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Devonian Brachiopods from Bird Fiord Formation, Arctic Canada

by

Rong-yu Li ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Earth and Atmospheric Sciences

Edmonton, Alberta

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September, 9, 2002

Dedicate to:

My mother Feng-yu Zhong

And the everlasting memory of my father Quan-shou Li

Abstract

The brachiopod fauna from the upper Lower to Middle Devonian Bird Fiord Formation of Arctic Canada includes 22 species that belong to 21 genera, among which *Borealistrophia, Arcticastrophia,* and *Grinnellathyris* are new genera, and *Borealistrophia rongi, Arcticastrophia costellata, Gypidula mega*, *Grinnellathyris alvarezis, Spinatrypa* (*Isospinatrypa*) *parvia*, *Desquamatia* (*Independatrypa*) *fortis*, *Nucleospira stelcki, Warrenella grinnellensis*, and *Cranaena briceae* are new species.

Cluster analysis shows that the brachiopods belong to the *Atrypa-Elythyna* Community Group and the *Spinatrypina-Desquamatia* Community Group. The former encompasses the *Atrypa-Elythyna* and *Atrypa-Elythyna-Perryspirifer* communities whereas the latter includes the *Spinatrypina-Dequamatia* and *Spinatrypina-Desquamatia-Cranaena* communities. The distribution of these communities was fundamentally controlled by water depth. Thus, the *Atrypa-Elythyna* Community Group, which belongs to Benthic Assemblage 3, lived in a shallow, near shore shelf environment. The *Spinatrypina-Dequamatia* Community Group, which belongs to Benthic Assemblage 4, lived in a deeper, distal shelf environment.

Quantitative study of 316 Eifelian brachiopod genera from Arctic Canada and around the world, using similarity analysis, probabilistic analysis, and parsimony analysis of endemicity (PAE), shows that the Arctic Canada has a close faunal affinity with Western

Canada and Nevada and that they can be assigned to the Cordillera Region of the Old World Realm. The quantitative results also show that the Old World Realm and Malvinokaffric Realm can be readily recognized whereas the qualitatively defined Eastern Americas Realm (as represented by the Michigan and Appalachian basins) is unrecognizable during Eifelian time. In the Old World Realm, the Eurasia and Laurentia-South China subrealms are defined based on quantitative analysis. The qualitatively recognized Uralian, South China, and Cordilleran regions within Old World Realm are confirmed by the quantitative analysis, whereas the Rhenish-Bohemia region may be split into the Rhenish and Bohemia regions. The analysis of Emsian brachiopod data confirmed the existence of the Eastern Americas Realm during Emsian time. The disappearance of the Eastern Americas Realm in eastern North America may have taken place during late Emsian or early Eifelian due to the sea level rises represented by the T-R Cycles Ic, Id, Ie that were sufficient to breach the barrier that separated western (Old World Realm) and eastern America.

Acknowledgements

I am greatly indebted to my supervisor, Dr. Brian Jones, for his guidance, dedication, patience, encouragement, and support during the course of this study. I am especially appreciative of his editorial skills, which have improved this thesis considerably. Brian's help and friendship were invaluable.

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Chapter 1

Introduction

The Bird Fiord Formation, first defined by McLaren (1963), is an upper Lower to Middle Devonian carbonate-clastic succession that changes from marginal-marine carbonates in its lower part, to shelf, deltaic, and fluvial siliciclastics in its upper part (Embry and Klovan, 1976; Goodbody, 1989; Goodbody in Mayr et al., 1994). It crops out on southwest Ellesmere Island, North Kent Island, northwest Devon Island, Bathurst Island, and parts of Cornwallis Island. It varies from 465 m thick on eastern Grinnell Peninsula to more than 900 m on western Bathurst Island (Goodbody, 1989). This formation contains numerous brachiopods (Goodbody, 1985). Some of the brachiopods, collected from isolated localities, were described by Meyer (1913), Johnson and Perry (1976), Brice (1982), Jones (1982a, 1982b), and Jones and Boucot (1983).

