hemisphere, including projecting surfaces which would have been in contact with the sediment. Evenly distributed algal growth around a nucleus, which is common to many of the Crystal Harbour rhodolites, was therefore dependent on regular turning.

Even though turning appears to have been regular on most rhodolites, this has had little effect on their shape and growth form. An indication of this is that rhodolite shape is highly variable at each locality despite every rhodolite experiencing similar environmental conditions. By using algal layers to track the change in shape throughout growth, it appears that the nucleus form is the primary influence of rhodolite form (Fig. 3.7). This is because the algal growth form of *P. rubra* mimics the underlying layers, transmitting the shape of the substrate (*i.e.*, the nucleus + cortex) through each layer. Nucleus form therefore becomes of primary importance. In the case of spheroidal or prolate nuclei, algal growth form is laminar because the nuclei may be rolled relatively frequently, and experience a variety of resting positions. The opposite is true of discoidal or irregular

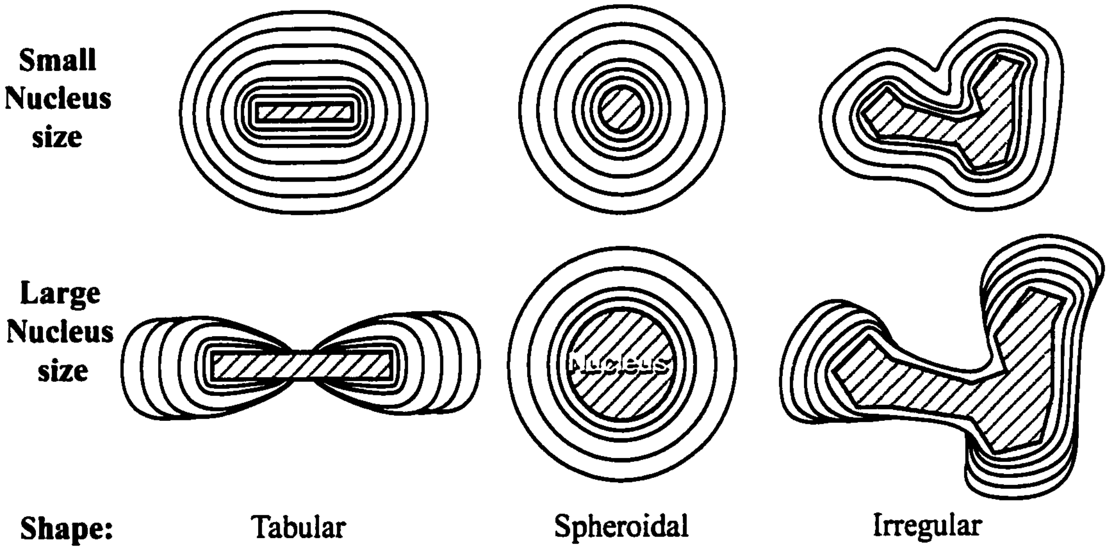

Figure 3.7: Relationship between nucleus size and shape and the resulting rhodolite shape.

nuclei. In these cases, algal growth is globular as it is only able to grow in a few stable resting positions. At its most extreme, columnar algal growth will develop when a nucleus has only one stable resting orientation, such as a highly convex bivalve or on stabilised substrates.

The size of the substrate may affect the relationship between nucleus and rhodolite form. Small objects on an uneven surface will experience a greater range of resting positions than a larger one of similar shape. Smaller rhodolites will therefore tend to develop laminar algae growth, regardless of shape (Fig. 3.8). At the other end of the scale, rhodolites with laminar algal growth will at some point reach a maximum size in which the turning mechanism becomes unable to regularly move it. This can be seen on spheroidal rhodolites where upon reaching ~ 8 cm diameter, globular growth around one axis replaces the concentric laminar growth.

A particularly common aspect of the rhodolite shape which is difficult to interpret

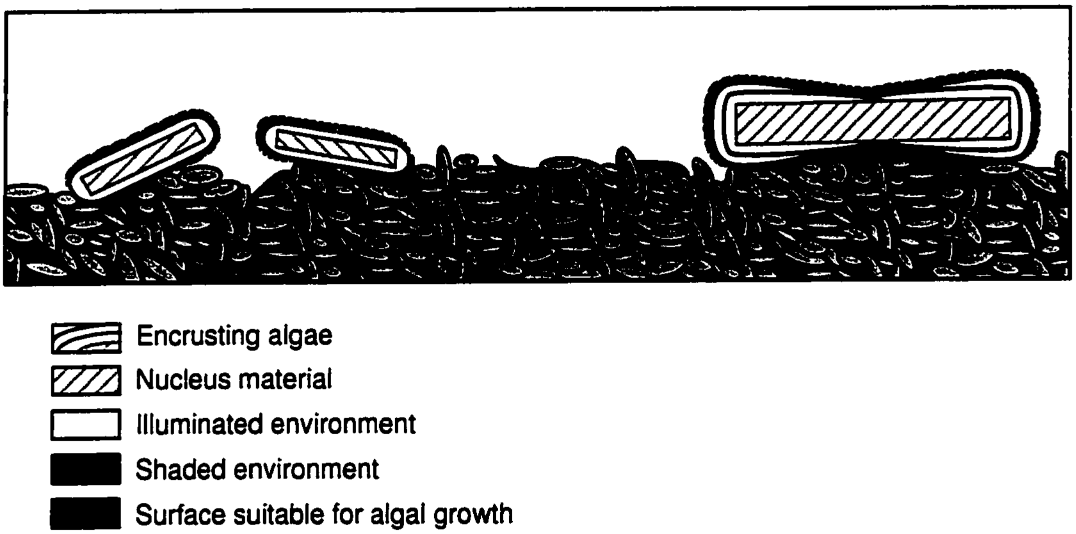

Figure 3.8: Relationship between rhodolite size, sediment grain size and encrusting algal distribution. Smaller rhodolites have more variable resting orientations than larger rhodolites of similar shape, hence the algal growth upon them is better distributed and laminar in form.

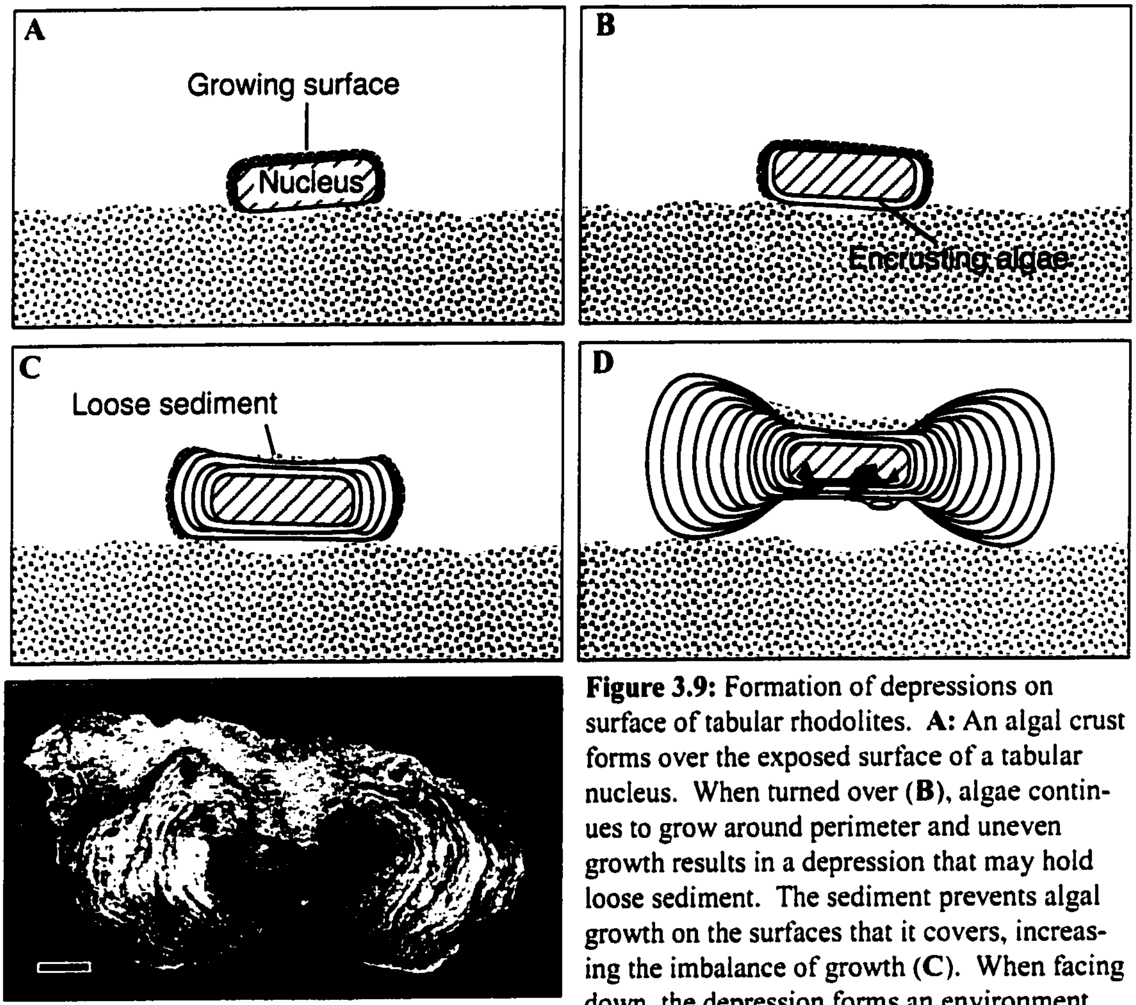

Figure 3.9: Formation of depressions on surface of tabular rhodolites. **A:** An algal crust forms over the exposed surface of a tabular nucleus. When turned over (**B**), algae continues to grow around perimeter and uneven growth results in a depression that may hold loose sediment. The sediment prevents algal growth on the surfaces that it covers, increasing the imbalance of growth (**C**). When facing down, the depression forms an environment suitable for sciaphyllic encrusters such as serpulid worms and endolithic organisms that attack the dead skeletal material (**D**). These depressions may form on one or both sides of a tabular rhodolite (**E**).

from external appearance, is a depression on one or both sides of discoidal forms (Fig. 3.9). Sectioned samples show that the depressions are the result of preferential growth around the rim and partial boring at the hubs. This is probably the result of the form of the rhodolite. During the growth period, one of the two faces would have been constantly in contact with the sediment, while the rims were continually free to grow. Growth around the rims could have therefore been up to double that of the hubs, resulting in the depressions observed. Further enhancement of the depressions may have resulted from the filling of the depressions with sediment which allowed access by boring organisms.

Rhodolite Distribution and Paleocurrents

The density of the rhodolites around the patch reefs, and their scarcity elsewhere, suggests that they were unaffected by wave or tidal currents. Conversely, grading of size between adjacent CHN-NS and CHN-SS localities, along with the evidence of frequent turning, suggests at least periodic currents occurred that were able to move them. It may be that paleocurrent velocities were high, but the rhodolites were restricted by a barrier. In Pease Bay, shallow troughs and basins that develop around patch reefs retain much of the debris that accumulates, despite frequent currents that are able to turn them (Chapter 2, this thesis). A similar situation may have developed at Crystal Harbour, where paleocurrents turned and distributed rhodolites in sandy depressions around the patch reefs, but were unable to move them out.

3.5 BIOTIC COMPOSITION

Encrusting red algae, along with lesser amounts of encrusting corals, foraminifera, serpulid worms and bivalves form the cortices of the rhodolites.

Red Algae

Corallinaceae and Peyssonneliaceae are the two superfamilies of carbonate producing, encrusting red algae present on the Crystal Harbour rhodolites. Representatives of the Corallinaceae family include *Lithoporella* sp., *Lithophyllum* sp., *Neogoneolithon* sp., *Hydrolithon reinboldii, Porolithon* sp., and *Lithothamnium* sp.. Peyssonneliaceae is dominated by *Peyssonnelia rubra*. A second unidentified species from a single sample is referred to as 'Unidentified peyssonnelid'. As the result of poor preservation and lack of identifying reproductive cells, many algae in this study have only been identified to genus level. Thus, brief descriptions of each species present are included to verify identification. Distribution on the Crystal Harbour rhodolites and in modern environments are also mentioned.

Corallinaceae (Crustose coralline algae or corallines)

Lithoporella sp.

Lithoporella sp. has foliose or laminar growth forms (Fig. 3.10A), both of which may be present on a single plant. The thallus is composed of a single layer of vertically elongate cells, 10 μm wide by 30 μm high. The horizontal cell walls are darker and more distinct than the vertical walls that separate the cells. Conceptacles, 200 μm wide by 130 μm high, have a single aperture. *Lithoporella* sp. was typically the initial encruster and developed thin crusts on protected and possibly shaded surfaces. Modern examples inhabit similar environments in shallow waters or may be present at greater depths (Minnery *et al.*, 1985).

Lithophyllum sp.

Lithophyllum sp. can form layers up to 6 mm thick that fill irregularities on the underlying substrate. The surface of *Lithophyllum* sp. has a distinct ornamentation formed of fine parallel ridges that are visible with the naked eye (Fig. 3.10B). Although the alga typically has a coaxial hypothallium (Johnson, 1961), this has not been identified on the Crystal Harbour specimens. The perithallium cells are arranged into strongly defined horizontal threads and weaker vertical threads (Fig. 3.10C). The horizontal threads are discontinuous, forming lenses up to 1 cm in length with the thickest section at the centre. Less distinct vertical cell threads are parallel and continuous throughout the thickness of the thallus. Cells are vertically elongate, 8 to 15 µm wide by 5 to 30 µm high, depending on which part of the lens they are situated. Conceptacles, approximately 200 µm wide by 150 µm high are numerous and well developed, with a single aperture in the roof. *Lithophyllum* sp. is the most common coralline algae on the rhodolites, with growths up to 2 mm thick and appears to be best developed on what were exposed surfaces. Studies by Adey (1979), Adey *et al.*, (1982) and Minnery *et al.*, (1985) have shown that the species is common to depths of 80 m in modern tropical waters.

