RUGOSE CORALS OF THE LATE ORDOVICIAN TO EARLIEST SILURIAN VAURÉAL, ELLIS BAY AND BECSCIE FORMATIONS, ANTICOSTI ISLAND, QUÉBEC

BY

ADAM A. MELZAK

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

Department of Geological Sciences
University of Manitoba
Winnipeg, Manitoba

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

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ABSTRACT

The rugose corals of the Late Ordovician (Richmondian-Gamachian) to earliest Silurian (Rhuddanian) Vauréal, Ellis Bay and Becscie formations of Anticosti Island, Québec, include 19 species belonging to 14 genera and five families, with three additional species placed in open nomenclature. Of the 19 species, five are new: *Streptelasma* n. spp. 1 and 2, *Bodophyllum* n. sp., *Rhegmaphyllum* n. sp. and *Palaeophyllum* n. sp.

Diversity is generally low in the entire stratigraphic interval except in bioherms. The Vauréal fauna is of low to moderate diversity (one to five species at a particular locality and stratigraphic interval), characterized by Red River-Stony Mountain Province species, four of which are also found in the Stony Mountain Formation of southern Manitoba. Two of the seven Vauréal Formation species disappear in the Mill Bay Member (first observed extinction interval). The Ellis Bay fauna is of low to moderate diversity (one to five species per locality) below the uppermost member and is characterized by "continental margin" forms. Three holdovers from the Richmondian disappear in the Prinsta Member (second observed extinction interval). The uppermost Ordovician Laframboise Member is distinguished by reef development and a peak in rugosan species diversity (seven species at one locality). The Ellis Bay fauna has affinities with Baltoscandian and Chinese rugose coral faunas in terms of generic makeup; no species are common to both the study area and non-Laurentian realms. All but one Ordovician species, *Eurogrewingkia pulchella*, disappear at the systemic boundary, placing the local extinction maximum (seven species) stratigraphically higher than mass extinction intervals recorded for other taxa from Anticosti Island. The three observed extinction intervals correlate with known brachiopod extinctions and reefal crises in the study interval. The Becscie fauna is of low to moderate diversity (one to five [possibly six] species per locality), consists of different species from those of the Ellis Bay Formation (except for *E. pulchella* which is present in the lowest 18 m), and is cosmopolitan in nature, including one species found at three other localities in North America and in Siberia and Iran. This fauna represents the earliest stage of rugose coral recovery from the end-Ordovician extinction.

ACKNOWLEDGMENTS

I would first and foremost like to thank my supervisor Dr. Robert Elias of the University of Manitoba, Department of Geological Sciences, who proposed the project and ensured that it was completed. Dr. Graham Young of the Department of Geological Sciences and the Manitoba Museum, as an advisory committee member, provided technical advice and moral support throughout the course of the project and many revisions, as did Dr. Nancy Chow of the Department of Geological Sciences and Dr. Ken Stewart of the Department of Zoology.

Many people from the University of Manitoba and the Department of Geological Sciences in particular provided assistance in one way or another. The following is, inevitably, incomplete and I apologize to anyone not included. Drs. Ayres, Halden, and Clark were helpful in a variety of ways. The staff were always friendly and helpful but, in particular, Elisabeth Ross, and Margo Watson provided equal parts support, encouragement and mild abuse. Sergio Mejia assisted with various aspects of image analysis and graphical production. A large number of students from this department (and others) have been helpful directly and indirectly over the years, particularly Andy, Derek, Eddy, Harvey, Myrna, and Tim.

Critical specimens from the Ellis Bay Formation and lowermost Becscie were obtained from Dr. Allen Petryk of the Québec Ministère d'Énergie, Mines et Resources. Many specimens and important locality data were obtained from Dr. Paul Copper of Laurentian University. Dr. Copper also served as external examiner and provided useful technical suggestions after reviewing the penultimate version of the dissertation. The Geological Survey of Canada's Invertebrate Paleontology Collections and Ms. Jean Dougherty loaned type specimens of several species, as did the Yale Peabody Museum and Mr. Tim White. The entire project was funded by Natural Sciences and Engineering Research Council operating grants to Dr. Elias. Dr. Dong-Jin Lee of Andong National University in Korea provided assistance during fieldwork.

I would particularly like to thank my family, without whose constant support the ultimate goal of familial quadridoctorality would never have been attained.

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1 INTRODUCTION

1.1 GENERAL

The latest Ordovician was a time of mass extinction and oceanographic and climatic change. The shallow-water shelf carbonate and siliciclastic rocks exposed on Anticosti Island in Québec form one of the world's most complete stratigraphic intervals of the Upper Ordovician-Lower Silurian containing abundant shelly fossils. These deposits are, therefore, particularly important because the systemic boundary is missing in most Paleozoic sections in North America and elsewhere throughout the world due to glacio-eustatic regression and erosion.

Anticosti fossils include a large solitary and colonial rugose coral fauna. Since corals were sessile and their distribution was controlled by environment, the variation in coral faunas should reflect the environmental changes that were occurring during this time interval, including a major glaciation and accompanying glacio-eustatic regression.

The rugose corals of the study interval on Anticosti Island were first examined over a century ago (e.g., Billings, 1857, 1858; Lambe, 1901). Subsequently, various authors (e.g., Schuchert and Twenhofel, 1910; Twenhofel, 1928; Bolton, 1979; Elias, 1982a) reviewed the rugose coral faunas. However, only Elias (1982a), and to a lesser extent Bolton (1979), used relatively modern taxonomic techniques, and the study by Elias was limited to previously collected solitary rugosans, including types. A thorough revision of the rugose coral taxa is, therefore, a central component of this study.

Many recent studies of Late Ordovician rugose (and tabulate) corals in North America (e.g., Elias, 1989; McAuley and Elias, 1990; Elias and Young, 1992, 1998; Young and Elias, 1995) have concentrated on biogeographic distribution and the Late Ordovician extinctions, particularly in the Edgewood Province of the east-central United States, where relatively continuous sections through the systemic boundary (N.B., these sections have significant hiatuses below and above the systemic boundary) include significant coral faunas. The present study will allow the comparison of survivorship patterns and general faunal characteristics in two geographically and geologically distinct regions (Anticosti Island and Edgewood Province) during an important time interval.

As Anticosti Island includes a virtually continuous section of the lowermost Silurian, a more complete picture of the earliest phase of rugose coral recovery following the mass extinction is available. By comparison, the lowermost Silurian in the American mid-continent is generally characterized by a depositional hiatus (Elias, 1989; McAuley and Elias, 1990). The Stonewall Formation of southern Manitoba, for example, may include a hiatus that represents a significant proportion of the Gamachian and lower Rhuddanian (Stearn, 1956; Norford et al., 1998). The Beaverfoot Formation of British Columbia, which spans the Upper Ordovician-Lower Silurian and has yielded rugose corals, is comparatively less fossiliferous (less "coralliferous") than Anticosti Island, and the precise location of the systemic boundary is unknown (Buttler et al., 1988). Other North American sections that are continuous across the Ordovician-Silurian boundary, such as the Hanson Creek Formation of the Great Basin (Finney et al., 1999) and the Cape Phillips Formation of the Canadian Arctic (Melchin et al., 1991), represent the shelf to basin transition. The Cape Phillips Formation generally lacks rugose corals and the carbonate platform (coralliferous section) of the Hanson Creek Formation lacks Gamachian corals and records a hiatus around the systemic boundary (Budge, 1972; Sheehan and Harris, 1997). Anticosti Island thus provides a unique opportunity to study rugose corals and the Ordovician-Silurian boundary.

1.2 OBJECTIVES

The objectives of this study are:

1) to describe the rugose coral faunas of the Vauréal, Ellis Bay and Becscie formations of Anticosti Island, Québec;

2) to study the temporal and spatial distribution of these corals, particularly in relation to the Richmondian-Gamachian and Ordovician-Silurian boundaries;

3) to examine intrageneric and intraspecific trends in evolution near and across the extinction boundaries;

4) to perform paleoecological and biostratinomic studies on the solitary and colonial rugosans in order to determine the environment during life and depositional environment after death;

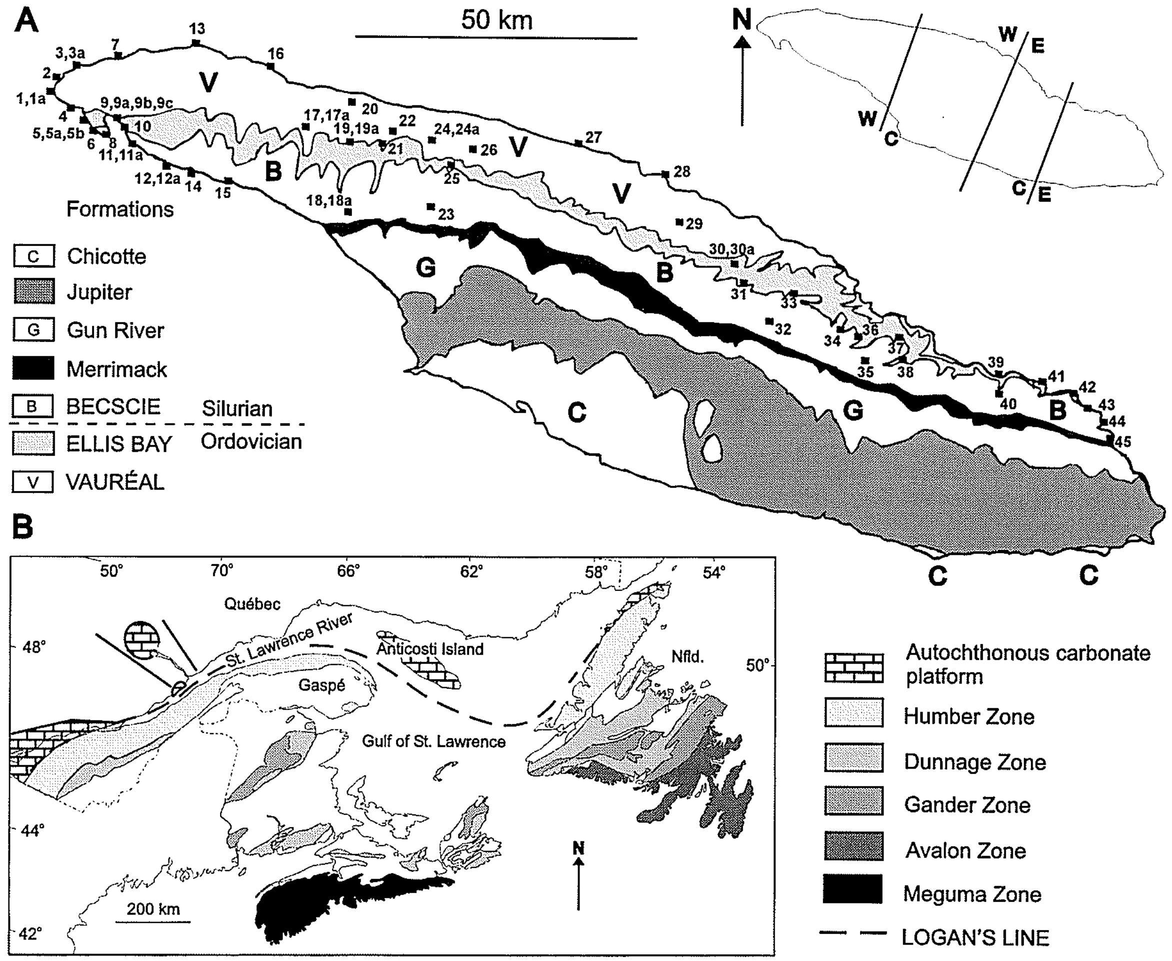
5) to combine data from 1-4 in order to characterize the corals' response to environmental changes associated with the mass extinction events and to compare the results of this study with data from elsewhere in North America and around the world;

6) to compare coral extinction data with those from other taxonomic groups to determine whether similar patterns of extinction and survivorship exist.

1.3 MATERIAL

Collection localities cover the whole geographic extent and stratigraphic range of the Vauréal, Ellis Bay and Becscie formations on Anticosti Island. There are, however, considerably more localities and specimens from the western end of the island around the Ordovician-Silurian boundary (Text-fig. 1A). The material from the Vauréal and Ellis Bay formations is generally well preserved externally and internally, while the Becscie Formation material is of variable quality, and is commonly silicified. Taxonomic identification at the species level is possible for all but the most heavily silicified or abraded/fragmentary specimens. All coralla found in the field were collected (except from extremely fossiliferous monospecific assemblages where a large number was collected) and their orientation (if possible) and stratigraphic position were noted. Coralla were sectioned transversely and longitudinally, and acetate peels or thin sections were made. In the following paragraphs, the count of solitary coralla includes individual corallites of two dendroid colonial species whose coralla tend to be fragmentary.

A stratigraphically continuous series of collections was made by Dr. Allen A. Petryk (Québec Ministry of Energy Mines and Resources) in 1983-1984 from Ordovician-Silurian boundary sections on the west coast at localities 6 and 8. These collections covered the uppermost few metres of the Ellis Bay Formation and the lowermost few metres of the Becscie Formation and are precisely located



Text-fig. 1. A. Map of Anticosti Island, Québec (after Long and Copper, 1994), showing formations (study interval named in upper case) and numbered collecting localities listed below (see Appendix A for detail). Small map (top right) shows arbitrary lines dividing collecting localities into west and east, and west, central, and east (Laframboise Member only). B. General location and tectonostratigraphic setting map, showing tectonostratigraphic zones and Logan's Line, the northernmost extent of Appalachian deformation (after Lavoie et al., 2003).

1,1a: Pointe de l'Ouest (PO-V), S of Pointe de l'Ouest (SPO-V)
2: Ruis Harvey (RH-V)
3,3a: Cap Anglais (CA-V), S of Cap Anglais (CAS, SCA-V)
4: N of Anse aux Fraises (NAF-V) + (A430)
5,5a,5b: Cap de la Vache-Qui-Pisse (CVP) + (A74, A85, A435, A438, A439), Fossil Cliff (FC), West Coast (WC)
6: Pointe Laframboise (PL,LaF) + (A86, A436, A442, A738) + various Petryk collections (see Appendix A)
7: Grand Ruisseau (GR-V)
8: Pointe aux Ivrognes (PI) + (A41) + various Petryk collections (see Appendix A)
9,9a,9b,9c: Canal de Saint Georges (CSG/SGC), Cap Blanc (CB-EB3), Baie des Navots (CB-Eb4), (A423)
10: Les Roselets (ROS)
11,11a: Cap à l'Aigle (CA-B1), S of Cap à l'Aigle (SCA-B1)
12,12a: Pointe de l'Ours (CO-B2), N of Pointe de l'Ours (CO-BB)
13: West of Cap de Rabast (WCR-V)
14: Petite Riviere mouth (A292)
15: Becscie River mouth (B-B2) + (A96, A97)
16: Cap Caron (CC-V)
17,17a: Lac Ste. Marie (LSM-V/RSM-V, A36)
18,18a: La Loutre Road (LLR 11.2), (LLR 16.1) + (A22)
19,19a: La Loutre Road (LLR 5.9) + (A4)
20: Havre du Brick Road (A35)
21: Jupiter River Road (A42)
22: Main Highway (MH-V)
23: Jupiter River 24 mile crossing (JR24), (JR24SE) + (A504)
24,24a: Beaver Cove Road (A5), S of Beaver Cove Road (A14)
25: Gravel road east of Jupiter Road (A72)
26: Tote Road (A80)
27: Baie MacDonald (BMac-V)
28: Carleton Point (Carl-V)
29: Observation Canyon (OC-V)
30,30a: Vauréal River (VRtop), (VR-Au)
31: Riviere des Petits Jardins (RPJ)
32: Salmon Road (A843)
33: Naciscotek Road (POR) + (A737)
34: Homard Road (A902)
35: Salmon River 16 mile pool (SR-16)
36: Homard Road (A892)
37: Homard Road (A894)
38: Salmon River 8 mile pool (SR) + (A743)
39: Mill Bay (MB) + A364(1)
40: Schmitt Creek (A590)
41: Prinsta River and Prinsta Point (A135, A359, A362, A362(2), A466)
42: Table Head (A357(1), A468a)
43: Lousy Cove (LC) +(A219, A466, A595)
44: Fox Point and Fox Bay (FP) + (A140, A142, A144, A146, A313)
45: Reef Point (A149)

stratigraphically. A total of 266 solitary coralla (and isolated corallites) from the Petryk collections was examined and identified in this study.

A series of discrete (not stratigraphically continuous) collections of solitary and colonial coralla was made by Dr. Paul Copper (Laurentian University) in the late 1980s and early 1990s over the full stratigraphic and geographic range. Each collection has stratigraphic information, although the precision ranges from anywhere within a member to an exact number of centimetres above a certain boundary. A total of 323 solitary coralla (and isolated corallites) and 22 colonial coralla from the Copper collections was examined. A few apparently monospecific collections of well preserved specimens were not sectioned or counted; 218 solitary coralla were identified to species level.

A series of collections was made in 1986 by Dr. Robert J. Elias (University of Manitoba) from localities at the western end of Anticosti Island from all three formations. The west coast collections are from stratigraphically continuous sections; the others are generally discrete. Each collection has stratigraphic information, except a few small collections in the Vauréal Formation which can only be located approximately within the section. Elsewhere, precision is to the centimetre although the locality 3 specimens are measured in centimetres from an arbitrary position (top of the section) rather than a member or formation boundary. A total of 762 solitary coralla (and isolated corallites) from the Elias collections was examined and identified.

A series of collections was made by the author, Dr. Elias, and Dr. Dong-Jin Lee (Andong National University, Korea), from localities across Anticosti Island during the summer of 1994. These collections include solitary and colonial coralla and were made in stratigraphically continuous sections on the west coast, along the east side of Ellis Bay, along Salmon River and on the northeast coast. Additional collections were made from discrete sections along the north coast and in the centre of the island. Stratigraphic information is precise to the centimetre (relative to the nearest stratigraphic boundary) where possible, although specimens from isolated outcrops are only referred to a member or in a few cases, a formation. A total of 1150 solitary coralla (and isolated corallites), of which 1079 were numbered and identified, and 64 colonial coralla from the 1994 collections was examined. Several slabs of well preserved specimens on bedding planes were not sectioned or counted, although the species in each collection were identified, either from distinctive external characters or from specimens from adjacent beds.

Data from previously published work, particularly Billings (1862, 1865b), Twenhofel (1928), Bolton (1979, 1981a) and Elias (1982a) were also used to examine taxonomic relationships to type material, delineate maximum stratigraphic and geographic ranges of certain species, and to study variability. Type specimens from the Geological Survey of Canada and the Yale University Peabody Museum were examined.

1.4 METHODS

This section will discuss the general methods employed in this study and, in particular, how they relate to the ultimate goals. Specific details of methodology will be covered in the introduction to each different area of study. Taxonomic methodology is discussed in Systematic Paleontology.

1.4.1 Paleoecology and Biostratinomy

Paleoecology was studied using a combination of the distribution of taxa (biofacies), the physical properties of the coralla (size, shape, degree of septal and axial dilation, presence of attachment structures), relationship with other organisms and local sedimentology and stratigraphy. Biostratinomy (the incorporation of fossils into sediment) was studied by examining the physical condition of each specimen (degree of abrasion) and, where possible, the orientation of the corallum in situ. A combination of paleoecologic and biostratinomic data enabled the analysis of environmental factors such as water depth, current strength, substrate type and sedimentation rates. These environmental data are important in analyzing the effects of extinction, in particular to determine whether a drop in diversity was a result of local environmental change or of global processes.

1.4.2 Biostratigraphy, Extinction and Recovery

In this study, the distribution of corals was determined using geographic and stratigraphic information recorded in the field and subsequently correlated with the taxonomic data. By using range information, in combination with results from previous work on Anticosti Island, vertical range charts were generated and patterns of diversity were revealed. These enabled the correlation of local patterns of diversity and extinction with data for other taxa from Anticosti Island and from corals (and other taxa) from elsewhere in North America and globally.

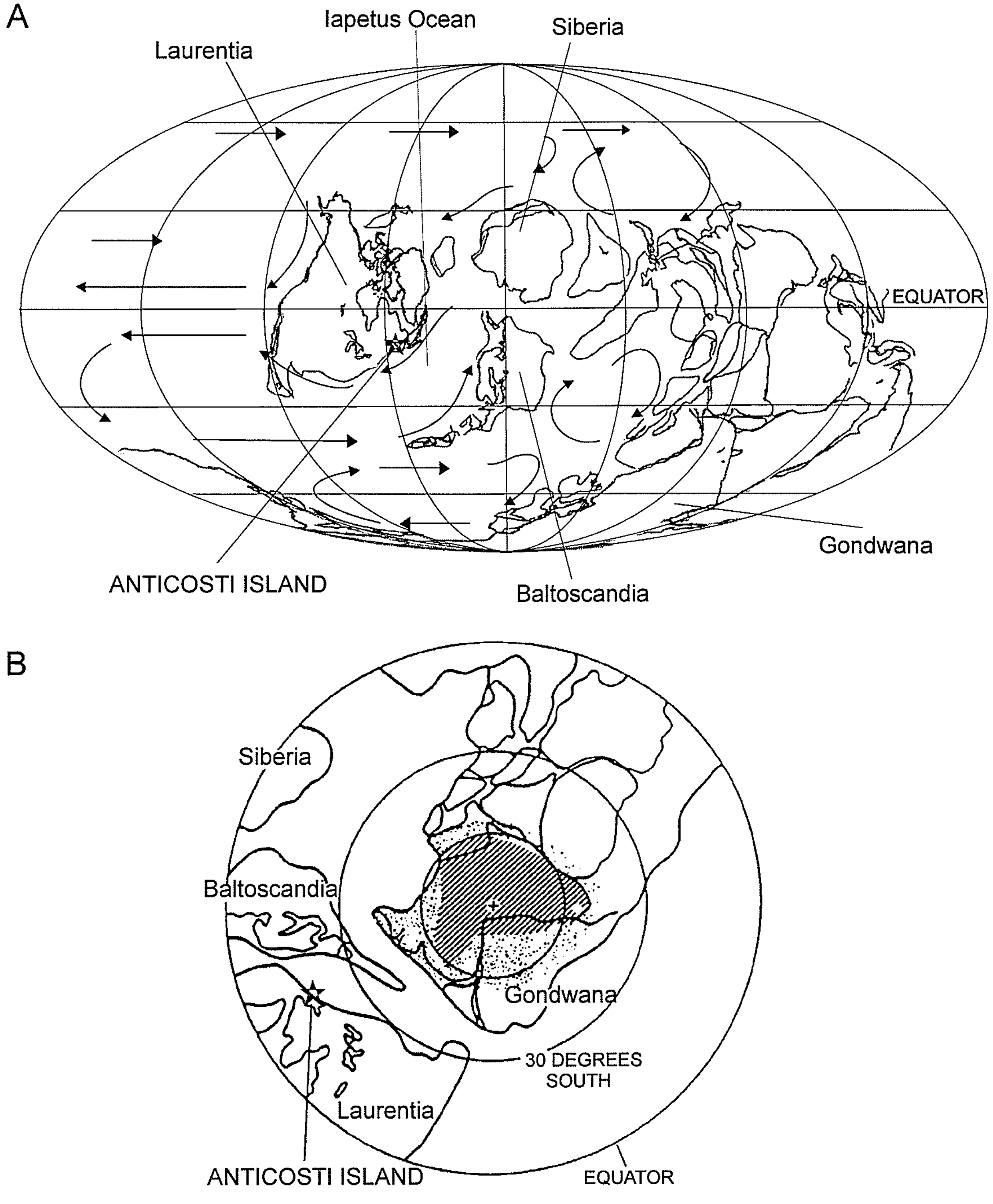
2 GEOLOGICAL SETTING

2.1 INTRODUCTION

This study focuses on the rugose coral faunas of the Late Ordovician Vauréal (Richmondian) and Ellis Bay (Gamachian) formations and the Early Silurian (Rhuddanian) Becscie Formation of Anticosti Island, Québec. This section includes discussions of: paleogeography, glaciation and associated events, previous geological work on Anticosti, general geology of Anticosti, stratigraphy and sedimentology of the three formations being studied and previous studies of corals from the study interval. The paleobiogeography of Late Ordovician corals from North America is also discussed.

2.2 PALEOGEOGRAPHY

A reconstruction of the positions of the continents during the studied time interval (McKerrow and Scotese, 1990; Copper, 2001, 2002; Text-fig. 2A) shows that Anticosti Island, at the eastern end of the Laurentian craton, was approximately 20 degrees south of the paleoequator. At the same time, the proto-Atlantic Iapetus Ocean was closing, bringing Baltoscandia and parts of what are now England and Ireland into relatively close proximity. The supercontinent Gondwana, which consisted of Africa, South America, Australia, Antarctica and parts of what are now Asia was situated at the South Pole, a significant factor in the resulting glaciation. Circulation in the Iapetus Ocean was counterclockwise (Copper, 2002) and the eastern Laurentian craton would have been affected primarily by a warm equatorial current.



Text-fig. 2. A. Map of the Late Ordovician world, showing position of continents and study area (star) and global current patterns (after McKerrow and Scotese, 1990; Copper, 2001, 2002). B. South polar projection of Late Ordovician world with approximate maximum extents of continental glaciation (diagonal lines) and marine glaciation (stippled), and positions of continental masses (after Brenchley et al., 1991).

2.3 GLACIATION

Glaciation developed during the latest Ordovician (Beuf et al., 1966; Allen, 1975; Brenchley and Newall, 1980; Marshall et al., 1997), centred on the South Pole in Gondwana (modern Sahara region of north Africa). Geological evidence includes tillites in north Africa, and diamictites and dropstones in southern Europe and South America (Brenchley, 1984, 1989; Text-fig. 2B).

The glaciation was accompanied by a eustatic drop in sea level (or series of regressive-transgressive cycles; Brenchley et al., 1994; Marshall et al., 1997), and, as a result, the uppermost Ordovician is missing from most stratigraphic sections due to erosion and nondeposition. With subsequent deglaciation, the ocean re-transgressed onto the generally exposed platforms in the earliest Silurian. The transgressions and regressions were accompanied by oceanographic crises as stratification was disturbed by cold water flowing from the polar regions (Wilde and Berry, 1984; Brenchley et al., 1995; Owen and Robertson, 1995).

In terms of climate, the Anticosti Island area would have been affected indirectly by the glaciation as it was in the tropical belt in the Late Ordovician. The sedimentation patterns in the latest Ordovician (see 2.4.3 Stratigraphy) show oscillations of paleodepth (Long, 1993b, 1997) that are comparable to global regression patterns (Brenchley et al., 1994). Oxygen and carbon isotopic shifts, which can be related to sea level changes as well as temperature and ice-cap related effects (Long, 1993a), are significant on Anticosti Island. The most significant effect is the pronounced positive shift both in $\delta^{18}O$ and $\delta^{13}C$ in the Laframboise Member of the Ellis Bay Formation just below the systemic boundary

(Long, 1993a, 1993b), which is comparable to isotopic shifts seen in contemporaneous rocks from Baltoscandia (Brenchley et al., 1994). The isotopic shift is thought to correspond to effects of final deglaciation (e.g., release of CO_2 from ice caps, change in organic carbon cycling, change in rates of carbonate deposition; Brenchley et al., 1994).

2.4 ANTICOSTI ISLAND

2.4.1 Introduction

The Anticosti Basin generally encompassed the area between Newfoundland and Gaspé and northwest to the Precambrian craton on the mainland north of Anticosti (see Text-fig. 1B). The basin is largely (and Anticosti Island is completely) situated north of Logan's Line and was, therefore, generally free of the direct influence of the Appalachian Orogeny (Lavoie et al., 2003). As a result, post-depositional deformation has been minimal in the study area. The Anticosti Basin was in a continental margin setting in which sedimentation was nearly continuous from the Cambrian to the Carboniferous, although the study area includes only Ordovician and Silurian rocks. The Taconic Orogeny temporarily activated regional tectonics in the Middle Ordovician, resulting in the deposition of large volumes of fine siliciclastics, which predated deposition of the sediments of the study interval. Subsequently, mixed carbonate and siliciclastic deposition continued in the passive margin setting, producing the Ordovician-Silurian section now exposed on Anticosti Island (and the lower ca. 800 m of Vauréal Formation known only from drillholes) (Bolton, 1972; Long and Copper, 1987a, 1994; Copper and Long, 1998). The closing of the Iapetus Ocean would have affected current patterns during the study period, while the subsequent closing of the Rheic Ocean to the south would have postdated Anticosti Island deposition by almost 30 million years.

Anticosti Island records the thickest and best exposed shallow-water section of the Ordovician-Silurian boundary in the world. The island is located near the meeting of the St. Lawrence River and the Gulf of St. Lawrence (see Text-fig. 1B). The Ordovician-Silurian strata of Anticosti were deposited in a shallow ramp or platform setting in tropical or sub-tropical conditions (Petryk, 1981a; Long and Copper, 1994). The paleo-shoreline corresponded approximately to the modern shoreline of mainland Québec (Sept-Iles to Havre St. Pierre) to the north (see Text-fig. 1B). Regional dip is to the southwest at approximately 2 degrees (Petryk, 1981a; Long and Copper, 1987a, 1987b, 1994). Carbonate lithologies dominate with locally abundant interbeds of siliciclastics. There is an east-west lateral differentiation: locally well developed sand bodies are present at the eastern end of the island (Long and Copper, 1987a, 1987b), but not in the west. The strata are of Late Ordovician and Early Silurian age and are divided into six (Petryk, 1981a) or seven (Copper and Long, 1989) formations. The lower two, the Vauréal and the Ellis Bay formations, are of Ordovician age and the Becscie, Merrimack (Copper and Long, 1989), Gun River, Jupiter, and Chicotte formations are of Silurian age.

2.4.2 History of Geological Study

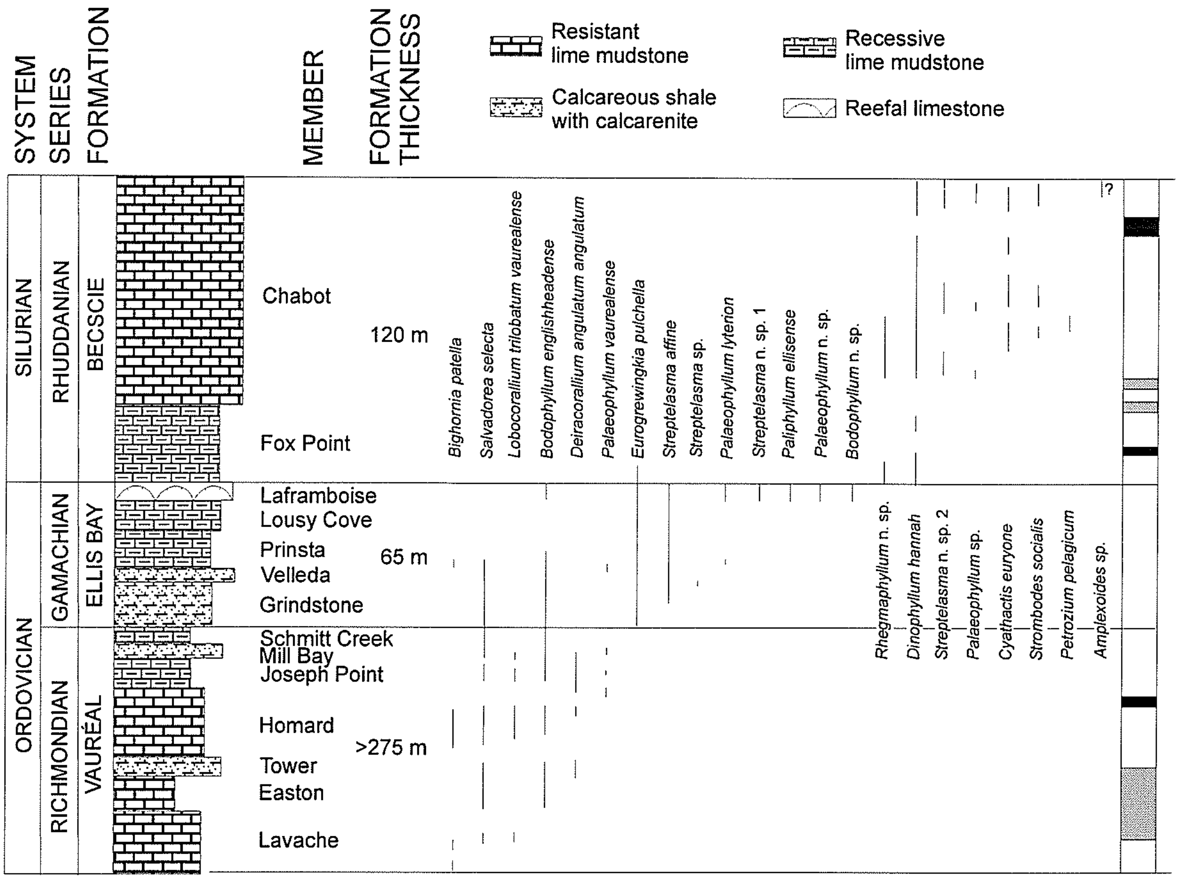
The geology of Anticosti Island was first investigated by Richardson (1857). He divided the strata into six units labelled A to F, which include Ordovician and Silurian rocks.

Logan et al. (1863) referred the lower beds to the Hudson River Group and named the upper beds the Anticosti Group. Their division was close to the modern definition of the Ordovician-Silurian boundary (Long and Copper, 1987a). Schuchert and Twenhofel (1910) were the first to name formations. They determined that the rocks of what is currently known as the Ellis Bay Formation are younger than the Richmondian Series, and proposed the name Gamachian Series for this interval. Twenhofel (1921, 1928) made major revisions of the geology and paleontology of Anticosti Island and added lithologic and paleontologic zonations. Bolton (1961, 1970, 1972) redescribed the Anticosti strata and numbered the members of the Ellis Bay Formation. Petryk (1981a) made a further revision of the stratigraphy of the upper part of the Ordovician section (Vauréal and Ellis Bay formations) and subdivided the Ellis Bay Formation into seven members. Long and Copper (1987a) have since described sections from the eastern part of the island (most previous investigations had concentrated on the western part of the island) and revised the subdivisions of the Ellis Bay Formation and added the Merrimack Formation (Copper and Long, 1989) by subdividing the Becscie Formation. The nomenclature of Long and Copper (1987a) for the Ellis Bay Formation is generally followed here, although a large number of specimens used in this study were collected by Petryk and their stratigraphic information is based on his nomenclature.

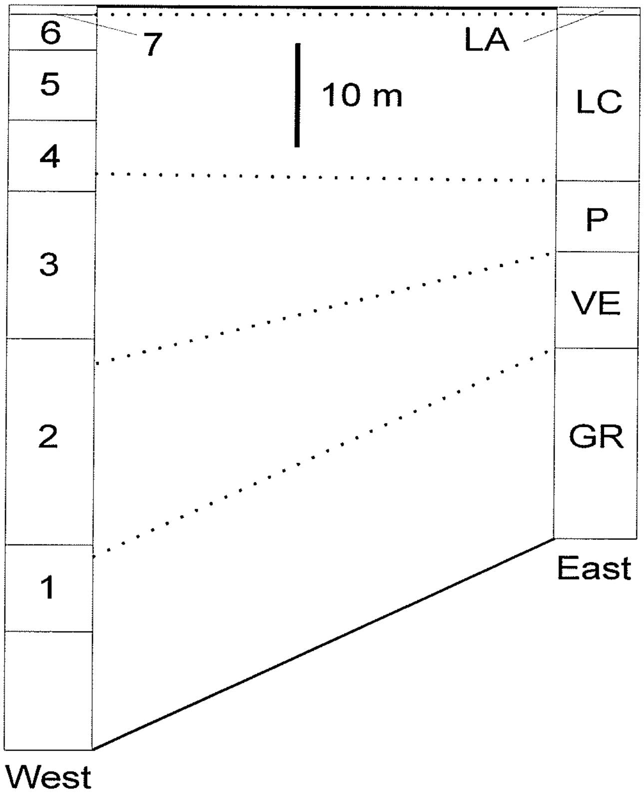
2.4.3 Stratigraphy

The Vauréal Formation comprises seven members: the Lavache, Easton, Tower, Homard, Joseph Point, Mill Bay and Schmitt Creek members, in ascending order (Text-fig. 3). Only the upper two of these members have been formally defined (Long and Copper, 1987a). The Ellis Bay Formation comprises five members (*sensu* Long and Copper, 1987a): Grindstone, Velleda, Prinsta, Lousy Cove and Laframboise in ascending order (Text-fig. 3). Petryk (1981a) divided the Ellis Bay into seven numbered members; that nomenclature is used only at sections where collection was based on the maps of Petryk (1981a) (Text-fig. 4). The Becscie Formation comprises two members, both of which are informal (Jin, 1989; Long and Copper, 1994): the Fox Point and Chabot, in ascending order (Text-fig. 3).