Between 1979 and 1983, Q. H. Goodbody and B. Jones collected 47026 brachiopod specimens in 140 collections from 34 localities throughout the outcrop belt of this formation. Goodbody (1985), however, only provided a brief overview of this fauna. This thesis, therefore, focuses on the taxonomy, paleoecology, and paleobiogeography of the brachiopod fauna. Specifically, this thesis:

1) systematically describes the brachiopod fauna, including three new genera and nine new species. This study, together with previous studies, provides a comprehensive overview of this important Devonian biota from Arctic Canada;
2) statistically delineates the brachiopod communities based on the large collections; and determines their distribution in terms of their stratigraphic and paleogeographic settings;

3) Examines the Eifelian paleogeography of brachiopods by quantitatively analyzing the data from Arctic Canada and around the world.

The thesis is presented in the format of four papers:

1) New brachiopod genera from Bird Fiord Formation (Devonian), Arctic Canada [*Li and Jones, 2002, Journal of Paleontology, 76(4): 648-658*)];
2) Middle Devonian Brachiopods from Bird Fiord Formation, Arctic Canada [*Li and Jones, 2003, Journal of Paleontology, 77(2)*];
3) Communities and Paleoecology of Eifelian (Mid-Devonian) brachiopods from Bird Fiord Formation of Arctic Canada (*Li and Jones, in press with the Canadian Journal of Earth Science*);
4) Eifelian (Mid-Devonian) Brachiopod Biogeography: A Quantitative Assessment *(Li and Jones, submitted to the Palaeogeography, Palaeoclimatology, Palaeoecology*).

The style/format among the papers varies slightly since the papers were submitted to different journals.

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Chapter 2

New Brachiopod Genera from Bird Fiord Formation (Devonian), Arctic Canada[*]

INTRODUCTION

THE UPPER LOWER to Middle Devonian Bird Fiord Formation (Embry and Klovan, 1976; Goodbody, 1989) crops out on southwest Ellesmere Island, North Kent Island, northwest Devon Island, Bathurst Island, and parts of Cornwallis Island (Fig. 2.1). This carbonate-clastic succession changes from marginal-marine carbonates in its lower part, to shelf, deltaic, and fluvial siliciclastics in its upper part (Goodbody in Mayr et al., 1994). The Bird Fiord Formation contains numerous brachiopods that have been described by Meyer (1913), Johnson and Perry (1976), Brice (1982), Jones (1982a, 1982b), and Jones and Boucot (1983). Between 1979 and 1983, Goodbody and Jones collected numerous brachiopods from 140 localities throughout the outcrop belt of this formation. Goodbody (1985), however, only provided a brief overview of this biota. During a recent taxonomic study of these brachiopods three new genera, which are described herein, were recognized.

Biogeographically, the study area is in the Old World Realm (Johnson and Boucot, 1973). With its numerous biogeographic divisions, the Old World Realm is taxonomically more variable than other contemporary realms (Boucot, 1988). Thus, the discovery of three new, monotypic brachiopod genera from Arctic Canada is not surprising given the remoteness of the area and the few studies that have focused on this biota in the past. The fact that these genera are monotypic may indicate that they are part of an endemic fauna or that further work is required on similar specimens from other areas.

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[*] This chapter has been published in the *Journal of Paleontology*, 76(4):648-658 (by Li and Jones, 2002).