Neogoneolithon sp.

The thallus of *Neogoneolithon* sp., 100 to 500 µm thick, consists of a poorly defined hypothallium and strongly developed perithallium (Fig. 3.10D). The structure of the hypothallium may be coaxial or plumose. The perithallium contains strongly developed vertical and horizontal threads made up of cells ~ 5 µm wide by ~ 5 µm high. Vertical stacks of 5-6 megacells are common throughout the perithallium. Laminar crusts of *Neogoneolithon* sp. have a constant thickness apart from small, poorly developed branches. Conceptacles with a single aperture, 500 µm wide and 200 µm high are regularly located at the base of the branches (Fig. 3.10E). *Neogoneolithon* sp. has a similar distribution on the rhodolites to that of *Lithophyllum* sp., though not as abundant. On modern, fixed substrates, the genus has been found growing from intertidal to 70 m (Adey *et al.*, 1982).

Hydrolithon reinboldii

Hydrolithon reinboldii has a laminar growth form similar to that of *Lithophyllum* sp.. The hypothallium has not been identified, but the species is readily recognisable by its distinct perithallium that is formed of cells grouped into lenses of variable width (100 μm to 1 mm) which are contiguous and juxtaposed to each other (Fig. 3.10F). Lens thickness is ~ 100 μm at the centre and tapers towards the edge. Cells, ~ 20 μm wide and high are arranged into three horizontal rows in each lens and have an irregular vertical alignment. The conceptacles which are 120 μm high and 180 μm wide, have a single aperture and are enclosed by many layers of perithallic cells. The few occurrences of *H. reinboldii* at Crystal Harbour, show the plant preferred protected surfaces on the irregularly shaped rhodolites. Modern examples of the genus are common in deeper waters or partly shaded regions of reef crests (Adey, 1979; Adey *et al.*, 1982; Minnery *et al.*, 1985; Chapter 2, this study).

Lithothamnium sp.

The hypothallium of *Lithothamnium* sp. may consists of cells that curve up from a horizontal orientation at the base, or may be plumose where the cells curve up and down from the centre (Fig. 3.10G). The perithallium consists of strong vertical cell threads that are evenly spaced with horizontal partitions between. The horizontal partitions may or may not be at the same level between vertical threads. Cells are ~ 5 μm wide and high. The multi-apertured conceptacles, a characteristic feature of this genus (Johnson, 1961), have not been recognised. *Lithothamnium* sp. occupied a similar niche to that of *H. reinboldii*, on protected surfaces. In the modern tropics, this genus develops in deeper waters or in shallow waters where shaded (Minnery *et al.*, 1985).

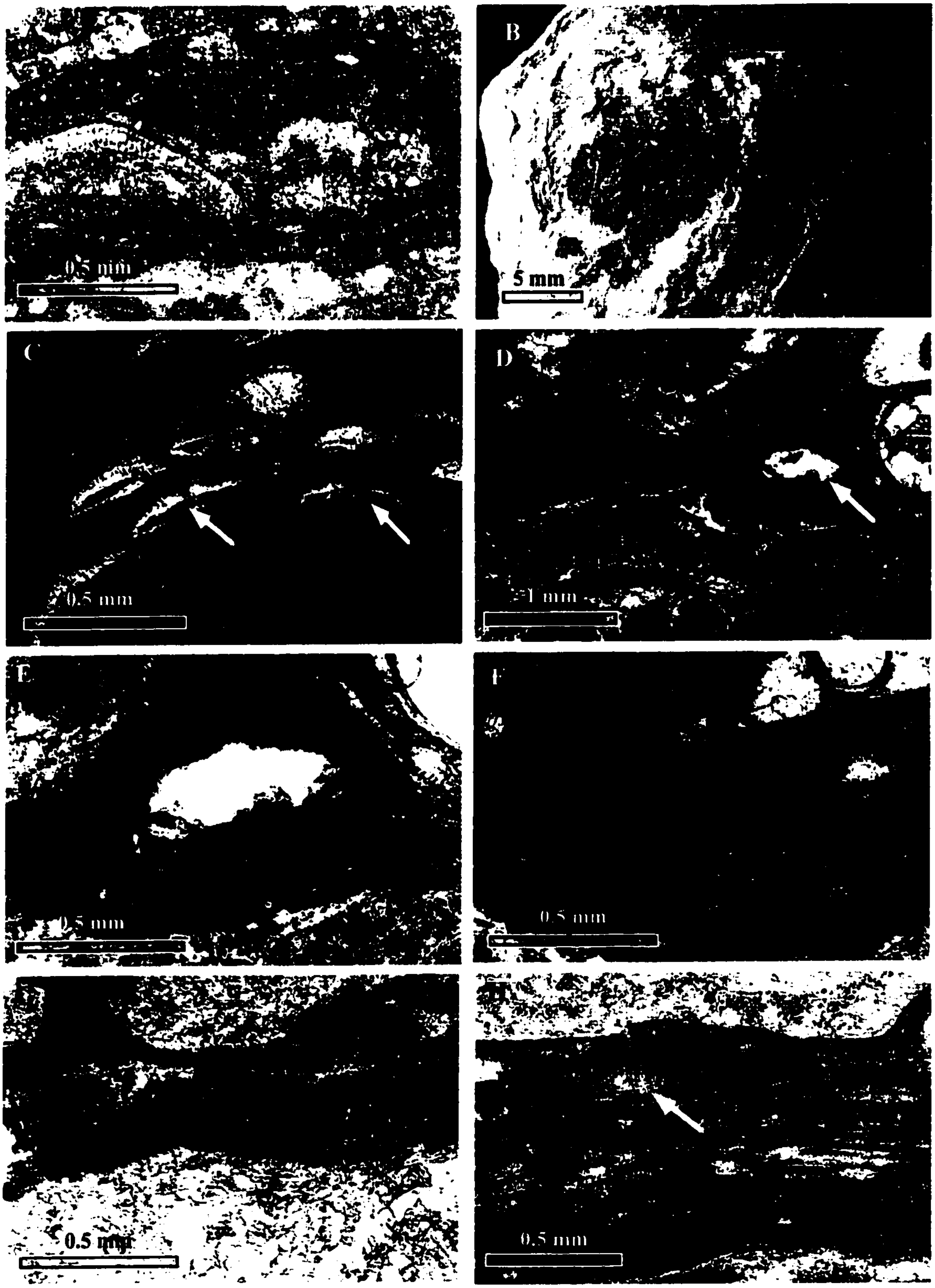

Figure 3.10 A: *Lithoporella* sp. with encrusting foraminifera. **B:** *Lithophyllum* sp. surface ornamentation. **C:** *Lithophyllum* sp. thallus. **D:** *Neogoneolithon* sp. thallus and **E:** conceptacle. **F:** *Hydrolithon reinboldii* with serpulid worm tube (top right). **G:** *Lithothamnium* sp. thallus. **H:** *Porolithon* sp. with megacells. Conceptacles shown by arrows.

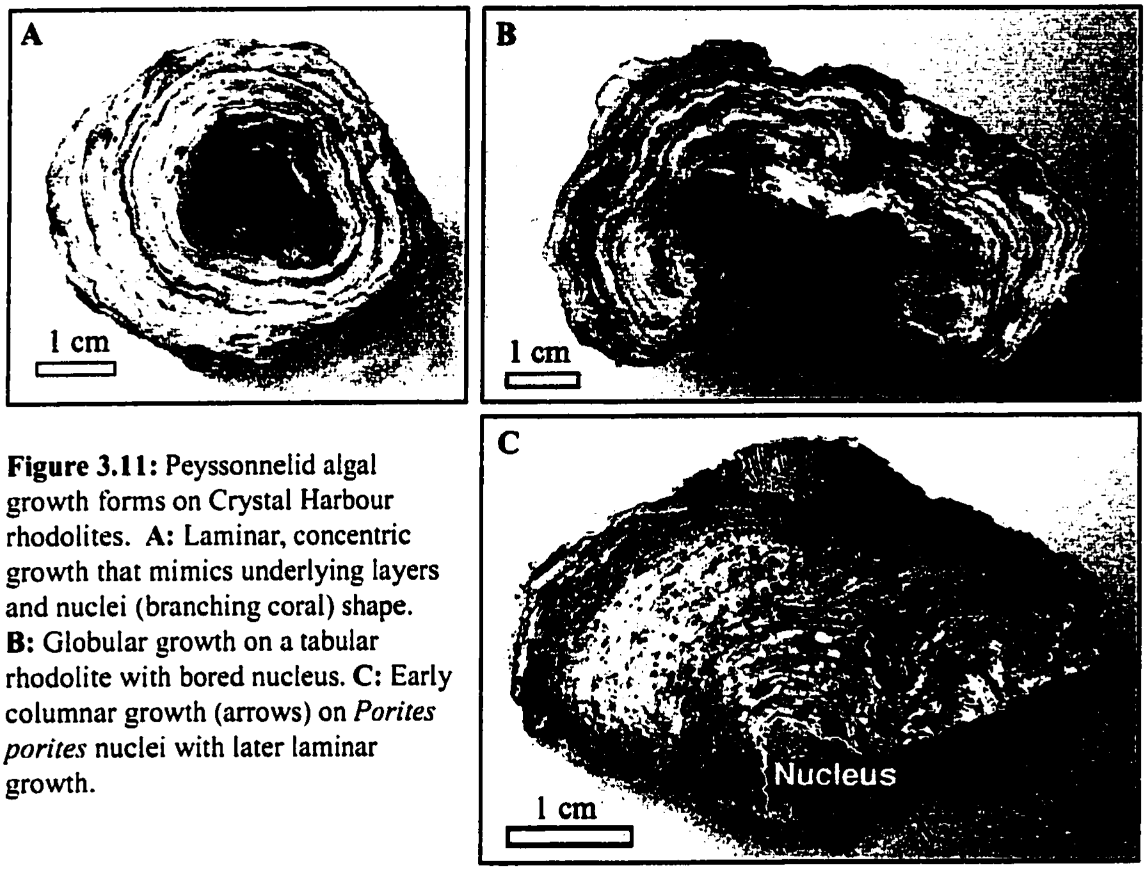

Figure 3.11: Peyssonnelid algal growth forms on Crystal Harbour rhodolites. **A:** Laminar, concentric growth that mimics underlying layers and nuclei (branching coral) shape. **B:** Globular growth on a tabular rhodolite with bored nucleus. **C:** Early columnar growth (arrows) on *Porites porites* nuclei with later laminar growth.

Porolithon sp.

This species of *Porolithon* forms crusts similar to that of laminar *Lithoporella* sp. The hypothallium has not been identified. The perithallium consists of strong horizontal threads of cells, parallel to each other, with weak vertical partitions (Fig 3.10H). Cells are ~ 4 μm wide and ~ 8 μm high. Megacells form throughout the perithallium as horizontal rows, a distinguishing feature of this genus. *Porolithon* sp. typically encrusted surfaces of the rhodolites that would have been exposed to abrasion and strong light. Correspondingly, modern forms are best developed on shallow substrates that are exposed to strong waves and currents, such as on reef crests (Adey, 1979; Adey *et al.*, 1982).

Peyssonneliaceae (peyssonnelid algae)

Peyssonnelia rubra

Much like a coat of paint, layers of *Peyssonnelia rubra* (Denizot, 1968) cover the substrate and mimic the underlying topography. In hand sample, *P. rubra* is buff in colour (modern living examples are a distinctively deep mauve) and has a finely stepped surface texture formed by exposure of underlying layers. The growth form of *P. rubra* ranges from laminar to columnar (Fig. 3.11).