2.4.3.1 *Vauréal Formation.* The Vauréal Formation is generally composed of fine grained carbonates and shales in its lower members, reflecting relatively deep water marine deposition with periodic episodes of storm deposition manifested as fine to coarse grainstones. The Homard Member contains channels and conglomerates (Long and Copper, 1994), indicative of high energy conditions at depths shallower than underlying units. The Joseph Point Member records a deepening period (Dewing, 1999) during which calcareous and carbonate mudstone deposition dominated. The Mill Bay Member consists predominantly of resistant coarse grainstones with abundant quartz sand in the eastern end of the island at locality 39. Sand waves and other high energy, shallow water features are present (Long and Copper, 1987b). In the western part of the



Text-fig. 3. Stratigraphy of the study interval with formation and member names (*sensu* Long and Copper, 1987a and Copper and Long, 1994; after Long and Copper, 1994) and stratigraphic ranges of rugose coral species (N.B., this includes data from other published sources). Thickness of formations not to same scale. Vauréal thickness represents only the exposed portion of the formation. Note that species ranges in lower Vauréal are only accurate to within 10-50 m. Column on right shows black intervals (not sampled), grey intervals (incompletely collected from imprecisely located discrete collections) and white intervals (continuously or nearly continuously sampled).



Text-fig. 4. Correlation between members of the Ellis Bay Formation sensu Petryk (1979; west coast) and *sensu* Long and Copper (1987a; east coast), showing relative thickness of generalized sections from western and eastern localities and approximate correlations based on Long and Copper (1987a, 1994) and analysis of specimens from this study. LA = Laframboise, LC = Lousy Cove, P = Prinsta, VE = Velleda, GR = Grindstone. After Long and Copper (1994).

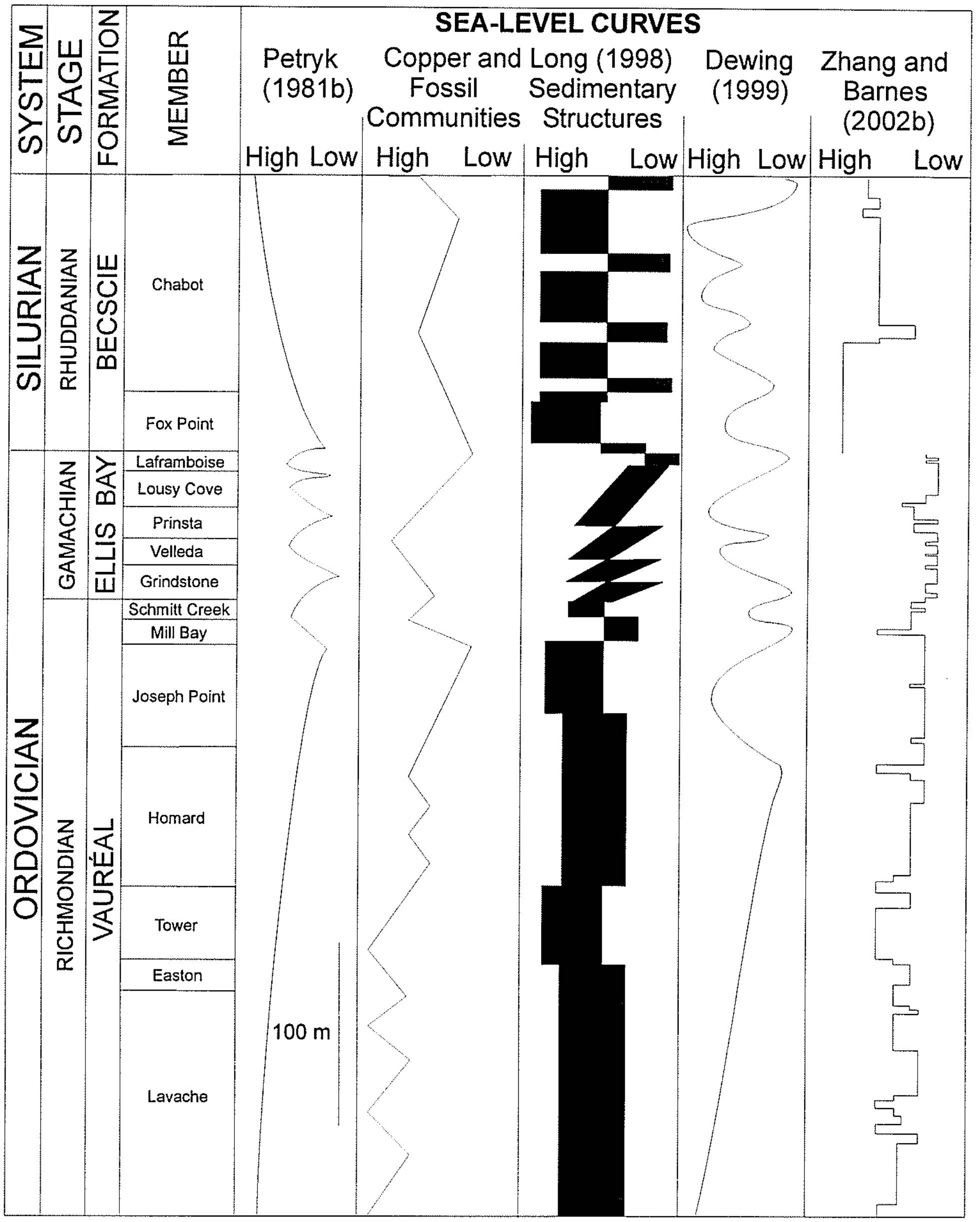
island, the Mill Bay Member includes small bioherms, indicative of increasingly shallow deposition with low sediment input. The Schmitt Creek Member occurs as nodular calcareous mudstones and carbonate mudstones-wackestones.

2.4.3.2 *Ellis Bay Formation.* The Ellis Bay Formation generally consists of carbonate mudstones in the western part of the island, while carbonate-siliciclastic sands are an important element of the Grindstone and Velleda members at the eastern end of the island (Long and Copper, 1987a). The Prinsta and Lousy Cove members are fine grained nodular limestones with minor carbonate mudstone and shale interbeds, and minor sandstone beds at the eastern end of the island. The Laframboise Member, at the top of the Ellis Bay Formation, is the thinnest but most recognizable stratigraphic unit in the entire study interval. It generally consists of a basal "oncolite platform bed" (Petryk, 1981a) overlain by coral-algal-stromatoporoid bioherms with interbedded bioclastic wackestones and floatstones. The Laframboise Member varies considerably across the island: in the west, bioherms are 1-2 m thick and the oncolite platform bed is relatively thin; in the centre of the island the oncolitic bed is 70+ cm thick; in the east-central part of the island, the bioherms are as much as 8 m thick (Lake, 1981; Copper and Long, 1998; Copper, 2001); and on the east coast, the member consists of a metre-thick oncolitic biostrome with metre-scale bioherms. At some exposures, the beds underlying the bioherms are downwarped and the overlying beds are draped over the mounds. This member apparently represents the shallowest depositional conditions in the study interval. Mudcracks or other evidence of prolonged exposure are not present, although evidence of hardground formation and a blackened surface suggestive of intertidal exposure have been found (Long, 1993a).

2.4.3.3 *Becscie Formation.* The Becscie Formation consists of a thin lower member, the Fox Point, which is formed of calcareous mudstones with minor coarser grained lenses and beds (wackestones), and a thick upper member, the Chabot, which generally consists of coarse-grained carbonates with extensive skeletal grainstone beds. Lateral variation within the units (e.g., thickness of grainstones) reflects the dominance of storm deposition during the time of the Becscie Formation and is a function of depth and proximal-distal position (Sami and Desrochers, 1992). The Fox Point Member is considerably thinner in the eastern part of the island than in the west (22 m vs. 3.6 m; Long and Copper, 1994). Individual beds cannot be traced across the island due to the degree of lateral variation.

2.4.4 Geological Events

Among the sea level curves published for the study interval are those based on sedimentation patterns (Petryk, 1981b; Long, 1993b, 1997), brachiopods (Dewing, 1999), conodonts (Zhang and Barnes, 2002b), and fossil communities and sedimentary structures (Copper and Long, 1998). Some of these curves (see Text-fig. 5) have significant differences but certain general patterns are consistent. The Vauréal Formation records an overall shallowing upwards from the Lavache to the Homard members (Petryk, 1981b; Dewing, 1999). Subsequently, sea level rose during deposition of the Joseph Point Member and then fell again, beginning a series of transgressive-regressive cycles that



Text-fig. 5. Schematic section of study interval with published sea-level curves showing glacio-eustatic cycles of transgression and regression (after Petryk, 1981b; Copper and Long, 1998; Dewing, 1999; Zhang and Barnes, 2002b).

continued through deposition of the entire Ellis Bay Formation (Petryk, 1981b; Dewing, 1999; Zhang and Barnes, 2002b; Text-fig. 5). While the sea level curves in Text-figure 5 are substantially different from each other, particularly the conodont-based curve of Zhang and Barnes (2002b), they all show fine-scale oscillations during deposition of the Ellis Bay Formation. These cycles are comparable in scale to transgressive-regressive cycles seen in Pleistocene sediments and are considered to be glacio-eustatic in origin. The associated shift from "greenhouse" (interglacial, transgressive) to "icehouse" (glacial, regressive) conditions during glaciation, and subsequent reversion to "greenhouse" conditions, drove oceanographic changes (e.g., disturbance of stratification, spread of anoxia; Brenchley et al., 1994, 1995; Armstrong, 1995) that are associated with mass extinction events.

Some authors (e.g., Brenchley et al., 1994) have considered that the shallowest point in the interval was in the oncolite platform bed, and their published sea-level curves have reflected this. Copper (2004, pers. comm.) considered this interpretation to have been based on incomplete biostratigraphic data for the upper Ellis Bay Formation and resulting faulty correlation with global sea-level patterns. According to other authors, the shallowest part of the interval was in the biohermal uppermost Laframboise Member (Long, 1993b, Copper, 2001); this conclusion is followed herein. The uppermost transgressive-regressive cycle ends in the biohermal Laframboise Member and the lower Becscie shows initial deepening that corresponds to the global megacycle of transgression in the Early Silurian (Long, 1993a, 1993b; Copper, 2001). Lake (1981) and Brenchley et al. (1994) suggested that there is an unconformity in the lowermost part of the

Laframboise Member, but Lake's analysis was based on data from the Prinsta Member and Brenchley et al. used incomplete data (Long, 1997; Copper, 2001; Copper, 2004, pers. comm.). Other authors, however, do not note a gap (e.g., Long and Copper, 1994) and Copper (2001) explicitly stated that there are no hiatuses in the Ordovician-Silurian boundary interval. The overall Early Silurian transgression is modified by smaller scale regressive-transgressive events (Sami and Desrochers, 1992; Dewing, 1999). The sea-level curve that Zhang and Barnes (2002b) generated from conodont data (see Text-fig. 5) shows a much sharper transgression at the systemic boundary followed by a relatively steady sea level with a depth of around 70 m. This pattern is in contrast with the steadily increasing depth described by Petryk (1981b; Text-fig. 5) and the oscillating, but increasing, depth described by Dewing (1999; Text-fig. 5). As the Zhang and Barnes (2002b) sea-level curve was based upon conodont assemblages, their data would be susceptible to distortion by storm reworking and other transportation. This was compensated for by using very large sample sizes and cluster analysis to distinguish recurring groups of conodont taxa (Zhang and Barnes, 2002c). Rugose corals in the study interval are useful only as general depth indicators. Rugose coral diversity is not high and, unlike conodonts and brachiopods, they are not present in (nearly) every bed in the section, making an analysis comparable to Dewing (1999) or Zhang and Barnes (2002b) impossible. Further work with other taxa and sedimentological evidence will be necessary to determine which pattern is most correct for the Becscie Formation.

2.4.5 Ordovician-Silurian Boundary

The systemic boundary on Anticosti Island is difficult to define precisely as there are very few graptolites in the shallow water carbonates in the uppermost Ellis Bay Formation. Melchin et al. (1991; Text-fig. 6) correlated the North American conodont zones with the global standard graptolite zonation (based on the section at Dob's Linn, Scotland) using sections in the Canadian Arctic. This enabled the correlation of graptolite zonation with the Anticosti Island section. The Ordovician-Silurian boundary on Anticosti Island has been defined as the first occurrence of the conodont genus *Ozarkodina* in the *Oulodus*? *nathani* Zone (McCracken and Barnes, 1981); however, both McCracken and Barnes (1981) and Melchin et al. (1991) showed that the *nathani* Zone is actually an overlap of Ordovician and Silurian faunas and does not sharply delineate a boundary. They defined a boundary interval that is approximately 1.5 m thick. The current boundary has generally been placed at the top of, or within the uppermost metre of, the Laframboise Member bioherms in the Ellis Bay Formation, as the overlying lower Becscie Formation lacks "diagnostic Ordovician" corals and brachiopods (McCracken and Barnes, 1981; McCracken and Nowlan, 1988; Long and Copper, 1987a; Copper, 2001).

A recent detailed analysis of the Silurian conodonts on Anticosti Island defined the *Ozarkodina hassi* Zone as the lowest conodont zone of the Silurian section (Zhang and Barnes, 2002a). The base of that zone coincides with the base of the Becscie Formation. A recent revision of the sparse graptolite fauna of the Ellis Bay and Becscie formations (Melchin, 2002) has shown that the Ellis Bay Formation is entirely within the *persculptus* and *extraordinarius* graptolite zones (Hirnantian age), in contrast with

PERIOD	STAGE	FM.	MBR.	Canadian Arctic (Melchin et al., 1991) Conodonts	Canadian Arctic (Melchin et al., 1991) Graptolites	Dob's Linn, Scotland (Williams,1986) Graptolites	Anticosti Island (Zhang and Barnes, 2002a) Conodonts	Anticosti Island (Copper, 2001; Melchin, 2002) Graptolites	Anticosti Island (Copper, 2001; Melchin, 2002) Fm.
SILURIAN	Rhuddanian	BECSCIE	Fox Point	*kentucky-ensis*	*sinitzini*	*acuminatus*	*Ozarkodina hassi*	*ascensus*	BECSCIE
					mademii-lubricus				
				nathani					
ORDOVICIAN	Gamachian	ELLIS BAY	Laframboise BH	*ordovi-cicus*	*persculptus*	*persculptus*	Fauna 13	*persculptus*	ELLIS BAY
			Laframboise OPB		*bohemicus*	*extraordinarius*		*extra-ordinarius*	
			Lousy Cove		*pacificus*	*anceps* *pacificus*		*anceps*	VAURÉAL
					fastigatus	*complexus*			

Text-fig. 6. Correlation of conodont and graptolite biostratigraphic schemes with the uppermost Ellis Bay Formation and lowermost Becscie Formation. BH = biohermal Laframboise member, OPB = oncolite platform bed. Melchin (2002) column shows position of formations relative to graptolite zones from Dob's Linn(after Melchin et al., 1991; Long and Copper, 1994; Copper, 2001; Zhang and Barnes, 2002a; Melchin, 2002).

previous analyses which placed between one and six members of the sub-biohermal Ellis Bay Formation (*sensu* Petryk, 1981a) in the *anceps* Zone (Rawtheyan age). For the purposes of this study, the Ordovician-Silurian boundary is considered to coincide with the Ellis Bay-Becscie boundary and the Ellis Bay Formation is considered to be entirely Gamachian in age, as defined by Schuchert and Twenhofel (1910).

2.5 PREVIOUS CORAL STUDIES

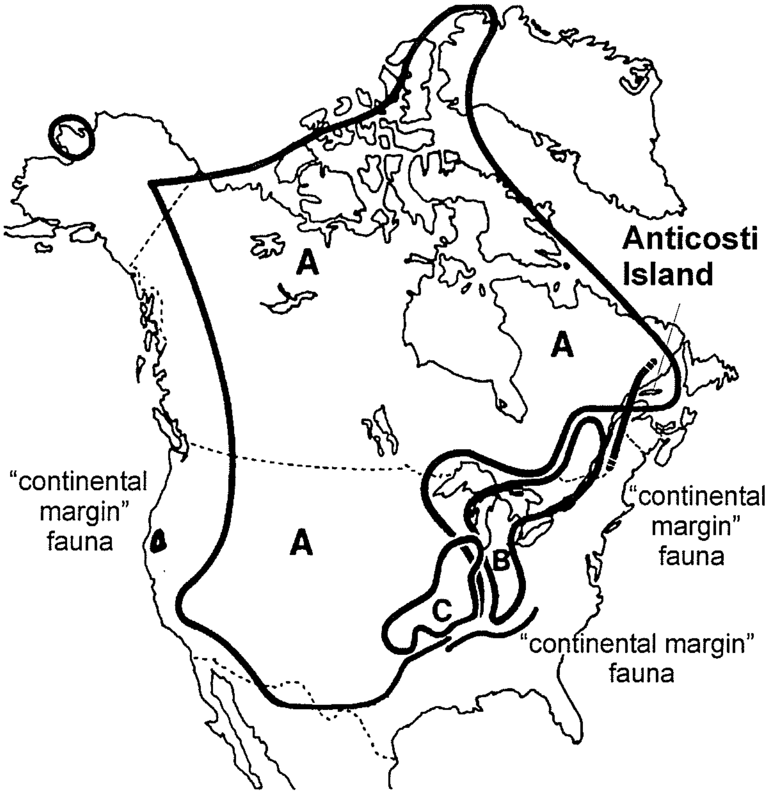
Billings (1862, 1865b, 1866) was the first to examine fossil rugose corals (and other taxa) from Anticosti Island. Subsequently, Lambe (1901) revised the taxonomy of Canadian Paleozoic corals including several Anticosti rugosan species. Twenhofel (1914, 1928) described many new taxa from Anticosti Island, in addition to revising the earlier descriptions. His rugose coral species are generally still valid, although generic taxonomy has been considerably altered. Bolton (1970, 1972, 1980, 1981a, 1981b) described or illustrated a number of rugose coral species of Anticosti and Gaspé, but some taxa were only described in general terms. Elias (1982a) revised the Ordovician solitary rugose corals of Anticosti based on previously collected specimens, and his nomenclature is followed here. Several studies on tabulate corals from Anticosti Island (e.g., Dixon et al., 1986; Noble and Lee, 1991) have been published relatively recently.

Several species of solitary rugosans found on Anticosti Island have also been described as occurring in the Late Ordovician Stony Mountain Formation of southern Manitoba (Elias, 1983), and *Bighornia patella* is widely known from Late Ordovician rocks of North America (Elias, 1982a, 1983, 1985; Buttler et al., 1988). Flower (1961) published a monograph on colonial corals from the Upper Ordovician of west Texas and New Mexico, including many rugose and tabulate taxa found on, or similar to taxa found on, Anticosti Island. Fedorowski and Jull (1976) and Bolton (1979) discussed some colonial rugose coral species, including *Palaeophyllum vaurealense*, from the Ordovician of Anticosti Island and nearby areas.

The Silurian rugose coral fauna of the Becscie Formation has not been revised recently, except in Bolton (1981a) which includes only plates and extended figure captions. Laub (1979), in a monograph on the corals of the mid-Llandovery Brassfield Formation in the Cincinnati Arch region, described several species that occur on Anticosti Island, in addition to several other related species. Buttler et al. (1988) and McAuley and Elias (1990) discussed some Early Silurian solitary rugose corals from other parts of North America, but these are sparse and/or poorly preserved faunas.

2.6 RUGOSE CORAL BIOGEOGRAPHY

The Late Ordovician solitary rugose coral faunas of North America have been divided into three provinces by Elias (1982a, 1985, 1989, 1992; Young and Elias, 1995; Elias and Young, 1998): Red River-Stony Mountain Province, Richmond Province, and Edgewood Province (see Text-fig. 7). A fourth, as yet informal division, is represented by a "continental margin" fauna. The distribution of these faunas was generally a function of paleogeography and environmental factors, and each province's fauna was morphologically or taxonomically distinct. *Palaeophyllum*, a cosmopolitan genus (Kaljo and Klaamann, 1973) found on Anticosti Island, occurs at various North American



Text-fig. 7. Map of North America showing extent of solitary rugose coral provinces in the Late Ordovician, the "continental margin" fauna, and the study area. A = Red River-Stony Mountain Province, B = Richmond Province, C = Edgewood Province (after Elias, 1982a, 1984; McAuley and Elias, 1990; Young and Elias, 1995).

localities in all three provinces. The variability within this genus is pronounced (and not easily quantifiable; see discussion of the genus in Systematic Paleontology), so *Palaeophyllum* is of little use in biogeographic analysis.

2.6.1 Red River-Stony Mountain Province

The largest area of the Laurentian craton was characterized by Red River-Stony Mountain (RRSM) Province corals from Edenian-Richmondian time (Elias, 1982a), when the craton was covered by a shallow epicontinental sea and carbonate deposition was widespread (Flower, 1965). The RRSM Province is characterized by solitary rugose corals with noncircular cross-sectional shape and dilated septa, indicating adaptation to high energy environments (Elias, 1982a). The taxa include the compressed genus *Deiracorallium*, the subcalceoloid genus *Bighornia*, the trilobate genus *Lobocorallium* and triangulate to trilobate forms of *Grewingkia*. Some species, especially *Bighornia patella*, were very widespread, occurring throughout the province, from Ellesmere Island to the southern Canadian Rocky Mountains, Manitoba, Wyoming, Texas, New Mexico and east to Québec. Various species of *Palaeophyllum*, some similar to *P. vaurealense* (this study), occur in the RRSM Province, but none are conspecific with Anticosti species. The province was largely eliminated at the end of Richmondian time when glacio-eustatic regression drained the epicontinental sea; however, two RRSM species (*Salvadorea selecta* and *Bighornia patella*), survived into the Gamachian on Anticosti Island.

2.6.2 Richmond Province

The Richmond Province occurs in a band that stretches from Tennessee north to the Great Lakes and northeast along the St. Lawrence Lowlands. The area was characterized during the Richmondian by mixed clastic and carbonate deposition in restricted to open marine conditions. Rugose coral diversity was low. The fauna includes four solitary species: *Grewingkia canadensis*, *G. deltensis*, *G. rustica* and *Streptelasma divaricans*. The primary characteristic of the low diversity faunas is the high degree of intraspecific variability in *G. canadensis* and *S. divaricans*, possibly a reflection of the varying environmental conditions at the time. *Cyathophylloides wellsi*, a species similar to *Palaeophyllum lyterion*, is found in the Richmond Province in Kentucky (Browne, 1965). The province disappeared at the end of the Richmondian.

2.6.3 "Continental Margin" Fauna

The continental margin in the Late Ordovician was characterized by solitary rugose corals with circular cross sections and generally nondilated septa, indicative of low energy conditions (Elias, 1982a). Fossils considered to be part of the "continental margin" fauna are known primarily from California (Elias and Potter, 1984; Elias et al., 1994), Maine (Elias, 1982a), Gaspé (Elias, 1982a) and Anticosti Island (Elias, 1982a; this study). Taxonomic composition varies and information is sparse. The California and Maine regions were characterized by open marine conditions with relatively close proximity to arc volcanism, while the Gaspé-Anticosti region was generally passive, indicating significant variation of environments represented by the "continental margin" fauna.

The continental margin corals from the California region are known from exotic terranes that are considered to have originated somewhat outboard from, but in close proximity to, Laurentia (Potter et al., 1990).

The Horseshoe Gulch Formation of California (Elias and Potter, 1984) has a sparse rugose coral fauna of *Eurogrewingkia callahanensis*, *E. penobscotensis* and *Streptelasma etnaense*, all with coralla that are circular in cross section with moderately dilated septa and other skeletal elements. *Eurogrewingkia penobscotensis* is also known from Maine, where it is associated with *Streptelasma rankini* and *Bodophyllum neumani* (Elias, 1982a) and the Montgomery Limestone of California (Elias et al., 1994). The association of *Grewingkia* and *Streptelasma* is similar to the *E. pulchella-S. affine* fauna that dominates most of the Ellis Bay Formation, but there are insufficient data to determine if one of the California species is numerically dominant. Additionally, the Richmond Province fauna is dominated by the same pair of genera, suggesting that the association of the two genera may be of limited significance. A solitary rugosan similar to *E. pulchella*, the dominant "continental margin" fauna species from Anticosti Island, has been reported from the Late Ordovician (Richmondian?) of Georgia and Alabama (Buttler et al., 1988), indicating that the "continental margin" fauna may have existed off the southeastern "coast" of Laurentia (present-day orientation). "Continental margin" faunas include at least one species (*E. pulchella*) that survived into the Silurian (Elias, 1982a; this study).

2.6.4 Edgewood Province

The Edgewood Province was developed in a carbonate belt deposited in the east-central United States as a result of transgressions onto the exposed platform. It existed from Gamachian to earliest Silurian (Rhuddanian) time and was largely isolated from the oceanographic effects of deglaciation (Elias and Young, 1998). The rugose coral faunas are characterized by the dominance of *Streptelasma subregulare*, a pattern similar to the dominance (except in biohermal settings) of Ellis Bay Formation faunas by *Eurogrewingkia pulchella*. Less important elements include *Streptelasma amsdeni*, *S. leemonense*, *Bodophyllum shorti*, *Palaeophyllum* sp. and *Grewingkia* sp. A, in addition to several species of tabulate coral belonging to the genera *Paleofavosites*, *Propora* and *Halysites* among others (Elias and Young, 1992; Young and Elias, 1995). There are no common species between the Edgewood Province and the Anticosti Island rugose coral faunas, although some specimens of *S. subregulare* are similar to *S. affine* (Ellis Bay Formation, this study), and *Palaeophyllum* sp. (Young and Elias, 1995) is similar to *P. vaurealense*. Some elements of the rugose coral faunas (primarily *S. subregulare*) survived into the earliest Silurian, evidence of the isolation of the Edgewood fauna from large scale oceanic effects associated with the terminal Ordovician extinction. Following an interval of nondeposition, the Edgewood fauna was replaced by a distinct Silurian assemblage characterized by *Dinophyllum*, *Rhegmaphyllum*, *Cyathactis* and *Dalmanophyllum* (Elias, 1982a, 1992; Elias and Young, 1998). The first three of these genera are the numerically dominant elements of the Becscie Formation fauna of Anticosti Island.

3 RUGOSE CORAL PALEONTOLOGY

3.1 INTRODUCTION

This section discusses the distribution of corals in strata, paleoecologic and biostratinomic data, and paleoecology and biostratigraphy. The paleoecology section includes analysis of the physical parameters of coral skeletons and their associations. At the end of the paleoecology section, the data are integrated into a summary of environmental conclusions, for each species as well as for each stratigraphic interval. An analysis of the application of rugose coral depositional orientation to the study of current orientation is presented separately. Unless otherwise specified, the discussion is confined to solitary rugosans or to single-corallite fragments of dendroid species.

3.2 DATA

Of the 2304 solitary and 103 colonial specimens described in Material (see 1.3), not all were usable for paleoecologic/biostratinomic study because many specimens were incomplete or the relevant features were covered and/or obscured. Where possible, for each specimen, the types of data described in the following subsections were recorded.

3.2.1 General

3.2.1.1 *Stratigraphic interval.* The interval from which each specimen was collected was recorded as precisely as possible. Where the interval could be exactly located in the Anticosti stratigraphic framework, the position relative to a known horizon was measured to the centimetre. In other cases, the position within the measured interval is given and the member is identified.

3.2.1.2 *Substrate conditions.* In most specimens, substrate could only be inferred from associated matrix, notes from the collector or published information on the locality. For specimens collected in the summer of 1994, substrate type was recorded for individual collections if it was unusual or distinctive, or was analyzed from collected slabs. Otherwise substrate conditions were generally recorded for a locality or portion of a section.

3.2.1.3 *Orientation.* The orientations of solitary coralla on a limited number of well exposed bedding planes were observed, with the azimuthal orientation of the calice, and at one locality, the cardinal side, being measured. These data are analyzed in detail in the section on rugose coral orientation. Additionally, a small number of coralla considered to be in growth orientation were noted.

3.2.2 Physical Properties - External

The properties described in the following subsections apply to solitary coralla, except where otherwise noted.

3.2.2.1 *Size.* The length of the corallum along the growth axis was measured with a flexible ruler.

3.2.2.2 *Form.* The shape of the corallum was identified as trochoid, ceratoid, cylindrical, or other. These categories are somewhat subjective, and are based on illustrations in Hill (1981) (see Systematic Paleontology).

3.2.2.3 *Curvature*. The curvature of the corallum was arbitrarily divided into straight, slightly curved, curved and bent categories (cf. Hill, 1981).

3.2.2.4 *Cross-sectional shape*. The cross section of the corallum was classified as circular, compressed, depressed, angulate, triangulate, or trilobate (Hill, 1981; Elias, 1981).

3.2.2.5 *General degree of abrasion*. The exterior was categorized as abraded, moderately abraded or nonabraded. A corallum is considered nonabraded if the external ornament (septal grooves and interseptal ridges, growth lines, rugae) is intact on all sides; moderately abraded if the external ornament is effaced on all or part of the corallum but the wall is generally intact; and abraded if a significant proportion of the wall is missing or heavily pitted.

3.2.2.6 *Presence/absence and nature of epi- and endobionts*. This can include the taxonomic identity, location on the corallum (solitary or colonial), numbers and size of epi- or endobionts, and in the case of certain elongate epi- or endobionts, their orientation.

3.2.2.7 *Other features*. These include distortions of the wall or calice and attachment structures.

3.2.3 Physical Properties - Internal

3.2.3.1 *Degree of dilation*. Dilation is the thickening of skeletal elements. Septal dilation is expressed as nondilated (septa very thin), moderately dilated (septa less than 50% as thick as interseptal space), or greatly-completely dilated (septa thicker than interseptal space or in lateral contact). Weighting towards the apex or calice or to one side was noted, if present.

3.2.3.2 *Endobionts*. The presence as well as orientation and location of endobionts was recorded.

3.3 DISTRIBUTION OF RUGOSE CORALS IN STRATA

The following data are based on all the collections of Anticosti Island rugose corals used in this study in addition to some previously published data (Billings, 1862, 1865b; Twenhofel, 1928; Bolton, 1979, 1981a). A range chart of rugosan species from the study interval is shown in Text-figure 4. The exact stratigraphic position is not known for certain collections, particularly some in the Vauréal Formation, where thick continuous sections lacking any marker beds produced only single collections (see Text-fig. 4). For most collections, however, precise stratigraphic information is available. Previously published data from older collections are discussed separately.

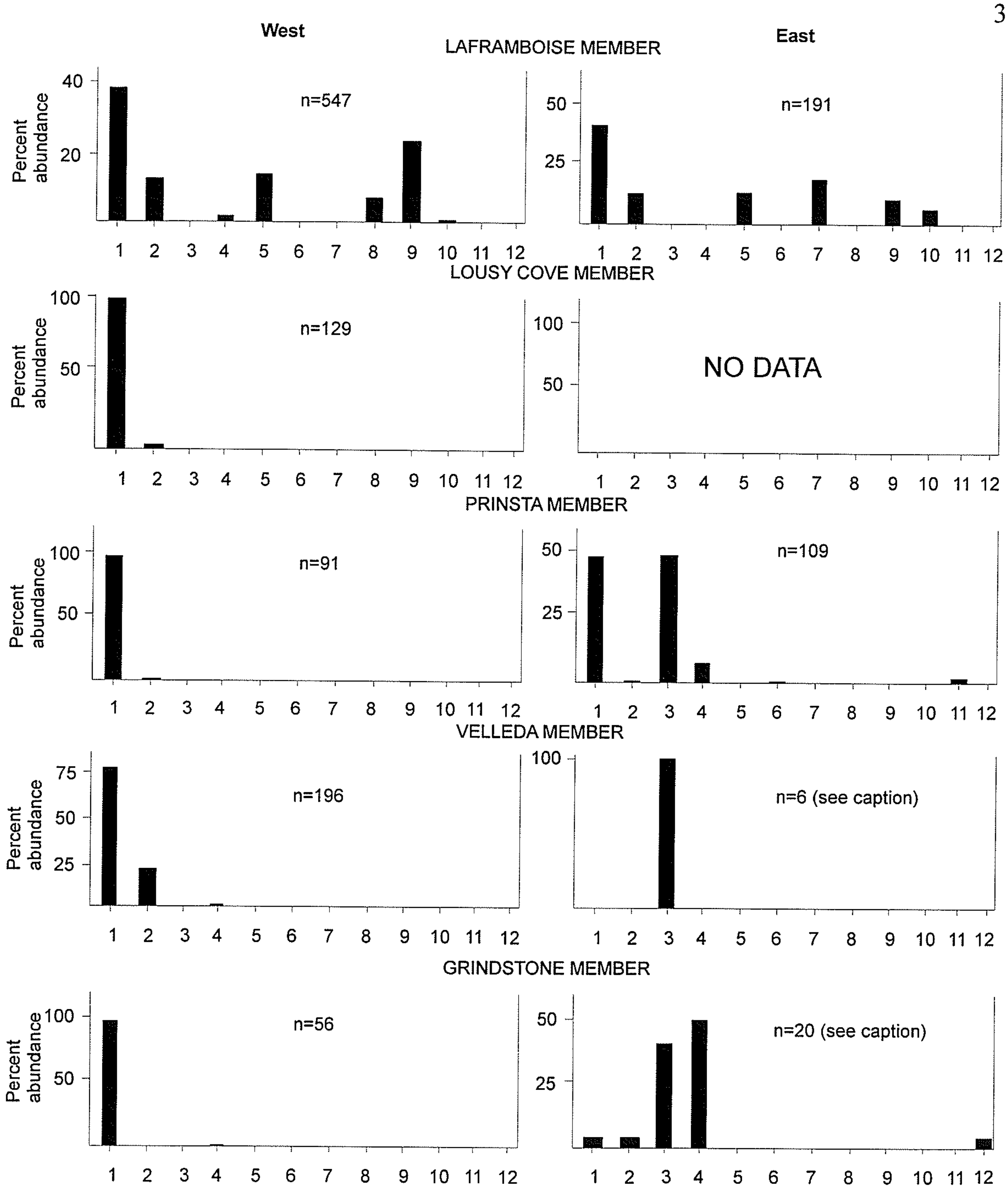
As specimens could have been transported and/or reworked, range data are more precise for those specimens with a comparatively low degree of abrasion. Transportation and/or reworking is most significant in biostratigraphic analysis at the top of the Ellis Bay Formation (approximately the Ordovician-Silurian boundary), where reef mounds project up into the lower Becscie Formation and some specimens in the lower Becscie are considered to have been reworked from the Ellis Bay Formation. The upper two members of the Vauréal Formation, the entire Ellis Bay Formation and the lowest Becscie Formation (entire Fox Point Member) were represented (and sampled) in nearly continuous sections at the western and eastern ends of the island.