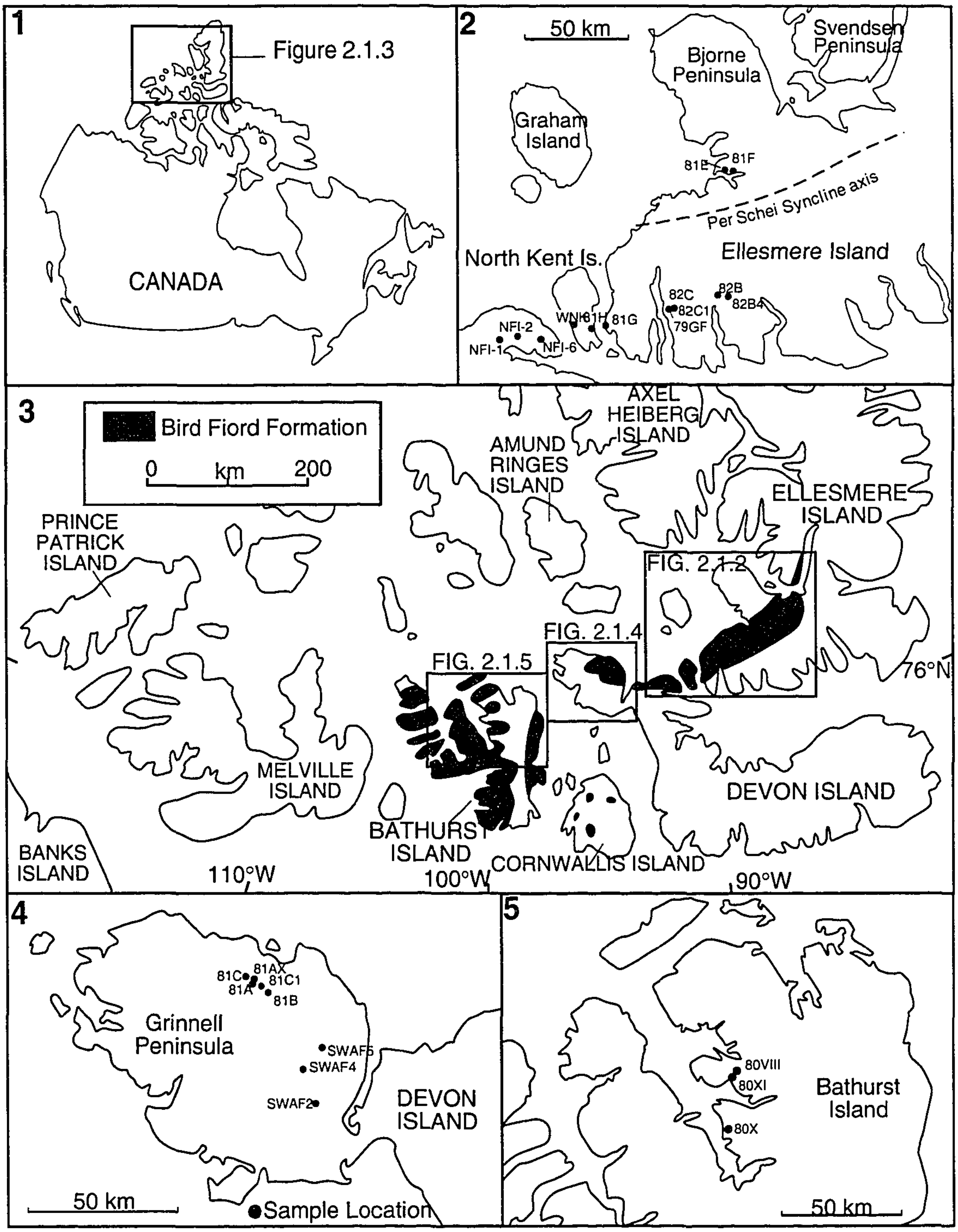


Figure 2.1—(1) Map showing general location of study area. (2) Location of measured sections on SW Ellesmere Island and North Kent Island. (3) Distribution of the Bird Fiord Formation in the Arctic islands (modified from Goodbody, 1985).(4) Location of measured sections on Grinnell Peninsula, Devon Island. (5) Location of measured sections on Bathurst Island. Section numbers are the same as those used by Goodbody (1985).

BIRD FIORD FORMATION

THE BIRD Fiord Formation, first defined by McLaren (1963), ranges from 465 m thick on eastern Grinnell Peninsula to more than 900 m on western Bathurst Island. Goodbody (1985) initially divided this formation into units A-F. Later, Goodbody (1989) formally named these units as the Cross Bay, Blubber Point, Baad Fiord, Norwegian Bay, Cardigan Strait, and Grise Fiord members (Fig. 2.2). The Cross Bay Member, which overlies the Blue Fiord/Disappointment Bay Formation, is formed of interbedded dolostone, limestone, siltstone, shale, and evaporites that probably accumulated in a sabkha setting. The Blubber Point Member, characterized by impure limestone and calcareous sandstone with minor shale, represents shallow, inner carbonate shelf deposition. The overlying Baad Fiord Member is formed of interbedded dark grey shale, dark grey-brown argillaceous siltstone and siltstone, and calcareous sandstone. The coarsening-upward shale to sandstone cycles of this member formed in response to variable clastic input and re-distribution in a shallow, nearshore, marine setting. The Cardigan Strait Member, which is dominated by orange-brown, non-calcareous, fine to medium grained sandstone, and some shale, formed as deltas advanced onto the shelf. The Grise Fiord Member comprises non-calcareous, fine to medium grained sandstone along with some light brown siltstone, dark argillaceous siltstone, and carbonaceous shale. This succession formed in a non-marine, delta plain setting. The Norwegian Bay Member is formed of interbedded shale, siltstone, impure limestone, and sandstone that formed in an intertidal to shallow shelf setting (Goodbody, 1985; in Mayr et al., 1994). The distribution of these members is governed by structural and sedimentological controls (Goodbody, 1989); for example, the Norwegian Bay Member is confined to the north limb of the Schei Syncline (Fig. 2.2).