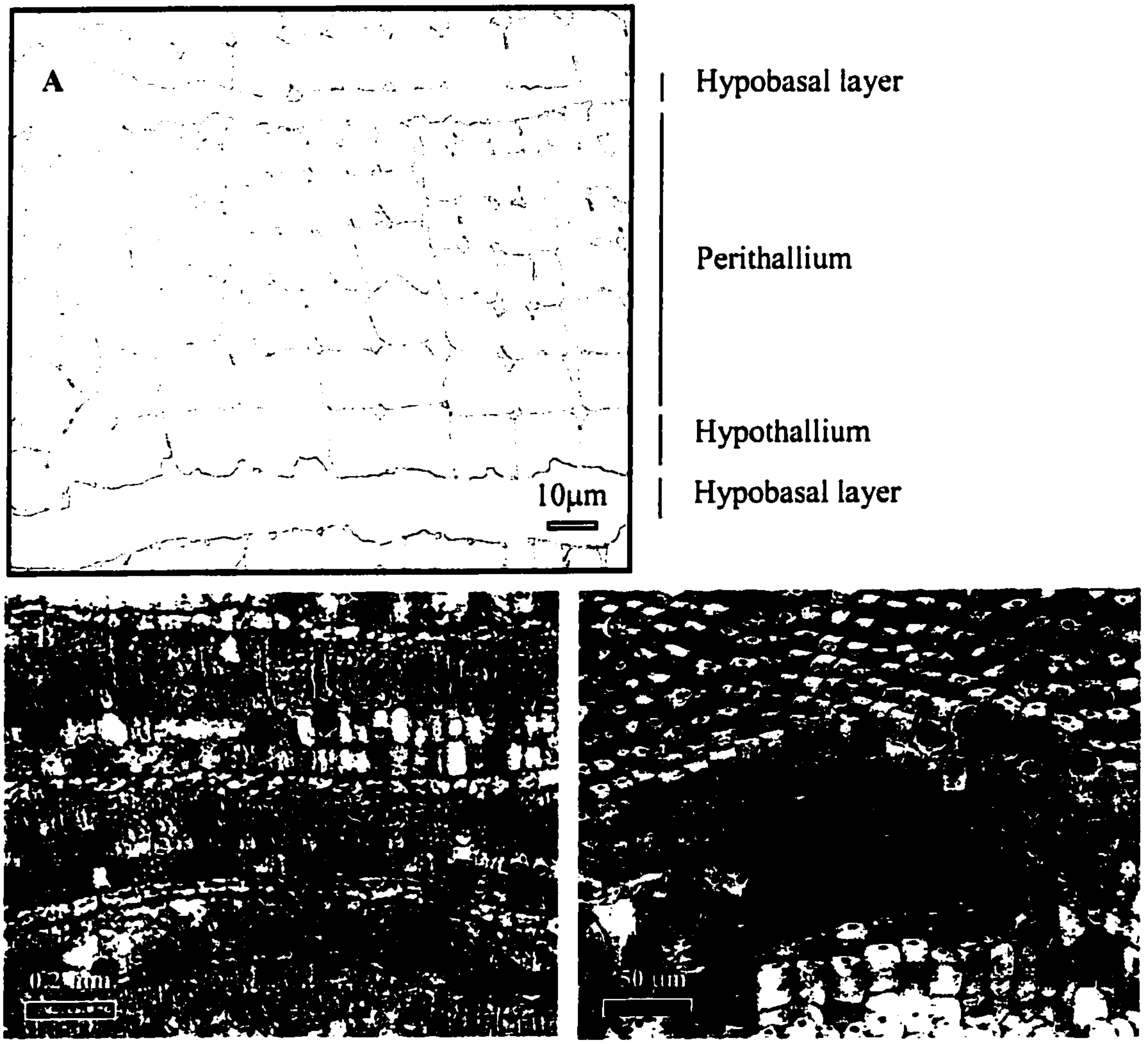

Figure 3.12 A: Structural composition of *Peyssonnelia rubra*. **B:** Thallus layers of *P. rubra* in plain polarised light. **C:** Scanning electron micrograph of *P. rubra* cross-section and upper surface.

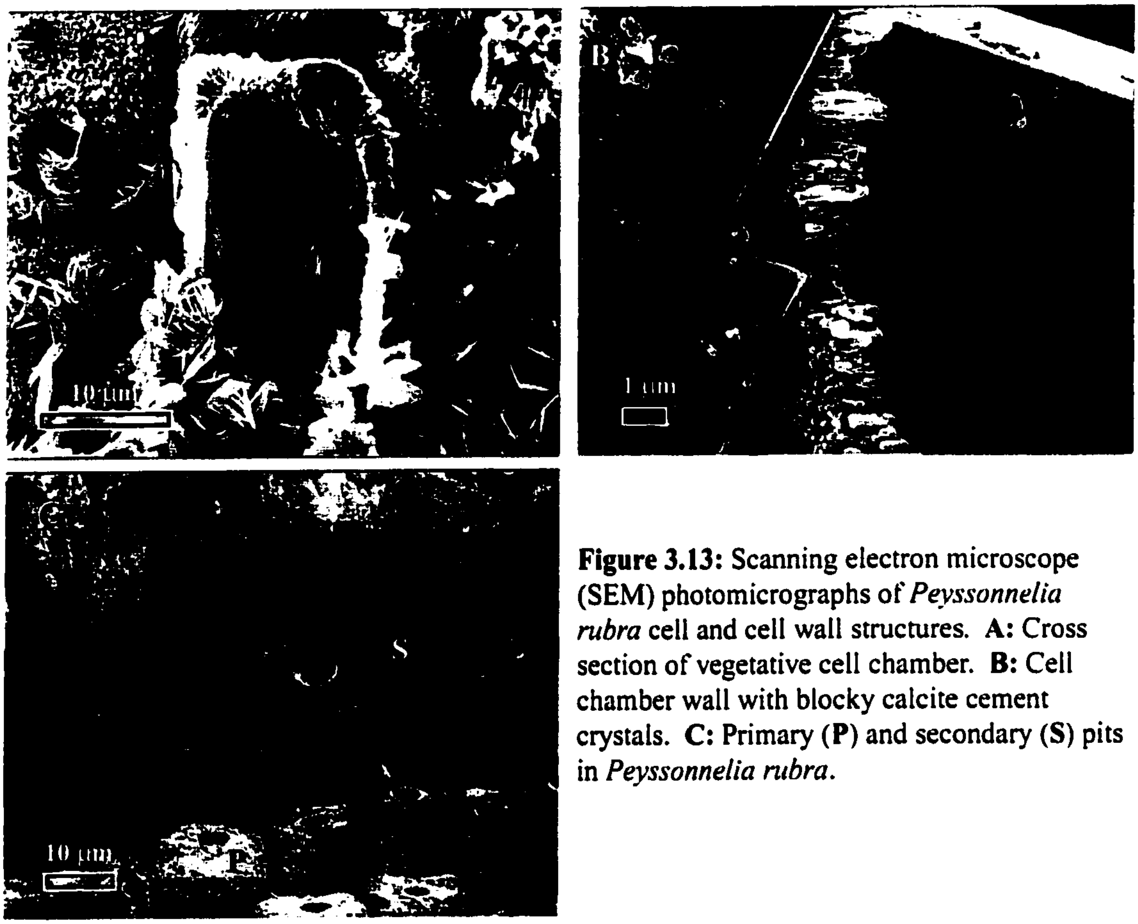

Figure 3.13: Scanning electron microscope (SEM) photomicrographs of *Peyssonnelia rubra* cell and cell wall structures. **A:** Cross section of vegetative cell chamber. **B:** Cell chamber wall with blocky calcite cement crystals. **C:** Primary (**P**) and secondary (**S**) pits in *Peyssonnelia rubra.*

P. rubra is distinctive in thin section because of the transparent tan colour of its thallus in plane polarised light. In comparison, coralline algae appear to have dark and opaque wall structures (*cf.*, Buchbinder and Halley, 1985; Elliot, 1963; Wray, 1977). The thallus of *P. rubra* is 70 to 150 µm (typically 90 µm) thick and may extend laterally up to 8 cm. Each thallus is composed of a hypobasal layer at the base, an overlying layer of hypothallium cells, and vertical threads of perithallium cells on top (Fig. 3.12A). The 2-10 µm thick hypobasal layer, composed of dense crystalline calcite or aragonite, has no apparent internal structure and is probably the product of extracellular precipitation (James *et al.*, 1988). The bottom surface of this layer is irregular and fills the spaces between the cells of the underlying thallus. The top surface is flat. The hypothallium is composed of a single layer of cells, usually square in cross section, 10 to 15 μm wide and high. Positioned above each hypothallium cell is a column of 3 to 7 perithallium cells, similar in form to the hypothallium cells. The cells regularly branch towards the top of the column, which is accommodated by a decrease in cell width. Cell size and shape vary from 10 to 15 μm wide and high at the base, to 5-7 μm wide by 10-15 μm high at the top (Fig. 3.12 B, C).

Cells in the hypothallium and perithallium are composed of a vegetative cell chamber enclosed by a cell wall (Fig. 3.13A). Cell walls, 1 to 1.5 μm thick, are formed of packed, non-interlocking aragonite crystals that are perpendicular to the wall surface (Fig. 3.13B). Individual crystals are anhedral, 0.2 to 1.5 μm long and 0.1 to 0.2 μm in diameter. Primary and secondary pits in the cell walls, ~ 6 μm in diameter, are present between horizontal and vertically adjacent cells (Fig. 3.13C).

P. rubra developed as the dominant encrusters on the Crystal Harbour rhodolites, forming envelopes up to 60 mm thick. They show little preference for exposed or protected surfaces.

Peyssonnelia are sciaphyllic plants, common to 200 m or in shaded regions. They are known as a minor but consistent component from tropical to polar seas and have been found encrusting hard limestone substrates, coral branches, and soft bottom sediments (Denizot, 1968). They are typically minor constituents among the more common coralline algae; however, in some cases they may dominate.

Unidentified peyssonnelid

A single specimen of a peyssonnelid algae, other than *P. rubra,* was found as the initial encruster on a bivalve nucleus. The structure of the thallus is similar to that of *P.*

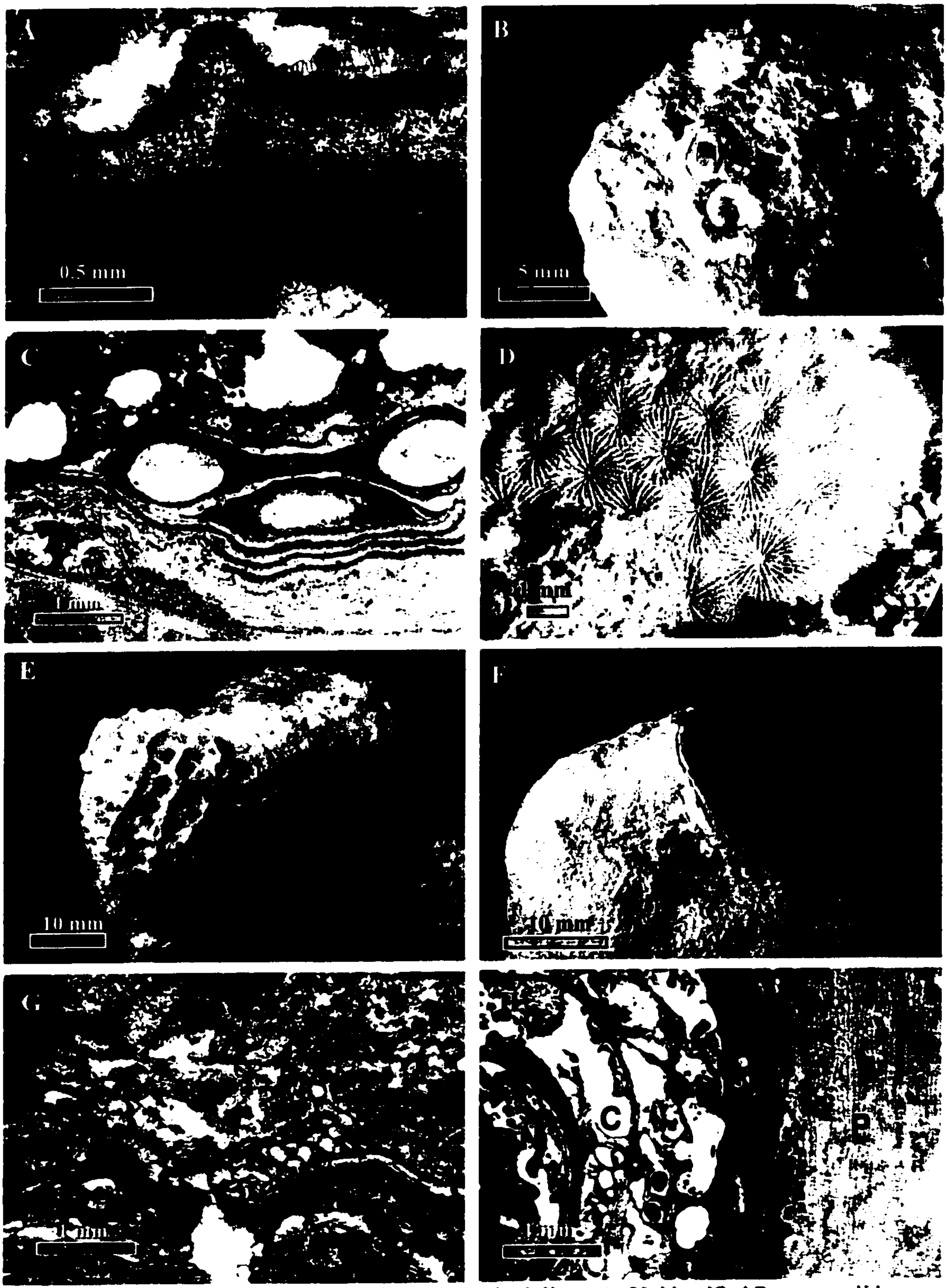

Figure 3.14: Epibionts and endoliths of Ironshore rhodolites. **A:** Unidentified Peyssonnelid. **B:** Serpulid worm tube on surface of *P. rubra*. **C:** Thin-section of a serpulid worm tube on the concave surface of a bivalve shell. **D:** *Siderastrea sideria* detail. **E:** Rhodolite with *Agaricia* sp. colony. **F:** *Spondylus americanis* attatched to rhodolite. **G:** *Carpentaria utricularis* section. **H:** Preferencial boring of nucleus (N) and coralline algae (C) leaving *P. rubra* (P) unaffected.

rubra, but has a smaller cell size of ~ 10 μm wide and high, and has a branching growth form (Fig. 3.14A).

Other encrusters

Serpulid worm tubes, the most common non-algal encruster, are found in protected chambers such as between columns of *P. rubra* or the concave surfaces of bivalves (Fig. 3.14 B, C). Encrusting corals *Siderastrea* sp. and *Agaricia* sp. developed as colonies < 5 cm^2 in area and 1 cm thick on a small number of rhodolites (Fig. 3.14 D, E). The Atlantic thorny oyster, *Spondylus americanis* (Warmke and Abbott, 1962) is the only species of bivalve that encrusts the rhodolites (Fig. 3.14F). It is 4 to 5 cm long and heavily ornamented with short, stubby spines that point away from the umbo. As a common late encruster, *S. americanis* can significantly alter the rhodolite shape after attachment. The foraminifera, *Planorbulina* sp. and *Carpentaria occulina* (Fig. 3.14G), are common on the protected surfaces amongst the coralline algae.