3.3.1 Vauréal Formation

The Vauréal Formation was sampled on the north and west coasts and along a few outcrops in the west-central portion of the island (Text-fig. 1). The stratigraphically lowest collections are from the Lavache Member (locs. 13, 16; carbonate mudstones-skeletal wackestones), and consist only of *Bighornia patella*. A small collection from higher in the Lavache Member (loc. 28; carbonate mudstones and shales) includes *Salvadorea selecta* and *Lobocorallium trilobatum vaurealense*. A small collection from the Easton or Tower member (loc. 7; wackestones) consists of *S. selecta* and *Bodophyllum englishheadense*. The collection from locality 27 (lime mudstones/shales) along the north coast is from somewhere in the lower Vauréal (Easton-Tower members?) and is composed of *Deiracorallium angulatum angulatum*. The Homard Member is exposed in a nearly continuous section along the west coast (locs. 2, 3, 3a; skeletal grainstones with minor finer grained wackestones-packstones) and its fauna includes common *Bighornia patella*, *Bodophyllum englishheadense* and *Salvadorea selecta*, and a small number of specimens of *Lobocorallium trilobatum vaurealense, Deiracorallium angulatum angulatum* and *Palaeophyllum vaurealense*. A small collection from the west central part of the island (loc. 20; carbonate mudstone-wackestone), probably from the Homard Member, consists of a single *P. vaurealense*. The Joseph Point Member was collected from localities 1 and 1a (bioclastic mudstones-wackestones) and in the middle of the island at locality 29 (nodular carbonate mudstones-wackestones). *Deiracorallium angulatum angulatum* is the most common element in this member, with *Salvadorea selecta*, *Bodophyllum englishheadense*, *Lobocorallium trilobatum vaurealense* and *Palaeophyllum vaurealense* (all of which only occur at loc. 1a in this member) as minor elements. The Mill Bay Member was collected from sandy grainstones at the type section at locality 39 and the fauna consists of *Bodophyllum englishheadense*, minor fragments of *Palaeophyllum vaurealense* and a single fragmentary specimen of *Salvadorea selecta*. The member was also collected from at several outcrops in biohermal limestones in the western part of the island (locs. 17, 22, 24, 26), where the fauna consists of *Palaeophyllum vaurealense*, *Bodophyllum englishheadense*, *Lobocorallium trilobatum vaurealense*, *Salvadorea selecta*, and *Deiracorallium angulatum angulatum*. The Schmitt Creek Member was examined at locality 39 on the eastern end of the island (nodular mudstones to wackestones with minor shales), yielding only *Salvadorea selecta*. The Schmitt Creek Member was also sampled at locality 4 on the west coast, where it yielded a small collection of *Bodophyllum englishheadense*.

3.3.2 Ellis Bay Formation

Text-figure 8 shows the distribution and abundance of rugose coral species in the Ellis Bay Formation. The Grindstone Member was collected from the western part of the island at localities 4, 5, and 9 (laminated lime mudstones-wackestones with lenses of skeletal grainstones). On the east coast, a single collection which includes *Bodophyllum*



Text-fig. 8. Histograms of abundances of rugose coral species from the Ellis Bay Formation, member by member, divided into western and eastern occurrences. N.B., All data shown for the Grindstone Member from the eastern part of the island are based on a single collection; stratigraphic position is not precisely known and could be in the Velleda Member. 1 = *Eurogrewingkia pulchella*, 2 = *Streptelasma affine*, 3 = *Salvadorea selecta*, 4 = *Bodophyllum englishheadense*, 5 = *Paliphyllum ellisense*, 6 = *Palaeophyllum vaurealense*, 7 = *Palaeophyllum lyterion*, 8 = *Palaeophyllum* n. sp., 9 = *Bodophyllum* n. sp., 10 = *Streptelasma* n. sp. 1, 11 = *Bighornia patella*, 12 = *Streptelasma* sp.

englishheadense, *Salvadorea selecta*, minor *Eurogrewingkia pulchella* and *Streptelasma affine,* and *Streptelasma* sp. from locality 42 (siliciclastic-carbonate sands) is from either the uppermost Grindstone or lowermost Velleda (Copper, 1994, pers. comm.). The overlying Velleda Member was sampled on the west coast at localities 5, 5a, and 9a (laminated-nodular mudstones with minor lenses of grainstone). The Velleda was sampled in the middle of the island (included in east, Text-fig. 8) at locality 30a. The Prinsta Member was sampled in the west at localities 5b and 9b (highly fossiliferous nodular lime mudstones with minor siliciclastic mudstones and grainstone beds), where the fauna is virtually identical to that of the underlying Velleda Member. Two isolated collections in the middle of this island (locs. 19a, 21; carbonate wackestones-packstones; included in west, Text-fig. 8), probably from the Prinsta Member, consisted of *Eurogrewingkia pulchella*. On the northeast coast (locs. 41, 43), the Prinsta Member is formed of nodular carbonate mudstones with minor siliciclastics, with a fauna similar to those of the underlying Grindstone/Velleda members, but definitely including three specimens of *Bighornia patella*, and *Palaeophyllum vaurealense*. The lowermost Prinsta Member bioherm described by Lake (1981) and Copper (1989) on the Vauréal River has yielded at least one specimen of *Palaeophyllum lyterion* (Bolton, 1979, p. 4). This specimen is included in studies of range data and diversity but not in Text-figure 8, as only a single selected specimen was available from this occurrence. The Lousy Cove Member was sampled in the west at localities 6, 8 and 10 (laminated to nodular carbonate mudstones with minor siliciclastics). The member was sampled in the middle of the island at localities 19 and 25 (skeletal wackestones; included in west, Text-fig. 8). The

Laframboise Member was sampled at localities 6, 8 and 11 in the west, localities 31, 33, 36, 37 and 38 in the east-central part of the island, and at localities 40 and 44 in the eastern part of the island. Lithologies from which samples were obtained include biohermal boundstones and floatstones, and skeletal and oncolitic grainstones with interreefal wackestones and packstones. The faunal composition and variation are discussed in detail under Paleoecology and Biostratinomy. Specimens of several Ellis Bay species were found in the basal Becscie Formation near the reefs at locality 6; however, all but *Eurogrewingkia pulchella* occur as isolated, abraded specimens that are considered to have been reworked from the adjacent Ellis Bay Formation reef mounds.

Specimens of *Streptelasma affine* have been reported from the lower Vauréal at Carleton Point and from the upper Vauréal at Wreck Point (Billings, 1865b; Elias, 1982a). Subsequent stratigraphic revision (Long and Copper, 1987a) has lowered the base of the Ellis Bay Formation, although probably not enough for those specimens to have been collected from the Ellis Bay. The collection (made by Richardson) said to be from Carleton Point (= loc. 28, which would place it in the Lavache [or possibly the Easton] Member) is almost certainly geographically (and as a result, stratigraphically) mislabelled. No specimens of *S. affine* were found in any of the four sets of collections used in this study (Petryk, Copper, Elias, Summer 1994) from any level within the Vauréal Formation (104 specimens from the Lavache Member alone were examined in this study).

Eurogrewingkia pulchella was reported by Billings (1866; Elias, 1982a) from beds that are now placed in the upper Vauréal. It is, however, possible that these specimens were actually from the lowermost Ellis Bay Formation, in which *E. pulchella* is abundant. Certain intervals in the Vauréal, particularly the Homard and Joseph Point members from localities 1, 1a, 2, 3, and 3a, were collected in detail during the present study and no specimens assignable to *E. pulchella* were found. The upper Mill Bay and lower Schmitt Creek members were also examined in detail at locality 39 and *E. pulchella* was not found. No specimens of *E. pulchella* were found in any of the four collections used in this study from any level within the Vauréal.

An additional problem with stratigraphic precision of these older collections is geographical error or ambiguity. An example is the Wreck Point locality (see above). The English name Wreck Point referred to by Billings (1866) is probably equivalent to Wreck Point as used by Twenhofel (1928). According to Bolton (1978, pers. comm.), however, the name Wreck Point could be applied either to a locality on the west coast (the sense in which it is used here) or to one on the east coast ca. 200 km away. There is also an east coast bay named Baie de Naufrage (English translation Wreck Bay) with which the name Wreck Point could be associated or confused. As another example of potential confusion, there are two places named Cap Blanc, one of which is used is this study (Ellis Bay, near Port Menier) and the other of which is on the north coast (near Cap Caron). Other data on the stratigraphic and geographic distribution of corals from previous authors (Billings, 1862, 1866; Twenhofel, 1928; Elias, 1982a) overlap with findings in this study.

3.3.3 Becscie Formation

The Fox Point Member of the Becscie Formation was sampled at localities 6, 8, 11 and 11a (laminated carbonate and siliciclastic mudstones with a basal grainstone and minor coarse grained lenses) in the west. Apart from the reworked coralla mentioned above, the fauna consists predominantly of *Eurogrewingkia pulchella* to a height of 15 m above the formational boundary. In addition, *Rhegmaphyllum* n. sp. occurs in the basal beds as a minor element and a single specimen of *Dinophyllum hannah* was found in these beds. *Rhegmaphyllum* n. sp. is considered to have first appeared in the Becscie Formation, as specimens from the basal metre are in relatively good condition and none were found in the adjacent Ellis Bay Formation reefs. *Dinophyllum hannah* is unknown in strata that definitely represent the Ellis Bay Formation. Copper (2004, pers. comm.) considered that the basal encrinite, previously assigned to the Silurian Becscie Formation, is Ordovician in age and thus assignable to the Ellis Bay Formation. This bed does contain abraded "Ellis Bay" solitary rugosans, but in addition also yields well-preserved *Eurogrewingkia pulchella* and rare *Rhegmaphyllum* n. sp. and *Dinophyllum hannah*. As substantive evidence that the encrinite is Ordovician in age has yet to be published, the bed is considered herein to belong to the Becscie Formation and to be of Silurian age (see Text-fig. 10). The Fox Point Member was also sampled at localities 34, 38, and 44 in the east. At locality 38, the Fox Point includes distal storm-generated beds with basal erosional surfaces and fine carbonate mudstones and shales on the upper surfaces. The upper surfaces are fossil pavements, with specimens generally well-preserved, some in life orientation or only minimally transported. *Eurogrewingkia pulchella* occurs as high as

4.60 m above the Ellis Bay Formation at locality 38. *Rhegmaphyllum* n. sp. and *Dinophyllum hannah* occur in the basal metre, with the lowest occurrence of *Dinophyllum hannah* 50 cm above the boundary. In a single collection 4.60 m above the boundary at locality 38, all three species co-occur. The three species also co-occur in the basal metre at locality 6, although *D. hannah* is represented by only a single specimen from localities 6 and 8.

The Chabot Member was sampled at localities 12, 12a, 14, 15, 18, 18a, 23, 35, 44 and 45 in storm-dominated carbonate lithologies (Sami and Desrochers, 1992). *Dinophyllum hannah* is the most important element except at locality 15 (skeletal grainstones) above the *Virgiana* interval (brachiopod marker beds) where *Cyathactis euryone* (uncommon elsewhere) is dominant. *Streptelasma* n. sp. 2 is also common at locality 15, but uncommon elsewhere. *Rhegmaphyllum* n. sp. ranges as high as 13.75 m above the base of the section at locality 35 (variable carbonate lithologies, mudstone-grainstone), and no higher in the member. *Strombodes socialis* was found as isolated coralla and corallites at localities 14, 15, 23 and 35. *Palaeophyllum* sp. occurs as fragments at localities 12, 12a and 15, and as a single moderately complete corallum with fragments at locality 23 (carbonate mudstones with nodular wackestone interbeds and lenticular grainstones), 3.5 m below the Merrimack Formation. *Dinophyllum hannah, Streptelasma* n. sp. 2 and *Cyathactis euryone* are all present within 4 m of the top of the formation. A single poorly preserved corallum of *Petrozium pelagicum* was found at locality 35, 17.2 m above the base of the section; isolated fragments were found at 4.47 m in the same section and at locality 15.

Billings (1862) reported specimens of *Cyathactis euryone* from the Gun River and Jupiter formations (see Systematic Paleontology), extending the range beyond the study interval. Twenhofel (1928) reported *Dinophyllum hannah* from the Gun River Formation. Both of these reports were confirmed by examination of the types. Bolton (1981a) illustrated a specimen of *Rhegmaphyllum* from the Jupiter Formation which may be conspecific with *Rhegmaphyllum* n. sp., but as it was not sectioned it could not be compared. Bolton (1981a) illustrated several specimens of *Petrozium pelagicum* and *Strombodes socialis* from the upper member of the Becscie Formation in what would be the Merrimack Formation (*sensu* Copper and Long, 1989), and Copper and Long (1998) mentioned the presence of *Petrozium* as high as the Chicotte Formation reefs.

Bolton (1981a, pl. 8, figs. 9, 10) reported a specimen of *Amplexoides* sp. from the "north bank Jupiter River, first section upriver from 24-mile lodge." This place is approximately the same as locality 23 (this study), which is at or near the top of the Becscie. As specimens for this study from this locality were collected from near the river level, and the boundary with the Merrimack is somewhere upslope in the same section, the Bolton specimen may be from either formation (*sensu* Copper and Long, 1989). An examination of the transverse sections has shown shortened major septa of a clearly amplexoid form. *Amplexoides* sp. was considered in studying diversity (see 3.4.3 Diversity and 3.4.4 Faunal Assemblages).

Other authors have reported isolated occurrences of species or genera from the Becsie Formation that are not discussed above. Billings (1862) and Twenhofel (1928) reported *Cyathophyllum wahlenbergi* Billings (1862) from member 4 of the Becscie

Formation and members 2 and 5 of the Jupiter Formation (*sensu* Twenhofel, 1928). According to Copper and Long (1989) and Long and Copper (1994), Twenhofel's member 4 of the Becscie is part of the new Merrimack Formation. *Cyathophyllum wahlenbergi* was, therefore, not considered in this study.

Bolton (1981a, pl. 7, figs. 6, 9) reported *Calostylis* sp. from the Becscie Formation on "Laloutre River Road, south from junction of Long Lake Road." This locality is probably within the Becscie Formation (*sensu* Copper and Long, 1989), based on its geographic location and correlation with geological maps. Close examination of the illustrated specimen has shown that while it has a cateniform structure and is perforate, it lacks septal and tabular structures and is apparently not a rugosan.

Bolton (1981a, pl. 8, figs. 7, 8) reported *Cyathactis* sp. aff. *C. cormorantense* (Twenhofel, 1928) from the "upper beds of the lower member [of the Becscie], Wilson pool road at top of ridge near La Loutre River." While this cannot be located precisely as the exact position of member boundaries is unclear in isolated sections, it is most likely within the Becscie (*sensu* Copper and Long, 1989); Copper (2004, pers. comm.) considers it to be so. Large size and narrow tabularium are distinctive characteristics of *C. cormorantense* (see discussion of *C. euryone*; Systematic Paleontology). The Bolton specimen is similar to *C. euryone* (Twenhofel, 1928; this study) in lacking a well developed cardinal fossula. Additionally, the Bolton specimen is not significantly larger than observed specimens of *C. euryone*, and the tabularium is not narrow relative to the dissepimentarium. The Bolton specimen appears to be a specimen of *Cyathactis euryone*, and is, in any event, much more like *C. euryone* than *C. cormorantense*.

3.4 PALEOECOLOGY AND BIOSTRATINOMY

Several features of the fossils and fossil assemblages were examined in order to study paleoecology and biostratinomy. Current direction (and to some extent strength) was determined from solitary rugose coral orientation. Sedimentation rate, sediment stability and degree of transportation were inferred from extent of abrasion and curvature of the coralla. The presence of talons and other fixing structures as well as the cross-sectional shape and degree of internal dilation of skeletal elements were also linked to energy and substrate conditions. The association of coralla with various epi- and endobionts was related to sedimentation rate, corallum size and corallum stability. The lateral differentiation of coral faunas at the same stratigraphic position was associated with sedimentation and energy conditions. This section includes background theory, data on physical characteristics of corals, epi- and endobionts, and rugose coral diversity. Subsequent sections include a summary of environmental conditions and an analysis of rugose coral orientations.

3.4.1 Physical Properties of Coralla

The physical characteristics and quality of preservation of the coralla, in addition to stratigraphic distribution, are the properties used here to study paleoecology and biostratinomy. For each feature being studied the physical characteristics of the corallum must be considered separately for each species as different morphologies will have different responses. As Ordovician solitary rugose corals rarely lived in an epizoic, or attached, state throughout ontogeny (Elias, 1984), they were liable to being overturned in the sediment and developed a number of strategies to offset this possibility.

Curvature of the corallum has been shown to contribute to corallum stability and is, therefore, an indicator of prevailing energy conditions (Elias, 1981, 1982b). It has been shown that life orientation could be determined from the distribution of epi- and endobionts and embedded particles, which would indicate which portion of the corallum was exposed during life (Elias, 1980, 1981, 1982b; Elias and Buttler, 1986; Elias, Zeilstra and Bayer, 1988). Straight coralla had upright positions in sediment and were inferred to have grown in low energy conditions. Curved coralla were oriented with their convex side down into the sediment and the concave side exposed so that the oral surface remain horizontal (Elias, 1984, fig. 2). These grew in higher energy environments and the growth orientation ensured stability, with greater degree of curvature being an indicator of stronger currents (Elias, 1981).

Curvature of the corallum is partially a function of sediment conditions since a hard substrate would not permit the gradual settling of the growing corallum into the sediment and would more likely result in overturning (Elias 1981, 1982b; Elias, Zeilstra and Bayer, 1988). As a result, the oral surface of the coral would reorient and the corallum would develop a pronounced bend, if possible. Stability could also be maintained by the development of a noncircular cross-sectional shape which would be less prone to rolling. Additionally, the development of highly dilated septa, particularly in the early stages of ontogeny, would contribute to stability (Elias, 1981).

Attachment structures would have contributed to corallum stability and have been found in the early stages of development of some coralla. They are comparatively rare in

North American Ordovician solitary rugose corals (Elias, 1984; Neuman, 1988; Scrutton, 1998), including the Anticosti fauna, and generally occur on the cardinal side (Elias, 1981, 1982b). An exception is *Streptelasma divaricans* (Elias, 1982a). The majority of solitary rugose corals from the Late Ordovician of North America, with the exception of *Bighornia*, have a convex cardinal side. As attachment structures generally occur on the cardinal side, the prevailing convexity suggests a biological reason for the cardinal side being down, probably associated with the initial attachment or larval settling orientation (Elias, 1981; Scrutton, 1998). Neuman (1988) illustrated small apical attachment structures on small solitary rugose coralla, structures that would be easily missed if the apex is covered, broken or even minimally abraded. The various methods of maintaining corallum stability are summarized in Table VI under "Stabilization Method."

Degree of abrasion of the corallum is an indicator of energy conditions and sedimentation rate. If the corallum is only mildly abraded (i.e., wall generally intact and external ornament preserved), a relatively rapid sedimentation rate and/or low energy conditions are inferred. If, however, the coral species being studied has a very thin wall, it will be particularly susceptible to abrasion. Analysis of abrasion data in this case would tend to result in inference of higher energy conditions or lower sedimentation rates than would be shown by thicker walled coralla in the same assemblage. Additionally, degree of abrasion serves as an indicator of transportation, which is important for biostratigraphic studies, especially around formation boundaries and near bioherms where relief can increase the likelihood of reworking of coralla.

3.4.1.1 *Results.* Table I summarizes the observed physical properties of solitary coralla collected from the study area on a species-by-species basis in terms of absolute abundance or occurrence of a particular feature. Table II summarizes the physical properties of solitary coralla on a stratigraphic basis. Note that data for members that are well exposed in more than one part of the island (usually west and east) are subdivided geographically. The east-west division is placed approximately at the Vauréal River, and for the Laframboise Member of the Ellis Bay Formation, the central portion of the island is considered to range from Salmon River in the east to Jupiter River in the west (Text-fig. 1A; map in upper right of figure). Data include information collected from exteriors of coralla and from thin sections or acetate peels. The data only include those specimens for which a particular feature could be examined.

3.4.1.2 *Interpretation - Physical properties (species-by-species).* Following the model of Elias (1981, 1982b), species with generally curved coralla are inferred to have grown in high energy environments and species with generally straight coralla are inferred to have grown in relatively low energy environments. This can be correlated with frequency of abrasion, although abrasion may have resulted from postmortem transportation. There are two main exceptions to general models of current strength for solitary rugosans. *Cyathactis euryone* has generally straight coralla that are frequently abraded, which may be a function of a very thin wall, rather than high energy. *Bodophyllum englishheadense* has coralla that are frequently abraded, but generally straight. This is apparently related to the development of attachment structures as a preferred mechanism of maximizing

Table I. Physical characteristics of solitary coralla (see text) from the study area. Under Curvature, st = straight, sl = slightly curved, cur = curved, be = bent. Under Corallum shape, tr = trochoid, ce = ceratoid, cy = cylindrical (or subcylindrical). Under Abraded, no = number of specimens, % = percentage of specimens abraded. Att = attached, % = percentage of specimens with attachment structures.

[1] *Bighornia patella* is subcalceoloid and distinct from all other species in shape and curvature.

[2] *Paliphyllum ellisense* is a dendroid colonial species that tends to break into cylindrical corallite fragments; therefore, the count is not necessarily accurate.

Taxa	Curvature				Corallum shape			Abraded	Att
	st	sl	cur	be	tr	ce	cy	no (%)	no (%)
Bighornia patella	-[1]				-			55 (5)	109 (5)
Bodophyllum englishheadense	28	6	3	0	48	17	10	131 (79)	188 (48)
Bodophyllum n. sp.	27	4	2	10	5	14	21	63 (37)	86 (7)
Cyathactis euryone	11	4	1	1	12	2	26	54 (82)	51 (4)
Deiracorallium angulatum angulatum	1	3	16	0	29	0	0	34 (18)	31 (0)
Dinophyllum hannah	75	26	29	3	189	3	0	172 (30)	207 (2)
Eurogrewingkia pulchella	66	211	192	24	407	25	0	755 (34)	643 (1)
Lobocorallium trilobatum vaurealense	0	3	2	0	5	0	0	12 (58)	12 (0)
Paliphyllum ellisense	33	5	0	8	1	9	66	54 (31)	- -[2]
Rhegmaphyllum n. sp.	15	13	14	0	56	0	0	39 (18)	37 (2)
Salvadorea selecta	30	16	20	0	78	3	0	80 (51)	91 (5)
Streptelasma affine	26	15	3	7	29	11	7	113 (20)	79 (11)
Streptelasma n. sp. 1	2	0	1	1	2	1	2	6 (67)	7 (0)
Streptelasma n. sp. 2	5	0	2	0	8	0	2	20 (45)	35 (23)
Streptelasma sp.	0	1	0	0	0	1	0	1 (0)	1 (100)

Table II. Physical properties of coralla, by geographic and stratigraphic position. Member abbreviations: CH = Chabot, FP = Fox Point, LAF = Laframboise, LC = Lousy Cove, PR = Prinsta, VE = Velleda, GR = Grindstone, SC = Schmitt Creek, MB = Mill Bay, JP = Joseph Point, HO = Homard, TO = Tower, EA = Easton, LV = Lavache. Oth = other; for other abbreviations, see Table I.

[1] Collection A468a is considered here to be from the Grindstone Member (see Appendix A).

[2] The Lavache Member fauna is >90% *Bighornia patella*, which has a distinctive skeletal growth form that cannot be classified conventionally.

Stratigraphic interval	Curvature				Corallum shape				Abraded	Att
	st	sl	cur	be	tr	ce	cy	oth	no (%)	no (%)
CH east	34	15	6	1	96	1	1	1	39 (28)	126 (2)
CH west	52	13	12	2	93	4	25	1	166 (51)	229 (6)
FP east	24	13	31	0	67	0	0	0	83 (17)	114 (3)
FP west	5	69	16	1	82	3	0	0	142 (36)	177 (8)
Becscie Fm. total	**115**	**110**	**65**	**4**	**338**	**8**	**26**	**2**	**430 (46)**	**646 (5)**
LAF east	26	20	8	1	57	9	1	0	64 (39)	93 (4)
LAF central	21	7	0	4	22	2	19	0	23 (57)	55 (4)
LAF west	61	81	22	27	52	33	77	0	335 (30)	500 (7)
LC	9	15	46	1	74	6	0	0	99 (56)	129 (5)
PR east	36	23	22	3	80	10	0	0	90 (47)	112 (8)
PR west	5	13	39	1	61	1	0	0	62 (13)	91 (7)
VE	4	23	37	13	41	4	0	0	169 (30)	202 (5)
GR east[1]	10	3	1	0	34	3	2	0	16 (75)	20 (25)
GR west	7	2	21	0	34	1	0	0	48 (32)	56 (40
Ellis Bay Fm. total	**179**	**187**	**196**	**46**	**455**	**69**	**99**	**0**	**906 (33)**	**1258 (60)**
SC	1	1	5	0	9	0	0	0	7 (57)	13 (8)
MB east	12	2	1	0	22	0	1	0	17 (77)	37 (27)
MB west	4	2	1	0	4	4	0	0	7 (86)	11 (9)
JP central	0	1	11	0	13	0	0	0	13 (0)	30 (0)
JP west	2	3	3	0	20	3	1	0	32 (38)	49 (18)
HO	6	3	4	0	26	4	7	0	103 (83)	134 (41)
TO	0	0	0	0	1	0	0	0	1 (0)	3 (0)
EA	0	0	0	0	0	0	0	0	0 (0)	0 (0)
LV	-[2]	-	-	-	1	0	0	104	49 (18)	109 (6)
Vauréal Fm. total	**25**	**12**	**25**	**0**	**96**	**11**	**9**	**104**	**229 (56)**	**386 (21)**
Total	**319**	**309**	**286**	**50**	**889**	**88**	**134**	**106**	**1565 (39)**	**2290 (8)**

stability, obviating the development of curvature. Postmortem reworking may also have resulted in significant abrasion.

Four of the solitary rugose coral species have varying ratios of curvature types and/or corallum shape: *Salvadorea selecta*, *Eurogrewingkia pulchella*, *Streptelasma affine* and *Dinophyllum hannah*. This is probably a reflection of their adaptability to varying environments, a hypothesis that is reinforced by their long stratigraphic range and occurrence in a variety of substrates. The other species (in which the physical properties are relatively constant) are assumed to have been less tolerant of variable environmental conditions (see 3.5 Intraspecific Variability).

Four species have coralla with moderately frequent bending, indicative of partial overturn and reorientation of growth. As two of these species (*Eurogrewingkia pulchella* and *Streptelasma affine*) are the only corals that occur throughout the Ellis Bay Formation, it is possible that the ability to reorient (rare, and species-specific, in rugose corals; Elias, 1984; Scrutton, 1998) contributed significantly to their success. The other two species (*Bodophyllum* n. sp. and *Paliphyllum ellisense*) have dominantly cylindrical coralla (corallites?), and grew exclusively in reefal environments.

The only two species in which attachment structures are common are *Bodophyllum englishheadense* (48%) and *Streptelasma* n. sp. 2 (23%). In both species, the apical end of the corallum is substantially distorted, although in only a few cases can the object to which a corallum is attached be determined. In several specimens of *B. englishheadense* from Cap Anglais, the coralla are attached to bryozoans. As some specimens of *B. englishheadense* were missing their bases or the base was covered, it is possible that the frequency of attachment was even higher, and it is probable that attachment was obligate for that species. This may also be true for *Streptelasma* n. sp. 2, but data are insufficient for rendering any conclusion. Attachment structures are uncommon in *Streptelasma affine* and rare in all other species except *Bodophyllum* n. sp. The latter species occurs in clusters and exclusively in reefal settings, suggesting that basal or other distortions (i.e., apparent attachment structures) may be results of close proximity, similar to the corallites in colonial taxa.

Deiracorallium angulatum angulatum is the best example of how physical properties of the corallum correlate with each other and reflect environment of deposition. Coralla are generally straight, degree of abrasion is extremely low and attachment structures are absent, all indicators of low current strength. The straightness of the coralla and lack of attachment structures indicate that there was no need for further stabilization (beyond internal dilation), suggesting a low energy environment. Additionally, there was a unique occurrence of several coralla of *D. angulatum angulatum* in a mechanically unstable (long axis vertical, calice up) life orientation, which corroborates Elias' (1982b) model of life position in low energy environments. *Deiracorallium angulatum angulatum* was most common in the Joseph Point Member, which was deposited in an environment of deeper water (Dewing, 1999) and lower energy than the under- and overlying Homard and Mill Bay members (Long and Copper, 1987b, 1994). Its physical characteristics appear to be responses to known environmental characteristics.

3.4.1.3 *Interpretation - Physical properties (stratigraphic variation).* The data in Table II show that corallum curvature remains relatively constant from member to member. Curvature (ratio of straight to slightly curved to curved) is close to 1:1:1 overall. The Fox Point and Chabot members (western localities) have particularly low and high proportions of straight coralla, respectively. The stratigraphic variation in physical properties of coralla is a reflection of changing faunal composition except in the cases discussed above where there is intraspecific variability.

The variation in curvature of coralla from the Becscie Formation (apart from the Fox Point Member in the west) is attributable to the different corallum morphologies of *Dinophyllum hannah*, which occur in different environments (see 3.5.2.6 Intraspecific Variability; *Dinophyllum hannah*).

Cylindrical coralla have a relatively high frequency in the Laframboise Member reefs (all locs.) and at locality 15 in the Chabot Member. The high proportion of cylindrical coralla in the Laframboise reefal environment indicates that stability was either not as important (i.e., sheltered environment) or was accomplished by means other than development of a trochoid corallum (e.g., attachment structures, noncircular cross-sectional shape, mutual support). The high proportion of (sub)cylindrical coralla at locality 15 is due to the high frequency of *Cyathactis euryone* which is most common at this locality. As attachment structures were not found in *C. euryone*, it is unclear how it maintained corallum stability.

The proportion of abraded coralla varies dramatically from member to member and across the island, as a response to varying conditions. The degree of variation makes it difficult to perceive overall trends or to relate anomalously high or low proportions of abrasion to a specific type of sedimentation. The exceptions are the Mill Bay Member (east) and the Homard Member (west), where a high frequency of abraded coralla is related to the high energy and probable low sedimentation rate.

3.4.2 Epi- and Endobionts

A number of taxa of epi- and endobionts (or traces thereof) are found associated with rugose coral skeletons: bryozoans, algal coatings, the alga *Wetheredella*, stromatoporoids, cornulitids, tabulate corals and solitary rugose corals. In some cases these grew while the host coral was still alive; however, many are considered to have grown after death as they are found on a side of the corallum that would not have been exposed during life. Table III summarizes the occurrence of epi- and endobionts associated with solitary Rugosa on a species-by-species basis and Table IV shows the same data on a stratigraphic basis. Unusual vermiform epibionts are discussed below, and a detailed examination of *Trypanites* borings is also presented. Subsequent interpretation is presented species-by-species and member-by-member.

3.4.2.1 *Vermiform epibionts on solitary coralla.* Elias (1986) documented a unique specimen of *Streptelasma affine* from the Laframboise Member bioherms in which the outer wall of the corallum is distorted around circular (cylindrical) openings. This was a rare case of biological interaction between the living coral and a vermiform epizoan in which the epizoan apparently gained a firm anchoring point. It is not known whether the relationship was beneficial or detrimental to the coral, but as the corallum was moderately

Table III. Absolute rate of occurrence of various epi- and endobionts with each solitary rugosan species (and *Paliphyllum ellisense*). Bry = bryozoans, alc = algal coat, *Weth* = *Wetheredella*, stro = stromatoporoid, cor = cornulitids, tab = tabulate corals, soli = solitary rugose corals, *Try* = *Trypanites*, other = miscellaneous unidentified epizoans. Under ep/en, % = % frequency of epi-/endobionts, no = number of specimens examined.

[1] *Bodophyllum englishheadense* is frequently attached to clasts or bryozoans or other coralla, and it is not always possible to determine which organism is epizoic.

[2] *Paliphyllum ellisense* is a dendroid colonial species that tends to break into cylindrical corallite fragments; therefore the count is not necessarily accurate.

Taxa	bry	alc	*Weth*	stro	cor	tab	soli	*Try*	other	ep/en no (%)
Bighornia patella	0	0	0	0	0	0	0	2	3	93 (5)
Bodophyllum englishheadense	26[1]	5	2	0	2	1	14[1]	28	1	166[1] (38)
Bodophyllum n. sp.	21	45	72	0	9	2	1	5	5	123 (85)
Cyathactis euryone	5	3	0	13	0	1	1	1	3	58 (47)
Deiracorallium angulatum angulatum	0	0	0	0	0	0	0	0	0	47 (0)
Dinophyllum hannah	2	3	0	2	0	0	0	1	1	201 (8)
Eurogrewingkia pulchella	49	122	16	0	0	2	0	20	16	841 (24)
Lobocorallium trilobatum vaurealense	2	0	0	0	0	0	1	2	0	12 (42)
Paliphyllum ellisense	28	36	34	0	4	2	3	1	3	90[2] (88)
Rhegmaphyllum n. sp.	1	1	0	0	0	0	0	0	1	60 (5)
Salvadorea selecta	10	3	0	0	0	2	1	24	12	94 (48)
Streptelasma affine	19	26	29	2	6	3	1	5	8	133 (57)
Streptelasma n. sp. 1	2	8	0	0	0	1	0	2	1	11 (100)
Streptelasma n. sp. 2	3	3	0	3	0	1	0	3	3	24 (42)
Streptelasma sp.	1	0	0	0	0	0	0	0	0	1 (0)
All taxa	**169**	**255**	**158**	**20**	**21**	**15**	**21**	**94**	**47**	**1954 (34)**

Table IV. Absolute rate of occurrence of various epi- and endobionts associated with solitary rugose corals (and *Paliphyllum ellisense*) differentiated by stratigraphic and geographic position. For member abbreviations, see Table 2. No = number of specimens examined, bor = miscellaneous borings other than *Trypanites*. For other abbreviations see Table III. N.B., this table also includes data for a small number of unidentified coralla with identifiable epi- or endobionts.

Stratigraphic Interval	bry	alc	*Weth*	stro	*Try*	bor	other	ep/en no (%)
CH east	1	2	0	1	0	1	0	71 (6)
CH west	8	7	0	17	2	8	14	177 (30)
FP east	4	1	0	0	0	0	0	98 (10)
FP west	29	0	0	0	2	0	2	130 (27)
Becscie Fm. total	**42**	**10**	**0**	**18**	**4**	**9**	**16**	**476 (21)**
LAF east	6	21	4	0	0	2	1	84 (32)
LAF central	2	17	9	0	4	1	2	46 (63)
LAF west	74	178	145	2	8	1	39	453 (76)
LC	2	9	0	0	5	2	2	121 (18)
PR east	10	7	0	0	16	7	1	104 (42)
PR west	4	6	0	0	5	9	1	86 (31)
VE	3	2	0	0	4	4	0	185 (11)
GR east	2	1	0	0	9	0	1	20 (60)
GR west	1	0	0	0	3	1	1	50 (12)
Ellis Bay Fm. total	**104**	**241**	**158**	**2**	**54**	**27**	**48**	**1149 (46)**
SC	0	0	0	0	5	2	1	12 (58)
MB east	6	1	0	0	5	0	0	37 (24)
MB west	3	0	0	0	3	0	1	10 (55)
JP central	0	0	0	0	1	3	0	30 (13)
JP west	3	1	0	0	0	1	0	43 (18)
HO	15[1]	2	0	0	21	0	1	117 (31)
TO	0	0	0	0	0	0	0	3 (0)
EA	0	0	0	0	0	0	0	0 (0)
LV	0	0	0	0	1	3	0	86 (4)
Vauréal Fm total	**27**	**4**	**0**	**0**	**36**	**9**	**3**	**338 (19)**
Total	**173**	**255**	**158**	**20**	**94**	**46**	**67**	**1963 (35)**

large and not significantly distorted, it apparently did not suffer greatly. In the present study, a similar phenomenon is seen in a single specimen of *Bodophyllum* n. sp. from the Laframboise Member bioherms, in which the outer wall is apparently distorted around vermiform grooves, one of which may contain a foreign tube (Pl. 12, fig. 14).

3.4.2.2 *Vermiform epibionts on colonial coralla.* Seventeen out of 37 specimens (46%) of *Palaeophyllum lyterion* (cerioid-phaceloid) from the Laframboise Member in the central part of the island (locs. 31, 33, 38) are associated and intergrown with previously undocumented large calcareous vermiform tubes (Pl. 15, fig. 4, Pl. 16, fig. 6, Pl. 17, figs. 3, 4). Such tubes were also found associated with stromatoporoids and the tabulate coral *Propora* in the same beds.