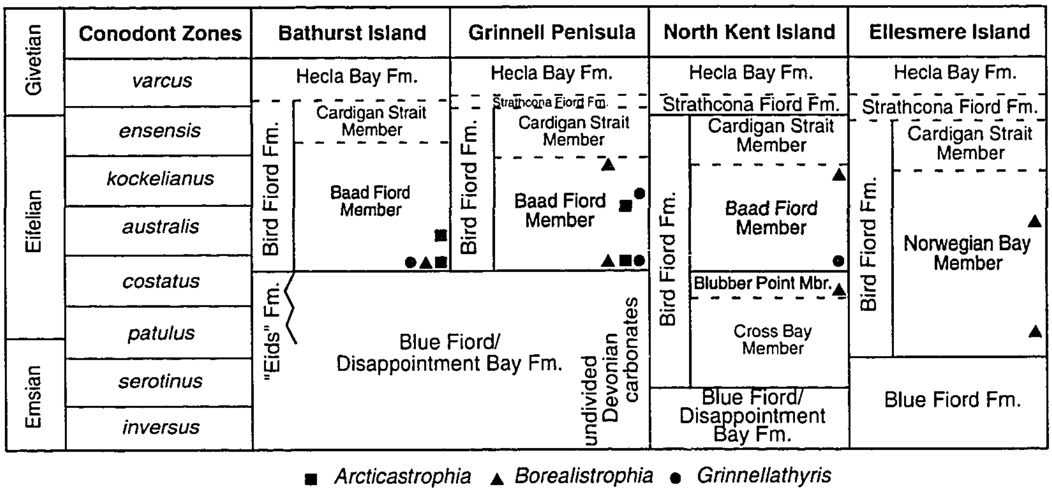


Figure 2.2--Correlation of members of Bird Fiord Formation. Solid horizontal lines indicate boundaries with biostratigraphic control, dash lines indicate inferred age boundaries (after Goodbody, 1989; Mayr et al., 1998). New genera of brachiopods come from the shaded members.

The age of the Bird Fiord Formation is difficult to establish from the biota that it contains. It is, however, sandwiched between the Blue Fiord Formation and Strathcona Fiord Formation or Hecla Bay Formation (Fig. 2.2). Thus, the lower part of the formation is probably late Emsian in age whereas the upper part of the formation is no younger than latest Eifelian (Goodbody in Mayr et al., 1994).

Goodbody (1985), during his stratigraphic and sedimentological study of the Bird Fiord Formation, examined successions throughout the outcrop belt (Fig. 2.1). He showed that most of the brachiopods are found in the Blubber Point, Baad Fiord, and Norwegian Bay members (Fig. 2.2). Borealistrophia n. gen. (175 specimens) was found at 18 different localities on southwest Ellesemere Island, Devon Island, and Bathurst Island. It should be noted, however, that only one specimen of this genus was found on Bathurst Island. Arcticastrophia n. gen. (88 specimens) was collected from six localities on Bathurst Island and Grinnell Peninsula, Devon Island. It was not found on southwest Ellesmere Island. Grinnellathyris n. gen. (66 specimens) was found at nine localities on Bathurst Island, Grinnell Peninsula, Devon Island, and North Kent Island. It was not found on southwest Ellesmere Island. These genera are important elements of the brachiopod biota that had a widespread distribution in near-shore, shallow marine settings.

SYSTEMATIC PALEONTOLOGY

Repository of illustrated specimens.-- All specimens are housed in the Paleontology Museum, Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, T6G 2E3, Canada.

Order STROPHOMENIDA Öpik, 1934

Superfamily STROPHOMENOIDEA King, 1846

Family DOUVILLINIDAE Caster, 1939

Subfamily PROTODOUVILLININAE Harper and Boucot, 1978

Genus BOREALISTROPHIA new genus

Type species.--Borealistrophia rongi n. sp. Monotype.