Endoliths

Endolithic attack is evident to some degree on all of the rhodolites examined. Most heavily affected are irregular or discoidal rhodolites with surfaces that had been free of live algae. In some of these rhodolites, up to 95% of the nucleus material had been destroyed. Most borings are irregular in shape and therefor unidentifiable, however, some appear to be the result of sponges. Borings range from sub-millimetre to 2 cm in diameter where they are most prevalent. Margins of the bores are typically micritised in a band of up to 2 mm. Curiously, the thalli of peyssonnelid algae are only rarely affected by endoliths, even when situated adjacent to heavily bored coralline algae (Fig. 3.14H). Studies of modern and fossil peyssonnelid algae have also noted this apparent immunity

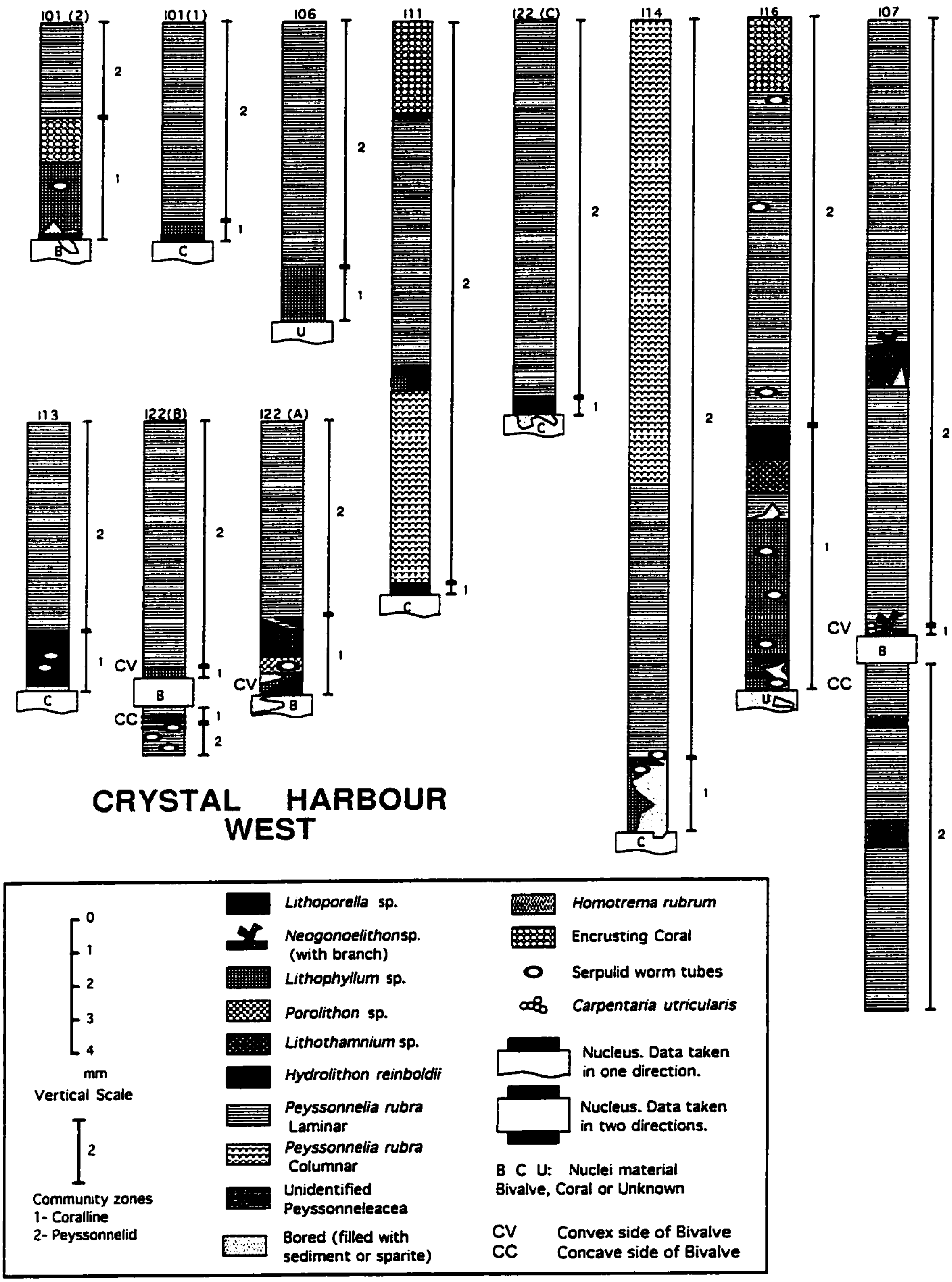

Figure 3.15: Algal successions in Crystal Harbour rhodolites. Diagramatic representation of species successions from nucleus to outer surface.

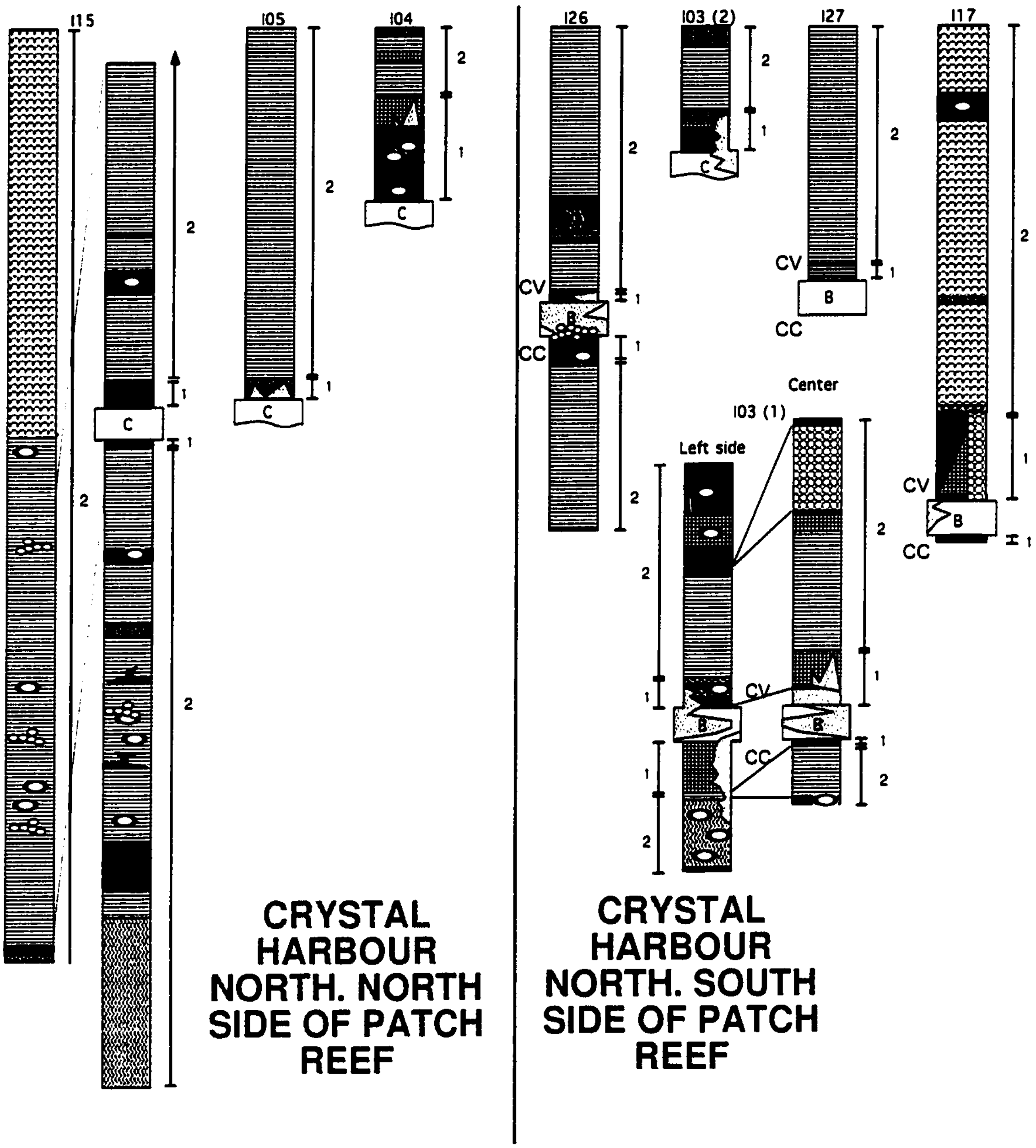

Fig. 3.15: continued.

to bioerosion (Adey and Vassar, 1975; Buchbinder and Halley, 1985); however, the reasons for this are not understood.

Colonisation Succession

All of the rhodolites that were sectioned displayed similar algal growth histories of two distinctly separate communities (Fig. 3.15; Fig. 3.16). The first community is domi-

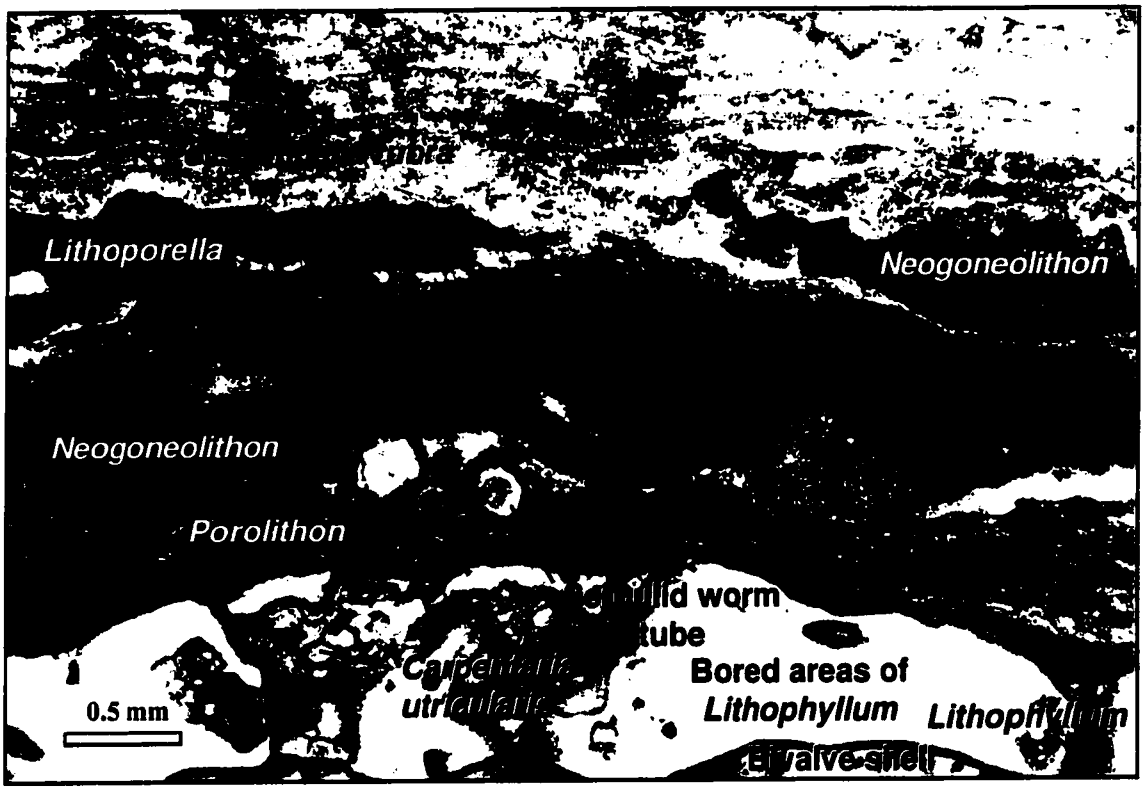

Figure 3.16: Example of succesion from nucleus to *Peyssonnelid Community* (see 'I22 A' on fig. 3.15), from convex surface of a bivalve shell. The bivalve nuclei has been bored, as has much of the initial encruster, *Lithophyllum* sp. Successive layers of *Porolithon* sp., *Neogoneolithon* sp. and *Lithoporella* sp. are present as discontinuous coatings. Encrusting foraminifera and serpulid worm tubes are also present between coralline species. *Peyssonnelia rubra* is the last encruster and is 3 cm thick.

nated by coralline algae, and so has been named the *Coralline Community*. It forms a partial or complete envelope directly around the nucleus, which is up to 10 mm thick but is typically ~ 2 mm. *Lithoporella* sp., *Lithophyllum* sp., and *Neogoneolithon* sp. are the most common forms of algae and *Peyssonnelia rubra, Hydrolithon reinboldii, Lithothamnium* sp., and *Porolithon* sp. are minor components. Surrounding the coralline community are thick successions of *P. rubra* in a near monospecific community named the *Peyssonnelid Community*. Other encrusting biota such as coralline algae, serpulid worms, foraminifera and bivalves may be minor components of the Peyssonnelid Community.

Determination of growth period

The growth period of a rhodolite may be estimated from the lateral growth rate of the algae, the surface area of the rhodolite, and the number of successive layers. In the case of the Crystal Harbour rhodolites, there are no known measurements for *P. rubra*, therefore, the rate for tropical coralline algae (1 - 2.3 mm/month (Adey and Vassar, 1975)) is assumed. Therefore, the approximate growth period of a 13.5 cm diameter rhodolite, with a 3 cm diameter nucleus is between 267 and 594 years old. The pioneering coralline community lived for only ~ 7 years.