The tubes range in diameter from 0.7 to 3.4 mm and generally occur parallel or subparallel to associated corallites, running the full height of the corallum in most cases (up to 100+ mm in length). The tubes occur in all parts of the coralla from the core to the outer edges, but are more common in cerioid areas than in phaceloid areas. Microstructure of the tubes is lamellar (Pl. 15, fig. 4). As many as 11 tubes were counted on the growth surface of a single corallum of *Palaeophyllum lyterion* (and over 100 tube openings were counted from one side of a single tabulate corallum). An apparently regular annulation is visible on nonabraded exterior portions of the tubes; however, as only the ends of a few tubes were exposed, and they were weathered, the intervals cannot be measured precisely.

The tubes are of comparable diameter to the corallites and fit into the coralla with a few occurrences of displacement of adjacent corallite walls (Pl. 15, fig. 4, Pl. 17, fig. 4). The tubes were not seen to intersect or truncate any corallites. In cerioid portions of coralla, the tubes are surrounded by corallite epitheca, in some cases with an intervening space. The close proximity and lack of truncation (of either corallite or tube) suggest that the tube-dwelling organisms grew concurrently with the corals. The upper surfaces of tubes do not protrude beyond the tops of coralla although their upper edges appear to be abraded/truncated in many cases and may have extended farther. As growth of adjacent corallites was apparently not disturbed, although possibly slightly shifted, the tube-dwelling organisms do not appear to have been parasitic.

The tubes are generally similar to those developed by cornulitids but grow considerably longer (>100 mm) and wider than any reported cornulitid (Fisher, 1962). The tapering proximal ends, sometimes with associated coiling, found in cornulitids cannot be compared to the tubes found in this study as no proximal ends were found.

3.4.2.3 *Microborings.* Clusters of microborings that are generally straight and penetrate perpendicular or subperpendicular to the outer surfaces of solitary coralla were found in many specimens, particularly those found in bioherms. The borings are frequently filled with blackened, possibly pyritic, material. These are similar to microborings, attributed to algae, that have been documented in numerous corals from the Upper Ordovician of North America (e.g., Elias, 1982a).

The proportion of coralla with such borings is difficult to determine as these structures are microscopic and extensive silicification of specimens from the Becscie

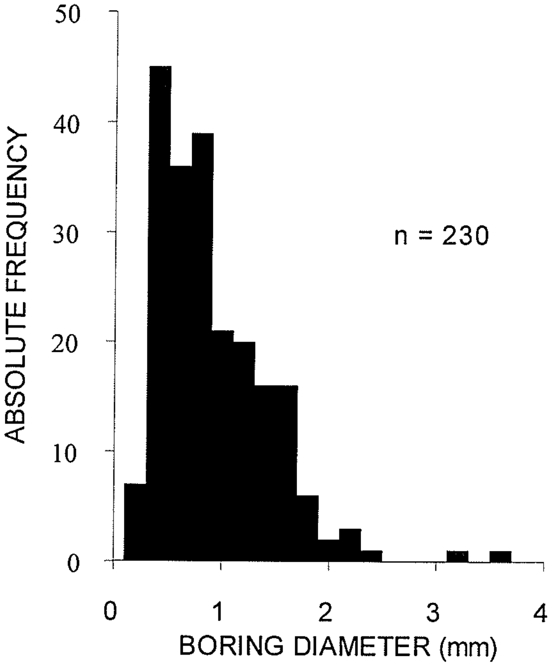
Formation obscures the outer wall in the majority of specimens. Silicification was less common in coralla from the sub-Laframboise Member portion of the study interval. Additionally, microborings are not always visible in acetate peels. Minor silicification and/or alteration obscures the outer wall and stereozone in many specimens from the Laframboise Member of the Ellis Bay Formation. These microborings are generally comparable to those seen in solitary rugose corals from the Late Ordovician Red River (Elias, 1980) and Stony Mountain (Elias, 1982b) formations of Manitoba, although the coralla from Anticosti have typically undergone a greater degree of alteration. The complex, reticulate pattern of borings in corals from the Red River Formation was not seen in the present study, but the size and branching are comparable.

3.4.2.4 Trypanites. The ichnogenus *Trypanites* is a relatively common trace fossil in coral skeletons from the Late Ordovician of North America (Elias, 1986), including Anticosti Island. *Trypanite*s is found in hard substrates, both skeletal and inorganic, in strata from Cambrian to Recent age (Kobluk et al., 1978). *Trypanites* is particularly common in Paleozoic rocks where massive stromatoporoid and coral skeletons can be completely infested (Nield, 1984). As with many other ichnotaxa, the precise nature of the *Trypanites* organism is unknown, and several different taxa may be responsible. Kobluk and Nemcsok (1982) found scolecodonts and other microscopic remnants of annelids in *Trypanites* boreholes, indicating an annelidan origin.

Of the 1963 solitary coralla that could be examined (i.e., had a sufficient proportion of their external surface exposed, or a sufficient volume to make a thin section), 94 (5%) were found to have *Trypanites* borings (e.g., Pl. 7, figs. 2-6, 11, 12, Pl. 8, fig. 9, Pl. 12, fig. 4). Detailed study was performed on thin sections and peels. Sixty-eight solitary rugose coral skeletons with a total 230 *Trypanites* borings were examined in detail (the remaining 26 solitary skeletons with *Trypanites* borings were poorly preserved or the boring was not seen in thin section).

The *Trypanites* borings found in Anticosti Island solitary rugose coral skeletons are circular in cross section and, in longitudinal section, generally terminate with a non-swollen rounded end. A few obliquely cut specimens (10) had small localized nipple-like extensions. One boring has a slight contraction and swelling at the tip that is unique among the borings in Anticosti corals. It is larger than and distinct from the nipple-like extensions mentioned above and may represent a different boring organism or a point at which the boring is turning. In cases of intersecting borings, there was no evidence of interaction between the boring organisms, comparable to the findings of Elias (1980). In most cases the borings cut across skeletal material with no apparent regrowth on the part of the coral. In two specimens (CA-V-340-30 and CA-V-450-1), however, there appears to be some septal regrowth across the opening, indicating that unlike most cases (Elias 1980, 1986; this study) the boring occurred during the life of the coral. The septal regrowth is not as clearly developed as in specimens documented by Elias (1986) from the Ordovician (Richmondian) of the Cincinnati Arch region. The borings are unlined.

The histogram in Text-figure 9 shows the distribution of diameters of *Trypanites* borings from the study area, as measured with a micrometer caliper or eyepiece under 20x magnification. The mean diameter is 0.95 mm, the mode is at 0.2-0.4 mm and the pattern



Text-fig. 9. Frequency histogram for diameters of *Trypanites* borings in solitary rugose corals from Anticosti Island. Mean diameter is 0.95 mm, class interval in 0.2 mm.

is generally unimodal and positively skewed. There are two outliers, at 3.2 and 3.6 mm, which may represent gerontic or otherwise exceptional development of the same boring organism, or may represent different taxa. The size distribution of *Trypanites* borings found in solitary rugosans from the Red River Formation of Manitoba (Elias, 1980) is similar to the distribution from this study (essentially unimodal, positively skewed), but with a higher mean value (1.4 mm) and mode (0.8-1.0 mm). The size distribution of *Trypanites* in solitary rugose coral skeletons from the Late Ordovician Stony Mountain Formation of Manitoba (Elias, 1982b) is also similar although there is a pronounced mode at 0.3 mm. The mode in this study is comparable (0.2-0.4 mm) but is not as pronounced. *Trypanites* in tabulate corals and stromatoporoids from Anticosti Island were found to be much larger than those from this study (mean diameter 2-3 mm; Tapanila and Copper, 2002). Other studies of *Trypanites* borings from the Ordovician of North America have shown results comparable to those from this study (i.e., mean diameter ca. 1 mm, unimodal, positively skewed; Cameron, 1969; Elias, 1982b).

Trypanites borings occur in five percent of solitary rugose corals from the study area (see Tables III and IV for occurrence). This is a much lower frequency than the 53 percent in solitary rugosans of the Selkirk Member of the Red River Formation (Elias, 1980) and the 42 percent in massive tabulates and stromatoporoids from Anticosti Island (Tapanila and Copper, 2002). Corallum size, curvature, degree of dilation and sedimentation rate are considered to be factors contributing to the frequency of *Trypanites* borings (Elias, 1985; Elias, Zeilstra and Bayer, 1988). As *Trypanites*-producing organisms needed a stable hard substrate in which to bore, size of the bored organism (i.e., available surface area), degree of internal dilation (i.e., solid, hard object for boring) and cross sectional shape (noncircular provided more stability, therefore more time for boring, therefore more and longer borings) would be significant factors in determining the distribution and size of *Trypanites* borings.

A comparison between the coral faunas of this study and the Selkirk Member of the Red River Formation shows that the corals of the Selkirk Member generally have large, thick-walled skeletons with a high proportion of noncircular cross sections. The Anticosti fauna includes several taxa that are small and/or have relatively nondilated internal elements (*Eurogrewingkia pulchella*, *Rhegmaphyllum* n. sp., *Bighornia patella*, *Deiracorallium angulatum angulatum*, *Dinophyllum hannah*, *Cyathactis euryone*) and all of the relatively abundant species, except *B. patella* and *D. angulatum angulatum*, have circular cross sections. All of these taxa have low frequencies of *Trypanites* borings (see Table III). *Bodophyllum englishheadense*, which is relatively small, but has a thick stereozone, has a high occurrence of *Trypanites* despite its size. Coralla of *B. englishheadense* are highly abraded, and are most commonly found in winnowed grainstones. These data suggest a low sedimentation rate, probably the main reason for the high frequency of *Trypanites* borings in this species. Low sedimentation rates (high degree of abrasion) were associated with frequent occurrence of *Trypanites* borings in solitary corals in the Stony Mountain Formation (Elias, 1982b). The degree of abrasion for *Cyathactis euryone* is also high but its wall is very thin and susceptible to abrasion. *Salvadorea selecta* is the only commonly occurring large coral species with highly dilated internal elements, tends to have abraded coralla, and is also the species with the highest frequency of *Trypanites*. *Streptelasma affine* is the largest solitary rugose coral species in the Anticosti fauna and can have a moderately thick sterozone, but most of the specimens occur in the biohermal uppermost Ellis Bay Formation, an environment with a high sedimentation rate that was possibly inimical to the *Trypanites* organisms.

The location of *Trypanites* borings in the skeleton of a coral is also partially a function of life position, according to Elias (1980) and Elias, Zeilstra and Bayer (1988). Elias (1980) observed that for curved, recumbent coralla, borings (as well as abrasion and epibionts) were most common on the counter side (67%). This would indicate a life position reclining on the cardinal side, with the boring, abrasion, and epizoic attachment taking place during the coral's lifetime. If the boring had taken place post mortem, it would have occurred most often on the alar sides which would have been facing up in the most hydrodynamically stable position (for curved specimens; straight specimens would have a random orientation if the cross section is circular). Of the 230 *Trypanites* borings examined in thin section or peel in this study, 116 occur in the alar quadrants, 50 in the counter quadrant, 43 in the cardinal quadrant, 7 in the axis and the remaining 14 occur in specimens too poorly preserved to determine the quadrant. A chi-squared test of *Trypanites* distribution by quadrant was performed to determine whether the distribution among quadrants is even. The data pass the test of observed vs. predicted values for even distribution ($\chi^2 = 2.99$, $\chi^2_{0.05/df=3} = 7.81$), indicating statistical isotropy; i.e., the borings do not preferentially occur in any particular quadrant of the coralla. Unlike borings in corals of the Red River Formation (Elias, 1980), the borings from this study are not concentrated on the counter sides. This is probably a function of the relatively low degree of corallum curvature in the more frequently bored taxa from the study area, which would have affected life orientation or burial position. Elias, Zeilstra and Bayer (1988) showed that macroborings in coralla from the Late Ordovician Maquoketa Formation are evenly distributed among the quadrants and concluded that this was because the coralla were relatively straight and that the life orientation was vertical, which allowed the boring organisms equal access to all quadrants. Their results are comparable to those from the present study, although currents and corallum shape are sufficiently variable that both life orientation and burial orientation are considered to be responsible for the even distribution of borings.

3.4.2.5 *Interpretation of epi- and endobiont data.* Occurrence of epi- and endobionts (see Tables III, IV) is a function of corallum surface area and various environmental factors. While approximately one third (35%; see Table IV, which includes a small number of unidentified coralla with epi- or endobionts) of observed solitary coralla had associated epibionts, the occurrence varies considerably between species with lows of zero (*Deiracorallium angulatum angulatum*) and five percent (*Rhegmaphyllum* n. sp., *Bighornia patella*) to highs of 57 *(Streptelasma affine*), 88 (*Paliphyllum ellisense*) and 100 percent (*Streptelasma* n. sp. 1) (Table III). The occurrence of epi- and endobionts also varies considerably from member to member, from lows of four (Lavache) and six percent (Chabot east) to highs of 60 (Grindstone east) and 76 percent (Laframboise west) (Table IV).

Deiracorallium angulatum angulatum and *Bighornia patella* have relatively small coralla (length 20-30 mm), a significant factor in their low frequency of epi- and endobiont association. These two species also have relatively low frequencies of abrasion (18% and 5% respectively), suggesting high sedimentation rates which would have resulted in rapid burial and low exposure time. In contrast, *Eurogrewingkia pulchella*, which produced even smaller coralla (length 10-20 mm), has a 24 percent epi- and endobiont association frequency. This is a result of the occurrence of a large number of *E. pulchella* in the biohermal Laframboise Member, where epi- and endobionts, particularly algal encrusters, are much more common.

Stromatoporoids are most commonly attached to coralla of *Cyathactis euryone*, and are only rarely found associated with any other species in the study area (Table III). As *Cyathactis euryone* is most common at a single locality (loc. 15) with a distinctive lithology (skeletal grainstones/biostromes), the stromatoporoid association is probably a function of environment, not of the presence of *C. euryone*. Bryozoans and *Trypanites* borings are the most common epi- and endobiont associations from non-reefal sediments, and bryozoa are most common in the Laframboise reefs, indicating that environmental factors that allowed reef growth (shallow water, low turbidity, stable substrate) are most significant in epi- and endobiont distribution (see 3.4.2.4 *Trypanites*).

3.4.3 Diversity

Diversity is a function of environmental conditions. A large dataset is required to correlate diversity and species assemblages with a particular factor or set of factors. Data from Anticosti Island are geographically limited as only the biohermal Laframboise

Member of the Ellis Bay Formation has multiple geographically separated collection sites, and only the Ellis Bay Formation was seen in its full extent in the west and in the east.

In this study, total diversity is defined as the number of species represented in a given stratigraphic unit (bed, member, formation). Local diversity is defined as the number of species present in a given outcrop (in a specific member if more than one is exposed). Local diversity in the Vauréal Formation reaches a high in the Homard Member and drops toward the base of the Ellis Bay Formation (Table V). Diversity remains low in the Ellis Bay Formation (with an isolated peak in the locally biohermal Prinsta Member [Lake, 1981]) below the Laframboise Member, where the total diversity and local diversity reach their maximum values in the study interval. Diversity is low in the Fox Point Member of the Becscie Formation and low to moderate in the overlying Chabot Member.

The Homard Member, as exposed at locality 3 (Long and Copper, 1994), where local diversity is highest, includes hardgrounds and bioclastic grainstones. The Chabot Member includes a number of sites with storm-generated bioclastic grainstones, and one of the higher diversity sites (loc. 15) has several grainstone beds. Locality 23 in the Chabot Member, at which local diversity may be as high as six species (the exact stratigraphic position from which the single specimen of *Amplexoides* sp. was collected is either uppermost Becscie or lowermost Merrimack), has mixed carbonate lithologies (wackestones to grainstones). The Laframboise Member of the Ellis Bay Formation is biohermal. Considering the former three intervals of high diversity (and possibly loc. 23

Table V. Rugose coral species diversity for study interval, by member and formation. See text for definition of total and maximum local diversity. N.B., While data from other sources were used for diversity numbers, they were not used for specimen totals.

[1] Some specimens (23) in the basal Becscie are abraded and transported from adjacent Ellis Bay Formation bioherms; number in brackets is in situ species diversity.

[2] Locality A468a was described by Copper (pers. comm., 1994) as uppermost Grindstone or lowermost Velleda member. The data are included in the Grindstone Member on this table.

Formation	number of specimens (total diversity / maximum local diversity)			
Member	West	Central	East	Total
Chabot	231 (7/6)	-	126 (6/3)	358 (8/5)
Fox Point[1]	179 (6[3]/6[3])	-	114 (4[3]/4[3])	293 (3/3)
Becscie Fm. total	**410 (9/6)**	**-**	**240 (7/3)**	**651 (9/6)**
Laframboise	547 (7/7)	102 (7/7)	94 (5/5)	743 (8/7)
Lousy Cove	129 (2/2)	-	4 (1/1)	133 (2/2)
Prinsta	91 (2/2)	-	112 (7/5)	203 (7/5)
Velleda	196 (3/3)	-	-[2]	223 (5/5)
Grindstone	56 (2/2)	-	27[2] (5/5)[2]	56 (2/2)
Ellis Bay Fm. total	**1019 (7/7)**	**102 (7/7)**	**237 (7/5)**	**1358 (12/7)**
Schmitt Creek	2 (1/1)	-	11 (1/1)	13 (2/1)
Mill Bay	20 (5/4)	-	39 (2/2)	59 (5/4)
Joseph Point	49 (4/4)	30 (1/1)	-	79 (4/4)
Homard	135 (6/5)	-	-	135 (6/5)
Tower	3 (2/2)	-	-	3 (2/2)
Easton	-	-	-	-
Lavache	109 (3/2)	-	-	109 (3/2)
Vauréal Fm. total	**318 (6/5)**	**30 (1/1)**	**50 (2/2)**	**398 (6/5)**
Total	**1747 (18/7)**	**132 (8/7)**	**527 (15/5)**	**2407 (20/7)**

as well), it is apparent that substrate type, and to a lesser extent terrigenous clastic input (low in all high diversity sections), or environmental conditions associated with those factors, are significant contributors to diversity. High rugosan diversity can be particularly related to the presence of grainstones.

3.4.4 Faunal Assemblages

3.4.4.1 *Introduction.* In the following section, the associations of rugose corals species will be discussed. The inferred living conditions for each species will be considered (water energy, substrate type, sedimentation rate), based on data from the previous sections on field observations, morphological characteristics (particularly the method of maintaining stability preferred by each species), degree of breakage and abrasion, association with other species of rugose coral, and some earlier studies on sedimentology and paleoecology. Data for the colonial species *Paliphyllum ellisense* are included in Table VI as specimens tended to break into individual corallites and were treated as such. The mutual support of the other corallites would have helped maintain corallite stability, and a few specimens have bent corallites which indicate that they were able to reattain a vertical living position in the event of destabilization. As monospecific assemblages can be a reflection of environmental specialization (as well as mechanical sorting), the percentage of each solitary species' total number of specimens that occurred in monospecific assemblages was calculated. These environmental data are summarized in Table VI.

Table VI. Data on, and interpretation of, environmental parameters controlling distribution of solitary rugose coral species and the dendroid colonial species *Paliphyllum ellisense*.

Species	Water energy	Substrate	Sedimentation rate	% monospecific assemblages	Stabilization method
Bighornia patella	low to moderate	soft	moderate	90	dilation, cross-section
Bodophyllum englishheadense	high	hard	low	21	dilation, attachment structures
Bodophyllum n. sp.	moderate to high	reefal	high (endogenic)	0	gregaria?
Cyathactis euryone	high	soft, hard	low	0	large size
Deiracorallium angulatum angulatum	low to moderate	soft	moderate to high	84	dilation, cross section
Dinophyllum hannah	low to high	soft	low to moderate	21	large size, trochoid
Eurogrewingkia pulchella	low to high	soft, hard, reefal	low to high (endogenic)	33	attachment structures
Lobocorallium trilobatum vaurealense	moderate to high	soft	low to moderate	7	dilation, cross section, large size
Paliphyllum ellisense	moderate	reefal	high (endogenic)	0	colonial, reorientation
Rhegmaphyllum n. sp.	low to high	soft	low	27	none
Salvadorea selecta	high	soft to hard	low to moderate	30	dilation, large size
Streptelasma affine	low to high	soft, hard, reefal	low to high (endogenic)	1	large size, attachment structures
Streptelasma n. sp. 1	moderate	reefal	moderate to high (endogenic)	0	dilation
Streptelasma n. sp. 2	high	hard	low	3	attachment structures, dilation
Streptelasma sp.	low	soft	low	0	large size, attachment structure

3.4.4.2 *Vauréal Formation.* The Vauréal Formation includes a wide variety of sediments representing varying environmental conditions. This is reflected, to a certain extent, in the rugose coral faunal composition. Some faunal variation, however, cannot be related to sedimentological characteristics or stratigraphic position.

The majority of specimens of two species, *Bighornia patella* (Lavache Member at loc. 13) and *Deiracorallium angulatum angulatum* (Joseph Point Member at loc. 29), occur in large monospecific assemblages (Table VI); and two species, *Bodophyllum englishheadense* (Mill Bay Member at loc. 39) and *Salvadorea selecta* (Schmitt Creek Member at loc. 39), commonly occur in monospecific assemblages. As *Bighornia patella* is the only species that occurs in the oldest rocks exposed on the island, it may have been the first available immigrant. The monospecific assemblages in the Lavache Member may, therefore, be a function of a lack of other available species rather than any narrow environmental control. The lower Vauréal Formation (where the majority of *Bighornia patella* specimens are found) generally represents deeper water deposition (see Text-fig. 5; Dewing, 1999). *Bighornia patella* is, however, found in considerably shallower, more restricted settings in the approximately coeval Stony Mountain Formation of southern Manitoba (Elias, 1982b, 1983) and in the lower Prinsta Member, which was apparently deposited in shallower water (Text-fig. 8; Petryk, 1981b; Dewing, 1999). Therefore, depth (and associated current strength and sedimentation rate) is not the control on the occurrence of *B. patella*.

Deiracorallium angulatum angulatum assemblages are apparently a function of unique environmental preference for low energy, high sedimentation rate settings. Their life orientation (corallum axis vertical) is generally unstable and may only remain stable during life of the coral if a high sedimentation rate keeps the corallum wedged in place. The subspecies *Deiracorallium angulatum gunni* from the Stony Mountain Formation of southern Manitoba is generally somewhat smaller and less angulate and occurs in an area of lower sedimentation rate (as seen by the high degree of abrasion). The two subspecies may be ecophenotypic variants, as a restricted, shallow water environment comparable to that of the Stony Mountain Formation is not represented in the study interval.

Bodophyllum englishheadense occurs primarily in two localities (locs. 3, 39), both of which are dominated by coarse grainstones. These data suggest environmental control (coarse substrate), particularly at locality 39 where the fauna of the Mill Bay Member (sandy grainstones) is over 90 percent *B. englishheadense* (with two fragmentary specimens of *Palaeophyllum vaurealense* and a highly abraded specimen of *Salvadorea selecta*?) and the fauna of the immediately overlying Schmitt Creek Member is 100 percent *S. selecta*. Other species distributions in the Vauréal are less obviously controlled by environmental factors. No species is restricted to a single environment or locality in the Vauréal Formation.

Young and Elias (1999) noted groupings of species in the Richmondian Stony Mountain Formation of Manitoba that corresponded to specific environmental variables. *Lobocorallium trilobatum trilobatum* and *Deiracorallium angulatum gunni* were associated with deeper open-marine environments and *Salvadorea selecta* (and minor *Salvadorea* sp.) and *Bighornia patella* (and minor *Bighornia* sp. cf. *B. integriseptata*) were associated with shallower, more restricted environments. Such a pattern is not present in the Vauréal Formation, where *Bighornia patella* is associated primarily with deeper water (lower Lavache Member) and *Lobocorallium trilobatum vaurealense* is associated with both deep (Lavache Member) and shallow (Mill Bay Member) water. *Deiracorallium angulatum angulatum* is most common in the Joseph Point Member which is an interval of local deepening (Long and Copper, 1994; Dewing, 1999). *Salvadorea selecta* is associated with both shallow and deeper water in the Vauréal and lower Ellis Bay formations. The difference in associations between two such comparable faunas can be attributed to the generally different setting; Anticosti Island sediments were deposited on an open marine carbonate ramp (even at the shallowest points), while the Stony Mountain Formation was deposited in a somewhat restricted epicontinental sea in the middle of the craton. The similar pattern of occurrence of *Deiracorallium* apparently indicates an actual environmental preference.

3.4.4.3 *Ellis Bay Formation.* Data from the Ellis Bay Formation can be divided into east and west collections. There are two significant results of an analysis of Ellis Bay Formation faunal composition: 1) diversity is low below the Laframboise Member, and 2) the Grindstone to mid-Prinsta members show a lateral variation in which *Salvadorea selecta* and *Bodophyllum englishheadense* are the major components in the eastern part of the island while *Eurogrewingkia pulchella* is the dominant component in the west (see Text-fig. 8). A temporal faunal differentiation is seen in the eastern part of the island within the Prinsta Member, as demonstrated at locality 43 where 26 specimens of *Salvadorea selecta* were found in the lower three units (*sensu* Long and Copper, 1987a), a single specimen was found in unit 4 and none were found in higher units. The temporal change in faunal composition (at loc. 43 and in the eastern end of the island as a whole) can be attributed to a general change in substrate type (no sandstones in the upper Ellis Bay Formation; i.e., less terrigenous input) and may also be a result of a drop in sea level (initiation of a regressive half-cycle; see Text-fig. 5; Dewing, 1999). Above this interval (i.e., upper Prinsta Member and above), the faunal compositions of the eastern and western exposures of the Ellis Bay Formation are comparable (i.e., dominated by *Eurogrewingkia pulchella* below the biohermal Laframboise Member).

The Ellis Bay Formation has been shown to be sedimentologically distinct in the east and west of Anticosti Island (Petryk, 1981a; Long and Copper, 1987a, 1994). Specifically, the eastern exposures contain a higher proportion of siliciclastics. The correlation of substrate type and coral species distribution data shows that faunal content of the sub-Laframboise Ellis Bay Formation is controlled by water depth and substrate-related environmental factors that vary across the island.

3.4.4.4 *Laframboise Member.* The Laframboise Member is unique in the study interval as it is: 1) the only stratigraphic interval recognized, studied and collected at multiple sites across the full extent of the island, 2) sedimentologically distinct, including an oncolite marker bed and the only widely and well developed bioherms in the study interval (Lake [1981] reported bioherms from the upper Prinsta Member [Copper, 1989; Long and Copper, 1994] in the eastern part of the island, but these were comparatively localized and were not examined in this study), and 3) the unit with the highest rugose coral diversity. Bioherms in the Laframboise Member vary in size and faunal content across the island (Lake, 1981; Copper, 1989, 2001; Long and Copper, 1994; Copper and Long, 1998). The bioherms are formed of coral-algal-stromatoporoid boundstones (Lake, 1981; Copper, 1989; Long and Copper, 1994; Copper and Long, 1998) sitting on, or surrounded by, an oncolitic platform bed (Petryk, 1981a; Copper and Long, 1998; Copper, 2001). The size of the biohermal masses varies from around 1 m high on the east coast (Long and Copper, 1987a) to up to 8 m high and >100 m long on Salmon River (Lake, 1981; Copper and Long, 1998).

There were six localities at which moderately large collections were made (Table VII). Diversity (5-7 species) and the composition of the solitary rugose coral faunas in the reefs is similar across the island, but the colonial faunal composition is significantly different. At the western localities (locs. 6, 8), *Paliphyllum ellisense* is common and *Palaeophyllum* n. sp. is a minor component (both dendroid-phaceloid forms). The central localities (locs. 31, 33) have a colonial fauna dominated by cerioid *Palaeophyllum lyterion* with lesser occurrence of *Paliphyllum ellisense*. The east-central locality (loc. 38) has *P. ellisense* and a generally subcerioid form of *Palaeophyllum lyterion* (see discussion of variability in *P. lyterion*). The eastern locality (loc. 44) has a sparse colonial fauna composed of *Paliphyllum ellisense*.

The variation in colonial faunal composition cannot be directly associated with a particular environmental factor, although the greater degree of reef development at locality 38 suggests that turbidity, nutrient availability, seafloor topography, or water depth may be responsible. Other potential controls on reef development (e.g., water

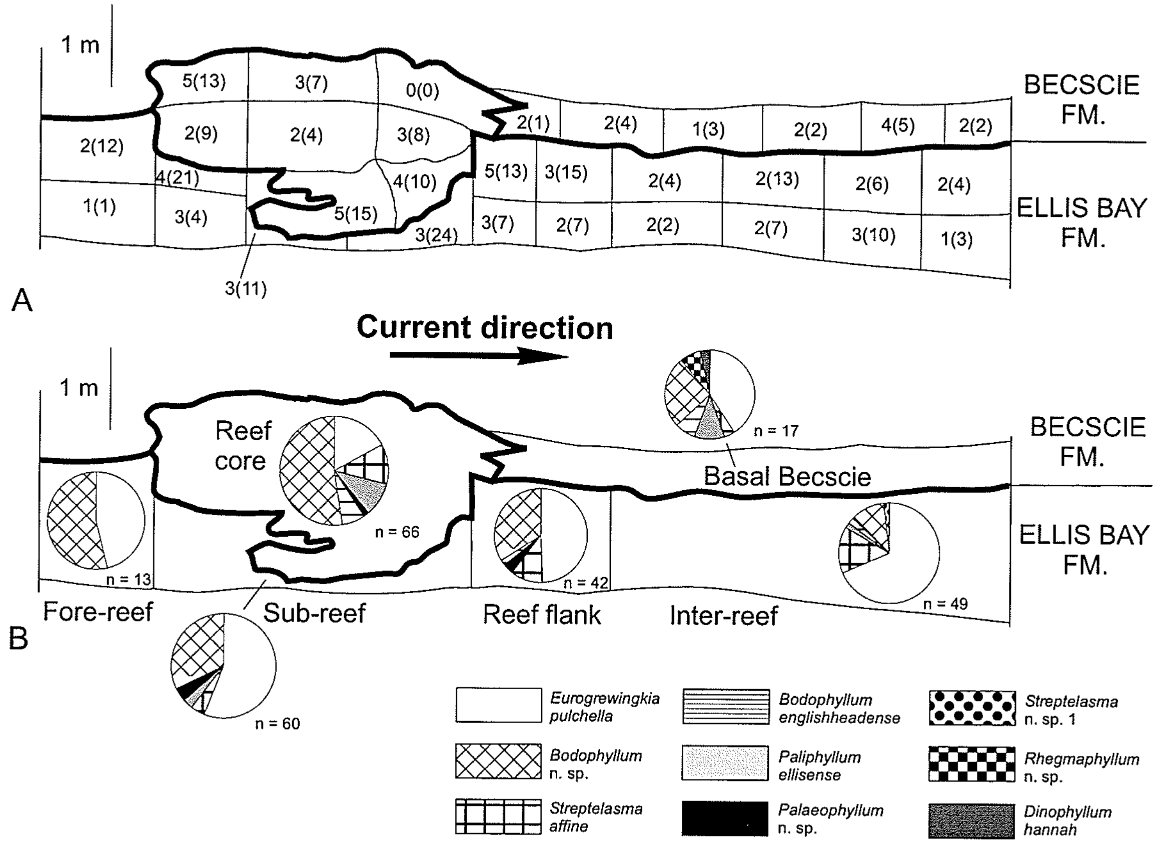
Table VII. Variation in reef development and colonial rugose coral faunal characteristics of the Laframboise Member, Ellis Bay Formation. See Text-fig. 1 for locality numbers.
[1] Only a small outcrop area was collected at this locality.

Locality	Reef development	Local diversity	Corallum structure
6	common, 2-3 m high	7	dendroid-phaceloid
8	common, 2-3 m high	6	dendroid-phaceloid
31	size unknown	2[1]	cerioid dominant
33	size unknown	7	cerioid dominant
38	common, >8 m high	7	phaceloid-subcerioid
44	uncommon, ~1 m high	5	dendroid-phaceloid

temperature) would probably not have varied significantly between the localities. The lateral variation between the reefs is clear, and additionally, the occurrence in the Laframboise Member of *Bodophyllum* n. sp., *Paliphyllum ellisense*, *Streptelasma* n. sp. 1 and *Palaeophyllum* n. sp., which do not occur lower in the Ellis Bay Formation (*Palaeophyllum lyterion* was also reported from reefs in the upper Prinsta Member [Lake, 1981; Copper, 1989]), indicates that environmental differences (e.g., substrate, water depth) were the primary control on the occurrence of those taxa.

A single bioherm at locality 6 was collected systematically, with collections laterally and vertically differentiated (see Text-fig. 10). Diversity is highest in the reef core and decreases away from the reef. The reef flank has a relatively high diversity but the degree of abrasion of those specimens (and of some specimens in the interreef and basal Becscie) indicates that they were transported, presumably from the adjacent bioherms.

Bodophyllum n. sp., *Paliphyllum ellisense*, *Palaeophyllum lyterion*, *Palaeophyllum* n. sp. and *Streptelasma* n. sp. 1 were apparently environmental specialists restricted to biohermal (stable substrate, low allogenic sedimentation rate, shallow water) or adjacent sediments. In contrast with the aforementioned species, *Eurogrewingkia pulchella* and *Streptelasma affine* were ecological generalists which could tolerate a far wider range of environmental variables, as shown by their occurrence in a variety of rocks at all levels of the Ellis Bay Formation. *Bodophyllum englishheadense* (see discussion for Vauréal Formation) is a rare element in the biohermal sediments. The availability of fossil skeletons as hard substrates (attachment sites) is probably the reason why *B.*



Text-fig. 10. Schematic of vertical section through a single Laframboise Member bioherm (dark outline) and associated beds at locality 6. A. Number of specimens (in parentheses) and number of species in each collection. B. Pie charts of relative proportions of each species from each facies, n = number of specimens. Facies interpretation and current direction based on Petryk (1981a, fig. 11). Dark line extending horizontally from bioherm is formational boundary. See Appendix B for collection names.

englishheadense occurs in the biohermal Laframboise Member, but not in the underlying upper Prinsta or Lousy Cove members.

3.4.4.5 *Becscie Formation.* Sami and Desrochers (1992) described the Becscie Formation as being dominated by a series of laterally differentiated storm deposits. Storm deposition may have overridden local topographic and substrate variations resulting in widespread, relatively uniform deposition. The primary lateral control on substrate variation would have been proximal-distal position. The Becscie Formation coral fauna is generally low in diversity. The lowermost Becscie Formation (Fox Point Member) fauna includes only three species, and *Eurogrewingkia pulchella* only occurs in the lowest 17 m. In the upper part of the lower Becscie Formation, below the lower-middle Chabot Member (locs. 15, 35), one or two species are present at any given locality. At this level, in the western part of the island where most of the Chabot Member collections were made, the coarse-grained carbonate-dominated sediments include faunas with up to six rugose coral species. At locality 35, and in most other Chabot Member outcrops other than locality 15, *Dinophyllum hannah* is dominant in a low-diversity assemblage (in mixed carbonate lithologies, often at least partially obscured by silicification and other alteration). As the Chabot Member is an interval dominated by bioclastic grainstones, substrate seems to have had an influence on diversity.

A single specimen of *Amplexoides* sp. has been reported from the uppermost Becscie or lowermost Merrimack (Bolton, 1981a); this taxon, however, was apparently only a minor element and was not present in the collections examined as part of this study (see 3.3.3 Distribution of Rugose Corals in Strata; Becscie Formation). Inclusion of this rare element in the Becscie data brings the total diversity in the upper Becscie to 9 species, comparable to the Laframboise Member of the Ellis Bay. The maximum local diversity of six is, however, still lower than the seven species seen in the Laframboise Member in the central and western parts of the island.