Diagnosis.-- Medium sized, rectangular, strongly plano-convex to concavo-convex protodouvillininae. Unequally parvicostellate, shallow broad sulcus may develop on ventral valve. Ventral muscle field clearly impressed, cordate, separated by low medium myophragm, low ridges laterally and anteriorly. Dorsal muscle field rectangular, ridged laterally and anterolaterally. Two pairs of side septa, inner ones long, strong, divergent, initiating at flanks of myophragm inside muscle field; outer ones short, low, anterior to muscle-bounding ridges, slightly convergent. Socket ridges strong, thick, widely divergent, almost parallel to hinge-line, with lateral ends wider than the muscular bounding ridge. Dorsal median ridge prominent, short, extending to about half shell length, not reaching subperipheral rim. Subperipheral rim well developed, relatively sharp and high.

Etymology.—Boreal-, Greek, north, and "-strophia", a suffix indicating Strophomenida.

Occurrence.—Baad Fiord, Blubber Point, and Norwegian Bay members, Bird Fiord Formation (late Early Devonian to Middle Devonian) in Arctic Canada (Fig. 2.2). This genus was found on SW Ellesmere Island (localities 81E, 81F, 81G, 82B4, 82B, 82C, 82C1, 79GF, Fig. 2.1.2), North Kent Island (locality 81H, Fig. 2.1.2), Devon Island (localities NFI-1, NFI-2, NFI-6, Fig. 2.1.2), Grinnell Peninsula (localities 81A, 81B, 81C, 81C1, SWAF2, Fig. 2.1.4), and Bathurst Island (locality 80XI, Fig. 2.1.5),

Discussion.-- The new genus is based on the distinctive pattern of the side septa, socket ridges, and median septum found in the dorsal valve. The decision to treat this as a new genus is based on the fact that Rong and Cocks (1994) have argued that characters such as the side septa are critical to the delineation of genera and families in the Strophomenida.

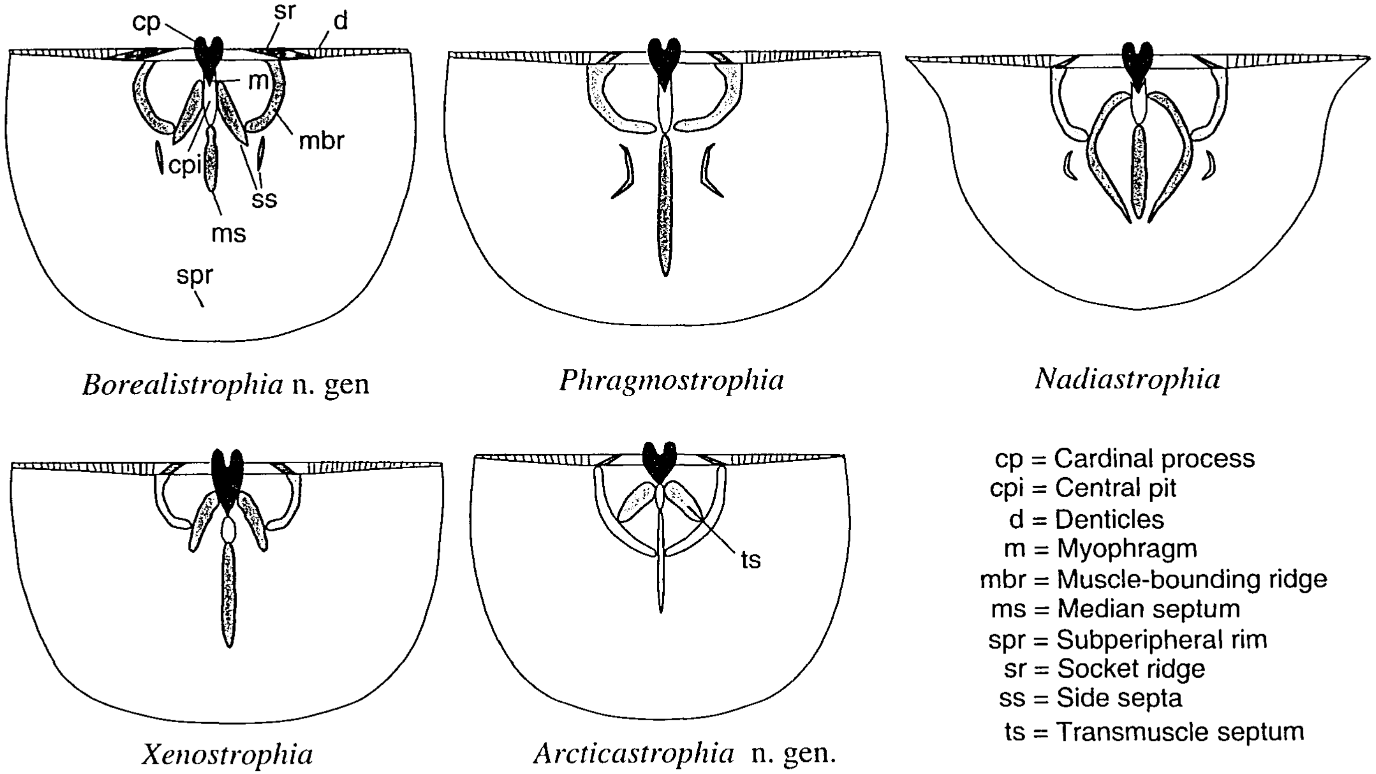
The new genus is similar to Phragmostrophia in shell shape, ornamentation, and ventral muscle field. Phragmostrophia, however, has only one pair of curved or "S"-shaped side septa that are located anterior to the muscle ridge (see Harper et al. 1967, p. 429, text-fig. 3b; pl. 7, fig. 6; pl. 8, figs. 1-4; Harper and Boucot, 1978, p. 44, pl. 49, figs. 20, 24, 26-27; Rong and Cocks, 1994, text-fig. 16H) (Fig. 2.3). Furthermore, its median septum is much longer than that of Borealistrophia (Fig. 2.3).