Determination of depth

As a result of the disturbed nature of the locality, there is no way to obtain an accurate paleodepth of rhodolite formation. However, the maximum possible depth is 13.8 m, as constrained by the thickness of the Ironshore Formation at Crystal Harbour, and the known maximum sea-level during the Pleistocene (Shourie, 1993; Wignall, 1996). The actual depth is likely to be much less, as this estimate assumes that the rhodolites developed prior to sediment deposition and during the period of maximum sea-level. Nonethe-

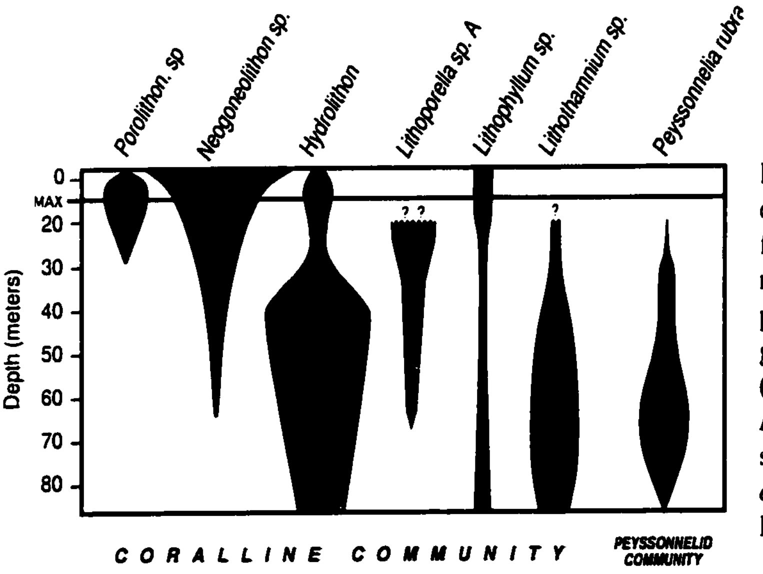

Figure 3.17: Modern depth distribution of calcareous algae found on Chrystal Harbour rhodolites. MAX - Maximum possible depth of rhodolite growth at Crystal Harbour (Depth distribution of *Porolithon* sp; *Neogoneolithon* sp., *Hydrolithon* sp. from Adey *et al.*, 1982; others from Minnery *et al.*, 1985).

less, even assuming the maximum possible depth, it is clear that most of the encrusting algae present on the rhodolites are indicative of much greater depths when compared to their modern equivalents (Fig. 3.17). In the case of *H. reinboldii* and *Lithothamnium*, their presence can be considered the result of the typically protected surfaces in which they encrusted. Other algae, in particular *Peyssonnelia rubra*, are found attached to what were exposed surfaces of the rhodolites. Therefore, if light had been the primary influence on species composition of this population, then they must have in some manner been shaded. Shade may have been provided by coral overhangs on the adjacent patch reefs. However, it is unclear why photophyllic algal dominated rhodolites did not develop outside of the shaded areas. With such rhodolites lacking, it seems unlikely that shading from the adjacent reefs was the primary cause in the deeper water algal community. There are other ways in which rhodolites could be shaded as a group. For example, turbulence may accomplish this; however, living algal crusts are unable to survive such conditions because the deposition of fine sediment will smother algae, preventing photosynthesis (Bosence, 1983b). Furthermore, there is no evidence of fine sediment deposition as a result of turbid conditions at Crystal Harbour. Another possibility is the development of a fleshy brown algal covering over the living encrusting algae. Relationships such as this are known on algal reefs in the Maldives (Denizot, 1968) where they allow sciaphyllic peyssonnelid species to dominate in shallow waters. If such an algal covering were present on the Crystal Harbour rhodolites, they have left no sign of their presence, and therefore cannot be proved either way.

The reason for *P. rubra* to dominate the Crystal Harbour rhodolites cannot therefore be fully explained by shading alone. This suggests that processes, other than light, were important in the determination of encrusting biota at Crystal Harbour.

3.6 DIAGENETIC ALTERATION

Crypto- to microcrystalline calcite fibre crystals are a common intraskeletal cement in *P. rubra* (Fig. 3.18A). The cement is formed by the extension of the cell wall crystals inside the cells, that develop a complex mesh in the centre of the cell. The crystals are ~ 0.1 μm wide and up to 15 μm long after regrowth. The restricted distribution of this cement to inside the vegetative cell chambers suggests that it is a chemical product of the living cells at the surface of the rhodolite. Metabolite products from living algae are known to promote precipitation of non-skeletal calcite in this way, even in sea water that is undersaturated with $CaCO_3$(Alexandersson, 1974, 1977; Freiwald and Henrich, 1994). The network of primary and secondary pits that connect the *P. rubra* vegetative cells chambers would have allowed sea water and metabolic fluids to pass freely and precipitate within the cell chambers.

Other cements present in the rhodolites include botryoidal aragonite and blocky, high magnesium calcite. The botryoidal aragonite fills many of the structural voids and conceptacles in the algae (Fig. 3.18B). The blocky, high magnesium calcite is a post-depositional cement found throughout the rhodolites and surrounding sediment (Fig. 3.18 C, D).

Cells with dense micritic fills are present in small areas of the peyssonnelid thallus in areas that were not covered by living algae, such as the lateral edge of columns (Fig. 3.18 E, F). During the period of growth, these portions of the thallus were open to external marine water and water that has passed through the living layer of algae. The micrite may therefore be the product of the mixing of these fluids inside the skeletal material.

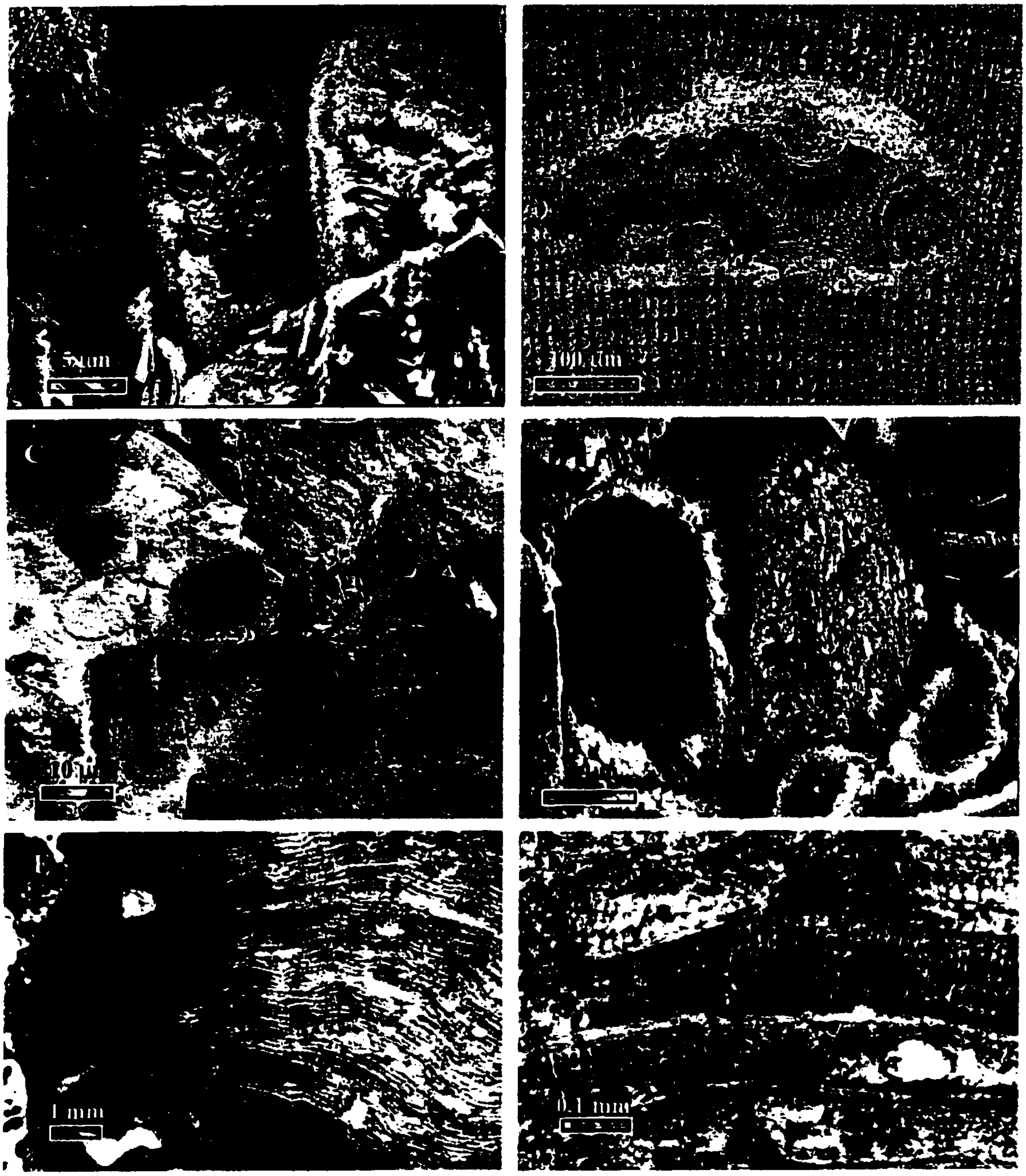

Figure 3.18: Cement types and micrite fills in Crystal Harbour rhodolites. **A:** Calcite fiber cement filling vegetative cell chamber in *Peyssonnelia rubra*. **B:** Aragonite botryoidal cement filling a *Lithophyllum* conceptacle. **C:** Near pervasive blocky, HMC cement in *P. rubra*. **D:** Early stages of blocky cement filling *P. rubra* vegetative cell chamber. **E:** Lateral edge of globular *P. rubra* growth with cells filled with dense micrite. **F:** Detail of dense micrite fills.

3.7 DISCUSSION

Ideally, a modern analogue of peyssonnelid rhodolites would serve best to explain the anomalous domination of *P. rubra*, a supposedly deep water alga, in a shallow water lagoon. Yet even without such analogues, the investigation of these fossil rhodolites may establish the conditions that led to the encrusting communities found on them. This problem is approached by first assessing the nature of the transformation from coralline to peyssonnelid, and then investigating the factors that allowed the peyssonnelid algae to remain the dominant encruster.

Distinct changes in encrusting community between the outer and inner layers of rhodolites are common and have been attributed to changes in local and global climate and sea-level (*e.g.*, Logan *et al.*, 1969; Toomey, 1975). Considering that the culmination of the Sangamon sea-level highstand may have been concurrent with the formation of the rhodolites at Crystal Harbour (*cf.*, Jones and Hunter, 1991), the community change observed may have been the result of environmental forcing. One major conflict with this theory, is that every rhodolite shows peyssonnelid algal domination over a similar thickness of the coralline algae (~ 2 mm). This would require every rhodolite to have developed a similar thickness of coralline algae before the change in environment that favoured peyssonnelid algae. Furthermore, new rhodolites would still be formed after the change in environment, which would be evident as purely peyssonnelid community rhodolites. The lack of such rhodolites, and the consistent thickness of the coralline community suggest that a community change due to an environment change is an unlikely scenario.

Other workers (*e.g.*, Adey and Macintyre, 1973; Bosence, 1983a) have suggested that

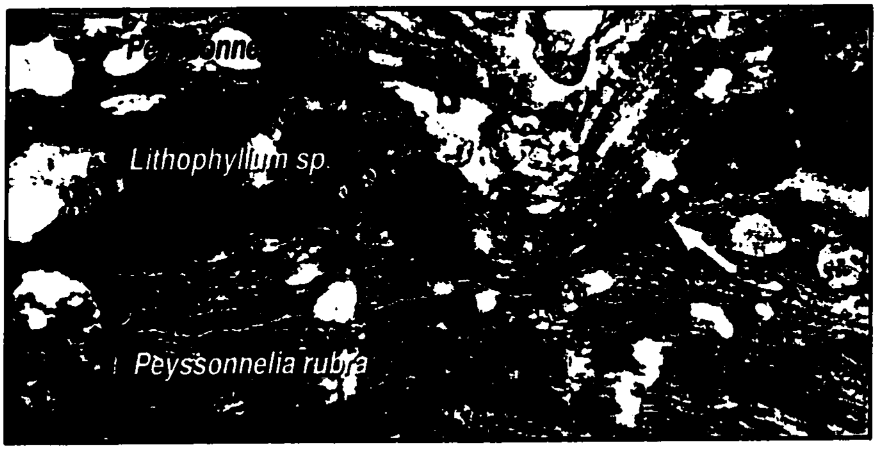

Figure 3.19: Lateral thin section photograph showing recolonisation of damaged *P. rubra* surface (arrow) by coralline algae (*Lithophyllum* sp.), and eventual resumption of *P. rubra* growth (top).

community changes can be forced by the increase of rhodolite size throughout growth. This is also unlikely in the case of Crystal Harbour, as rhodolites of different nuclei size have similar thickness of the coralline community.