The low diversity in the lower Becscie is probably due to an unstable, fine grained, storm-generated substrate (Sami and Desrochers, 1992) as stable coarse-grained carbonates were shown to support the highest diversity in the lower formations. Both *Rhegmaphyllum* n. sp. and *Dinophyllum hannah* appears to have been opportunists, and *Dinophyllum* in particular occurred in a wide variety of paleoenvironments in the Becscie Formation. *Cyathactis euryone* is most common in the skeletal grainstones at locality 15 (and rare elsewhere), suggesting either intolerance of fine-grained sedimentation or preference for environmental conditions that resulted from deposition of skeletal grainstones (e.g., substrate stability). The only observed (temporal) faunal transition is at locality 15 where the fauna of the lower part of the section (exposed on the tidal flats) consists of *Dinophyllum hannah* and *Streptelasma* n. sp. 2 while the fauna of the upper part of the section consists mainly of *Cyathactis euryone*, with a little mixing between the two. The upper part of the section is more recessive and contains abundant skeletal grainstones while the lower part is more massive and resistant bioclastic mudstones-wackestones; therefore substrate appears to be the most important variable affecting faunal composition. *Strombodes socialis* and *Petrozium pelagicum* are only known from a few localities (in this study) and their occurrence cannot be related to specific environmental variables.

3.5 INTRASPECIFIC VARIABILITY

3.5.1 Introduction

Intraspecific variability was studied for those species for which a large enough sample size was obtained. This variability was correlated with spatial and stratigraphic distribution in order to determine to what extent variability was a function of temporal change (evolution) or environmental response (ecophenotypic variability). *Streptelasma* n. sp. 1 and *Streptelasma* n. sp. 2, *Palaeophyllum* n. sp., *Palaeophyllum* sp., *Streptelasma* sp., *Petrozium pelagicum* and *Strombodes socialis* were too uncommon for spatial or temporal variability to be studied. *Rhegmaphyllum* n. sp., *Paliphyllum ellisense*, *Bodophyllum englishheadense*, *Bodophyllum* n. sp., *Cyathactis euryone*, and *Palaeophyllum vaurealense* were moderately variable but no particular temporal or spatial trends were apparent. The latter five species were generally restricted to particular environments, and *Bodophyllum* n. sp. and *Paliphyllum ellisense* were restricted to a single stratigraphic interval as well. *Deiracorallium angulatum angulatum* had too low a degree of variability to be analyzed spatially or temporally. The features discussed below are explained in Systematic Paleontology under Biometric Methods (6.2) and in the description of each species.

3.5.2 Variability and interpretation: species-by-species

3.5.2.1 Bighornia patella. *Bighornia patella* shows generally little variability, and was found mainly in the lower Vauréal Formation. The coralla are generally depressed and triangulate in early stages and subrounded in later stages. Three specimens from the Prinsta Member of the Ellis Bay Formation at locality 43 are much younger than all other specimens from Anticosti Island and appear to be more rounded in earlier stages. On a graph of cardinal-counter length vs. alar-alar length, their values plot on the 1:1 line (or above in one case which was apparently a result of a section having been cut obliquely; Text-fig. 24B). However, as only three specimens were obtained from such a high level in the stratigraphic column, it cannot be determined whether the unusual degree of roundness is an evolutionary or ecophenotypic product or even a random variation. The columella in two of the specimens (A-595-1, 5) appears to be slightly larger than in comparable specimens from the Vauréal, but the size difference could not be quantified due to the highly variable nature of columella development (shape and size),. The columella of the third specimen from the Prinsta Member (A-595-9; Pl. 5, fig. 13) is not particularly large.

3.5.2.2 Eurogrewingkia pulchella. *Eurogrewingkia pulchella* is by far the most common (>900 specimens) solitary rugose coral species from the study interval, and is also highly variable. External characters (e.g., length, curvature) and internal characters (e.g., number of major septa at a given diameter, axial region characteristics) are highly variable (see Systematic Paleontology). Table VIII shows how external characters vary, member-by-member, as well as the variation in presence/absence of a median lamella, the most significant of the internal characters.

Table VIII. Features of *Eurorewingkia pulchella*, by stratigraphic position. EB = Ellis Bay, B = Becscie. For "axial structure with median lamella," the numbers given are: number of specimens with median lamella/number of specimens observed; percentage of specimens with median lamella is given in parentheses. For curvature, st = straight, sl = slightly curved, cur = moderately curved, be = bent; numbers given are number of specimens with each type of corallum curvature.

Member (Formation)	Axial structure with median lamella	Curvature (st / sl / cur / be)	Average length
Fox Point (B)	5/159 (3.1%)	11 / 67 / 21 / 3	16.2 mm
Laframboise (EB)	41/275 (14.9%)	24 / 89 / 26 / 5	18.6 mm
Lousy Cove (EB)	18/126 (14.3%)	8 / 12 / 46 / 1	15.9 mm
Prinsta (EB)	10/181 (5.5%)	11 / 29 / 59 / 6	17.4 mm
Velleda (EB)	8/134 (6.0%)	3 / 10 / 20 / 9	15.7 mm
Grindstone (EB)	3/52 (5.8%)	1 / 4 / 20 / 0	15.1 mm

Corallum curvature varies between members; the slightly curved to curved ratio is between 1:5 and 1:2 below the Laframboise Member and ca. 3:1 in the Laframboise and Fox Point members. This suggests that the Laframboise and Fox Point members were deposited in quieter water conditions. Corallum length varies between members; coralla from the Laframboise Member are significantly longer than in under- or overlying strata as shown by a z-test ($z = 5.44$, $z_{0.01} = 2.58$). This suggests that the biohermal environment may have been particularly favourable to growth.

A chi-squared test of median lamella frequency ($\chi^2 = 27.01$, $\chi^2_{0.01/df=5} = 15.09$), indicates significant differences from member to member. Median lamella frequency is highest in specimens from the Lousy Cove and Laframboise members of the Ellis Bay Formation. This enabled the division of specimens of *E. pulchella* into three statistically significant groups (Grindstone-Prinsta members, Lousy Cove-Laframboise members and Fox Point Member; see discussion of *E. pulchella* in Systematic Paleontology).

In a plot of number of major septa relative to corallum diameter, data for the upper Ellis Bay Formation (Lousy Cove and Laframboise members) specimens have a steeper regression line than the data for specimens from the rest of the Ellis Bay and the Becscie. This indicates that septal insertion relative to corallum diameter was faster (or corallum expansion relative to time was slower) for specimens in that interval (Text-fig. 28C). As the lines for the two other intervals are similar to each other (as is the relatively infrequent development of median lamellae), it would suggest that conditions that affected *E. pulchella* morphology were comparable. An overall pattern of morphological change is apparent from the study of *E. pulchella*: 1) initially a relatively low number of major septa/diameter (n/d) ratio with infrequent median lamella development (lower to middle Ellis Bay), 2) higher d/n ratio, with more frequently developed median lamellae (upper Ellis Bay), 3) followed by a return to a lower n/d ratio and infrequent median lamella development (Becscie Formation) (Table VIII). The mean corallum length data (Table VIII) show that coralla of *E. pulchella* from the Laframboise Member are longer than coralla from under- and overlying strata. This pattern may be either a temporal or environmental response or both. The stratigraphically lowest group occurred in water of variable depth (but deeper than the Laframboise Member) with at least moderately siliciclastic-rich substrate, the middle group primarily occurred in the sedimentologically distinctive Laframboise Member and the upper group occurred in the deepening, storm-dominated lower Becscie Formation (Sami and Desrochers, 1992). The changes in n/d ratio indicate a heterochronic cyclical pattern which may be "evolutionary" (i.e., temporal), but is more likely an ecophenotypic response as the environment of the Laframboise Member is so different from that of other strata.

3.5.2.3 *Lobocorallium trilobatum vaurealense*. While very few specimens of *Lobocorallium trilobatum vaurealense* were found in this study, the stratigraphically lowest specimen is significantly more depressed than the other specimens (see Text-fig. 26B), and more comparable to *L. trilobatum trilobatum* from the approximately coeval Stony Mountain Formation of southern Manitoba. Whether or not the single depressed specimen has any evolutionary significance (see discussion of *L. trilobatum vaurealense*) cannot be determined, but it may represent an intermediate between the two subspecies.

3.5.2.4 *Salvadorea selecta*. Specimens of *Salvadorea selecta* from the study interval do not display a high degree of intraspecific variability. A comparison with specimens from the Stony Mountain Formation of Manitoba, however, shows that coralla from Anticosti were considerably larger (up to ca. 100 mm in length compared to a maximum of 47 mm for Stony Mountain specimens; Elias, 1983). As the Stony Mountain specimens were approximately coeval (i.e., Richmondian), the difference in size was presumably environmental. The Stony Mountain Formation was deposited in an epicontinental sea in a somewhat restricted environment while the Anticosti sequence was deposited in an open water continental margin setting. It has, however, not been possible to identify a specific environmental variable responsible for the differences between the Manitoba and Anticosti specimens.

3.5.2.5 *Streptelasma affine*. *Streptelasma affine* is the second most common solitary rugosan species in the Ellis Bay Formation and occurred in a wide variety of environments, as reflected in a high degree of variability. Coralla of *S. affine* were divided into three groups: sub-Laframboise Member, biohermal Laframboise and nonbiohermal Laframboise, and number of major septa, stereozone thickness, and major and minor septum length relative to the corallum diameter were compared (see Text-figs. 22A-D). Corallum size could not be compared quantitatively as too many of the larger specimens were incomplete, but in general terms, the biohermal specimens were usually much larger than non-biohermal specimens. Number of major septa, major septum length and stereozone thickness do not appear to show a temporal variability pattern, but a plot of minor septum length shows generally greater length relative to corallum diameter for the sub-Laframboise specimens (Text-fig. 22D). The larger size of coralla in the bioherms is an indication that corallum size is at least partially a function of environment, comparable to the corallum size variation for *Eurogrewingkia pulchella.*

3.5.2.6 *Dinophyllum hannah.* There is a geographic/sedimentologic differentiation of degree of curvature and abrasion from four localities where n >10 (see Table IX). As corallum curvature is an indicator of current strength during life and abrasion is an indicator of current strength prior to burial (or speed of burial), the curvature and abrasion data for the four localities appear to yield opposite results. The data appear to indicate that the coralla from localities 18a and 38 lived in relatively strong currents but were abraded only by weak to moderate currents or were rapidly buried, and that coralla from localities 12 and 35 lived in relatively weak currents and were abraded by moderately strong currents post mortem or were subjected to extensive reworking and abrasion.

These interpretations show that living conditions and burial conditions can leave completely different evidence in a corallum. The corallum data from locality 38 can be correlated with taphonomic and sedimentologic evidence from the outcrop and collected slabs, in which the coralla are found in near life orientation and with very low degrees of abrasion or breakage, indicating that they have not been transported and were rapidly buried. The sedimentary environment of locality 38, and specifically of the fossiliferous beds (fine grained distal tempestites; Sami and Desrochers, 1992), is distinct from higher

Table IX. Variation in physical properties of coralla of *Dinophyllum hannah* from the largest collections. See Text-fig.1 for locality numbers. st = straight, sl = slightly curved, cu = curved. Under abraded, number is number of specimens analyzed for abrasion characteristics, number in parenthese is percent of coralla with abrasion.

Locality	st / sl / cu	Substrate type	abraded
12	24 / 2 / 0	coarse skeletal grainstones	28 (36%)
38	7 / 5 / 13	distal tempestites (fine carbonate mudstones/shales)	32 (16%)
35	27 / 9 / 1	variable wackestones-grainstones	25 (20%)
18a	3 / 3 / 9	coarse skeletal grainstones/biostromes	14 (0%)
All *D. hannah*	75 / 26 / 29	-	172 (30%)

in the Becscie Formation, and a soft substrate may have resulted in corallum wedging and instability (and resulting curvature) that is distinct from that caused by high energy currents (Bolton and Driese, 1990). At the localities other than those in Table IX, particularly locality 11, post-burial alteration makes it impossible to be definitive about the depositional environment, but the curvature data clearly show that conditions differed between the localities.

3.5.2.7 *Palaeophyllum lyterion.* Although *Palaeophyllum lyterion* is restricted to the biohermal Ellis Bay Formation, the combination of inter- and intracolonial variability data yields a distinctive spatial pattern. Corallum mean diameter, number of major septa, and number of neighbours (number of other corallites touching a given corallite if circular, or sharing a wall if polygonal), vary by locality. A Student t-test for small populations (non-paired) was used to determine the significance of the differences between corallum parameters from the three main localities (see Tables X, XI). The number of degrees of freedom is the number of specimens from each locality being compared minus two, and weighted means were calculated (using Corel Quattro Pro 8). The t-score was compared against the 95th and 99th percentile values. The data show that all three parameters are significantly different between localities 38 and 31, that two out of three are significantly different between localities 38 and 33 and that only one out of three is different between localities 31 and 33. As all three sets of specimens are from the biohermal top member of the Ellis Bay Formation, the variability suggests subtle environmental differences between the three localities. Localities 31 and 33 (the most

Table X. Data for mean corallum parameters of *Palaeophyllum lyterion*, by locality. See Text-fig.1 for locality numbers. No = number of sections, n = number of major septa, c.v. = coefficient of variation, d = corallite diameter (mm), nn = number of neighbours.

Locality	no	Mean n	c.v. n	Mean d	c.v. d	Mean nn	c.v. nn
38	12	17.9	6.2	4.6	20.4	3.2	55.8
33	11	17.2	9.5	4.2	23.5	5.6	29.5
31	8	16.1	9.1	3.8	24	5.6	35

Table XI. Student t-test results comparing n, d, and nn (for abbreviations, see Table X) for *Palaeophyllum lyterion* by locality. The number is the level of significance at which the values can be considered to be different.

Locality		33			31		
		n	d	nn	n	d	nn
38	n	0	-	-	99	-	-
	d	-	99	-	-	99	-
	nn	-	-	99	-	-	99
33	n				95	-	-
	d				-	0	-
	nn				-	-	0

similar pair of localities) are relatively close to each other (about 10 km apart). Since locality 38 is about 30 km east of the other two, the differences between the localities apparently represent an ecophenotypic gradient, but more data would be required to confirm this or to determine the specific environmental variable(s) responsible.

3.6 SUMMARY OF PALEOECOLOGICAL INTERPRETATIONS

The interpretation of environments in which rugose corals lived (Table VI) is based on the data from Tables I-V and VII, field observations and previously published data on the sedimentology of beds on Anticosti Island. Additional results in Table VI are based on occurrence data ("% monospecific assemblages") and analysis of morphological data ("stabilization method") from this study. Energy conditions were inferred from the degree of curvature (more curved = higher energy), sedimentation rate was inferred from the degree of abrasion and occurrence of epi- and endobionts, and substrate conditions were determined from field and published data and occurrence of attachment structures. As noted in the sections on diversity (3.4.3) and faunal assemblages (3.4.4), certain species occur frequently in monospecific assemblages, suggesting preference for specific environmental conditions. The "stabilization method" information in Table VI is given to illustrate the variety of methods used to maintain a stable life position by solitary (and colonial phaceloid, in the case of *Paliphyllum ellisense*) rugose corals in the study interval.

A number of taxa from the Laframboise Member reefs have a high occurrence of epibionts (Tables III, IV) and occurred in environments with high sedimentation rates

(Table VI). This is due to the fact that sedimentation in a biohermal setting will be high but endogenic (i.e., not causing turbidity), and other factors (e.g., depth, availability of hard substrate for larval settling or algal growth) are optimal for all reefal organisms.

Abrasion data for *Cyathactis euryone* (Table I) require that the thin wall (and resulting ease of abrasion) be considered. The frequent association with stromatoporoids corroborates a low sedimentation rate that would be inferred from the apparently high degree of abrasion. *Deiracorallium angulatum angulatum* is exceptional in that no epibionts and only a few borings were associated with it. *Eurogrewingkia pulchella*, by far the most common species, also has the highest degree of variability in external features, evidence of its ability to live in varying environments.

3.7 RUGOSE CORAL ORIENTATION

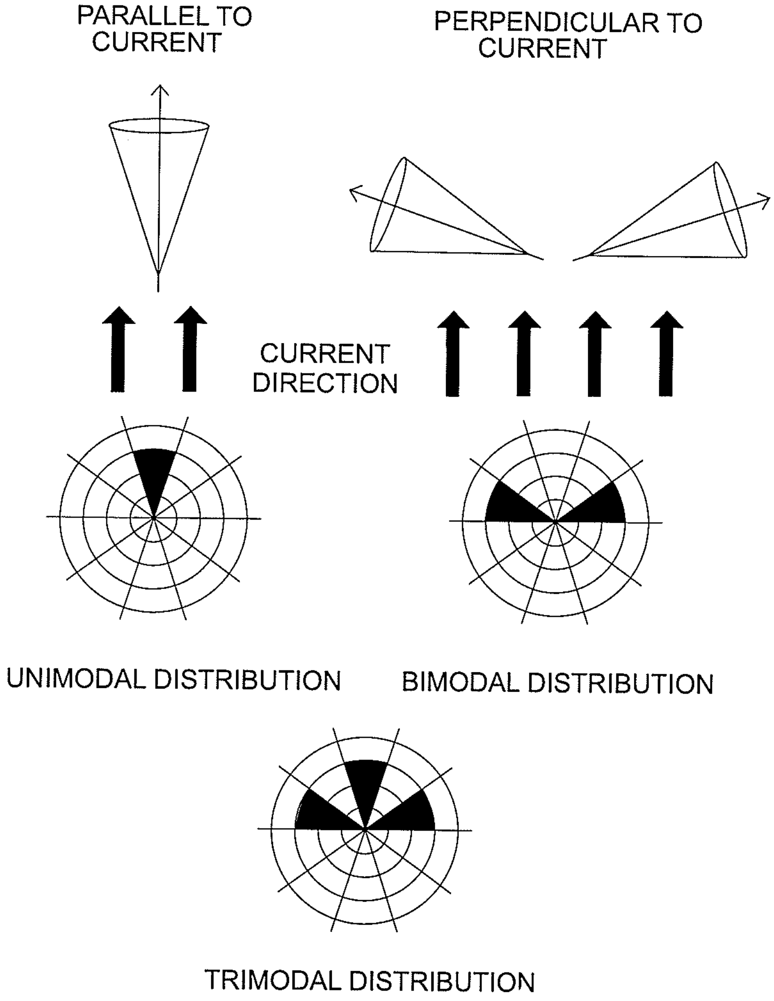
The orientation of skeletal fossils in sedimentary rocks can provide paleocurrent information that is useful in interpretation of basinal history. Information on paleoecology (recognition of in situ and transported assemblages) and sedimentology (differentiation of hard and soft substrates) is also obtainable from orientation data. Orientation studies have been performed on cephalopods, gastropods and other elongate fossils from Paleozoic rocks; solitary rugose corals have, with few exceptions (e.g., Nagle, 1967; Elias et al., 1987; Elias, Zeilstra and Bayer, 1988; Bolton and Driese, 1990; Elias, 1992; Wendt, 1994) not been examined.

This section will present rugose coral orientation data from the Upper Ordovician and lowermost Silurian of Anticosti Island, and compare data from transported assemblages with a rare in situ (life orientation and minimally transported) assemblage. These data will be compared with paleocurrent data obtained by other authors from elsewhere in the Anticosti Island sequence and from other localities in the Ordovician of North America, and will be used to refine the use of solitary rugose corals as paleoenvironmental indicators.

3.7.1 Model

Rugose corals can be treated in general as straight to usually curved cones weighted at the apical end by thickened internal skeletal elements. Most have been interpreted as living in a "calice up" position, with the cardinal side (usually convex in curved forms) facing downstream and long axis orientation varying from vertical to horizontal depending on current strength (Elias, 1982b; Elias, Zeilstra and Bayer, 1988). In a transported assemblage, an apically weighted, elongate conical object will tend to be deposited parallel to current direction with the apical end upstream because of its greater weight and optimized hydrodynamics (Nagle, 1967; Laub, 1979), or it will be oriented perpendicular to the current (parallel to wave crests) (Nagle, 1967; Seilacher, 1973). The resulting orientation rose diagram distributions would be either unimodal (parallel to current), bimodal but slightly skewed (perpendicular to current with calice slightly downstream), or trimodal (combination of parallel and perpendicular orientations) (Text-fig. 11).

Because some species of rugosans have coralla that are curved, noncircular in cross section, operculate, or otherwise atypical, the general model (for straight, smooth cones) has to be modified in rugose coral studies. Richter (1929) showed that the



Text-fig. 11. Orientation distribution models for conical rugose corals.

calceoloid *Calceola*, with its flattened counter side and calice-weighted operculum, would tend to be oriented parallel to current with the calice upstream. Elias et al. (1987) examined the orientation of *Bighornia patella*, a subcalceoloid species with a weighted apex and no operculum, and obtained a bimodal orientation that was parallel to current direction as indicated by other sources. They concluded that the short stubby shape of *B. patella* and its flattened counter surface would minimize rolling perpendicular to current direction, and that the calice could be oriented either upstream or downstream, producing an atypical bimodal plot with peaks that are directly opposite one another.

3.7.2 Methodology

Directional orientation data were obtained from large (>35 specimens) transported assemblages (inferred from corallum orientations) of rugose corals at three localities representing different stratigraphic levels in the Vauréal Formation (Lavache, Joseph Point and Mill Bay members) and from one in situ assemblage at a fourth locality in the Becscie Formation (Fox Point Member) (see Appendix D for orientation data). Tidal flat and riverbank exposures provided sufficient surface area for acquisition of large datasets. Orientation measurements were taken for every exposed corallum from which orientation could be determined at the studied localities. Commonly only a truncated calice was exposed and, for such specimens, the measurement was taken perpendicular to the calice (parallel to the long axis of the corallum); where most of the skeleton was exposed, orientation was measured parallel to the long axis from the apex towards the calice. Data for locality 38 were obtained from a large slab (extracted in situ) with an arbitrary "north" and used to compare the degree of current-related orientation in a relatively undisturbed assemblage to the more highly transported settings.

The four assemblages were apparently monospecific and included 1) small depressed patellate forms, 2) small compressed forms, 3) moderately large, straight to slightly curved, ceratoid forms with circular cross-sections, and 4) moderately large, slightly curved to curved, trochoid forms. The small compressed forms were usually found with the cardinal-counter plane parallel to the substrate surface; for these specimens, the orientation of the cardinal side was also measured (perpendicular to corallum orientation, from the corallum axis towards the cardinal side).

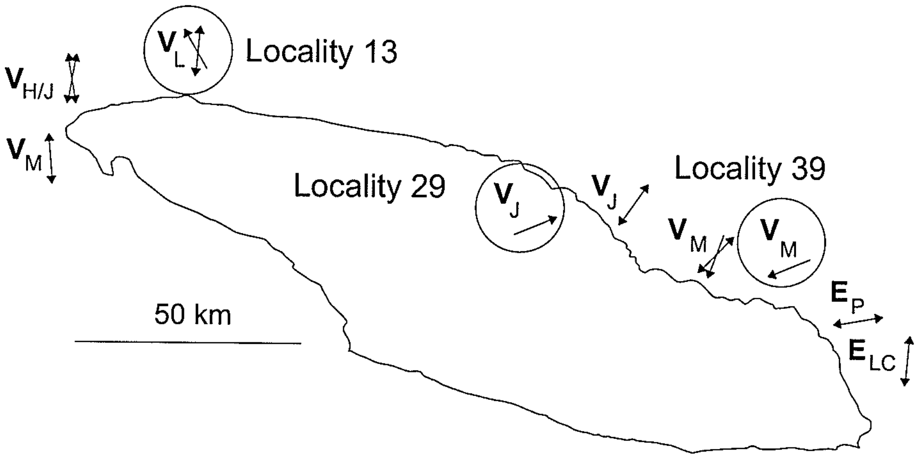
Following Reyment (1975) and Elias et al. (1987), a chi-square test was used to check for anisotropy of orientation data; this compared the observed data to a hypothetical isotropic distribution where frequencies in all classes are equal. The class sizes were chosen to be as small as possible (for maximum refinement) but always resulting in an average frequency of greater than five to ensure that the chi-square test would remain valid (Reyment, 1975). For the chi-square test, the 95 percent confidence interval was used. Individual frequencies were considered to be anomalously high or low if they differed from the mean frequency by more than one standard deviation (Reyment, 1975; Elias et al., 1987).

3.7.3 Results and Interpretation

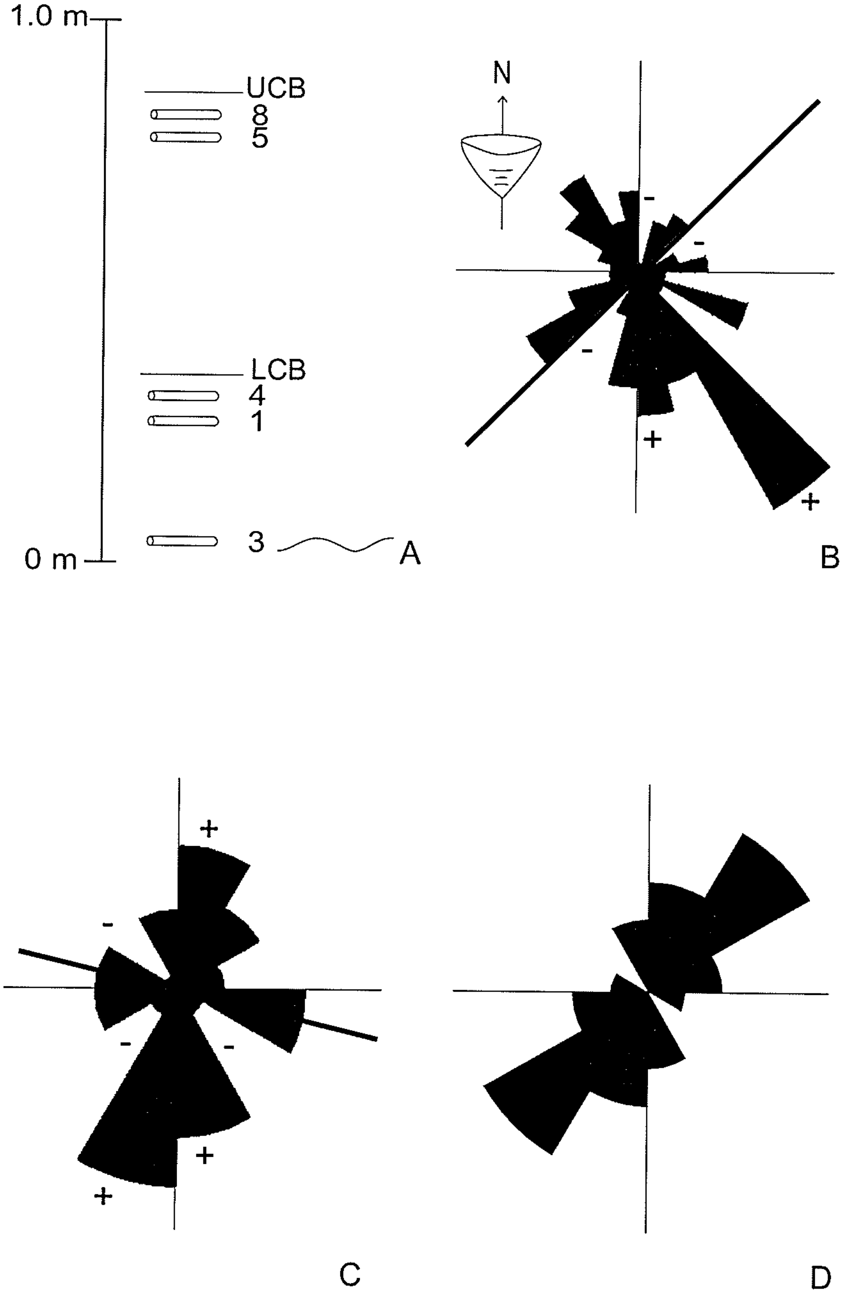
3.7.3.1 *Locality 13*. In the stratigraphically lowest occurrence (Vauréal Formation, Lavache Member), data were obtained for specimens of *Bighornia patella* from locality

13 on the north coast of Anticosti Island (Text-fig. 12). The lithology is mixed carbonate mudstones to wackestones with minor fine siliciclastics. The coralla were generally deposited on their flattened counter sides but as many were weathered, only the axial orientation could be determined. Thirty-four percent of specimens at this locality were abraded, and the delicate calice rims were only rarely preserved. The overall indication is limited or low energy transportation. Coral orientation data were obtained mainly from two beds stratigraphically separated by 54 cm (Text-fig. 13A). Additional data were obtained, for comparison, from other large elongate bioclasts (primarily crinoid stems) in associated beds. Corals from the upper coral bed display a statistical anisotropy ($\chi^2 = 69.25$, $\chi^2_{0.05/23df} = 35.71$), with anomalously high frequencies between 135° and 150° ($n = 19$, $x + \sigma = 9.23$) and between 165° and 180° ($n = 10$). The frequencies between 0° and 15° ($n = 1$, $x - \sigma = 1.19$), 45° and 60° ($n = 1$), and 210° and 225° ($n = 1$), are anomalously low (Text-fig. 13B). Two classes with anomalously high frequencies are close to one another and are considered to be part of the same mode. Secondary (non-anomalous) modes appear opposite the main mode as well as perpendicular and slightly skewed to the northwest.

Coral orientations from the lower of the two coral beds show statistical anisotropy, ($\chi^2 = 22.39$, $\chi^2_{0.05/11df} = 19.68$) with a bimodal distribution (Text-fig. 13C). Anomalously high frequencies occur between 0° and 30° ($n = 9$, $x + \sigma = 8.95$), and between 150° and 180° ($n = 9$) and 180° and 210° ($n = 12$). Anomalously low frequencies occur between 120° and 150° ($n = 2$, $x - \sigma = 2.21$), 210° and 240° ($n = 2$), and 300° and 330° ($n = 1$). There are secondary modes approximately perpendicular to the main



Text-fig. 12. Map of Anticosti Island with paleocurrent data from this study (circled) and previous work (uncircled) by Long and Copper (1987b, 1994). Single- and double-ended arrows represent uni- and bidirectional currents, respectively. Formation names: V = Vauréal, E = Ellis Bay; member names as subscripts: L = Lavache, H = Homard, J = Joseph Point, M = Mill Bay, P = Prinsta, LC = Lousy Cove.



Text-fig. 13. Corallum orientation data and associated data from the Lavache Member, Vauréal Formation, at locality 13. A. Schematic of section showing relative positions of the coral beds (UCB = upper coral bed, LCB = lower coral bed), crinoid data (cylinders on figure with number of measured stems), and megaripples (wavy line). B. Upper coral bed (n = 127, bold line is orientation of associated crinoid stems from D). C. Lower coral bed (n = 67, bold line is orientation of associated ripple crests). Orientation convention illustrated using N arrow in B; + and - indicate anomalously high and low frequencies. D. Crinoid stem orientation data, upper part of section (n = 13).

modes.

Orientation data (measured parallel to long axis) were also obtained for 21 crinoid stems (index of elongation 10:1 or greater) from the locality 13 section. Of these, 13 were obtained from the upper part of the section and 8 from the lower part (Text-fig. 13A). Because the two coral beds yielded differing orientation patterns, data from the upper and lower coral beds are compared only with crinoid data from the upper and lower parts of the section, respectively. Although the dataset is small, there is a distinct pattern of crinoid orientations in the upper set: a single high frequency (not statistically significant; sample size too small) between 30° and 60° (210-240°) and anomalously low frequency between 120° and 150° (300-330) (Text-fig. 13D). The crinoid orientations are approximately perpendicular to the largest mode of the coral orientations (Text-fig. 13B). The orientation pattern for crinoid stems from the lower beds is not as sharply bimodal. Four out of eight stems fall in the 30-60° range, two fall in the 90-120° range and two in the 150-180° range. The two that fall in the 90-120° range occur in the bed 30 cm below the lower coral bed, where a megaripple orientation of 103° was measured (Text-fig. 13C).

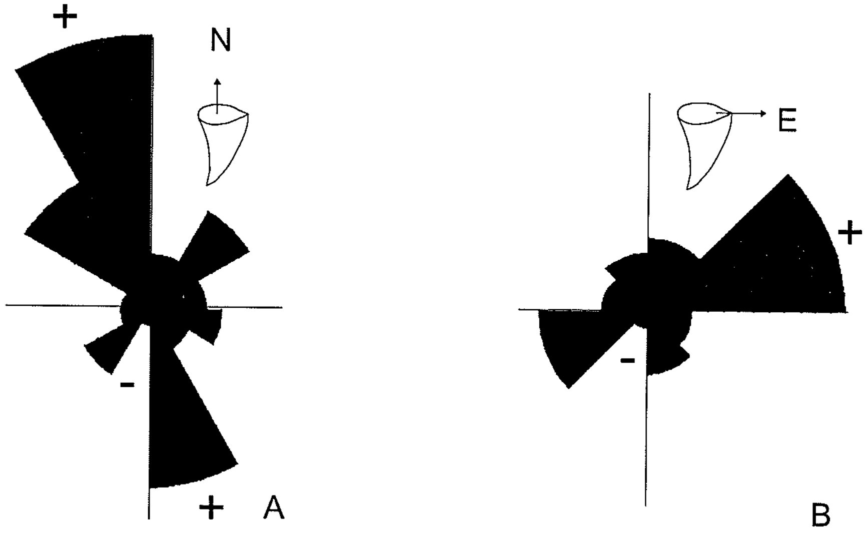
Coralla of *Bighornia patella* have septa that are completely dilated until just below the calice and a prominent columella is present. The extra weight near the calice and unusual subcalceoloid external form produce atypical orientation patterns. Following the general model and previously observed data from the Penitentiary Member of the Stony Mountain Formation of southern Manitoba (Elias et al., 1987), the predicted orientation of *B. patella* is parallel to the current with the apical end pointing either way, with a bimodal orientation parallel to wave crests unlikely as one side of the coral is flattened, restricting rolling. In this study, the presence of perpendicular (but slightly skewed) modes, in addition to a primary mode in the southeast and a smaller mode in the northwest, indicates that subcalceoloid coralla can also be oriented perpendicular to current with a slight downstream skew (Text-fig. 13B). The orientation of the crinoid stems (upper bed) is perpendicular to the main mode and as elongated symmetrical objects would tend to be oriented perpendicular to current, the crinoids are further evidence of a southwest-northeast current.

Data from the lower coral bed, in which the coralla are comparable to those from the upper bed in size and frequency of abrasion, show a bimodal distribution in a north-south direction (Text-fig. 13C). Both the north and south modes are significant although the south mode (two adjacent significant classes) is larger, suggesting a pattern of asymmetry comparable to the upper bed, although less pronounced. Coralla in the lower bed were oriented perpendicular to a north-south oscillating current with secondary modes oriented perpendicular to current. The crinoid data are somewhat isotropic, and are thus of limited usefulness; however, apparently symmetrical megaripples from 30 cm below the lower coral bed were oriented at 103°, approximately perpendicular to the primary modes, providing strong evidence for a north-south current. The current in the lower beds may have been oscillating as the secondary perpendicular modes are not skewed; the combined south mode, however, is larger than the north mode. Note that the current direction shifted significantly between deposition of the lower and upper beds (from N-S to SE-NW). No independent current data have been published from the

Lavache Member of the Vauréal Formation, but, data from higher in the Vauréal at the western end of Anticosti Island show a generally comparable north-south current (Long and Copper, 1994; Text-fig. 12).

3.7.3.2 *Locality 29.* Orientation data were obtained for specimens of *Deiracorallium angulatum angulatum* from a single bed in carbonate mudstones-wackestones of the lower Joseph Point Member of the Vauréal Formation exposed 4.9 m below the culvert above the waterfalls at locality 29 (Text-fig. 12). The coralla are mildly abraded suggesting limited transportation. A bed 1.2 m below that from which the orientation data were obtained contained greater than 50 percent of coralla in calice-up life orientation (19 of 30 in collected slabs), indicating weak currents and/or rapid burial. Prevailing current conditions appear to have changed between the deposition of the two beds as the coralla in the measured bed were reclined and mildly abraded. The distribution of observed orientations in the measured bed is statistically anisotropic ($\chi^2 = 41.96$, $\chi^2_{0.05/11df} = 19.68$) (Text-fig. 14A). There are anomalously high frequencies between 330° and 0° ($n = 19$, $x + \sigma = 11.47$) and between 150° and 180° ($n = 12$). There is an anomalously low frequency between 180° and 210° ($n = 1$, $x - \sigma = 1.03$).