Borealistrophia has straight side septa, whereas the two pairs of side septa in Nadiastrophia Talent, 1963 are curved and convex outward (Harper et al., 1967, p. 425, pl. 9, figs. 1-3; also see Talent, 1963, pl. 31, figs. 7-9; pl. 33, figs. 1-2; Lenz, 1973, pl. 1, figs. 6, 7, 11; Harper and Boucot, 1978, p. 140, pl. 29, figs. 1-3, 5; Lenz and Johnson, 1985, pl. 13, fig. 14; Rong and Cocks, 1994, text-fig. 16D) (Fig. 2.3). The socket ridges of Borealistrophia are more prominent and thicker than those of Nadiastrophia (Fig. 2.3). The ventral muscle fields and ventral medium septum of these two genera are different: Borealistrophia is cordate with a myophragm, whereas Nadiastrophia is elongate, like an inverted "Y", with a short and weak medium septum (Talent, 1963, p. 62-63, pl. 31, fig. 6; pl. 32, figs. 7, 10, 12, 14, 15; pl. 33. figs. 3-6; Harper et al., 1967, pl. 8, figs. 10-11; Lenz, 1973, pl. 1, fig. 1; Lenz and Johnson, 1985, pl. 13, figs. 3, 7, 9, 10, 11) (Fig. 2.4).

The side septa of Borealistrophia are similar to those of Malurostrophia Campbell and Talent, 1967. These two genera, however, can be distinguished by their shell outlines and ventral muscle fields. Malurostrophia has an indented anterior margin with sharp acute cardinal angles. The ventral muscle field of Malurostrophia is elongate and the myophragm bifurcates anteriorly (Campbell and Talent, 1967; Cocks and Rong, 2000).