Alternatively, the change in species may have been the response to a developmental succession of the encrusting community. An indication of this is shown where damaged surfaces of *P. rubra* have been recolonised by coralline algae (Fig. 3.19). In the few cases which have been found, the recolonisation is always initiated with coralline algae before *P. rubra* returns. Similar patterns of initial colonisation to those of the rhodolites have been observed on modern fixed substrates by Adey and Vassar (1975). In an experiment to investigate colonisation successions of coralline algae, they distributed a number of sectioned PVC tubes in various light conditions around the reefs of St. Croix. The tubes were designed and placed to mimic the surface of *Acropora palmata* in life position and were then observed over a 350 day period in order to investigate the surface distribution of encrusters and evidence of grazing. On most, coralline species dominated the substrate throughout (Fig. 3.20A). However, on tubes that were protected from parrotfish

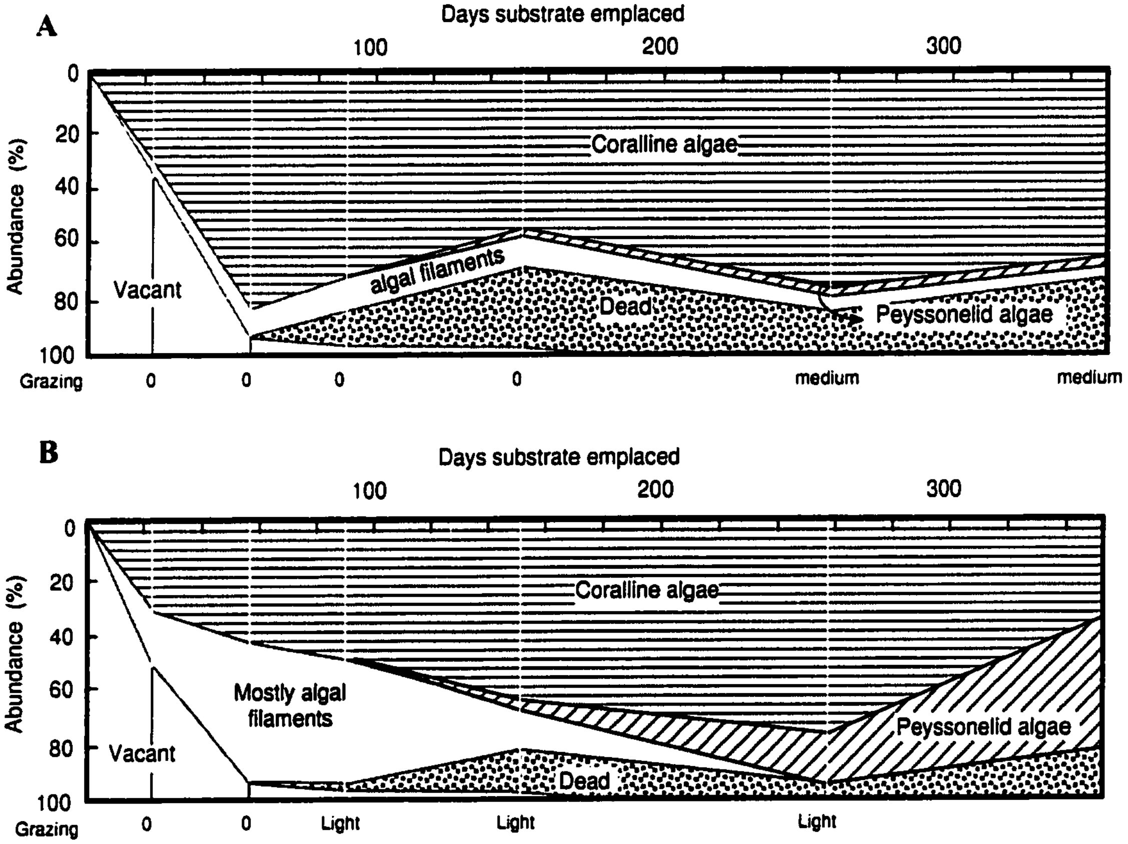

Figure 3.20: Colonisation and temporal succession of encrusting organisms on artificial substrate that mimics the surface of *Acropora palmata*. **A:** Typical succession on exposed surface; **B:** Succession on protected surface. Vertical axis represents total area of artificial substrate with each segment representing different groups (modified from Adey and Vassar, 1975).

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grazing by surrounding *A. palmata*, an early coralline community was almost completely replaced by peyssonnelid algae after 350 days (Fig. 3.20B). Although the species and genera differ between those documented by Adey and Vassar (1971) and those of Crystal Harbour, the pattern of colonisation between the coralline and peyssonnelid algal families is the same. This suggests that there are some similarities between the environment in which the rhodolites developed at Crystal Harbour and those of the protected substrates of Adey and Vassar (1975), and the lack of abrasive mechanisms, such as grazing organisms appears to be the most important factor.

In consequence, this means that the Crystal Harbour rhodolites were protected from abrasive mechanisms, such as wave and current energy and destructive grazers, for periods of up to 594 years (the approximate age of the largest rhodolite). Parrotfish (*Sparisoma viride*), which first appeared in the Eocene, are among the most destructive feeders in modern reefs (Frydl and Stearn, 1978; Steneck, 1985), using a hard beak to rasp through the skeletal surface of coral or coralline algae. They prefer to feed in open, well lit areas, where they are free to manoeuvre and are at less a risk of predation (Adey and Vassar, 1975). It is possible that this is a factor that prevented their grazing upon the rhodolites at Crystal Harbour. Close proximity to the patch reefs, as is apparent from the CHN localities, may have offered the rhodolites protection from this kind of attack.

To remain free of abrasion, the rhodolites must also have been protected from the effects of tropical storms. Tropical storms and hurricanes that affect the island at present, come from the south to east (Burton, 1994) and are capable of removing the rhodolites along with vast quantities of sediment on the lagoons of the south coast (Kalbfleisch and Jones, 1997; chapter 2, this thesis). During the Pleistocene, the weather patterns were similar to that of today, and the Ironshore Lagoon would have been largely protected from storm wave energy, as land barriers bordered its south, east and northern sides (Jones and Hunter, 1990). It must also be considered that some amount of hydraulic energy was a necessity for rhodolite development. Probably of equal importance in the formation of the rhodolites, was their exposure to the moderate wave energy from the west. In this way, energy remained high enough to prevent fine material from settling, and to periodically turn the rhodolites, but did not reach levels that could have damaged or removed the rhodolites out of the area of accumulation.

3.8 SYNOPSIS

Rhodolites, dominated by aragonitic peyssonnelid algae developed during the Pleistocene, on the western side of Grand Cayman. Dense accumulations of these rhodolites were collected in areas adjacent to patch reefs and analysed to determine the ecological and environmental conditions in which the rhodolites developed.

Unlike many other examples of rhodolite formation, rhodolite form cannot be used as an indicator of turning frequency, rather, variation in form throughout each locality population is influenced by nucleus form and resulting distribution of algae.

Initial growth of the rhodolites commenced with a crust ~ 2 mm thick, representing ~ 7 years of growth, of various coralline algae. This was then overgrown by a single species of peyssonnelid algae *P. rubra* that dominated henceforth developing a cortex up to 60 mm thick over periods of up to 594 years. The change in biota is a product of a biologically forced colonisation succession in the absence of mechanical or biological elements that could damage the living algal surface. This suggests that the rhodolites were well protected from destructive elements that regularly affect the modern rhodolites on the Grand Cayman's southern coast caused by destructive grazing, and periodic tropical storms.

The area of Crystal Harbour was therefore protected from south easterly storms by land barriers that have been proposed by Jones and Hunter (1991). Meanwhile, moderate wave energy entered from the west that possibly turned the rhodolites on a frequent basis and maintained adequate circulation for the development of rhodolites.

From the analysis of the rhodolites, the Crystal Harbour area during the Pleistocene experienced moderate wave energy from the western open end of the lagoon, but was protected from violent tropical storms by land masses proposed by Jones and Hunter (1991) to the south and east.

CHAPTER 4
MODEL FOR THE DEVELOPMENT OF TROPICAL LAGOONAL RHODOLITES

4.1 INTRODUCTION

The determination of rhodolite distribution, morphology, and ecology is the result of a combination of environmental influences. These include light, temperature, hydraulic energy, salinity, turbidity, grazing, nuclei availability as well as the intrinsic factors of species competition. Many studies have established (*e.g.*, Reid and Macintyre, 1988; Adey and Vassar, 1975; Steneck, 1985; Chapters 2 and 3, this thesis) that some of these environmental factors influence rhodolites more than others. Nonetheless, all have the potential to be the primary influence in certain situations, therefore making interpretations difficult.

By restricting the geographic distribution of rhodolites being considered, a number of environmental factors may be assumed to be constant. This will reduce the number of variable influences, thus simplifying the model. The restriction of a paleoenvironmental model to a particular geographic setting may seemingly defeat its purpose. However, use of established techniques such as sediment or coral analysis, will allow the determination of the basic environment. Rhodolites may then be used to enhance the paleoenvironmental details. Variability in rhodolite morphology throughout a depositional area, or sequence of deposits may therefore be associated with fewer, if not a single environmental factor.

In this chapter, rhodolites are considered in the context of a tropical lagoonal environment, where their value as paleoenvironmental indicators is approached in two ways. The first establishes the environmental criteria that must be met for rhodolites to form. This approach allows for a number of assumptions concerning the environment of formation to be made, eliminating the need to assess the complex relationships between rhodolite morphology and environment. The second approach determines the local environment by investigating rhodolite morphology and its variability. This approach addresses the relationship between morphology and environment and may provide a sensitive record of that environment. These techniques will then be discussed in terms of common lagoonal forms and resulting rhodolite morphologies.

4.2 FACTORS INFLUENCING RHODOLITE DISTRIBUTION

Although rhodolites are found from boreal seas to the tropics, and from shallow intertidal waters to a depth of almost 100 m, they are not ubiquitous throughout this range of environments. For example, despite the inspection of over 150 localities of the Ironshore Formation across Grand Cayman (Jones pers. comm.), rhodolites were found only in small areas near Dolphin Point and Crystal Harbour. Even at Paul Bodden Quarry (Fig. 1.1), where almost identical facies to those at Crystal Harbour are well exposed, no rhodolites were found. Such restricted rhodolite distributions and others like it (*e.g.*, Bosellini and Ginsburg, 1971, Scoffin *et al.*, 1985) indicate there are a variety of limiting factors other than latitude and depth.

Possible limiting environmental factors in rhodolite distribution are light, salinity, turbidity, hydraulic energy, and nucleus supply. In considering only those rhodolites of tropical lagoons, a number of assumptions can be made. Light can be assumed to be non-limiting because encrusting algae are generally tolerant of light levels much lower than those found in shaded areas of lagoons (*e.g.*, Littler *et al.*, 1991). Salinity and turbidity may also be ignored. Although these factors may be limiting, they affect lagoons as a whole and are not a factor in local distribution. Hydraulic energy and nucleus supply, however, are variable throughout tropical lagoons and therefore influence rhodolite distribution.

The level of hydraulic energy must be within a specific 'window' to allow rhodolite development (Fig. 4.2). Too much energy causes the brittle algal thallus to be abraded and destroyed; too little energy, and the alga may suffocate in fine sediment, or develop

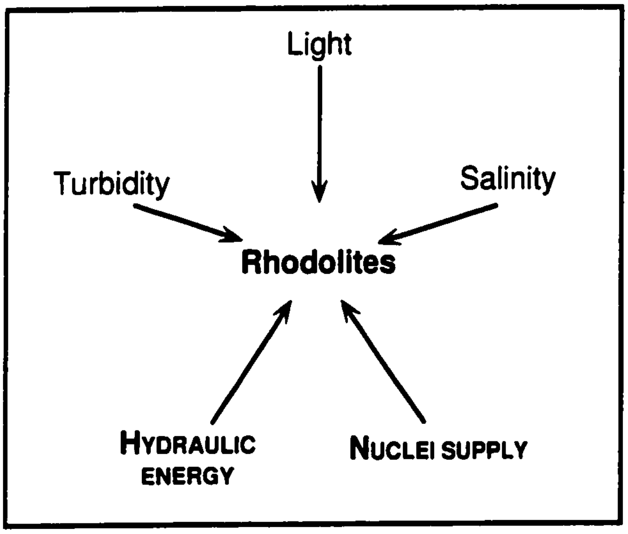

Figure 4.1: Environmental factors that may potentially limit rhodolite distribution. Of these, hydraulic energy and nuclei supply are major influences in the distribution of lagoonal rhodolites.

laterally across the sediment as a pavement (Denizot, 1968). As a result, rhodolite distribution across a lagoon depends upon the combination of wave and tidal energy entering the area, local geography and bathymetry, and hydraulic energy barriers (Fig. 4.3). It is the upper boundary of the window which is most critical, because it represents energy levels that are significantly lower than typical open water wave energy. This boundary is evident in the rhodolite distributions of Muri Lagoon, Rarotonga (Scoffin *et al.*, 1985). There, despite the lagoon's large size and shallow waters, rhodolites are only found in the wave shadows behind reef islands. Similarly restricted rhodolite distribution has been found on Grand Cayman, where despite the considerably higher energy conditions present, rhodolites were only found on the windward margin of the island (Jones, pers. comm.). This takes place because only the windward margin has a well developed reef to

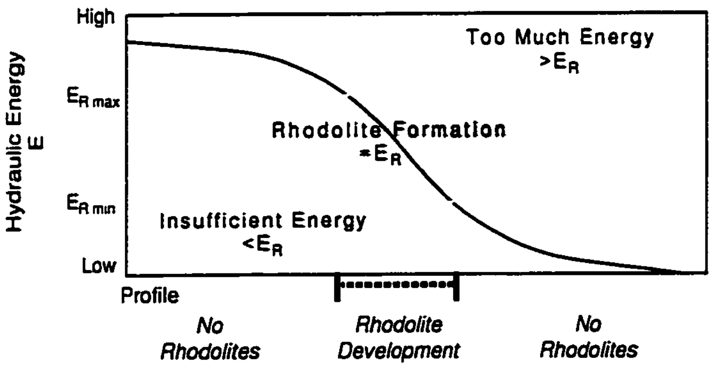

Figure 4.2: Response of rhodolite distribution to hydraulic energy across a hypothetical lagoonal profile.