The noncircular, compressed cross section and slight curvature of the skeleton of *D. angulatum angulatum* result in the most common depositional orientation being alar side up. The orientation of the convex cardinal side (measured perpendicular to long axis of the corallum) was recorded to determine if there was any preferential orientation (Text-fig. 14B). The resulting distribution is statistically anisotropic ($\chi^2 = 29.53$, $\chi^2_{0.05/7df} =$

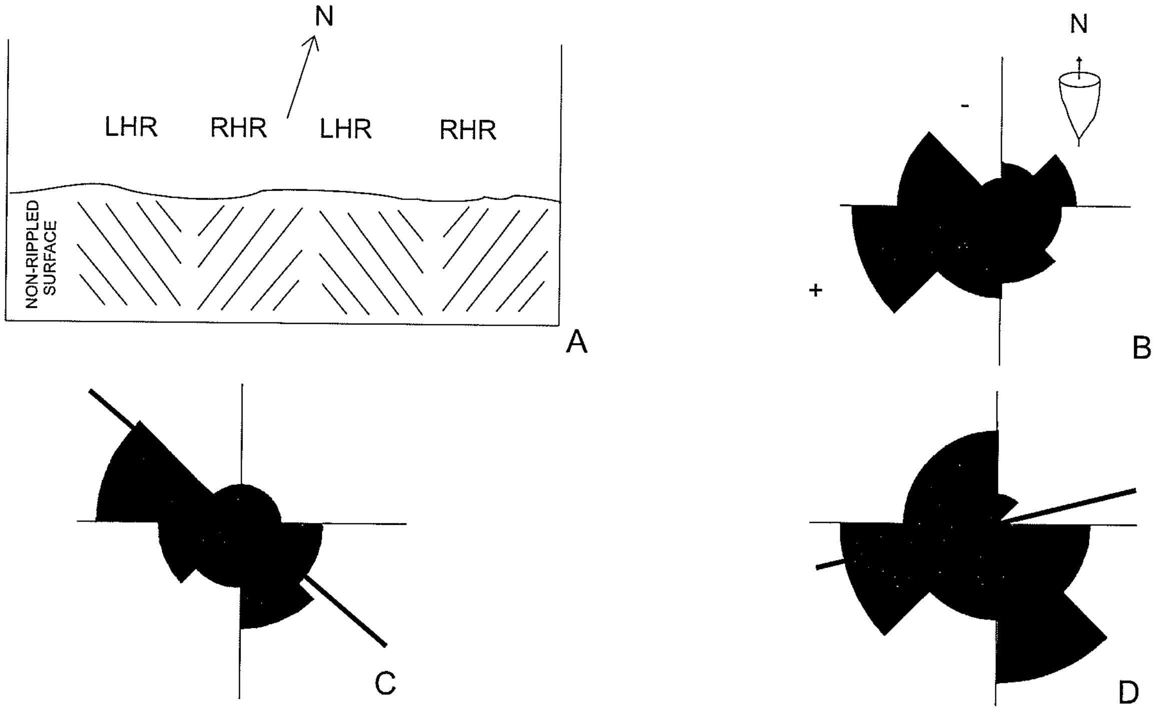


Text-fig. 14. Corallum orientation data from the Joseph Point Member, Vauréal Formation, at locality 29. A. Corallum orientation (n = 75). B. Cardinal side orientation (n = 40). Orientation convention illustrated using N and E arrows; + and - indicate anomalously high and low frequencies.

14.07) with a single significant mode between 45° and 90°. This rose diagram is similar to that for corallite long axis azimuths but rotated 90° to the east.

Following the general model, the apparently bimodal distribution of corallum long axes should indicate orientation perpendicular to current direction, which would be from the east or west. The unimodal cardinal side orientation pattern (Text-fig. 14B) would tend to indicate that prevailing currents were from the west-southwest, as the angulate, convex cardinal side of the corallum would most likely prevent rolling when deposited facing downstream. This result is similar (but rotated ca. 30°) to data from aulacerids in the Joseph Point Member at Battery Point (not sampled in this study; Text-fig. 12), which indicate a northeast-southwest current direction (Long and Copper, 1994). As the Battery Point locality is several kilometres distant and from lower in the member, the similarity of the results may indicate an actual prevailing pattern or may be an artifact of more local variables.

3.7.3.3 *Locality 39.* Data were obtained from the top bed of the Mill Bay Member of the Vauréal Formation as exposed at the type locality (Text-fig. 12) The bed is covered with laterally constrained symmetrical ripple sets with intervening nonrippled surfaces, and was deposited in a tidal embayment (Long and Copper, 1987b) (Text-fig. 15A). For the purposes of data collection in the field, the ripple sets were grouped into left- (ca.131°) and right-handed (ca. 76°) sets. Orientations were measured for specimens of *Bodophyllum englishheadense* from both the rippled and nonrippled surfaces. Data from the nonrippled surfaces are statistically isotropic ($\chi^2 = 11.39$, $\chi^2_{.05/7df} = 14.07$) with a



Text-fig. 15. Corallum orientation data from the Mill Bay Member, Vauréal Formation at locality 39. A. Schematic map of multiple ripple sets on wave cut surface, water is to the north. Ripple sets labelled as left hand (LHR) and right hand (RHR). Several sets of ripples were measured. B. Non-rippled surface (n = 42, + and - indicate anomalously high or low frequencies). C. Left-hand ripple sets (n=27, bold line is orientation of ripple crests). D. Right-hand ripple sets (n = 23, bold line is orientation of ripple crests). Orientation convention illustrated using N arrow in B.

single mode between 225° and 270° (Text-fig. 15B). The left hand ripple sets did not yield sufficient data for statistical analysis (n = 27). A qualitative examination, however, shows a bimodal pattern with the modes at 135° to each other (Text-fig. 15C). The coral orientations from the right hand ripple sets show a bimodal distribution with the two modes 90° apart (Text-fig. 15D), but this sample size is also too small for statistical purposes (n = 23).

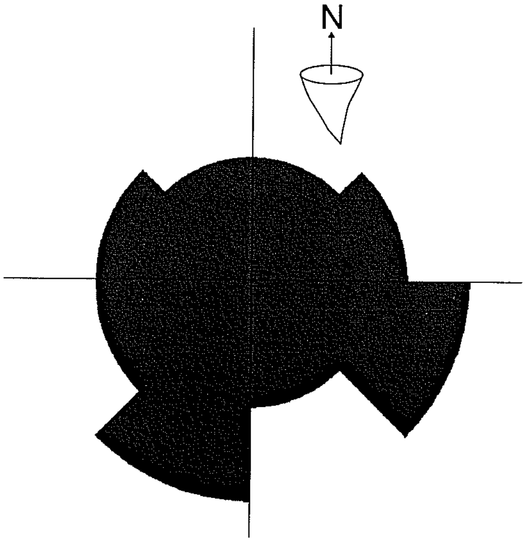
Because *Bodophyllum englishheadense* has a ceratoid to subcylindrical, straight to slightly curved skeleton with a circular cross section, it should closely follow the general model. The single mode in the nonrippled portion of the bed at locality 39 therefore suggests alignment parallel to current direction (from the northeast). In the left hand ripple sets, the limited data show two modes at ca. 135° to each other. As the two modes are nearly parallel to the average trend of the ripple sets, the coralla appear to conform to the bimodal, slightly skewed model for deposition perpendicular to flow. As the ripples are apparently symmetrical, flow was probably bidirectional, northeast-southwest although the skewing of the positions of the modes suggest that the current from the northeast was dominant. Additionally, weathering of the modern tidal platform may have removed the asymmetry of the ripples. Long and Copper (1987b) described larger scale sedimentary structures from the Mill Bay tidal platform with cross beds that indicated a unidirectional current from the northeast (200°; Text-fig. 12). Additionally, they described the depositional pattern of aulacerids from the same locality, which also indicate a northeast-southwest current direction, but slightly shifted from the cross-bed data (224°; Text-fig. 12). These results are comparable to those from this study where the non-rippled and rippled beds both indicate current direction from the northeast.

Data from Long and Copper (1994) for aulacerids in the Mill Bay Member on the west coast of Anticosti Island indicate a north-south current direction. These data are geographically distant enough that subtle basinal architectural differences could be responsible for the different results. While the data from locality 29 are from the underlying member and ca. 70 km away, the apparent rotation of the current direction (nearly 180° difference between the two localities) suggests a significant shift in basinal current dynamics, although considerably more data would be needed to analyze this further. Data from the Ellis Bay Formation at the eastern end of Anticosti Island (Text-fig. 12) indicate local current orientation to be nearly east-west (bimodal) in the Prinsta Member and north-south in the Lousy Cove Member. These cannot be correlated with Mill Bay orientation data and suggest general shifts in the overall current pattern through time.

In the right hand ripple sets at locality 39, a bimodal orientation distribution is present, but only one of the two modes is parallel to the ripple crests. Qualitative examination of the orientation plot (Text-fig. 15D) suggests that the orientations are following the general model for deposition perpendicular to current direction with two modes oriented slightly downstream of perpendicular to the current direction. Rigourous conclusions are not drawn, however, because the dataset is small (n = 23) and associated ripple sets indicate different current directions.

3.7.3.4 *Locality 38*. The coralla of *Dinophyllum hannah* from the Fox Point Member of the Becscie Formation as exposed at locality 38 represent a rare occurrence of a large number of minimally transported specimens. Abrasion is minimal and, where present, was mostly produced by recent weathering. The delicate calice rims are mostly undamaged (except by crushing, probably caused by burial). The data were obtained from a slab in the laboratory and the orientations are relative to an arbitrary north. The purpose of including these data in this study is to contrast the orientation distribution of a nontransported assemblage with transported assemblages as studied here and in previous work (Elias et al., 1987; Elias, Zeilstra and Bayer, 1988). The distribution of orientations on the slab is statistically isotropic ($\chi^2 = 1.85$, $\chi^2_{0.05/7df} = 14.07$) although peaks in two sectors are slightly anomalous ($n = 7$, $x + \sigma = 6.30$) (Text-fig. 16).

Dinophyllum hannah has a trochoid, slightly curved corallum. The calice is deep and dilation decreases toward the calice, thereby maximizing the apical weighting of the corallum. Although the sample size is small, it is apparent that there was minimal response of the coralla to currents. The two peaks in the orientation distribution may represent a weak response to a current, with deposition perpendicular to current direction but slightly skewed downstream. The generally isotropic nature of the orientation data suggests that the high frequency classes may not be statistically meaningful. The rest of the bed is coated with numerous well preserved fossils including brachiopods, domical and branching bryozoans, small tabulate coral colonies, a number of which are in inferred life orientation and only a few of which are obviously overturned. The implication is that current was weak and sedimentation was rapid. The relatively minimal curvature of the coralla is also indicative of low current strength (Elias and Buttler, 1986). It is possible



Text-fig. 16. Corallum orientation data for Fox Point Member, Becscie Formation at locality 38 (n = 41), orientation convention illustrated using arbitrary north arrow.

that there was a prevailing current whose effects were masked by the wedging of the coralla into mechanically unstable positions (e.g., apices pointing downstream; Bolton and Driese, 1990).

3.7.4 Conclusions

A comparison with data from Long and Copper (1987b, 1994) on current orientations within the Vauréal Formation show that the general north-south trend indicated by solitary rugose corals from locality 13 is also reflected in aulacerids, gutter casts and other bidirectional indicators (see Text-fig. 12). The Long and Copper data were, however, taken from localities (and stratigraphic intervals) different from those studied here; therefore any correlation between localities may be the result of regional trends or of coinciding local variables. The results from locality 39 (this study) are quite similar to results of Long and Copper (1987b) for paleocurrent indicators from the same locality. As the paleocoastline was approximately east-west during Anticosti deposition, the prevailing current during the Late Ordovician appears to have been onshore-offshore, possibly varying between the two due to changes in basin geometry (Copper and Long, 1987b).

The locality 13 data are an unusual example of deposition of coralla in combined parallel and perpendicular (but skewed) orientations. Elias et al. (1987, fig. 1d) showed a corallum orientation distribution with perpendicular and parallel modes; however, the perpendicular modes were dominant. Locality 13 data also confirm that orientation results for *Bighornia patella* from the Stony Mountain Formation of Manitoba (Elias et al., 1987) do indeed show deposition parallel to current. The locality 13 data are also significant in showing that coralla that are calice-weighted (dilated septa and a columella) may be deposited with the apex pointing downstream contrary to the general model. The locality 29 data indicate that the cardinal side orientation of compressed, curved and angulate coralla may be useful as current direction indicators when the long axes of coralla are oriented perpendicular to current. The locality 39 results indicate that presence of channels or other localized hydrologic features can obscure prevailing current data as indicated by solitary rugose corals. Further examples from rippled sediments will be necessary to confirm the utility of studying coral orientations in such deposits. The locality 38 data show that in quiet water settings and soft sediments, solitary rugose corals are not preferentially oriented. The apparent isotropy of the data may have been partially influenced by sediment conditions which would hold the coralla in mechanically unstable positions (Bolton and Driese, 1990).

4 RUGOSE CORAL EXTINCTION AND RECOVERY

4.1 INTRODUCTION

The following section is in five parts: first, a brief review of mass extinction data and proposed forcing mechanisms for the Late Ordovician events; second, an analysis of the extinction and recovery of rugose corals from Anticosti Island, related to environmental data and data from other taxa from Anticosti Island; third, a comparison of the extinction of the Anticosti rugose coral fauna with faunas from elsewhere in North America and around the world; fourth, a discussion of recovery of Anticosti and other lowermost Silurian faunas; and finally, a synthesis of paleobiogeography, extinction and recovery of rugose corals from the study area and elsewhere.

4.2 LATE ORDOVICIAN EVENTS

The Late Ordovician mass extinction was the greatest in magnitude (number of families/million years) of the five documented by Raup and Sepkoski (1982) and Sepkoski (1993). This is partially an artifact of the measurement of extinctions per million years (the Ordovician event was particularly rapid), and the total loss of diversity was considerably less than the "slower" Permian/Triassic extinction (Teichert, 1990; Sepkoski, 1993, 1995). Despite these arguments about the magnitude of the extinction, there is no doubt that there was a significant drop in the diversity of many marine groups during the Ordovician. The affected groups included sessile benthic forms (e.g., echinoderms, brachiopods and corals), vagile benthic forms (e.g., trilobites), nektobenthic forms (e.g., conodonts) and planktic forms (e.g., graptolites) (Brenchley, 1989; Droser and Sheehan, 1995; Sepkoski, 1995). The total magnitude of the Late Ordovician extinctions (at the species level) is difficult to assess because data on many taxa are insufficient, and differing taxonomic structures between groups minimize the value of combined data.

The major extinction events occurred in the last million years of the Ordovician, in the Cincinnatian Series, Richmondian and Gamachian stages of the North American standard (or Ashgill Series, Rawtheyan and Hirnantian stages of the European standard), with a minor extinction event that occurred in the Late Caradoc (Brenchley, 1989). There are significant problems in correlation between facies and continents during this time interval. In Europe, the Rawtheyan-Hirnantian and Ordovician-Silurian boundaries are recognised on the basis of graptolite biostratigraphy in deep water shales, while most of the contemporary sections exposed in North America are in shallow water and/or carbonate facies and the biostratigraphy is based largely on conodonts. Additionally, the Richmondian-Gamachian and Rawtheyan-Hirnantian boundaries were not exactly contemporaneous, and a Late Ordovician glacio-eustatic regression appears to have been diachronous (Brenchley, 1989). A section from Arctic Canada records the facies change between basinal shales and platform carbonates, and affords a unique opportunity to correlate directly between conodont and graptolite faunas (Melchin et al., 1991). This allowed the first calibration between the two time scales (see 2.4.5 Geological Setting; Ordovician-Silurian Boundary, Text-fig. 6). Sections from the Great Basin have added to the correlation between adjacent shelf-slope and basinal settings in the latest Ordovician

(Finney and Berry, 1999; Finney et al., 1999). Data from these sections show that extinctions were stepwise and diachronous, depending on water depth; shallow shelf and shelf edge faunas disappeared first, followed by deeper water faunas. Additionally, these sections added to the correlation between the global graptolite standard and the North American conodont biostratigraphic scheme; however, the biostratigraphy of the Silurian portion of the sections was not discussed. Zhang and Barnes (2002a) refined the Silurian conodont biostratigraphy of Anticosti Island and improved precision of the Ordovician-Silurian boundary, but, correlation with global schemes remains challenging.

The extinction events of the Late Ordovician had different effects on different taxa in terms of magnitude, timing and spatial pattern. The following is a summary of the effects on a number of important taxa for the purpose of comparison with coral extinctions.

4.2.1 Crinoids

Crinoid generic diversity in North America dropped suddenly (70% of genera) at the Richmondian-Gamachian boundary (Eckert, 1988). There was another drop in diversity at the Ordovician-Silurian boundary (30% of genera). These data are, however, on a zonal scale and artificially concentrate extinctions. The extinction at the Richmondian-Gamachian boundary is attributed to the glacio-eustatic regression, and resulting loss of living space. Evidence for this is found in the pattern of extinctions in the Cincinnati Province which deepened to the north. The faunas in the shallower southern environments became extinct earlier (Eckert, 1988). The pattern of survivorship of crinoid genera was distinctive, as the stenotopic taxa that were restricted to hard substrates were unsuccessful, and the more eurytopic taxa were successful.

4.2.2 Brachiopods

The brachiopods underwent drastic faunal changes in the Late Ordovician. Like the crinoids, they reached a high in diversity in the Caradoc and then declined into the Ashgill (Williams, 1965; Brenchley, 1989; Harper and Rong, 1995; Copper, 1999). The end of the Rawtheyan (~ Richmondian) saw a major extinction of brachiopods coinciding with the first glacio-eustatic regression. Approximately 25 percent of genera disappeared at this time. A later phase of extinction in the mid-Hirnantian eliminated 40 percent of brachiopod genera (Brenchley, 1989). An analysis of 300 genera from the latest Ordovician and earliest Silurian showed a two stage drop in diversity in the Ordovician followed by a rapid increase in the Silurian (Harper and Rong, 1995). More recent analysis of Sepkoski's (1995) database showed that 45 percent of genera became extinct in the first phase and 30 percent became extinct in the second phase (Brenchley et al., 2001).

The brachiopod faunas of the Hirnantian Stage (named for the cosmopolitan brachiopod genus *Hirnantia*) were markedly different from older faunas. During the Rawtheyan, provinciality was well developed among brachiopods (Owen et al., 1991; Jin, 1999), and degree of morphological complexity and variability was high. In contrast, the Hirnantian faunas had simpler morphologies and were far more cosmopolitan.

Owen et al. (1991) noted that deeper water faunas were more affected by the extinctions, suggesting that an oceanographic overturn and related phenomena were responsible, as the glacio-eustatic regression and climatic cooling would intuitively have had a greater effect on shallower faunas. Jin (1999) noted that epicontinental faunas were considerably different from continental margin faunas, and the extinctions in the midcontinent were due to intolerance of hypersalinity and siliciclastic influx triggered by the regression. Dewing (1999), studying strophomenids from Anticosti Island, noted that extinctions in the epicontinental strophomenid fauna happened earlier than on the continental margin, suggesting that loss of habitat was an important factor in the extinction of epicontinental taxa. Brenchley et al. (2001) also showed that extinction at the base of the Hirnantian was concentrated in the deeper benthic assemblage zones, particularly in the deep-water *Foliomena* Zone, a fauna that was not replaced in subsequent recovery phases. The number of communities represented by the *Hirnantia* Fauna was lower than pre-extinction, showing that the first extinction was a function of both within-community (alpha diversity) loss and loss of communities (beta diversity) (Brenchley et al., 2001). Brenchley et al. (2001) also showed that the second phase of extinction was a function of loss of provincialism (gamma diversity) as the number of provinces before the Hirnantian was 10, the number during the Hirnantian was 9, and the number in the Early Silurian was only five. The *Hirnantia* Fauna was almost completely wiped out before the end of the Hirnantian Stage (Owen et al., 1991; Copper, 1999); isolated holdovers have been found in lowermost Silurian *Parakidograptus acuminatus* Zone rocks in England and Kazakhstan (Rong, et al., 2002).

4.2.3 Graptolites

The graptolites reached a high of diversity during the Caradoc and then declined slowly into the Ashgill (Koren, 1991; Berry and Finney, 1999). A revision of graptolite taxonomy showed that the magnitude of the Late Ordovician extinctions was greater than previously suspected (Melchin and Mitchell, 1991), indicating that only one genus (*Normalograptus*) survived. Xu and Zhang (1995) observed a three phase extinction of graptolites in the Late Ordovician in China. They also noted that the more endemic taxa became extinct before more cosmopolitan forms. A comparable pattern was noted by Finney and Berry (1997, 1999); epipelagic taxa (normalograptids) survived while mesopelagic taxa became extinct.

Melchin and Mitchell (1991) suggested that an oceanographic overturn model was likely responsible for the extinction of the graptolites. As they occupied relatively deep and offshore waters, they would have been insulated from effects of climatic cooling. A regression would not have had any direct effect as graptolites were planktic. Wilde and Berry (1984) suggested that, during the glaciation, cold waters would flood out from the poles into the deeper water areas and possibly drive an overturn, causing upwelling of anoxic waters, to which the graptolites would have been susceptible. The oceanographic model has been further refined, relating the extinctions of graptolites (and other groups) to "ocean states," a shift from a low latitude, stratified ocean to a high latitude mixed ocean (Armstrong, 1995, 1996; Finney and Berry, 1997; Berry and Finney, 1999).

4.2.4 Trilobites

Jaanusson (1979) showed that only 14 families of trilobites survived from the mid-Ashgill into the Llandovery. These data are based on worldwide compilations; data for lower level taxa are more localised. In North America, Sloan (1991) showed that of 62 genera of trilobites extant in the Richmondian, only 27 survived into the Gamachian; however, only 50 of the genera from the Richmondian survived to the end of that stage. This illustrates the value of precise stratigraphic methods in properly assessing extinctions. Owen et al. (1991) showed that there was a limited number of morphologically simple cosmopolitan genera in the Hirnantian Stage, comparable to the *Hirnantia* Fauna of the brachiopods.

The trilobites did have a well developed environmental differentiation, and the effects of the end-Rawtheyan and end-Hirnantian extinctions are demonstrably variable from biofacies to biofacies (Owen et al., 1991). The data show that effects were more pronounced in deeper shelf settings. It has been suggested that during the regression, the faunas were forced basinwards and the deepest faunas were forced off the shelf and extinguished (Brenchley, 1989; Owen et al., 1991). The deepest faunas, however, include the mesopelagic cyclopygids which would not have been affected in such a way, and the extinction is attributed to a probable oceanographic cause.

4.2.5 Conodonts

The conodonts reached a high of generic diversity in the Ordovician that was never regained in post-Ordovician times. Up to 80 percent of conodont species became extinct in the Late Ashgill (Sweet and Bergström, 1984; Barnes and Bergström, 1988). This extinction was shown to have occurred in multiple steps (Barnes and Bergström, 1988; Armstrong, 1995), with the main extinction even taking place in the *extraordinarius* graptolite zone of the Gamachian Stage (Text-fig. 6). The conodont extinction, which is not synchronous with the main graptolite extinction, is also attributed to a change in oceanic conditions (Armstrong, 1995) although the exact mechanism is different as graptolites were strictly planktic and conodonts were generally nektobenthic (Finney and Berry, 1999).

4.2.6 Chitinozoans and Acritarchs

Information on Late Ordovician extinction of chitinozoans and acritarchs is generally lacking as previous studies have tended to focus on paleobiogeography and biostratigraphic correlation. Initial studies, however, showed that chitinozoans in particular suffered a profound extinction at the Rawtheyan-Hirnantian boundary (9/11 species; Grahn, 1988). The acritarchs also appear to have undergone extinction in the Late Ordovician, but the timing is not precisely known (Kaljo, 1996). A more recent study in the Great Basin showed that chitinozoan extinction occurred in a stepwise fashion, starting in the *pacificus* graptolite zone and continuing into the *persculptus* Zone (Finney et al., 1999). As a result of a study of marine palynomorphs in drillcores from Algeria, Paris et al. (2000) concluded that: 1) chitinozoan extinction was not associated with the initial onset of glaciation; 2) extinction was slow and progressive; and 3) because some species survived the glaciation (into the Silurian), that there was no mass extinction of chitinozoans in the Late Ordovician. These conclusions contrast with conclusions from the previously cited publications and review papers (e.g., Brenchley, 1989; Brenchley et al., 2001), suggesting that more work is necessary for a better understanding of the Late Ordovician history of organic microflora.

4.2.7 Tabulate Corals

It has been reported that the tabulate corals lost ca. 70 percent of genera in the Late Ordovician (Scrutton, 1988), although Scrutton (1997) considered that result to be questionable due to the crudeness of the database. Sepkoski (1995) noted a ca. 75 percent drop in genera in the late Ashgill, based on information from large taxonomic databases. That study would have been subject to several problems associated with large taxonomic databases (e.g., taxonomic inconsistency, excessive splitting, stratigraphic imprecision). The occurrence of a significant decline in tabulate genera in the Late Ordovician is, however, not in doubt. While tabulates had been the dominant group of Anthozoa before the end of the Ordovician, they became secondary to the rugosans in the Silurian (Scrutton, 1997). Tabulate corals in the latest Ordovician-earliest Silurian Edgewood Province in eastern North America include several species that cross the Ordovician-Silurian boundary, and the subsequent Silurian assemblages are dominated by the same genera (Young and Elias, 1995).

4.2.8 Rugose Corals

A series-scale examination of rugose coral diversity in Scrutton (1988) showed that rugosan diversity was not apparently affected by the end-Ordovician extinction; the Late Ordovician appears to have been a period of increasing diversity. This pattern is, however, an artifact of the use of overall diversity plotted at the series scale. Rate of extinction data (Scrutton, 1988) show a 75 percent extinction of rugose coral genera in the Late Ordovician. This extinction was matched by an equivalent (or greater) rate of origination, which masked the effects of the extinction. Sepkoski (1995) showed a ca. 66 percent decline in rugose coral genera in the Late Ordovician (see 4.2.7 Tabulate Corals).

Rugose corals originated in the Middle Ordovician and had not reached a high level of diversity by the time of the extinction events. As a result, the longer range pattern of diversity, particularly at the suprageneric level, is not directly comparable to other taxa which were fully diverse in the Ordovician. The most closely comparable taxon, the tabulates, were significantly more diverse (than the rugosans) before the extinction, while the rugosans continued to rise in diversity, surpassing the tabulates after the extinction (Scrutton, 1988, 1997).

Neuman (1982a) noted patterns of coral distribution in the Oslo area in which there was a limited overlapping of species ranges from Ordovician and Silurian faunas. Several of the coral taxa examined by Neuman are similar to those found in North America and in particular on Anticosti Island. *Densigrewingkia pyrgoidea* was shown by Neuman (1997b) to have ranged from the Rawtheyan (~Richmondian) to the Rhuddanian in an offshore drillcore from south of Oslo, and was apparently the only rugosan species from Baltoscandia to have done so.

In the Edgewood Province (see 2.6.4) of the south-central United States, a small rugose coral fauna replaced that which had become extinct at the end of the Richmondian (Elias, 1989, 1992; McAuley and Elias, 1990). These included the highly variable and numerically dominant species *Streptelasma subregulare* which survived into the lowermost Silurian before becoming extinct. Some less common elements of the Edgewood fauna, species of *Streptelasma* and *Grewingkia*, also survived into the lowermost Silurian (Elias, 1989, 1992; Elias and Young, 1998). The entire Edgewood fauna became extinct early in the Rhuddanian and was replaced by a distinctly Silurian rugose coral fauna (Elias, 1992, Elias and Young, 1998).

4.2.9 Summary of Ordovician Extinction Data

Certain patterns recurred in the analysis of various taxa from the Late Ordovician. Many groups reached a high in diversity in the Caradoc that was followed by a decline due to a drop in provinciality. Such a pattern was not observed in rugose corals as they were only beginning to diversify, having first appeared in the early Middle Ordovician. At the Richmondian-Gamachian (~ Rawtheyan-Hirnantian) boundary, most groups underwent a sudden and profound drop in diversity that was contemporaneous with a global glaciation and glacio-eustatic regression (Brenchley, 1984, 1989). Organisms representing sessile or attached faunas (brachiopods, corals, crinoids), vagile benthic faunas (trilobites) and pelagic faunas (graptolites, conodonts), were all affected. The taxa from each group that survived into the latest Ordovician were generally simpler, more eurytopic forms and tended to be cosmopolitan. There were further extinctions in the latest Ordovician (brachiopods, trilobites, graptolites, etc.) at the base of the *persculptus* graptolite zone when the cosmopolitan faunas that flourished in the early Hirnantian disappeared (Brenchley, 1989; Armstrong, 1995; Copper, 1999; Finney and Berry, 1999).

4.3 EXTINCTION: ANTICOSTI ISLAND

4.3.1 Rugose Corals

Although the stratigraphic sections that were sampled at Anticosti Island were not continuous through the entire interval (lower Vauréal Formation to upper Becscie Formation), a composite section including range data from this study (and previously published data) shows a relatively well defined pattern (Text-fig. 3). Extinction patterns based on species range and diversity data are compared with extinction data for other taxa from Anticosti Island and with rugose coral extinction data from around the world.

4.3.1.1 *Anticosti Island species ranges.* The rugose coral species of the Vauréal Formation can be divided into two groups: those whose last appearance datums are within the formation (*Lobocorallium trilobatum vaurealense, Deiracorallium angulatum angulatum*) and those whose ranges extend into the Ellis Bay Formation (*Bighornia patella*, *Bodophyllum englishheadense*, *Salvadorea selecta*, *Palaeophyllum vaurealense* and possibly *Eurogrewingkia pulchella*; see 3.3 Distribution of Rugose Corals in Strata). Both *L. trilobatum trilobatum* and *D. angulatum angulatum* last appear in the Mill Bay Member.

Three species have their final appearance datum within (but well below the top of) the Ellis Bay Formation; *Bighornia patella*, *Salvadorea selecta*, and *Palaeophyllum* *vaurealense* last appear in the mid-Prinsta Member on the eastern end of the island. The last appearance of *Bodophyllum englishheadense* is within the Laframboise Member at the top of the formation. *Streptelasma affine* and *Eurogrewingkia pulchella* range through the Ellis Bay Formation. *Palaeophyllum lyterion* was reported as appearing (Bolton, 1979; Lake, 1981) in reefs in the Prinsta Member (Long and Copper, 1987a) and was found in reefs in the Laframboise Member (Bolton, 1979, 1981a; this study). Some of the Prinsta reef occurrences may actually be cerioid *P. vaurealense* (see discussion of *P. lyterion* and *P. vaurealense*; Systematic Paleontology) but at least one specimen from the Prinsta Member was examined and confirmed to be *P. lyterion*. *Palaeophyllum* n. sp., *Paliphyllum ellisense*, *Bodophyllum* n. sp. and *Streptelasma* n. sp. 1 are all restricted to the Laframboise Member.

Eurogrewingkia pulchella is the only species that crosses the Ellis Bay-Becscie Formation boundary (last appearance ca. 18 m above the base of the Becscie). *Rhegmaphyllum* n. sp. (Becscie Formation, this study) is possibly conspecific with *Rhegmaphyllum* sp. (Bolton, 1981a) from the Jupiter Formation of Anticosti Island. *Dinophyllum hannah* ranges through the Becscie, possibly into the Merrimack Formation (Bolton, 1981a; Bolton's stratigraphic scheme did not include the Merrimack) and is also present in the Gun River Formation. *Cyathactis euryone* occurs at various levels in the Chabot Member of the Becscie as well as in the Gun River and Jupiter formations (Billings, 1862; Bolton, 1981a). *Streptelasma* n. sp. 2 was found to range from the lower Chabot Member to just below the top of the Becscie Formation. *Palaeophyllum* sp. apparently occurs through the entire Chabot Member and probably into the Merrimack

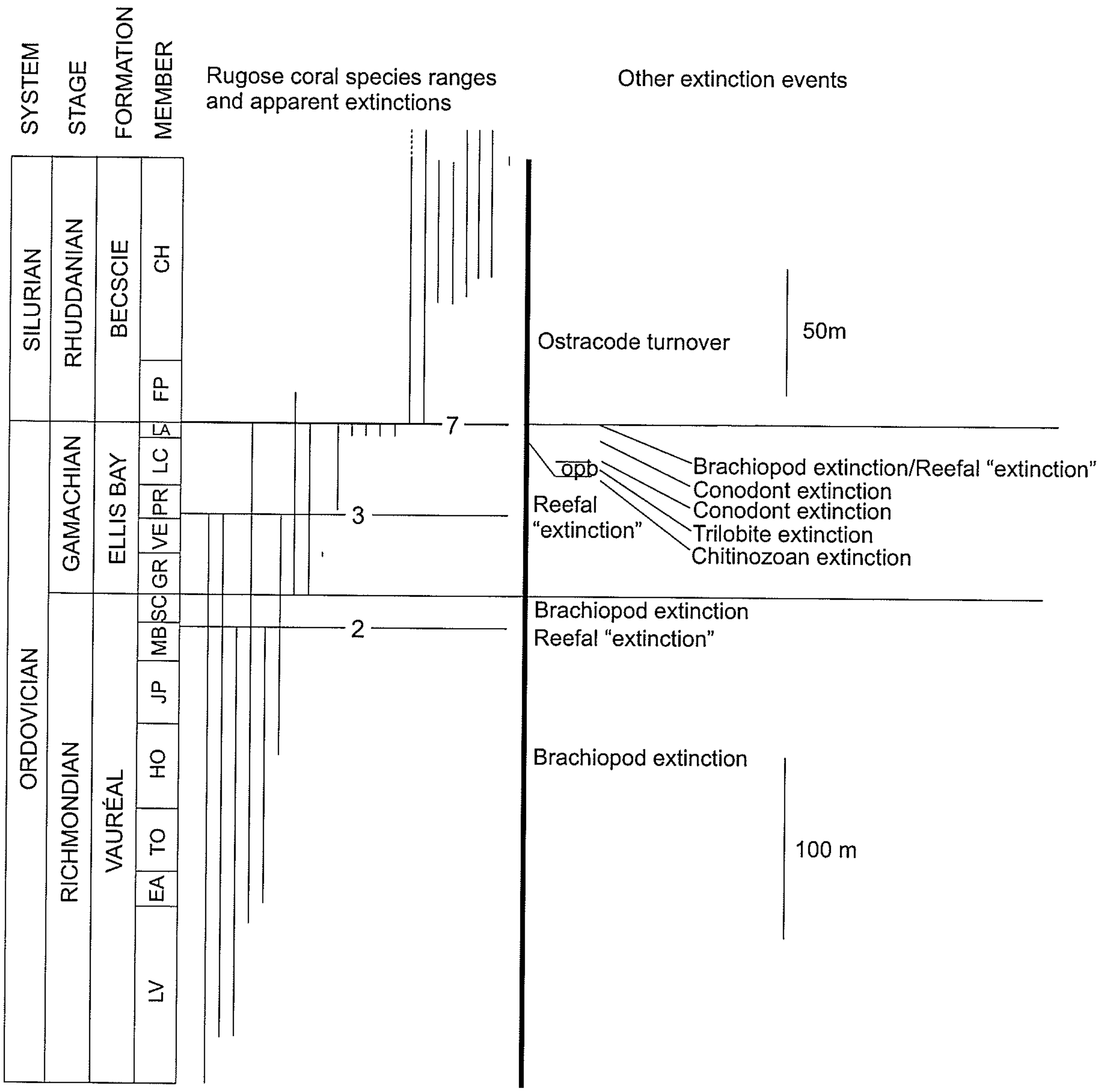
Formation (Bolton, 1981a). *Petrozium pelagicum* and *Strombodes socialis* are only moderately abundant in the Becscie but are known to range higher in the Silurian on Anticosti Island (Bolton, 1981a; Copper and Long, 1998) and elsewhere (Laub, 1979). *Amplexoides* sp. (Bolton, 1981a; this study) is a unique occurrence from (apparently) the upper Becscie, and as such, does not contribute significantly to knowledge of extinctions and originations.