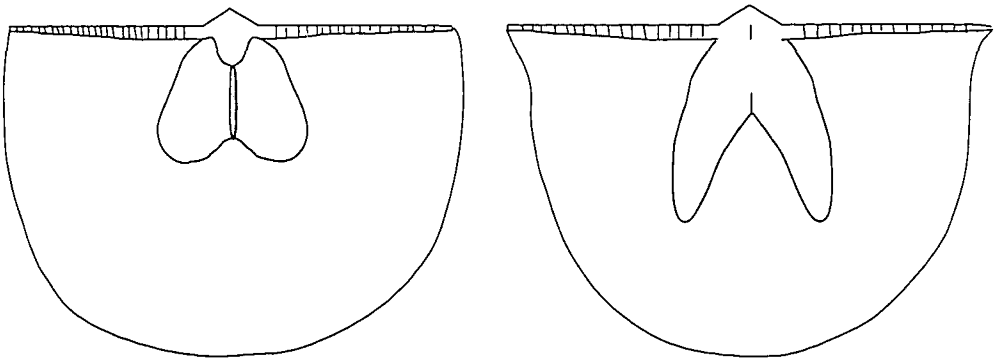
The new genus differs from Taemostrophia Chatterton, 1973, in the following aspects: (1) Borealistrophia has two pairs of side septa whereas Taemostrophia only has one pair; (2) the ventral muscle-bounding ridges in mature *Taemostrophia*, unlike those in *Borealistrophia*, converge at mid-length to give them a "waist-like" appearance (Chatterton, 1973, pl. 8, figs. 1, 6, 13, 17), and (3) *Taemostrophia* is characterized by a traverse, alate shell that has acute cardinal angles (Chatterton, 1973, pl. 8, figs. 1, 2, 4-6, 13, 17) whereas *Borealistrophia* has a rectangular shell with rounded cardinal angles.

The new genus can be readily distinguished from *Xenostrophia* Wang, 1974 (*in* Wang *et al*., 1974, p.37-38, pl. 5, figs. 1-7). According to Wang *et al*. (1974), *Xenostrophia* has only one pair of septa (similar to inner septa of *Borealistrophia*) (Fig. 2.3) and the adductor and diductor scars of ventral muscle field are clearly differentiated in *Xenostrophia* but not in *Borealistrophia*. Furthermore, the socket ridges of *Borealistrophia* are more prominent and the median septum is shorter than those of *Xenostrophia* (Fig. 2.3). Wang and Rong (1986) illustrated some specimens of *Xenostrophia* that had two pairs of septa (e.g. Wang and Rong, 1986, pl. 11, fig. 10; pl. 16, figs. 3, 4, 19). Those specimens, however, are more transverse than *Borealistrophia*, and their socket ridges, median septa, and ventral muscle fields are different from those of *Borealistrophia*. There is, however, a debate on the validity of *Xenostrophia*. Talent (1963), Harper *et al*. (1967), Hou and Xian (1975), and Harper and Boucot (1978) suggested that *Shaleria* (*Telaeoshaleria*) *yukiangensis* Wang, 1956, which is the type species of *Xenostrophia*, should be assigned to *Nadiastrophia*. If so, *Xenostrophia* becomes a junior synonym of *Nadiastrophia*. Johnson (1970, p. 130-131), on the other hand, suggested that the type species of *Xenostrophia* is closer to *Phragmostrophia*. Wang and Rong (1986) studied their large collection of *Xenostrophia* and concluded that *Xenostrophia* is a valid genus, because it differs from *Nadiastrophia* in its lateral profile and ventral muscle field. Cocks and Rong (2000, p. 271) treated *Xenostrophia* questionably as a synonym of *Nadiastrophia*. More specimens of *Xenostrophia yukiangensis* (Wang) from the type area are needed before this problem can be satisfactorily solved.



cp = Cardinal process
cpi = Central pit
d = Denticles
m = Myophragm
mbr = Muscle-bounding ridge
ms = Median septum
spr = Subperipheral rim
sr = Socket ridge
ss = Side septa
ts = Transmuscle septum

Figure 2.3--Dorsal internal structures of Borealistrophia n. gen., Phragmostrophia, Nadiastrophia, Xenostrophia, and Arcticastrophia n. gen.



Borealistrophia n. gen.

Nadiastrophia

Figure 2.4--Ventral muscle fields of *Borealistrophia* n. gen. and *Nadiastrophia*

BOREALISTROPHIA RONGI new species

Figure 2.5.1-2.5.14

Phragmostrophia. sp. JONES AND SMITH, 1980, p. 685, pl. 2, figs. 11-13.

Diagnosis.--As for genus.

Description.--Shell medium sized, up to 24 mm wide (Table 2.1), rectangular outline with anterior margin more or less parallel to hinge line; plano-convex to slightly concavo-convex in lateral profile; ventral valve strongly convex in most shells, geniculate in adult shells. Maximum width at straight hinge line in some specimens, slightly anterior to midlength in others. Length about 70 percent of width, thickness about 30 percent of width (Fig. 2.6, Table 2.1). Ventral valve may bear shallow and broad sulcus anteriorly. Ventral interarea well defined, nearly orthocline to apsacline; dorsal interarea anacline. Delthyrium filled by pseudodeltidium. Ornamentation of unequal parvicostellate, better defined on dorsal valve (possibly a function of preservation).