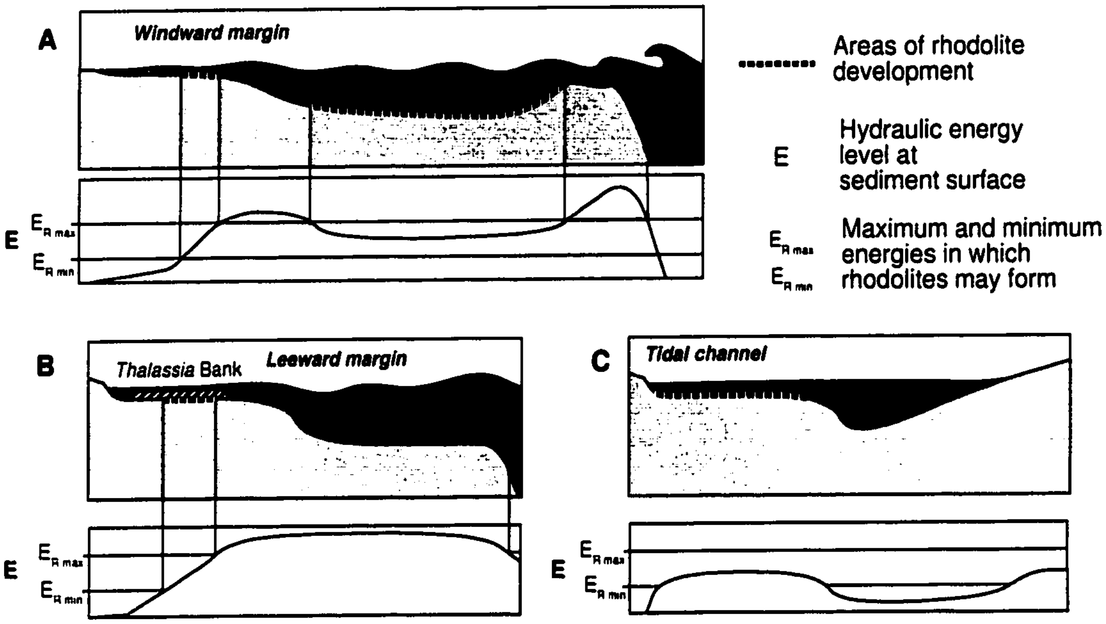

Figure 4.3: Variation in surface hydraulic energy over characteristic margins. **A:** A *Windward margin (e.g.* South Sound and Pease Bay) that sustains high energy input is baffled by the reef crest and may allow areas in the lagoon to develop rhodolites. The rise in sea floor towards the shore interacts with the remaining wave energy to produce areas too high for rhodolite formation. Areas close to the shore have little remaining energy, microbialites are better suited in these environments. **B:** A *leeward margin* (*e.g.*, Whalebone Bay, Bermuda) lacks a barrier, therefore waves interact directly with the shore. Alternatively, shelf, or off-shore shoals may act as a barrier, or banks of sea-grasses may baffle wave energy enough to allow rhodolite formation. **C:** *Tidal channels* (e.g., Muri Lagoon, Rarotonga, Cook Islands) may allow rhodolite development where waters are restricted where the tidal channel shallows, to maintain sufficient energy.

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act as a barrier from open water waves (Li, 1997). Wave barriers come in forms other than barrier islands and reefs. In Bermuda, the development of rhodolites in Whalebone Bay has probably been made possible by the banks of *Thalassia* that baffle the remaining wave energy entering from the leeward shelf (Bosellini and Ginsburg, 1971). Tides may also provide the hydraulic energy necessary for rhodolite development, as is the case on Rarotonga, where tidal currents of ~ 25 cm/sec. are sufficient for rhodolite development (Scoffin *et al.*, 1985). Where barriers reduce hydraulic energy below the lower boundary suitable for rhodolite development, microbial mats may dominate any nuclei material. In South Sound, areas in which microbialites develop have wave heights in the order of < 5 cm.

Where hydraulic energy levels are suitable for rhodolite formation, rhodolites may still only develop where there is a sufficient supply of nuclei. For example, despite optimum hydraulic energy over the mid lagoonal areas, rhodolites in South Sound and Pease Bay are only found around the patch reefs and where fore-reef debris has been deposited. It may not always be the case that nucleus supply is a limiting factor. Bosence (1976) described branching rhodolites from Western Ireland that had a self sustaining nucleus supply through the fragmentation of other rhodolites. However, as neither modern nor Pleistocene rhodolites of Grand Cayman appeared to have algal nuclei, this is not the case there. Self sufficiency in nucleus supply requires rugged algal growth forms (such as branching form) that continue to grow after fragmentation.

4.3 FACTORS INFLUENCING RHODOLITE DEVELOPMENT

Where they develop, rhodolites may display a broad range of characteristics unique to the individual population and to the conditions under which they form. Isolated into the separate elements of species (*i.e.*, encrusting algal species), algal growth form, and rhodolite form (*i.e.*, shape and size), rhodolite characteristics can be considered the result of intrinsic and extrinsic influences (Fig. 4.4).

The relationships between species, algal growth form, and rhodolite form comprise the intrinsic influences on rhodolite formation. Species exert a major influence on algal growth form because most encrusting algal species will develop as a range of growth forms between two particular end members. For example, the species of *Lithothamnium* described by Bosence (1976) was a branching type, that varied from open branching on stable substrates to dense branching on unstable substrates. In comparison, *Peyssonnelia rubra* at Crystal Harbour was a massive type, that ranged from massive columnar on stable substrates, to massive laminar on unstable substrates (Chapter 3, this thesis). Regardless of environmental conditions, *Lithothamnium* would *not* develop a massive growth form, nor would *P. rubra* develop a branching one. Hence, to associate an algal

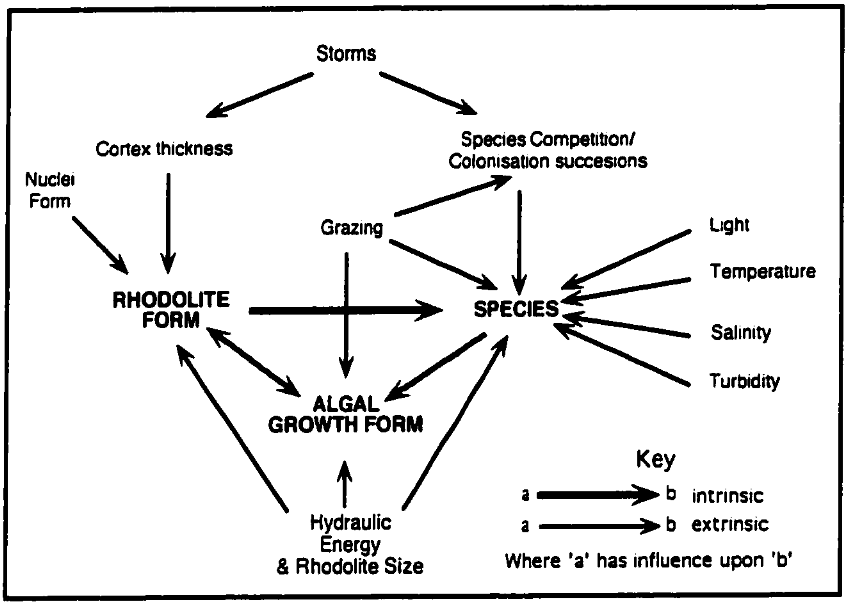

Figure 4.4: Possible influences that affect rhodolite characteristics of species, algal growth form and rhodolite form.

growth form to a particular extrinsic factor, the range of possible growth forms of the species in question must be known. Rhodolite form influences stability, which in turn will affect algal growth form. In this way, small and spheroidal or prolate rhodolite forms will lead to more even and/or laminar algal growth than discoidal and larger rhodolite forms (Chapter 3, this thesis). Less evident is the possible influence of algal growth form upon rhodolite form. This may be apparent in some algal growth forms where each thalli mimics the underlying layer to the extent that nucleus form may have an influence on rhodolite form (Chapter 3, this thesis).

The relationship between extrinsic factors and rhodolite morphology is much more complex than with rhodolite distribution alone. Foremost, every element of the environment is important in the determination of rhodolite morphology. This is because each factor may be a primary control under certain conditions. Light and temperature are most important in this respect, as they are typically the primary influence (Adey, 1970b; 1973; 1986; Adey *et al.*, 1982). This is illustrated by the common distributions of coralline algae with depth from different parts of the world (Adey *et al.*, 1982). However, other factors may also be of primary influence when they are at levels that may stress the algal population. This type of relationship is illustrated between algal communities between the mid-lagoon and back-reef channels of Pease Bay. In the mid-lagoon, algal populations reflect the expected composition for those light levels (*cf.*, Minnery *et al.*, 1985; Martindale, 1976; 1992; Adey *et al.*, 1982). The back-reef environment receives similar levels of light to that of the mid-lagoon; however, the algal composition of rhodolites there compares to deeper waters when similar comparisons are made. It is the added stress of hydraulic energy that modifies algal encrusters in the back-reef—at higher energy conditions, the mid-lagoon species cannot develop, which then opens a niche for energy tolerant species.

Of all of the possible extrinsic factors, the most influential in rhodolite variability in lagoons is hydraulic energy. If it is presumed that hydraulic energy affects the rhodolites through the process of turning, then rhodolite form must also be considered. Rhodolites of smaller size and/or prolate or spheroidal shapes have less stability and are turned more often than rhodolites of larger size and/or discoidal shapes. This is illustrated well at Pease Bay (Chapter 2, this thesis), where the alga *Neogoneolithon* sp. is found on rhodolites of all sizes throughout the mid-lagoon, but only on the largest rhodolites in the more energetic back-reef channels. Although seemingly complicating matters, the sensitivity of rhodolites to both size and turning will help distinguish hydraulic energy as the major influence. That is, if a particular characteristic is found on only small rhodolites at one locality, and the same characteristics are also found on larger rhodolites at another locality, then the latter must have experienced higher energy conditions. Therefore, with a variety of proximal rhodolite bearing localities, comparisons in morphology may allow the determination of hydraulic energy variation.

The effect of hydraulic energy upon algal growth form and rhodolite form (Bosellini and Ginsburg, 1971; Bosence, 1976, 1977; Bosence, 1983a) can be generalised as the development of more laminar and/or massive growth forms and spheroidal rhodolite forms with increased energy. Other mechanisms are also known to turn rhodolites (Reid and Macintyre, 1988), nonetheless, rhodolites that show signs of development in low energy conditions require the absence of all turning mechanisms to form, including hydraulic energy. Such low energy rhodolites may therefore be considered accurate indicators of environments.

Other extrinsic factors may have greater influence than hydraulic energy in particular situations. Shading can have a significant effect on the algal composition of rhodolites by allowing deep water species to dominate at shallow depths. In lagoons, overhanging corals around patch reefs provide small areas in which sciaphyllic algal rhodolites may develop. Such development can be easily identified in fossil localities if patch reefs are found adjacent to the site of rhodolite development. Other forms of shading may be less obvious. Rhodolites of Whalebone Bay for example, are dominated by the generally sciaphyllic genus *Lithothamnium*, which grew under the shading from the surrounding *Thalassia* (Bosellini and Ginsburg, 1971). As *Thalassia* is unlikely to be preserved, the correct assessment of depth by the analysis of algal composition may only be possible by identifying associated molluscs found only in these habitats (Cerridwen, 1989; Cerridwen and Jones, 1991). Destructive grazing and mechanical abrasion on the surface of living encrusting algae has the dual effect of promoting the development of laminar algal

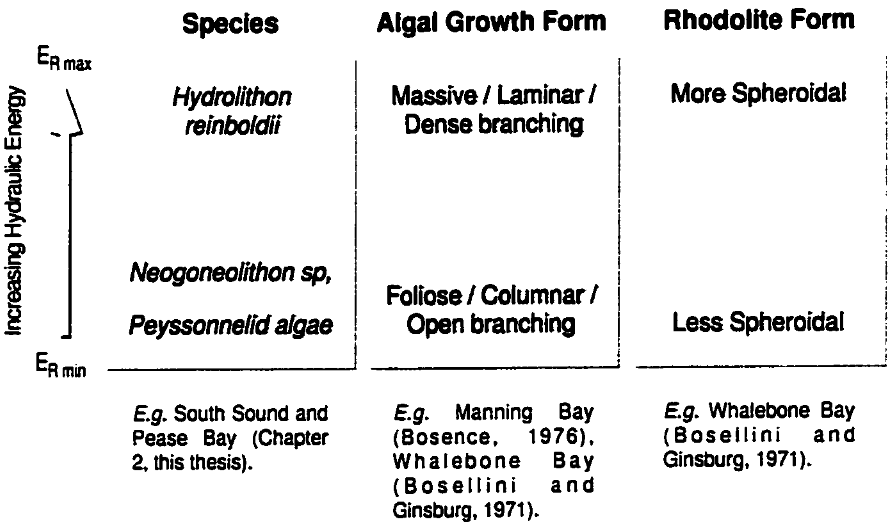

Figure 4.5: Response of rhodolite characteristics to increase in hydraulic energy.

growth forms (Steneck, 1985) and maintaining an immature algal community composition (Adey and Vassar, 1975; Chapter 3, this thesis). The resulting effects of grazing may therefore be mistaken for other processes, particularly hydraulic energy. Careful examination of the algal thalli may allow the effects of grazing and mechanical abrasion to be discerned from other mechanisms (see Fig. 3.19).

The effect of storms

The effect of storms on lagoonal rhodolites needs to be considered separate from other extrinsic influences. This is because storms do not affect day to day rhodolite development, but will have a significant effect by periodically removing a rhodolite population and initialising new rhodolite growth. This leads to a distinct difference between rhodolites from storm affected margins and those of protected margins. Storm affected rhodolites consistently display thin cortices throughout the population. The thickness of the cortex may be used to approximate the period since the last storm event before burial/collection. Rhodolites from protected lagoons will display a variety of cortex thickness. A secondary feature may be the change from immature to mature communities from the inner to the outer parts of the cortex. This, however, also relies on the absence of other damaging processes that are not related to storms.