4.3.1.2 *Summary.* The only significant discrete level of extinction is at the Ellis Bay-Becscie (Ordovician-Silurian) boundary. Two species (*Deiracorallium angulatum angulatum*, *Lobocorallium trilobatum vaurealense*) became extinct near the Richmondian-Gamachian boundary, three (*Bighornia patella*, *Palaeophyllum vaurealense*, *Salvadorea selecta*) became extinct in the mid-Ellis Bay (mid-Gamachian) and seven (*Streptelasma affine*, *Bodophyllum englishheadense*, *Bodophyllum* n. sp., *Paliphyllum ellisense*, *Palaeophyllum lyterion*, *Palaeophyllum* n. sp., *Streptelasma* n. sp. 1) became extinct at or near (within topmost metre of the Ellis Bay) the formational/ systemic boundary between the Ellis Bay and the Becscie.

4.3.2 Anticosti Island Extinctions: Other Taxa

4.3.2.1 *Graptolites.* The graptolite extinctions are not clearly defined on Anticosti Island as the sediments of the study interval were deposited in a shallow water, mixed carbonate-siliciclastic (nongraptolitic) ramp sequence (Riva, 1988). Graptolite extinctions elsewhere can be indirectly compared with the Anticosti section by correlation with conodonts (Armstrong, 1995). The main graptolite extinction is correlated to just below the oncolite platform bed (base of the *bohemicus* graptolite zone) of the Laframboise Member of the Ellis Bay Formation (Text-fig. 17). A revised graptolite biostratigraphy based on reexamination of the few graptolites known from the Ellis Bay Formation tends to indicate that the main extinction event occurred sometime during deposition of the lower-mid Ellis Bay (Melchin, 2002). Melchin's conclusions were, however, based on very limited data.

4.3.2.2 *Conodonts*. Conodont range data from Anticosti Island (and elsewhere) show that the Ordovician-Silurian boundary cannot be precisely defined in the study interval (McCracken and Barnes, 1981; Melchin et al., 1991) (see 2.4.5 Geological Setting; Ordovician-Silurian Boundary). The conodont species of the Vauréal generally range through the formation (Nowlan and Barnes, 1981) with varying ratios of the dominant taxa. McCracken and Barnes (1981) described *Gamachignathus*, a minor element that becomes dominant in the Ellis Bay Formation, from the top of the Vauréal, in the interval that was later assigned to the lower Ellis Bay Formation (Long and Copper, 1987a). Although Nowlan and Barnes did not describe an extinction event, an inspection of their data (Nowlan and Barnes, 1981, table 1) appears to show that diversity is lowest at the top of the Vauréal Formation and in the fourth highest collection (i.e., in the basal Ellis Bay Formation, *sensu* Long and Copper, 1987a) although this is difficult to quantify. McCracken and Barnes (1981), in their study of conodonts of the Ellis Bay Formation, indicated that although the faunas of the Vauréal and Ellis Bay are different, "Most of the



Text-fig. 17. Anticosti Island stratigraphy (N.B., Vauréal Formation at different scale) with rugose coral species ranges (this study), correlated with local extinction and turnover events observed for other taxa from the study interval. Numbers represent number of apparent rugose coral species extinctions at each horizon. Laframboise Member exploded to ca. x3 scale on right side of figure. See Text-fig. 3 for rugose coral species (order identical from left to right). Coral ranges not actually continuous (i.e., interpolated through all known occurrences). Solid lines continue above Becscie Formation for species known tooccur in younger rocks, dotted line for species that may occur in younger rocks. For member names, see Text-figure 3. opb = oncolite platform bed.

other species [other than species of *Gamachignathus*] range upward from Fauna 12 [Vauréal fauna], although some seem to show significant differences" (McCracken and Barnes, 1981, p. 65). The pattern of extinction (from a composite section correlated with the Canadian Arctic) in the upper Ellis Bay Formation shows two events, one in the oncolite platform bed and one higher in the Laframboise Member (Armstrong, 1995) (Text-fig. 17). The revised graptolite biostratigraphy of the Ellis Bay Formation (Melchin, 2002) suggests that the first of the conodont extinctions may have occurred below the level of the Laframboise Member (see 4.3.2.1 Graptolites).

4.3.2.3 *Brachiopods*. Two main brachiopod extinctions have been documented on Anticosti Island, in the upper Vauréal Formation (Copper, 1996, 1999) around the Richmondian-Gamachian boundary and at the top of the Laframboise Member (Copper, 1999; Dewing, 1999). Dewing (1999) noted an extinction of four species around the top of the Vauréal Formation, and that six species became extinct at the top of the Homard Member (Text-fig. 17).

4.3.2.4 *Trilobites*. The "Ordovician" trilobites disappear from the study interval at the level of the oncolite platform bed (Chatterton et al., 1983; Lespérance, 1985) (Text-fig. 17).

4.3.2.5 *Ostracodes*. The ostracodes undergo a significant extinction and change in faunal composition 35 m above the base of the Becscie Formation (Copeland, 1981), although the boundary interval is not precisely placed due to gaps in the fossil record of ostracodes in the lower Becscie Formation (Text-fig. 17).

4.3.2.6 *Chitinozoans*. According to Achab (1981) and Soufiane and Achab (2000) the chitinozoans of the Ellis Bay Formation show a pronounced lateral differentiation, associated with facies differences between the east and west ends of Anticosti Island. On both ends of the island, the chitinozoans demonstrate an extinction maximum just below the oncolite platform bed of the Laframboise Member of the Ellis Bay Formation. The bioherms are apparently devoid of chitinozoans, which reappear in draping inter- and super-reefal beds that Soufiane and Achab (2000) considered to be the uppermost Ellis Bay Formation. Some of the super-reefal chitinozoan species disappear at the "contact between the Ellis Bay and the Becscie formations" (Soufiane and Achab, 2000, p. 91). At least three species survived into the basal Becscie Formation (Text-fig. 17).

4.3.2.7 *Reefs*. Copper (2001) noted three distinct horizons of reefal "extinction" (destruction of the reefal ecosystem) in the study interval (Text-fig. 17): Mill Bay Member, mid-Prinsta Member and Laframboise Member. These horizons of reefal development are discrete (i.e., reefs are not developed throughout the study interval). Therefore, the apparent extinction horizons mark both initiation and extinction of reefal ecosystems.

4.3.2.8 *Tabulate Corals.* While the tabulates of Anticosti Island have not been fully revised recently, Copper (1999, fig. 2) published range data for tabulate genera. Of the eight genera listed, one became extinct in the mid-Ellis Bay, three in the uppermost Ellis Bay and four ranged well into the Becscie (one of which originated in the basal Becscie). These are genus-level data and can, therefore, obscure or artificially concentrate extinctions. There may have been extinctions at the species level that were missed, but it is apparent that no genera became (locally) extinct at the Vauréal-Ellis Bay (Richmondian-Gamachian) boundary and that the Ellis Bay-Becscie formational/systemic boundary was a time of significant faunal change.

4.3.3 Comparison of Anticosti Island Extinctions

The most significant extinction of rugose corals takes place at the Ellis Bay-Becscie boundary (Text-fig. 17), approximately correlative with the third brachiopod extinction, and slightly later than trilobite, conodont and chitinozoan extinctions. As brachiopods are benthic and sessile, and thus somewhat similar to corals in life habit, their reaction to environmental change might be expected to be similar. The similarity is at least somewhat coincidental. The concentration of rugose coral extinctions at the boundary is a reflection of the development of high-diversity reefal environments at the top of the Ellis Bay Formation; four species are restricted to the Laframboise Member and another occurs in the Laframboise reefs and in the isolated Prinsta Member reefs (*P. lyterion*, see 3.3 Distribution of Rugose Corals in Strata). In contrast, many of the brachiopod species that became extinct at the formational boundary also occur throughout the Ellis Bay

Formation (Copper, 1999; Dewing, 1999). The brachiopods, conodonts, and rugose corals all underwent extinction in the upper Vauréal (at or near the formational boundary; Copper, 1999), although the rugose coral extinction was minor.

The three levels of extinction of reefal environments in the study interval noted by Copper (2001) correspond with the three main levels of extinction of rugose corals (Text-fig. 17). Although the rugose coral fauna includes both reefal and nonreefal species, the correlation of extinction intervals indicates that the environmental parameters associated with reef development (most significantly water depth and substrate stability) are the same as those associated with rugose corals in general (see 3.4 Paleoecology and Biostratinomy). Comparison of extinction with sea level (Text-fig 5; Dewing, 1999) shows that the three extinction intervals were associated with shifts from regression to transgression. The greatest extent of regression was followed by the most significant extinction (i.e., in the uppermost Ellis Bay/lowermost Becscie).

4.4 COMPARISON WITH OTHER RUGOSE CORAL FAUNAS

4.4.1 Vauréal Formation

The Vauréal Formation rugose coral fauna is typically Red River-Stony Mountain (RRSM) in its composition, with four species that also occur in the Stony Mountain Formation of southern Manitoba (Elias, 1982a, 1983): *Salvadorea selecta*, *Bighornia patella, Lobocorallium trilobatum* and *Deiracorallium angulatum*. The latter two species are differentiated between the two localities at the subspecies level. *Deiracorallium* and *Lobocorallium* from the Stony Mountain do not range into the upper member of that formation (Elias, 1982b, 1983, 1991; Young and Elias, 1999). The RRSM components of the Anticosti fauna disappear at or below the Richmondian-Gamachian boundary except for *Salvadorea selecta* and *Bighornia patella* which survived into the Gamachian Stage (i.e., the species lasted longer on the continental margin, at Anticosti Island). *Bighornia patella* ranges as high in the Stony Mountain as *Salvadorea selecta* and higher than *Lobocorallium trilobatum trilobatum* and *Deiracorallium angulatum gunni.*

The Richmondian Caution Creek and Chasm Creek formations of northern Manitoba have a coral fauna that consists of two species of *Salvadorea*, two species of *Bighornia* including *B. patella*, two species of *Deiracorallium* including *Deiracorallium* sp. cf. *D. angulatum*, *Grewingkia haysii*, *Palaeophyllum raduguini*, *P. stokesi*, *Favistella alveolata stellaris* and *Paliphyllum*? *stummi* (Nelson, 1963, 1981; Elias, 1991). *Bighornia patella* and *Deiracorallium* sp. cf. *D. angulatum* disappeared first as regression progressed, followed by the rest of the coral species (Elias, 1991). The timing of disappearance of *Deiracorallium* sp. cf. *D. angulatum* is comparable to that in the Vauréal Formation, while in contrast, *B. patella* survived until the Gamachian on Anticosti and *Grewingkia haysii haysii*, a trilobate species similar to *Lobocorallium*, survived to the top of the Chasm Creek Formation (top of the Richmondian?), unlike its morphological counterpart from the Vauréal Formation which disappeared at the same time as *D. angulatum.*

The coral fauna of the Maysvillian to Richmondian Aleman Formation and the overlying Richmondian Cutter Dolomite of New Mexico and Texas includes *Bighornia patella*, three species of *Salvadorea*, and two species of *Grewingkia* (Elias, 1985, 1991).

The Richmondian fauna disappeared in a stepwise fashion, with the last three species (*B. patella*, *Salvadorea distincta cutterensis*, and *Grewingkia* sp. cf. *G. franklinensis*) disappearing before the end of the Richmondian in the upper Cutter Dolomite (Elias, 1985, 1991). Several species of *Cyathophylloides*, *Favistina* and *Palaeophyllum* have been reported from the Aleman and Cutter formations (Flower, 1961), including some forms that resemble *P. vaurealense* and *P. lyterion* from Anticosti Island, but no species of colonial rugosan are shared between the areas and range (extinction) data are lacking.

The Richmondian-Rhuddanian Beaverfoot Formation of British Columbia overlaps completely with the studied section, although the majority of rugose corals were obtained from the *Bighornia-Thaerodonta* Zone which is strictly Richmondian in age (Buttler et al., 1988). The solitary species identified from that zone are: *Salvadorea distincta distincta*, an unnamed species of *Salvadorea*, *Bighornia patella*, *Bighornia* sp. cf. *B. bottei, Grewingkia haysii haysii* and *Deiracorallium prolongatum*. The position of the Richmondian-Gamachian boundary is unknown, but all species' last appearance data are within the Richmondian. Colonial rugosan species from the interval include *Palaeophyllum halysitoides*, *P. primum*, *Favistina alveolata stellaris* and *Favistina* aff. *F. stellata* (Buttler et al., 1988). Association data were not given for the colonial species but the overall diversity (of colonial taxa) is higher than in the Vauréal, and the species are all distinct from *P. vaurealense*. The overall rugosan assemblage is comparable to the Vauréal assemblage in terms of morphology and generic makeup although *Bodophyllum* has not been reported from the Beaverfoot.

The rugose corals of the Richmondian portion of the Ely Springs and Fish Haven dolomites and the laterally equivalent Hanson Creek Formation of Nevada and Utah include *Bighornia solearis* (=*patella*?) and species of *Grewingkia*, *Streptelasma*, *Deiracorallium*, *Lobocorallium*, *Bodophyllum*, *Cyathophylloides*, and *Palaeophyllum* (Budge, 1972; Pandolfi, 1985; Sheehan and Harris, 1997). Deposition in the shallower carbonate ramp portion of the interval in the Great Basin was interrupted during the Gamachian and the pattern of extinction cannot be observed, except to note that *Palaeophyllum* is the only genus to range into the overlying Silurian beds (Sheehan and Harris, 1997). Otherwise, this fauna is almost identical to the Vauréal Formation fauna at the generic level. *Palaeophyllum* cf. *P. raduguini*, which is similar to *P. vaurealense*, has been reported from the Ely Springs Dolomite (Pandolfi, 1985).

A small rugose coral fauna of the Ashgill (Richmondian) White Head Formation and related Ordovician rocks of Gaspé, Québec includes *Lobocorallium trilobatum vaurealense, Salvadorea selecta*, an unnamed species of *Grewingkia*, an unnamed species of *Bodophyllum*, and the colonial species *Favistina honoratensis* (Billings, 1865b; Schuchert and Cooper, 1930; Bolton, 1979, 1980; Elias, 1982a). The latter species is similar to cerioid forms of *Palaeophyllum vaurealense* and *P. lyterion*. This is geographically the closest fauna to Anticosti Island and the co-occurrence of *L. trilobatum vaurealense* and *Salvadorea selecta* as well as the overall generic makeup indicate a close relationship between the two areas. More material from Gaspé is necessary to analyze the relationship further; range data and extinction information from Gaspé are insufficient for purposes of detailed comparison with Anticosti and other regions.

Bodophyllum englishheadense is unique to Anticosti Island. *Palaeophyllum vaurealense* is also unique to Anticosti Island although it resembles several Late Ordovician species from elsewhere in North America. In general, the Richmondian (and older) faunas from around North America have comparable generic makeup to the Vauréal fauna, although *Eurogrewingkia* apparently does not appear in the study interval until the Ellis Bay Formation (Gamachian). As the Richmondian-Gamachian boundary is usually missing or unidentifiable at localities other than Anticosti Island, comparison of extinctions is difficult.

The Rawtheyan (~Richmondian) of Baltoscandia has a rugose coral fauna that is generically distinct from that of Anticosti; *Streptelasma* and *Eurogrewingkia* are dominant components. The faunas in Sweden, Norway, and Estonia are generally distinct from each other except that *Grewingkia buceros* and *Streptelasma primum* occur in all three areas (Neuman, 1969, 1986, 1997a, 1997b). The solitary rugose coral faunas in the coeval Richmondian beds of North America (including Anticosti Island) are dominated by taxa with strongly dilated internal elements and noncircular cross-sections, adaptations to high energy environments, while Baltoscandian forms have circular cross-sections and generally no more than moderately dilated internal elements (except *Bighornia orvikui* in the Pirgu Stage of Estonia; Neuman, 1997a). Diversity in the Rawtheyan of Baltoscandia reaches a high of six species in the Herøya Formation in the Ringerike area and in an offshore drill core south of Oslo (both in Norway; Neuman, 1997a, 1997b). While this number is comparable to the diversity high in the Vauréal Formation, the faunal composition is distinct and precise stratigraphic information are lacking (e.g., member-by-member diversity). No species of rugose coral is common to both areas.

The upper Rawtheyan (~upper Richmondian) of Wales has yielded small rugose coral faunas from the Conway Castle Grit at Llandudno and from the Dolhir Formation at Glyn Ceiriog in the northern part of the country. The overall fauna comprises several species of *Bodophyllum* including *B. oilense*, *Borelasma crassitangens*, *Leolasma holtedahli*, *Streptelasma* sp., *Helicelasma* and *Grewingkia* sp. cf. *G. europaea* (Orita and Ezaki, 2001). None of the species occur in the Vauréal Formation. The Welsh fauna has a generally Baltoscandian aspect and shares at least three species with Baltoscandia (Neuman, 1997a, 1997b; Orita and Ezaki, 2001). Range data are not available for the Welsh fauna, so extinction patterns cannot be compared. The Welsh fauna is composed exclusively of species with circular cross-sections, in contrast with the Richmondian Red River-Stony Mountain fauna (including that of the Vauréal Formation) of North America.

4.4.2 Ellis Bay Formation

The Ellis Bay Formation rugose coral assemblage is composed of a "continental margin" type (Elias, 1982a) fauna with *Eurogrewingkia pulchella* dominant and *Streptelasma affine* a significant component although always less abundant than *E. pulchella*. *Eurogrewingkia pulchella* is also known from an unnamed Late Ordovician unit near Ashland, Maine, and *Eurogrewingkia* sp. cf. *E. pulchella* has been reported in the Late Ordovician (Richmondian?) Sequatchie Formation of Alabama and Shellmound Formation at Pope Spring, Georgia (McAuley and Elias, 1990). The upper Ellis Bay Formation reefs include species (*Paliphyllum ellisense*, *Streptelasma* n. sp. 1) that are generally restricted to Anticosti Island. It is significant to note that *Grewingkia* is the dominant genus in many Richmondian and older faunas around North America (Elias, 1981, 1982b, 1983, 1985, 1991; Nelson, 1963, 1981). Elias (1991) interpreted *Grewingkia*-dominated assemblages in the RRSM Province as signifying relatively deep, open marine conditions; these assemblages were replaced during regressive phases. In contrast, *Eurogrewingkia* is the dominant form on Anticosti Island during the comparatively shallow water (but still open marine) conditions represented by the Ellis Bay Formation.

The rugose coral fauna of the Stonewall Formation of southern Manitoba (Richmondian-Gamachian) includes *Palaeophyllum pasense pasense* and *P. pasense parvum*, both of which are similar to *P. vaurealense* of the Vauréal and lower Ellis Bay formations. Other species from the Stonewall Formation, including *Bighornia* sp. cf. *B. integriseptatum* and *Streptelasma*? *hindi* (Stearn, 1956; Elias, 1991), belong to genera common to the two areas, but are distinctly different from Anticosti species.

The rugose coral fauna of the Edgewood Province existed at the same time as that of the Ellis Bay Formation (and lowest Becscie), but there are no rugosan species common to the two areas. The generic makeup of the Edgewood fauna is similar to that of the Ellis Bay: *Streptelasma*, *Bodophyllum* and *Palaeophyllum* are genera common to the two regions. *Keelophyllum* is not found on Anticosti Island and *Paliphyllum* is not found in the Edgewood Province. The Anticosti species *Streptelasma affine* is comparable to some forms of the Edgewood *S. subregulare* (McAuley and Elias, 1990). Other species are not similar, particularly *Bodophyllum englishheadense* and

Bodophyllum n. sp. of Anticosti, both of which differ considerably from the Edgewood *B. shorti* (Elias, 1982a). Unlike at Anticosti Island, where only one species survived into the Silurian, more than one species of the Edgewood fauna survived into the lowermost Silurian. In the Edgewood Province and on Anticosti Island, the most variable and numerically dominant species, *Streptelasma subregulare* and *Eurogrewingkia pulchella*, respectively, were survivors. The surviving fauna of the Edgewood became extinct in the lowermost Silurian and was replaced after a hiatus by a completely distinct assemblage.

The Richmondian-Rhuddanian Beaverfoot Formation of British Columbia includes the "poorly fossiliferous interval" and *Eostropheodonta* Zone of latest Gamachian and Rhuddanian age (Buttler et al., 1988). The lowest occurrence of solitary rugosans in this interval is *Rhegmaphyllum* sp., which may be within the Gamachian. If so, the occurrence is distinct from Anticosti Island where *Rhegmaphyllum* occurs in the lowest Rhuddanian, but not in the Gamachian (see 4.4.3 Becscie Formation).

The Ellis Bay solitary rugose coral fauna is most closely comparable to faunas from the Hirnantian (Gamachian) of central Sweden, Norway and Estonia (Neuman, 1968, 1969, 1977, 1986, 1997a, 1997b). Baltoscandia was geographically close across the Iapetus Ocean (McKerrow and Scotese, 1990), during the Late Ordovician. The Baltoscandian coral faunas include *Streptelasma*, *Bodophyllum*, *Paliphyllum*, *Palaeophyllum* (and *Cyathophylloides*), *Eurogrewingkia* and *Grewingkia* (Neuman, 1968, 1969, 1975, 1977, 1986, 1997a, 1997b); every genus from the Ellis Bay Formation (except *Salvadorea* and *Bighornia*) is represented in the Baltoscandian faunas. The latter faunas also include *Densigrewingkia*, *Helicelasma* (similar to *Salvadorea*; Nelson, 1981;

Elias, 1985), *Borelasma*, *Ullernelasma*, *Leolasma, Crassilasma*, and *Tryplasma* (Neuman, 1969, 1977, 1997a, 1997b), all genera not present in the Ellis Bay Formation. The Hirnantian Baltoscandian rugose coral faunas are distinct from those in the underlying Rawtheyan beds and are endemic. Diversity is generally low (one to two species) except in the Boda Limestone in the Siljan District of Sweden where as many as ten species may be present (Neuman, 1986, 1997a, 1997b). As the Boda is at least partially formed of algal mound facies, it appears that substrate type may be the strongest control on diversity, as on Anticosti Island. The other moderately diverse Hirnantian interval is the Langøyene Formation in the Ringerike area of Norway (Neuman, 1997a, 1997b), in which small bioherms are present. Colonial species, representing *Palaeophyllum* and *Cyathophylloides*, are present in the Ringerike bioherms (Neuman, 1997a, 1997b) but apparently not to the extent that they are in the Laframboise bioherms. Published data from the uppermost Hirnantian beds (*Dalmanitina* Beds), glacial erratics and Tommarp Formation in Sweden, the Langøyene Formation in Norway and the Porkuni Stage in Estonia (Neuman, 1969, 1997a, 1997b) do not yield sufficiently precise ranges to analyze patterns of extinction. *Densigrewingkia pyrgoidea* has been found in Rawtheyan, Hirnantian, and Rhuddanian beds (offshore drillcore at Kristiansand, Herøya Formation?; Neuman, 1997b) crossing both stadial (and extinction) boundaries, unlike any species in North America, except possibly *Eurogrewingkia pulchella*. *Bodophyllum euthum* and *Ullernelasma svartoyensis* have been reported from the basal Silurian Sælbonn and Solvik formations of the Oslo region (i.e., they cross the systemic boundary).

Neuman (1997a), in considering the correlation between the Laurentian and Baltoscandian realms, stated that no species are common to the two and that trends in rugose coral development are generally not comparable. He noted that cardinal fossulae are rare in Baltoscandian rugose corals below the Hirnantian (~Gamachian), the opposite pattern to what is seen on Anticosti Island, where the Richmondian fauna is generally formed of fossulate corals and the Gamachian fauna of nonfossulate corals. The timing of these trends (i.e., the shift to fossulate or nonfossulate forms) is, however, approximately coeval in both realms (i.e., at the Rawtheyan-Hirnantian, or Richmondian-Gamachian boundary), suggesting that there may be some global control on overall rugose coral development. Neuman (1997a) suggested that provinces (and realms) can only be compared where they overlap. Kaljo and Klaamann (1973) compiled the global distribution of rugose coral genera, and their work, though generalized and based on possibly flawed taxonomy, showed the affinity between North America and Baltoscandia in the Late Ordovician, which can be seen in the similarity between the Ellis Bay and Baltoscandian faunas. Webby (1992) used global genus level rugose coral data to compile similarity information for various regions during the Middle-Late Ordovician. Webby showed that while three colonial genera (*Cyathophylloides*, *Palaeophyllum*, *Favistina*) were cosmopolitan, no solitary genus had as wide a range. Using Otsuka and Simpson correlation coefficients, Webby (1992) showed that North America was most similar to Baltoscandia, and northern and western parts of the former U.S.S.R. These data are, however, genus level, and, as such, are not very useful for direct comparison of Anticosti faunas (or any two localized faunas from different regions).

The solitary rugose coral fauna of the Late Ordovician (late Ashgill) Guanyinqao Beds of China (Wang and Ho, 1981; He, 1985a) includes *Streptelasma* and *Bodophyllum*, indicating some affinity with the Anticosti fauna (and with the Baltoscandian fauna). The Chinese faunas also include *Borelasma*, which is the "most representative" genus (Wang and Ho, 1981, p. 55), and other genera (*Sinkiangolasma*, *Siphonolasma*, *Brachyelasma*, *Kenophyllum*, *Crassilasma*, *Pycnactis* and *Paramplexoides*) (Wang and Ho, 1981; He, 1985a; He and Chen, 2003) which show the overall dissimilarity between the two faunas.

4.4.3 Becscie Formation

The Becscie Formation fauna (apart from *Eurogrewingkia pulchella*, which only occurs in the lowermost 18 m) is completely distinct from the preceding faunas. *Dinophyllum*, *Rhegmaphyllum*, and *Cyathactis* are widespread in North America, being characteristic components of the Early Silurian recovery fauna that followed the demise of the Edgewood Province (Elias, 1982a, 1989; McAuley and Elias, 1990; Elias and Young, 1998). The post-Edgewood forms are not identified at the species level (McAuley and Elias, 1990) and therefore cannot be directly compared with the Becscie fauna.

The Becscie fauna cannot be directly compared with most other Llandovery faunas as the majority of Silurian sections are missing the lowermost Silurian (Rhuddanian), or the Rhuddanian portion of the section is in a basinal setting that does not yield rugose corals. The following discussion of Early Silurian faunas from North America (Laurentia), Baltoscandia, and China is intended to illustrate the general faunal makeup of the Early Silurian in geographically associated regions. The Brassfield fauna is discussed because it is the best documented Early Silurian rugose coral fauna in North America, and to contrast it with the older Becscie fauna.

The coral fauna of the Chaleurs Group (Llandovery) of the Gaspé Peninsula, Québec, includes *Palaeophyllum* sp. (Clemville Formation), *Dinophyllum stokesi* (Anse à Pierre-Loiselle Formation) and *Cyathactis* sp. (La Vieille Formation) (Bolton, 1981b). *Cyathactis* sp. was examined in this study and appears to be conspecific with *C. euryone* from the Becscie Formation (and higher) on Anticosti. *Dinophyllum stokesi* is also found in higher strata on Anticosti Island (Bolton, 1981a). The entire Chaleurs Group is probably younger than the Becscie Formation.

The Beaverfoot Formation of British Columbia (see 4.4.2 Ellis Bay Formation) spans the Gamachian-Rhuddanian boundary although the position of the boundary is unknown (Buttler et al., 1988). The lowest definitively Silurian rugose coral occurrence is considered to be *Dinophyllum* sp., which was found ca. 180 m above the Richmondian *Bighornia-Thaerodonta* Zone. *Rhegmaphyllum* sp. occurs as low as 47 m lower in the section, possibly within Gamachian strata (Buttler et al., 1988). As such, it would represent a pre-Silurian occurrence of a typically Silurian genus that predates the Anticosti Island occurrence of *Rhegmaphyllum* n. sp.

Rhegmaphyllum sp. occurs in Richmondian strata in the southeastern United States (Buttler et al., 1988) and in the Gamachian at the base of the Cason Öolite in Arkansas (McAuley and Elias, 1990). The occurrence of *Rhegmaphyllum* in the Cason is considered be a precursor of a post-Ordovician fauna as represented on Anticosti Island and in units overlying strata bearing the Edgewood fauna. *Rhegmaphyllum* co-occurs with

Eurogrewingkia sp. cf. *E. pulchella* in the Late Ordovician Sequatchie Formation of Alabama and the Late Ordovician Shellmound Formation at Pope Spring, Georgia (McAuley and Elias, 1990). *Rhegmaphyllum* is also found in the Lady Burn Starfish Beds of the South Threave Formation near Girvan in Scotland (Neuman, 1997b). These beds are late Hirnantian in age, further showing that *Rhegmaphyllum*, which was a component of the cosmopolitan Silurian fauna, was present in more than one realm in Ordovician times.

The early to middle Llandovery Manitoulin Formation of Manitoulin Island, Ontario, contains the largest known early Llandovery reef complex in the world (Copper and Fay, 1989). These reefs may be temporally equivalent to the Becscie Formation and the fauna includes: *Strombodes* sp., *Evenkiella gracilis*, ?*Entellophyllum vennori* and *Palaeophyllum* (Copper, 1978). Underlying and laterally equivalent level bottom communities also include "small cup corals" which have not been identified (Copper, 1978). Copper (1978) and Copper and Fay (1989) noted variations in the biohermal faunas of the Manitoulin Formation from colonial rugose coral-dominated to stromatoporoid-tabulate coral-dominated to stromatoporoid-dominated. In all cases, solitary rugose corals are rare to absent. These faunas are not comparable to the general makeup of the Becscie fauna and there are no species in common, although the illustrated *Strombodes* sp. (Copper, 1978, pl. 9, figs. 1, 2) may be *Petrozium pelagicum* and the illustrated ?*Entellophyllum vennori* (Copper, 1978, pl. 9, figs. 3-5) has tabulae and dissepiments similar to *Strombodes socialis* (although there is no evidence in the illustrations of periodic expansions). *Evenkiella gracilis* and *Strephophyllum* (Copper and Fay, 1989, fig. 5d, outcrop photograph only) are not similar to any Becscie species and the fauna as a whole is distinct. As no bioherms are known in the Becscie, this may represent an environmental (biofacies) differentiation. The immediately overlying Cabot Head Formation is barren and consists of shallow sub- to intertidal shales (Copper, 1978). Subsequent formations (Dyer Bay, Wingfield, St. Edmund, Mindemoya) contain increasingly abundant shelly fossils including favositids, but no rugosans. The Fossil Hill Formation of Manitoulin Island, ca. 60-70 m above the Manitoulin, has yielded a rugosan fauna that includes *Arachnophyllum mamillare*, *Ptychophyllum stokesi*, *Dinophyllum* sp. and other colonial and solitary species (Copper and Fay, 1989). These suggest a correlation with the Chicotte Formation on Anticosti Island (Copper and Long, 1998), the La Vieille Formation of the Gaspé region (Bolton, 1981b) and the Brassfield Formation of Ohio (Laub, 1979); all three formations are younger than the Becscie Formation.

The rugose coral fauna of the mid-Llandovery Brassfield Formation of the Cincinnati Arch region (Laub, 1979) is much more diverse than that of the Becscie Formation (29 species vs. 9). All the genera of the Becscie are represented in the Brassfield fauna. Two species are common to the Becscie and the Brassfield, *Petrozium pelagicum* and *Strombodes socialis*. In addition, *Arachnophyllum mamillare* and *Dinophyllum stokesi* from the Brassfield (Laub, 1979) are also known from higher in the Anticosti Island section (Jupiter and Chicotte formations; Twenhofel, 1928; Bolton, 1981a).

The Llandovery (late Rhuddanian) to early Wenlock (Johnson and Lescinsky, 1986) Interlake Group of southern Manitoba includes numerous solitary and colonial rugose coral species (Stearn, 1956). The taxonomy, however, is dated and comparison with Anticosti Island is difficult. No species are common to the two areas, and *Dinophyllum* and *Amplexoides* appear to be the only genera in common (Stearn, 1956). Rugose coral diversity in the Interlake Group apparently reaches a maximum of seven species in the Cedar Lake Formation. Unlike the Brassfield Formation, the Interlake Group does not include any species that also occur in younger parts of the Anticosti sequence. The presence of colonial, amplexoid taxa, such as *Synamplexoides*, in the Interlake, shows that at least some portion of the Interlake fauna is distinct at family or higher levels.

Apart from Anticosti Island and the Brassfield Formation, *Strombodes socialis* is also found in the Manistique Group (late Llandovery to early Wenlock) and Kendricks Dolomite (early late Llandovery) of Michigan (Rominger, 1876; Laub, 1979); the Thornloe Formation (late Llandovery or early Wenlock) of Ontario (Bolton and Copeland, 1972); the Silurian Niur Formation of Iran (Flügel and Saleh, 1970); and the type locality, Layer B5, Kochumdeskoy Suite (middle to late Llandovery) of the Siberian Platform (Soshkina, 1955). Laub (1979) considered that the corals from the above localities are conspecific. The widespread occurrence of this Anticosti species (and *Petrozium pelagicum*, see above) illustrates the contrast between the comparatively endemic latest Ordovician fauna and the cosmopolitan Silurian fauna.

Dinophyllum (Högklint Beds and Visby, Gotland; Lindström, 1882; Laub, 1979) and *Rhegmaphyllum* (Visby, Gotland; Lang et al., 1940) occur in the Lower Silurian (Llandovery) of Sweden and elsewhere in Baltoscandia (Kaljo and Klamaan, 1973; Laub, 1979). Neuman (1982b) also noted *Dinophyllum* and unnamed species of *Bodophyllum* and *Streptelasma* from the Early Silurian (Llandovery) Sælbonn and Solvik formations of the Oslo area. However, as there is a hiatus between the latest Ordovician and the earliest Silurian represented in the rocks in this area, the beds may be entirely younger than the Becscie. An additional problem in correlation of these rocks with the Becscie is that the biostratigraphic scheme used in the Oslo region placed the *Normalograptus persculptus* graptolite zone (considered to be uppermost Ordovician in more recent work; e.g., Melchin et al., 1991) in the Silurian, and the exact position of the Ordovician-Silurian boundary was not confirmed (Worsley, 1982, fig. 3). Younger rocks in the area yield rugose corals that include *Palaeocyclus porpita* (Neuman, 1982b) which is also found in the Chicotte Formation (Bolton, 1981a) indicating at least a limited relationship between the two regions. No species are shared between Baltoscandia and the Becscie Formation, indicating that the common genera may be a reflection of the greater degree of cosmopolitanism of Silurian (as compared to Ordovician) corals as described by Kaljo and Klaamann (1973).

The mid-Llandovery Xiangshuyuan and Leijatun formations of eastern China are slightly younger than the Becscie Formation and contain a rich rugose coral fauna which includes *Rhegmaphyllum*, *Crassilasma*, *Brachyelasma*, *Grewingkia*, *Dinophyllum*, *Dalmanophyllum*, *Schlotheimophyllum*, *Prototryplasma*, *Pycnostylus*, *Tryplasma*, *Cantrillia*, *Neocantrillia*, *Tunguselasma*, *Shiqianophyllum*, *Briantelasma* and *Gyalophyllum* (He and Chen, 1997, 2003). While bed-by-bed diversity data are not available, the Chinese faunas are apparently much more diverse than the Becscie fauna.

Rhegmaphyllum and *Dinophyllum* are common genera between the two areas, but no species are shared by China and Anticosti. The other genera are not found in the Becscie Formation (although *Schlotheimophyllum* has been reported from the Chicotte Formation on Anticosti Island; Bolton, 1981a), and the Chinese faunas show affinity with early Silurian faunas of Siberia and Kazakhstan (He and Chen, 1997).

4.5 RECOVERY

4.5.1 Anticosti Island Rugose Corals

As the Becscie Formation represents the lowermost Silurian, an interval that is missing from most stratigraphic sections, it is difficult to compare the recovery of the corals. Rugose coral diversity in the Becscie Formation is relatively low (total number of species = 9). One species disappears in the lowest Silurian, two species first appear in the lowest Silurian and five species first appear higher in the section. Although the rugose coral diversity higher in the Anticosti sequence is not known exactly, it is apparently greater than that of the Becscie fauna (Twenhofel, 1928; Bolton, 1981a).

The earliest Silurian rugose coral faunas in the east-central United States that succeeded the Edgewood Province are comparable to the Becscie fauna (*Cyathactis* sp., *Dinophyllum* sp. and *Rhegmaphyllum* sp.), although these faunas are relatively poorly known (McAuley and Elias, 1990; Elias, 1992; Elias and Young, 1998). The rugose coral diversity in the mid-Llandovery Brassfield Formation of the Cincinnati Arch region is much higher than in the Becscie (29 species vs. 9).