4.4 DISCUSSION

Even when restricting a model to that of tropical lagoons, the possible combinations of environmental factors contributing to a set of rhodolite characteristics may still be overwhelming. Nonetheless, as generalisations may be made as to the typical forms of lagoons, so too can they be made as to the rhodolites that develop in them. In keeping with the distinction between lagoonal types, tropical lagoonal rhodolites may be separated at the most basic level into those of narrow windward lagoons, and those of protected and leeward lagoons (Fig. 4.6).

Generally, a distinguishing feature of rhodolites from narrow windward lagoons is a

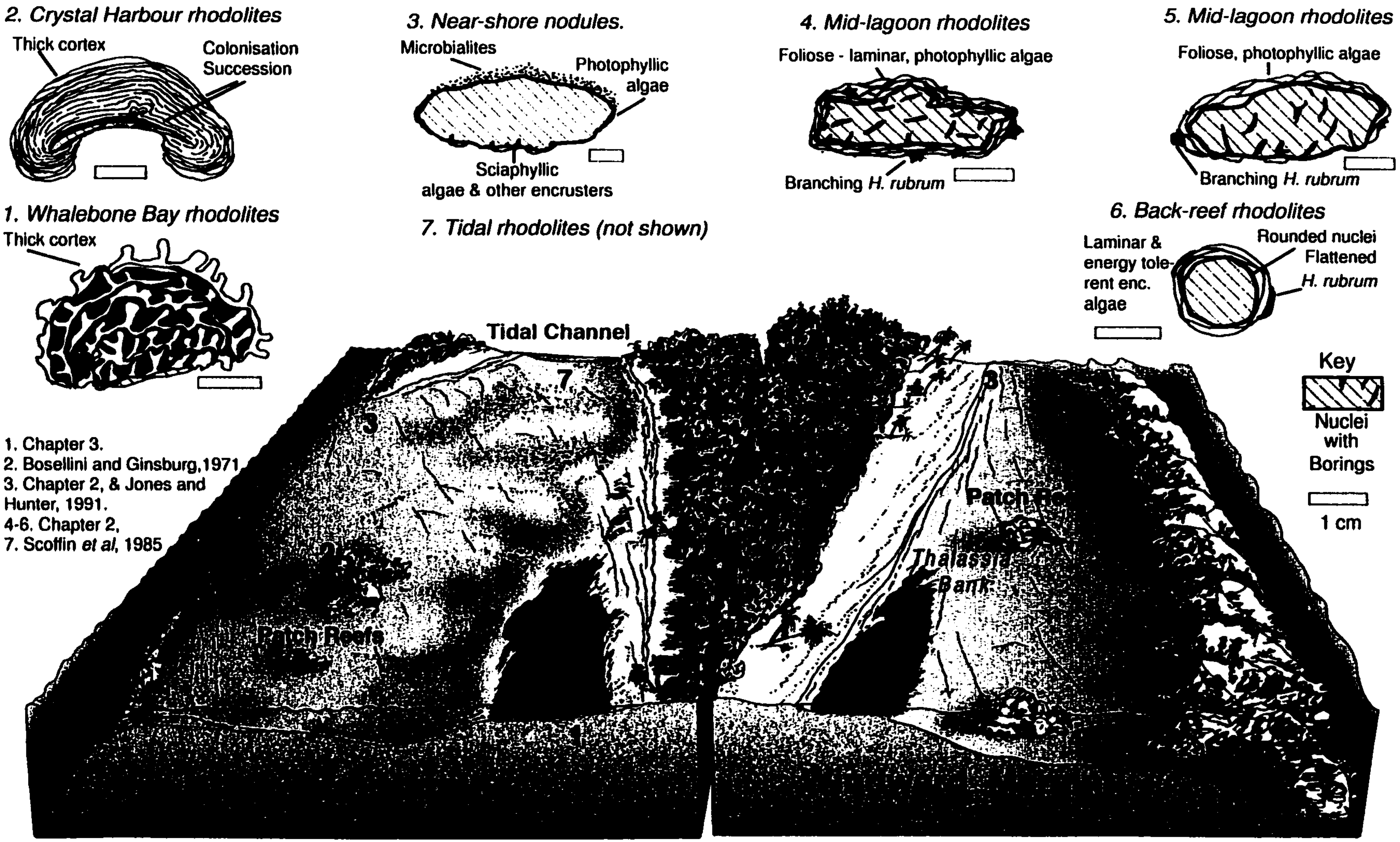

Figure 4.6: Rhodolite morphology from different lagoonal environments.

thin cortex that results from frequent storms. As a result, rhodolite form has little interpretative value. Rhodolites will develop in areas that are protected from open water energy and where nuclei are supplied (apart from rhodolite types that are self sufficient for nuclei). As a result of abrupt changes in hydraulic energy between the reef crest and the shore, the rhodolites may be biotically diverse over short distances. If the rhodolites and microbialites from South Sound and Pease Bay can be assumed typical of such environments, then biotic zonation into back-reef, mid-lagoonal and near-shore types may be considered a distinctive feature of windward lagoons.

Rhodolites may be distinguished as those of back-reef channels by the signs of frequent turning. This includes a laminar to slightly foliose algal growth form, and an algal community dominated by high energy tolerant species. Few other encrusting organisms are present on these rhodolites apart from *Homotrema rubrum*, which has a flattened growth form (Martindale, 1976, 1992) and coral. In the mid-lagoon, rhodolites are distinguishable by photophyllic algal encrusters with a more foliose growth form. *Homotrema rubrum* is present also, but has a thick and branching form. On larger rhodolites that have few but stable resting positions, sciaphyllic encrusters may be interleaved with the photophyllic algae. In the near-shore environment, deposited nuclei material will develop as microbialites, not rhodolites. They are likely to display a partitioned community over the surface, with few signs of having been turned. The top surface during development is covered by a microbial mat of adhered fine sands. Photophyllic algae may encrust around the perimeter, and sciaphyllic encrusters develop a patchy distribution on the undersides.

The environments in leeward or protected lagoons are in many cases similar to those of the mid-lagoon and near-shore environments of narrow, windward lagoons. This promotes the development of rhodolites and microbialites with similar encrusting communities and morphological features (*e.g.*, Jones and Hunter, 1991). The main distinction between them is that rhodolites may develop thick cortices and they lack the parallel biotic zonation. Furthermore, if they are well protected from grazing and mechanical abrasion, they may also display species successions throughout the cortex. Rhodolite distribution in leeward and protected lagoons depends upon wave and tidal hydrology. In the absence of a wave barrier in the form of a reef crest, rhodolite formation is dependent on other forms of wave baffling (*e.g.*, *Thalassia* banks). In lagoons with strong tidal currents, rhodolites may develop in tidal channels. The unidirectional currents associated with tides may distribute rhodolites by size (Davies *et al.*, 1986), however, similar results may develop in wave dominated lagoons (Bosellini and Ginsburg, 1971).

It is the case that basic morphological characteristics may be associated with particular lagoonal types, confirming that rhodolites may be valuable as paleoenvironmental indicators. However, many more modern examples will be needed before the picture of rhodolite formation in lagoons is complete.

4.5 CONCLUSIONS

From the interpretations of the modern and fossil rhodolites on Grand Cayman, and other studies of lagoonal rhodolites, the following conclusions may be made.

- Rhodolites may serve as valuable paleoenvironmental indicators when used as a supplement to other more established techniques.
- The development of rhodolites is dependent upon too many independent variables to allow a single variable to be quantitatively established. Through comparisons of rhodolite morphology between proximal populations, variation in particular environmental factors between the localities may be identified.
- The distribution of rhodolites in tropical lagoons is primarily controlled by hydraulic wave energy and the supply of nuclei.
- Rhodolite morphology in lagoonal environments is determined by extrinsic and intrinsic influences. The variation in morphology in a single lagoon is primarily controlled by changes in hydraulic energy.

- Rhodolites may display characteristic morphologies that could enable them to be identified with particular lagoonal environments.

CHAPTER 5
SYNOPSIS

Rhodolites were collected from South Sound and Pease Bay on Grand Cayman for use in establishing a model of rhodolite development in lagoons which may be used as a tool to interpret ancient environments.

Modern rhodolites from South Sound and Pease Bay show distinct variation between the back reefs, mid-lagoons, and near-shore environments. This variation is predominantly the result of changes in hydraulic energy across the lagoons. High energy back-reef environments are characterised by rhodolites with generally spheroidal shape, laminar algal growth forms, and are dominated by *H. reinboldii*. Under the moderate hydraulic energy conditions of the mid-lagoons, rhodolites have variable rhodolite forms, laminar and foliose algal growth forms, and are dominated by *Neogoneolithon* sp. Lower energy near-shore environments result in microbialites with minor encrusting algal development.

Pleistocene rhodolites from the Ironshore Formation at Crystal Harbour are dominated by peyssonnelid algae. The dominance of this algal family on rhodolites is unusual because these algae typically inhabit waters deeper than those possible at Crystal Harbour during the Pleistocene. The dominance of peyssonnelid algae has resulted from colonisation succession. It is suggested that the colonisation succession and Peyssonnelid dominance resulted from protection against the abrasive effects of storms or grazing animals.

The determination of rhodolite distribution, morphology, and ecology is the result of a combination of environmental influences. As many of these result in similar morphological characteristics, rhodolites cannot be used to distinguish individual environmental factors. By restricting a model to lagoonal environments many environmental factors can be considered to remain constant across a lagoon (*e.g.*, light intensity). Once general lagoonal characteristics are determined using other analytical methods (*e.g.*, coral, mollusc or sediment analysis) changes in rhodolite form and growth throughout a given lagoon can be attributed to the remaining variable environmental factors. Rhodolites may therefore serve as valuable paleoenvironmental indicators of proximal localities within a given lagoon.

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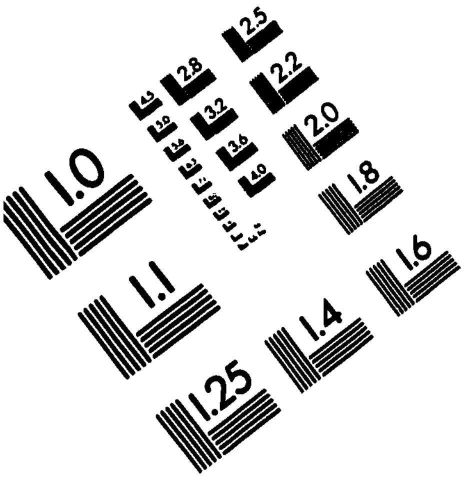
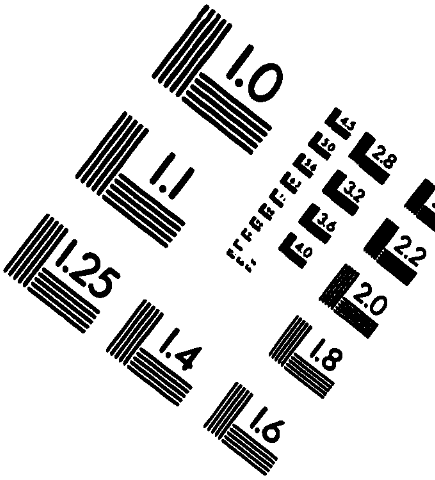
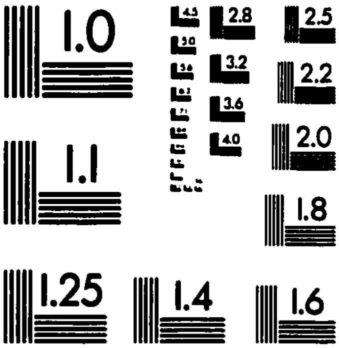
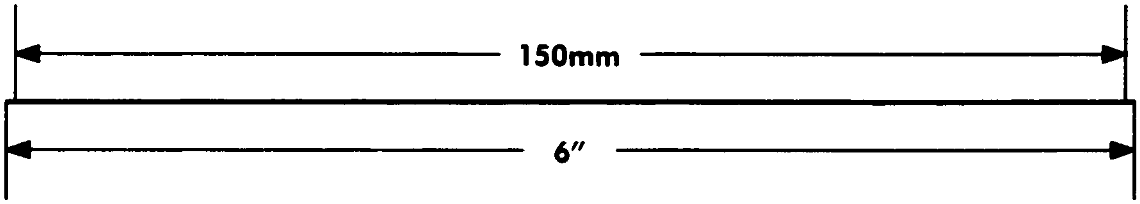
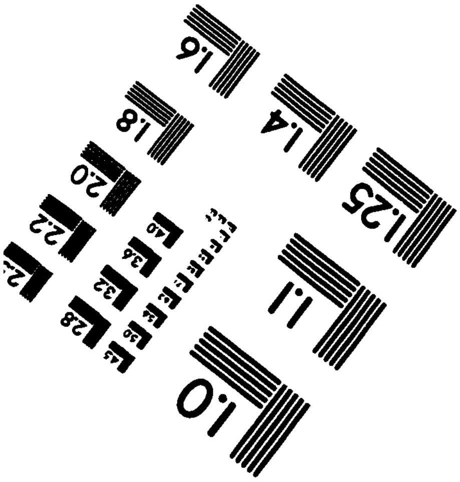
IMAGE EVALUATION TEST TARGET (QA-3)

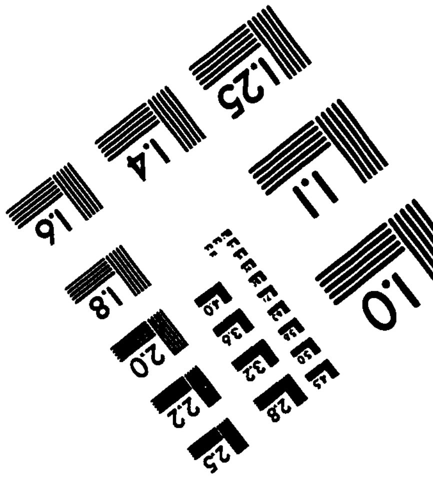












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