4.5.2 Other Taxa from Anticosti Island

4.5.2.1 *Graptolites*. The graptolites were already recovering from the end-Richmondian extinction and diversifying before the end of the Ordovician (Finney and Berry, 1999). As relatively few graptolites have been found in the study interval on Anticosti Island, the recovery cannot be observed or analyzed meaningfully.

4.5.2.2 *Conodonts*. According to Armstrong (1996), the conodont recovery was relatively rapid, having already been initiated during the *persculptus* Zone (i.e., the latest Ordovician). Barnes and Zhang (1999) described the Silurian conodont faunas on Anticosti Island as having three cycles of radiation. The first cycle was initiated at the base of the *Oulodus* (?) *nathani* Conodont Zone (i.e., the Ordovician-Silurian "boundary zone") (Melchin et al., 1991). Barnes and Zhang (1999) considered that the Anticosti Basin was an "important evolutionary radiative centre" and that the conodont recovery recorded in the Lower Silurian of the Becscie Formation may be the earliest such recovery in the world. Zhang and Barnes (2002a) documented a fairly diverse lowermost Rhuddanian conodont fauna on Anticosti Island, which relatively suddenly increased in diversity in the Gun River and Jupiter formations.

4.5.2.3 *Brachiopods*. Copper (1996, 1999) described two stages of recovery of the Silurian brachiopods on Anticosti Island: a low diversity fauna (with locally high abundance) from the basal Becscie to the mid-Jupiter formations and a high diversity fauna in the upper Jupiter and Chicotte formations. Dewing (1999) noted a similar pattern in the strophomenid brachiopods, in which the diversity that existed earlier in the Ordovician is finally regained only in the Jupiter Formation. Copper (1996) considered that the recovery of brachiopods (and other shelly benthos) on Anticosti (and elsewhere during the lowermost Silurian) was slow due to changing ocean states (from icehouse to greenhouse; Armstrong, 1996).

4.5.2.4 *Trilobites*. According to Lespérance (1985), there are no characteristically Silurian trilobites in the lower 45 m of the Becscie Formation, indicating a post-extinction delay in trilobite recovery and establishment of new faunas. This gap is considerably greater than that for the brachiopods and rugose corals, although preservational bias may account for a gap in the trilobite fossil record.

4.5.2.5 *Ostracodes*. An endemic fauna of ostracodes appears in the upper Becscie (upper part of *Virgiana* interval; Copeland, 1974; Lespérance, 1985). This fauna is distinct from the Ordovician-type fauna which, in contrast to nearly every other taxon studied, ranges a considerable distance (35 m) into the lowermost Becscie (Lespérance, 1985). As the pattern of survival and replacement is completely distinct from those of other shelly faunas, it cannot be compared meaningfully.

4.5.2.6 *Chitinozoans*. All three of the species of chitinozoans that survived into the basal Silurian on Anticosti disappear before the top of member 1 (*sensu* Petryk) of the Becscie Formation (Soufiane and Achab, 2000). There is a gap between the disappearance of the survivors and the appearance of a low diversity (3-4 species) fauna in the upper part of the Becscie. The chitinozoans did not become diverse (8-10 species) until the mid-Gun River Formation (Soufiane and Achab, 2000), indicating a delayed recovery from the extinction.

4.5.2.7 *Reefs*. Reefs do not occur in the Silurian on Anticosti Island below the Jupiter Formation (Copper, 1989; Long and Copper, 1994) and the reefal ecosystem in general was not reestablished until the late Aeronian (Copper, 2001). An exception to this is the development of a ca. 100 km long complex of small bioherms in the early-mid Llandovery Manitoulin Formation of Ontario (Copper, 1978; Copper and Fay, 1989; Cuffey and Copper, 1989). The fauna includes rugosans, tabulates, stromatoporoids and bryozoans. While none of the buildups is large, the widespread local development of bioherms indicates that reefal recovery started early in the Llandovery, although possibly only in protected cratonic areas.

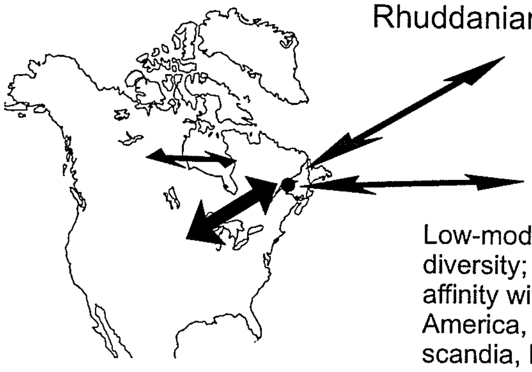
4.5.3 Discussion

The earliest Silurian rugose coral fauna on Anticosti Island is almost completely distinct from the fauna of the underlying Ordovician strata and, as such, must have consisted of immigrants rather than locally evolved taxa. *Rhegmaphyllum*, which first occurs in the Late Ordovician in the southern United States, may constitute a crisis progenitor (Kauffman and Harries, 1996) as the genus appears to have spread around the continental margin from a possible point of origin to the south of the Laurentian realm.

Kauffman and Erwin (1995) described a general model of post-extinction recovery in which there are two intervals: the survival interval and the recovery interval. Rapid speciation and diversification occur in the recovery interval; therefore the low diversity of the Becscie Formation fauna suggests a "survivor" state, although only one species was a holdover from the Ordovician. Younger faunas on Anticosti Island (Jupiter Formation; Twenhofel, 1928; Bolton, 1981a) and elsewhere in North America (Brassfield Formation; Laub, 1979) are more diverse and are more representative of the high diversity "recovery" fauna. As the Chabot Member has a higher rugose coral diversity than the Fox Point Member, and as there was only a single species that survived the Ordovician-Silurian transition, the Becscie Formation appears to preserve a brief "survivor" stage and the beginning of the "recovery" state. The reefal ecosystem was not restored on Anticosti Island or elsewhere (except Manitoulin Island) until Aeronian time (Jupiter-Chicotte formations; Copper, 2001), apparently coincident with diversification of rugose corals. It is unclear why the Manitoulin Island reef fauna was so successful while reefs were not flourishing elsewhere. As diversity of rugose corals in the study interval is highest in reefal settings (see 3.4.3 Diversity), the return of reefs is apparently related both temporally and causally to the recovery of rugose corals.

4.6 SUMMARY OF PALEOBIOGEOGRAPHY, EXTINCTION AND RECOVERY

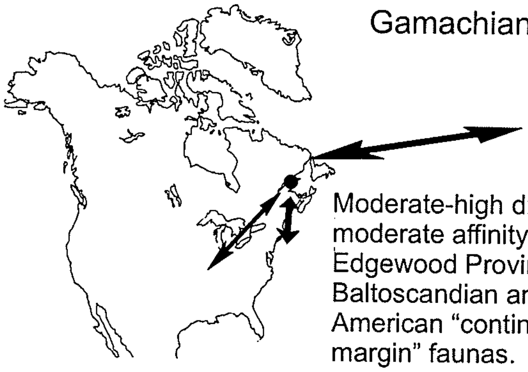
The Anticosti Island coral faunas from the study interval show a distinct three-stage pattern (Text-fig. 18). The first stage (Richmondian) was characterized by an assemblage dominated by species characteristic of the Red River-Stony Mountain Province (with a



Rhuddanian

Low-moderate diversity; strong affinity with N. America, Balto-scandia, Middle East.

End-Gamachian extinction of Anticosti Island rugose coral faunas (and brachiopods, etc.); Silurian faunas new, possibly originating around continental margin before spreading across Laurentia.



Gamachian

Moderate-high diversity; moderate affinity with Edgewood Province and Baltoscandian and N. American "continental margin" faunas.

End-Richmondian extinction of Red River-Stony Mountain corals, brachiopods, graptolites, etc. Influx of "continental margin" forms.

Richmondian

Moderate diversity; strong affinity with Red River-Stony Mountain Province, especially Williston Basin.

Text-fig. 18. Rugose coral affinities of the Anticosti fauna and related events during the three stages represented in the study interval.

minor affiliation with the continental margin). The second stage (Gamachian) was characterized by a "continental margin" type fauna which had moderate affinities with Baltoscandia, China and the coeval Edgewood Province. The third stage (Rhuddanian) was characterized by a sparse but increasingly cosmopolitan fauna with strong affinities with North America, Baltoscandia and to a lesser extent, Siberia and Iran.

The end-Richmondian phase of extinction, related to initial drop in sea level (Brenchley, 1989; Brenchley et al., 1995), was not particularly drastic for rugose corals on Anticosti Island, as only two (of four) of the Red River-Stony Mountain species became extinct close to the Richmondian-Gamachian boundary (Mill Bay Member): *Deiracorallium angulatum angulatum* and *Lobocorallium trilobatum vaurealense*. By comparison, the strophomenids show a moderate extinction at the top of the Homard Member (six species) and another moderate extinction at the top of the Vauréal Formation (four species) (Dewing, 1999). The brachiopods in general suffered a major extinction in the upper Vauréal (Mill Bay-Schmitt Creek members) (Copper, 1999) which correlates with the minor rugosan extinction.

The second phase of extinction (Owen and Robertson, 1995) associated with global deglaciation and oceanographic overturn in the late Hirnantian (Gamachian) was not apparent in the rugose corals of Anticosti Island. The greatest rugose coral diversity in the study interval (8 species in the biohermal Laframboise Member: *N. persculptus* graptolite zone; Melchin et al., 1991) occurred immediately following the time of the second "global" phase of extinction (graptolites, conodonts, trilobites in the oncolitic lower Laframboise Member: *C. extraordinarius* graptolite zone; Melchin et al., 1991).

The most significant "extinction" (drop in diversity) in the study interval occurs at the end of the Ordovician as the Laframboise reefs were extinguished (7 species lost). A low diversity fauna was developed earlier in the Gamachian Stage, but it was not comparable to the cosmopolitan trilobite and brachiopod faunas. The rugosan (and reefal; Copper, 2001) extinction in the mid-Prinsta Member is not generally reflected in other taxa, indicating particular sensitivity to environmental changes (i.e., transgression).

The lowermost Silurian Becscie Formation rugose coral fauna includes cosmopolitan genera (*Rhegmaphyllum*, *Cyathactis*, *Stombodes*, *Dinophyllum* and *Petrozium*). The five genera and three of the species (*Strombodes socialis*, *Cyathactis euryone, Petrozium pelagicum*) occur elsewhere, including North America, Baltoscandia, Iran and Siberia. The first appearance of *Strombodes socialis* was apparently in the Becscie Formation (other occurrences of this species are mid-Llandovery to Wenlock). As *Rhegmaphyllum* occurs in Ordovician and basal Silurian strata around North America, it is possible that the Silurian fauna had multiple sources (i.e., locally evolved taxa and immigrants).

5 OVERALL SUMMARY AND CONCLUSIONS

The results of this project have implications for taxonomy, biostratigraphy, paleoecology, and extinction and recovery. This section will summarize the results and their significance. Rugose coral studies will be considered first, followed by Anticosti Island paleoecology, biostratinomy, and extinction and recovery.

5.1 RUGOSE CORAL STUDIES

A large number of specimens was collected, enabling the revision of the taxonomy of rugosans from the Ordovician Vauréal and Ellis Bay and Silurian Becscie formations. The use of "modern" quantitative methods added significantly to knowledge of variability of the genera and species in question and of variability in general.

5.1.1 Taxonomy

Five new species were found: *Streptelasma* n. spp. 1 and 2, *Bodophyllum* n. sp., *Palaeophyllum* n. sp. and *Rhegmaphyllum* n. sp. The first three species, while only known from a limited number of specimens, have extended the morphologic ranges of already highly variable genera. Future work may show that the two new species of *Streptelasma* are better assigned to another genus.

5.1.1.1 *Colonial rugosans*. The application of quantitative techniques to the study of *Palaeophyllum vaurealense* and *P. lyterion* has extended the knowledge of those two species but, more importantly, will enable more rigorous comparison between species of

Palaeophyllum in the future. Quantitative techniques, now commonly used in studies of tabulate corals, have not been widely applied to phaceloid colonial rugosans. In particular, the application of quantitative techniques helped to show that *Palaeophyllum clion* Bolton, 1979 is a junior synonym of *Palaeophyllum lyterion* (Bolton, 1979) and that the spatial variation of *P. lyterion* in response to environmental variables is significant. The comparison of coefficient of variation of means vs. mean coefficient of variation of internal biometric parameters in *P. lyterion* and *P. vaurealense* showed that degrees of intra- vs. intercolonial variation were approximately equal in the two species. This technique has the potential to be used to compare degrees of intra- and intercolonial variability in other colonial taxa. *Palaeophyllum* n. sp. was shown to have reproduced by octipartite parricidal offsetting, apparently a unique feature in this well known, cosmopolitan, genus. *Paliphyllum ellisense* was shown to be a colonial species, unique for the genus.

5.1.1.2 *Solitary rugosans.* *Salvadorea selecta*, while identical to specimens from the Stony Mountain Formation of Manitoba, was shown to attain much greater size on Anticosti Island. *Streptelasma* n. sp. 1 and *Streptelasma* n. sp. 2 both have more highly dilated internal elements than other species of the genus and the former species has distinctively highly arched tabulae. The median lamella (a generic characteristic of *Bodophyllum*) was shown to be weakly developed in late stages of *Bodophyllum englishheadense*, but the smaller specimens and early stages of larger specimens show that the median lamella is present. Examination of a large number of specimens of

Eurogrewingkia pulchella enabled quantification of variability of external and internal characters, particularly the frequency of occurrence of the median lamella, which was shown to increase with greater height in the stratigraphic section. Corallum length and number of major septa relative to corallum diameter also increased with increasing stratigraphic position, and the overall pattern of intraspecific change through time appears to be a change in rate (heterochrony) rather than addition of new features. As the uppermost Ellis Bay Formation represents a distinct biohermal environment within the section it cannot be determined whether the variation in *E. pulchella* is a purely "evolutionary" (temporal) effect or an ecophenotypic (environmental) response. The morphologic range of the genus *Dinophyllum* Lindström, 1882 was extended by the inclusion of *Dinophyllum hannah* (Twenhofel, 1928), a species with slightly axially depressed tabulae. The holotype of *Zaphrentis anticostiensis* Twenhofel, 1928 was shown to have been incorrectly assigned to *Dinophyllum* (Bolton, 1981a); its taxonomy is uncertain but it may belong to *Amplexoides*. Analysis of the taxonomy of the two new species of *Streptelasma* has illustrated the overall difficulty in attaining consistency in analysis of the Streptelasmatidae, a family in which the genera have overlapping characteristics and few truly distinctive features.

5.2 ANTICOSTI ISLAND

5.2.1 Paleoecology and Biostratinomy

The paleoecology of the rugose corals of Anticosti Island was studied using a combination of skeletal properties (primarily curvature, growth form, degree of internal dilation, distortions/talons), associated substrate (sedimentology) and biological associations (epi- and endobionts, faunal assemblages). Degree of transportation and mixing and sedimentation rates (determined by analysis of external abrasion and breakage) were also used in paleoecological study, at least partially to determine if associated taxa were parts of life or death assemblages. These data combined to show that some species were generally restricted to particular environments (*Bodophyllum englishheadense*, *Bodophyllum* n. sp., *Deiracorallium angulatum angulatum*, *Paliphyllum ellisense*, *Streptelasma* n. sp. 1, *Streptelasma* n. sp. 2, *Palaeophyllum lyterion*, *Palaeophyllum* n. sp.), some were moderately adaptable (*Salvadorea selecta*, *Bighornia patella*, *Palaeophyllum vaurealense*, *Cyathactis euryone*, *Rhegmaphyllum* n. sp., *Lobocorallium trilobatum vaurealense*) and a few species occurred in a wide variety of environments (*Eurogrewingkia pulchella*, *Streptelasma affine*, *Dinophyllum hannah*). The latter group consists of common and highly variable species, particularly *Eurogrewingkia pulchella*, which shows that ability to adapt to various environments helped some species to maximize their geographic range as well as their population size.

Palaeophyllum lyterion was also shown to be highly variable, despite being restricted to the biohermal Laframboise Member of the Ellis Bay Formation (and possibly isolated bioherms of the Prinsta Member). The differences between specimens from three localities were shown to be statistically significant, but the particular environmental characteristic responsible for the variability could not be identified. It appears that fairly subtle differences in environment caused measurable differences in *P. lyterion*.

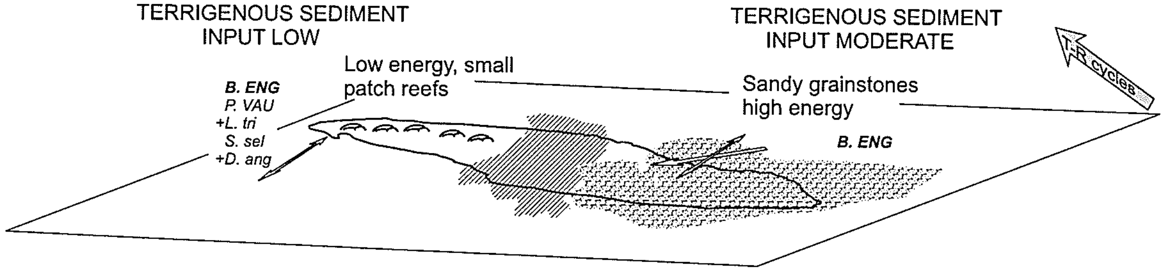
Using a combination of results of paleoecologic and biostratinomic studies, previously published information on the sedimentology of the study interval (primarily Petryk, 1981a, 1981b; Long and Copper, 1987a, 1987b, 1994), and data on rugose corals from the Upper Ordovician and Lower Silurian of North America, the history of rugose coral faunas on Anticosti Island was reconstructed (Text-fig. 19). The temporal divisions in Text-figure 19 are arbitrary, based on the ranges of significant rugose coral species or groups of species and related environmental changes (transgression, regression). Faunal events (immigration, extinction) and composition are correlated with substrate and energy conditions where data are available.

5.2.2 Extinction and Recovery

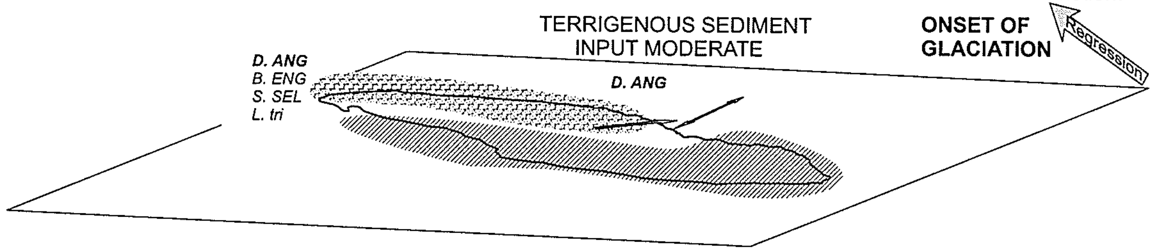
The rugose coral fauna of the study interval apparently underwent three phases of extinction. The first, in the uppermost Vauréal Formation (uppermost Richmondian), was approximately correlative with the onset of brachiopod, trilobite and graptolite extinctions worldwide, suggesting that global effects (glaciation, oceanographic overturn, regression) were contributing factors. The second phase of extinction, in the mid-Prinsta Member of the Ellis Bay Formation (mid-Gamachian), was coeval with a minor local "extinction" of the reefal ecosystem (and possibly with a global reefal extinction; Copper, 2001). It was probably a result of a glacio-eustatic sea-level oscillation. The third and most significant level of extinction was at the formational (Ellis Bay-Becscie) and systemic (Ordovician-Silurian) boundary. It was contemporaneous with certain local and global extinctions, while being younger than local and global conodont and trilobite extinctions. The only survivor into the basal Rhuddanian was *Eurogrewingkia pulchella*,

Text-fig. 19 (see subsequent two pages). Environmental variables and associated rugose coral faunas from study interval on Anticosti Island. Sedimentology generalized from Petryk (1981a) and Long and Copper (1987a, 1987b, 1994). Current arrows are single- or double-ended, depending on whether current is uni- or bidirectional. Under species frequency, dominant = 50+%, common = 10-50%, and uncommon = <10% of fauna from a given member(s) (in multi-member stages, listed species may not actually have co-occurred). Species appearance data apply only to study area (N.B., *Amplexoides* sp. may be from the Merrimack Formation); some species occur in older or younger units elsewhere. T-R cycles = transgressive-regressive cycles. Species abbreviations are as follows:

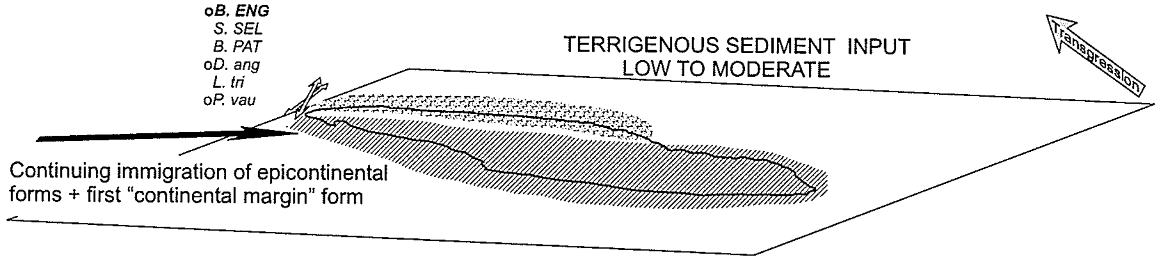
B. pat = *Bighornia patella*
L. tri = *Lobocorallium trilobatum vaurealense*
S. sel = *Salvadorea selecta*
D. ang = *Deiracorallium angulatum angulatum*
P. vau = *Palaeophyllum vaurealense*
B. eng = *Bodophyllum englishheadense*
E. pul = *Eurogrewingkia pulchella*
S. aff = *Streptelasma affine*
P. ell = *Paliphyllum ellisense*
P. lyt = *Palaeophyllum lyterion*
S. sp. = *Streptelasma* sp.
S. n. sp. 1 = *Streptelasma* n. sp. 1
R. n. sp. = *Rhegmaphyllum* n. sp.
D. han = *Dinophyllum hannah*
C. eur = *Cyathactis euryone*
P. sp. = *Palaeophyllum* sp.
S. soc = *Strombodes socialis*
P. pel = *Petrozium pelagicum*
A. sp. = *Amplexoides* sp.



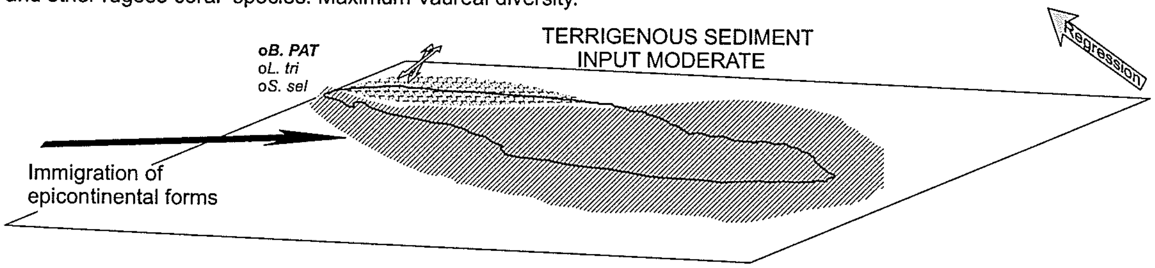
Stage 4. Mill Bay Member, first reef formation, considerable lateral environmental variation. First level of extinction.



Stage 3. Joseph Point Member, dominantly fine grained sediments in low energy, deeper water conditions.

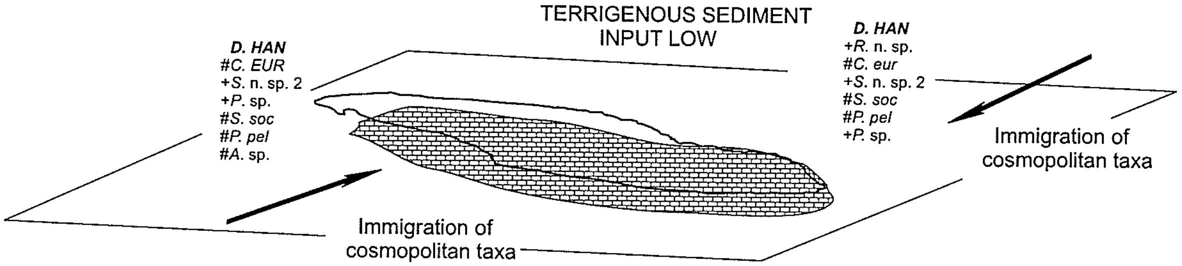


Stage 2. Easton-Homard members, lime mudstone to skeletal grainstones. Immigration of Red River-Stony Mountain and other rugose coral species. Maximum Vauréal diversity.

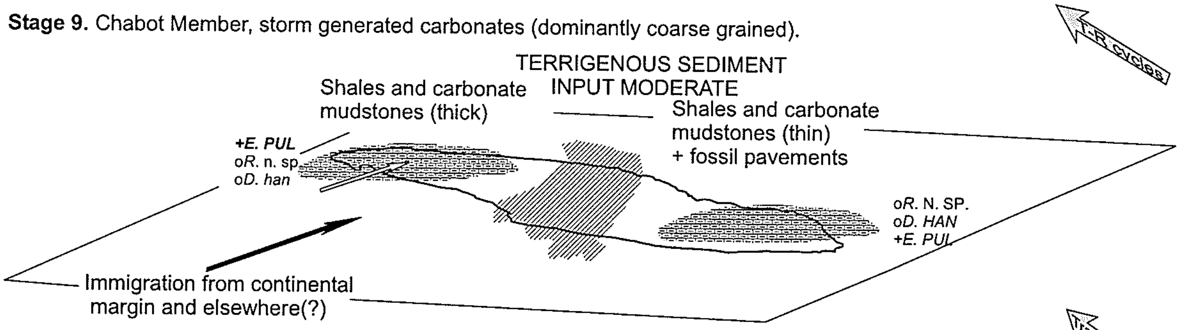


Stage 1. Lavache Member, first rugose corals immigrate into relatively deep, calm water. Immigration from epicontinental area (Red River-Stony Mountain Province). Species may be from unexposed, sub-Lavache Vauréal Formation.

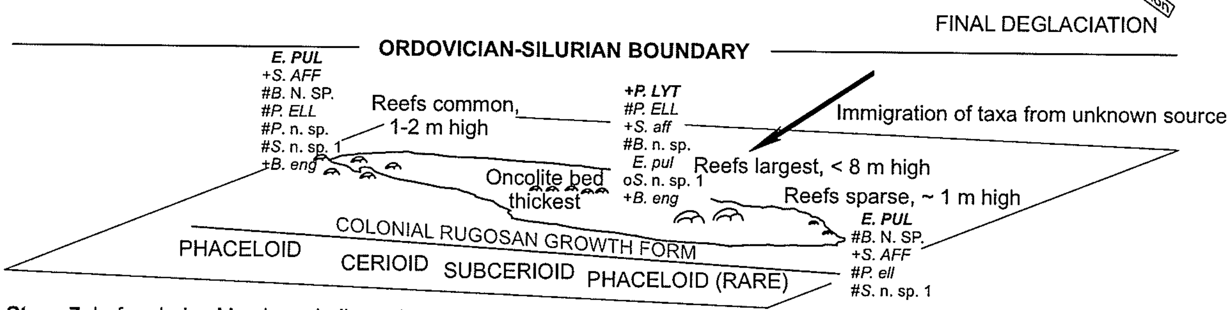
LITHOLOGY		SYMBOLS	SPECIES FREQUENCY/EVENTS	
▨ No data	▒ Coarse siliciclastics	/ Current direction	***SPECIES*** Dominant	o*Species* First appearance
▤ Sands/silts-carbonates	⌓ Bioherms	➞ Immigration	*SPECIES* Major	+*Species* Last appearance
▤ Shales-carbonates	▦ Carbonates	⇨ Sea - level events	*Species* Minor	#*Species* Only appearance



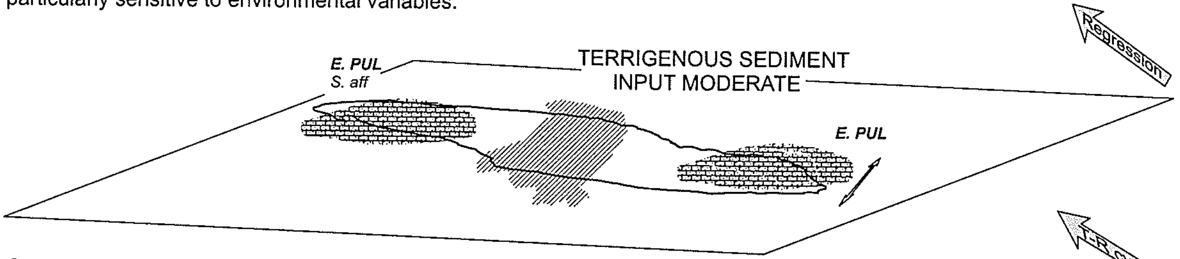
Stage 9. Chabot Member, storm generated carbonates (dominantly coarse grained).



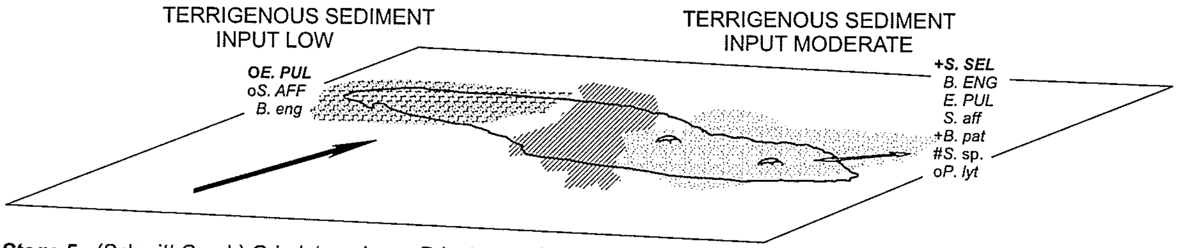
Stage 8. Fox Point Member, deepening, storm-dominated deposition. Fauna homogeneous.



Stage 7. Laframboise Member, shallowest part of sequence, extensive and variable reef development. Colonial rugose corals particularly sensitive to environmental variables.



Stage 6. Upper Prinsta-Lousy Cove members, terrigenous input equal in east and west; fauna uniform across island.



Stage 5. (Schmitt Creek) Grindstone-lower Prinsta members, siliciclastic (coarse) vs. carbonate-dominated sediments, with different faunal assemblages. Immigration possibly from continental margin of Laurentia. Final extinction of Red River-Stony Mountain taxa.

by far the numerically dominant (and most variable) species in the Ellis Bay Formation. This pattern is similar to that seen in the Edgewood Province of the east-central United States in which the Gamachian rugose coral fauna was dominated by the highly variable species *Streptelasma subregulare*, which also survived into the basal Silurian (Elias, 1989; Elias and Young, 1998).

The rugose coral fauna of Baltoscandia was comparable with the fauna from Anticosti Island during the Rawtheyan-Hirnantian (~Richmondian-Gamachian) at the generic level, with *Grewingkia* (and *Eurogrewingkia*) and *Streptelasma* as the dominant genera. No species were shared between the realms. Diversity in the Hirnantian was generally low except in the carbonate mound and biohermal facies of the Boda Limestone in the Siljan District in Sweden and the Langøyene Formation in the Ringerike area of Norway (Neuman, 1997a, 1997b). This pattern is comparable to the diversity highs in the biohermal units in the study interval on Anticosti Island. The Rawtheyan and Hirnantian faunas are distinct with the apparent exception of *Densigrewingkia pyrgoidea* which is common in rocks of Rawtheyan to Rhuddanian age in an offshore drillcore south of Oslo (Neuman, 1997b). Genus range data for rugose corals from Baltoscandia show stepped clusters of first and last appearances in the Ashgill, with concentrations at the base and top of the Hirnantian Stage (Neuman and Kaljo, 2004). According to a species diversity plot, the greatest drop in diversity occurred before the Rawtheyan Stage, in the early Ashgill (Neuman and Kaljo, 2004), in contrast with the pattern in Laurentia. Only one species apparently crosses the Ordovician-Silurian boundary (*Densigrewingkia pyrgoidea*) (Neuman, 1997a). Neuman and Kaljo (2004) described three intervals of extinction (Caradoc, Rawtheyan, Hirnantian) in Baltoscandia, although the timings are not known precisely. The latest Ordovician extinction(s) in Baltoscandia may have also been due to the loss of the reef habitat as a result of deglaciation, transgression, and associated oceanographic effects. At the genus level, only four of thirteen genera do not range across the Ordovician-Silurian boundary. This contrasts with Anticosti Island where the systemic boundary was the time of greatest extinction.

All three rugose coral extinction events on Anticosti appear to correlate with global events. Despite the temporal correlation, the third, and most significant, extinction event on Anticosti appears to have been a result of local environmental changes causing extinction of the reefal habitat, although it was probably related to the basal Silurian transgression. As more than half of the taxa lost (in the third extinction interval) only appear for the first time in the uppermost Ellis Bay Formation (latest Ordovician), the extinction event appears to have been a local reflection of a global environmental change, which can be correlated temporally if not causally with extinctions of other taxa and in other regions. The presence, and eventual extinction, of Red River-Stony Mountain species in the Gamachian shows that the continental margin acted as a refuge for species that were extinguished at the end of the Richmondian in the middle of the craton (Elias, 1989).

The study interval only includes the earliest stage of recovery of the rugose corals. As most Silurian sections (throughout the world) are lacking the basal Rhuddanian portion of the interval, it is difficult to compare the Anticosti section with sections from elsewhere. Consequently, relatively little could be concluded about the nature of the rugose coral recovery on Anticosti Island, except that the fauna included cosmopolitan forms. Some coeval sections in North America show that a few Ordovician rugose coral species survived into the earliest Silurian. These sections, however, include unconformities between earliest Silurian beds containing the Ordovician holdovers and younger beds containing a more typical Silurian fauna (Elias, 1989).

In general, the study of the Anticosti Island rugose coral fauna has shown that for rugose corals, local environmental variables are at least as important as global effects in determining spatial and temporal distribution, even if the former may be secondary effects of the latter. The rugose coral "contribution" to the Late Ordovician mass extinction is more likely a series of small, coeval events than a single large event, such as would result in the extinction of a pelagic, planktic taxon like the graptolites. This pattern found on Anticosti Island is similar to the larger scale pattern of extinction of rugose corals in North America in the Late Ordovician, in which whole provinces, each with distinctive environmental characteristics, come and go, taking their endemic faunas with them (Elias, 1989, 1992; Elias and Young, 1998). Within those provinces, local environmental variables further complicate the picture of rugose coral distribution. This pattern is also generally comparable to that of the Baltoscandian faunas in which each region (Sweden, Norway, Estonia) has distinct and endemic faunas with only a few widespread species (cf. *Bighornia patella* in North America). The lithologies (depositional environments) were also variable resulting in a condition similar to North America in which the rugose coral fauna is a function of local rather than realm-wide or global conditions.

The pattern of rugose coral extinction in North America is comparable to the pattern of final extinction of the Rugosa in the latest Permian in South China (Ezaki, 1994). Ezaki determined that extinction was driven by a combination of local and large scale factors. While the Permian extinction may have been a much slower event or series of events (Teichert, 1990; Erwin, 1994; Sepkoski, 1995; Jin et al., 2000) the overall pattern is that, in times of crisis, rugose corals are more sensitive to local than global environmental variables. Further study of rugose corals from the Silurian section on Anticosti Island and from the earliest Silurian elsewhere would help to increase understanding of the recovery of the rugose corals. As rugose coral diversity in the Ordovician was generally not high (i.e., the rugose corals, a relatively young taxon at the time had not fully diversified) the mass extinction and subsequent recovery were not as profound. Additionally, as the basal Silurian is characterized by unconformities globally, the earliest stages of recovery of the rugose corals can only be observed at a few localities.