Hinge line denticulate, ventral muscle field cordate, laterally and anteriorly bounded by low ridges, extending about half of valve length, medially separated by low myophragm; adductor scars not clearly visible. A low and weak subperipheral rim may develop.

Cardinal process bilobed, well developed, projecting posteroventrally, supported medially by myophragm that is broad posteriorly, becoming lower and narrower anteriorly, extending about one-fifth valve length. Socket ridges strong and thick, separated from cardinal process, widely divergent, almost parallel to hinge-line, with lateral ends wider than the muscular bounding ridge. Central pit located immediately anterior to myophragm. Dorsal muscle field rectangular, slightly elevated, bounded laterally and anterolaterally by muscle ridges. Two pairs of side septa, inner one long and strong, strongly pustulose in middle part, initiating at flanks of myophragm inside muscle field, diverging anterolaterally at about 30 degrees; outer pair short and low, anterior to muscle-bounding ridges, slightly convergent. Dorsal median septum prominent, short, beginning anterior to central pit, extending to about half of shell length, not extending to subperipheral rim which is well developed, relatively sharp, and high. Dorsal interior surface pustulose, especially adjacent to muscle impressions.

Etymology.-- Species named after Rong Jia-yu whose joint works with L. R. Cocks (1989, 1994, 2000) on Strophomenida are critical to the recognition of the new genus.

Types.-- Holotype, UA12075, from Baad Fiord Member of Bird Fiord Formation, Ensorcellement River, Grinnell Peninsula, Devon Island (locality 81B, Fig. 2.1.4). Paratypes, UA12076 (Baad Fiord Member, locality NFI-6), UA12077-12079 (Blubber Point Member, locality 81H), and UA12080 (Baad Fiord Member, locality 81B).

Material examined.--175 specimens, one with dorsal interior and three with ventral interior.

Occurrence.—As for genus.

Discussion.--Jones and Smith (1980, p. 685, pl. 2, figs. 11-13) reported Phragmostrophia sp. from the Bird Fiord Formation of southwest Ellesmere Island, Arctic Canada, but no interiors of the specimens were available at that time. Later, they reassigned these specimens to Parapholidostrophia harpi based on two poorly preserved dorsal interiors (Jones and Smith, 1985). A re-examination of Phragmostrophia sp. (Jones and Smith, 1980) showed that they have a ventral sulcus and that the ventral valves are not strongly convex. With the dorsal and ventral interiors now available from Ellesemere Island, it is evident now that these specimens belong to the new species Borealistrophia rongi.

Figure 2.5--1-14, *Borealistrophia rongi* n. sp. 1-3, holotype, dorsal exterior and interior, 1, 2, X 3, 3, X4.5, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA 12075; 4-8, paratype, ventral (4), dorsal (5), lateral (6), anterior (7), and posterior (8) views, X1.7, from Norfolk Inlet (locality NFI-6), Devon Island, UA 12076; 9, 10, paratype, ventral internal mould and dorsal exterior, X3.4, from North Kent Island (locality 81H), UA 12077; 11, 12, paratypes, ventral internal moulds, 11, X2.6, 12, X2.2, both from North Kent Island, UA 12078, UA 12079 respectively; 13, 14, paratype, dorsal and ventral views of same, X1.5, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA 12080; 15-28, *Arcticastrophia costellata* n. sp.; 15-19, paratype, lateral (15), ventral (16), dorsal (17), anterior (18), and posterior (19) views of same, X2.1, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA 12081; 20, paratype, ventral interior, X2.3, from Ensorcellement River (locality 81A), Grinnell Peninsula, Devon Island, UA 12082; 21, 22, paratype, dorsal view and dorsal interior, X1.9, from Ensorcellement River (locality 81A), Grinnell Peninsula, Devon Island, UA 12083; 23, 24, paratype, dorsal view and dorsal interior, X2, from Ensorcellement River (locality 81A), Grinnell Peninsula, Devon Island, UA12084; 25, 26, paratype, dorsal view and dorsal interior, X2, from Stuart Bay (locality 80XI), Bathurst Island, UA12085; 27, 28, holotype, dorsal view and dorsal interior, X2, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA12086.

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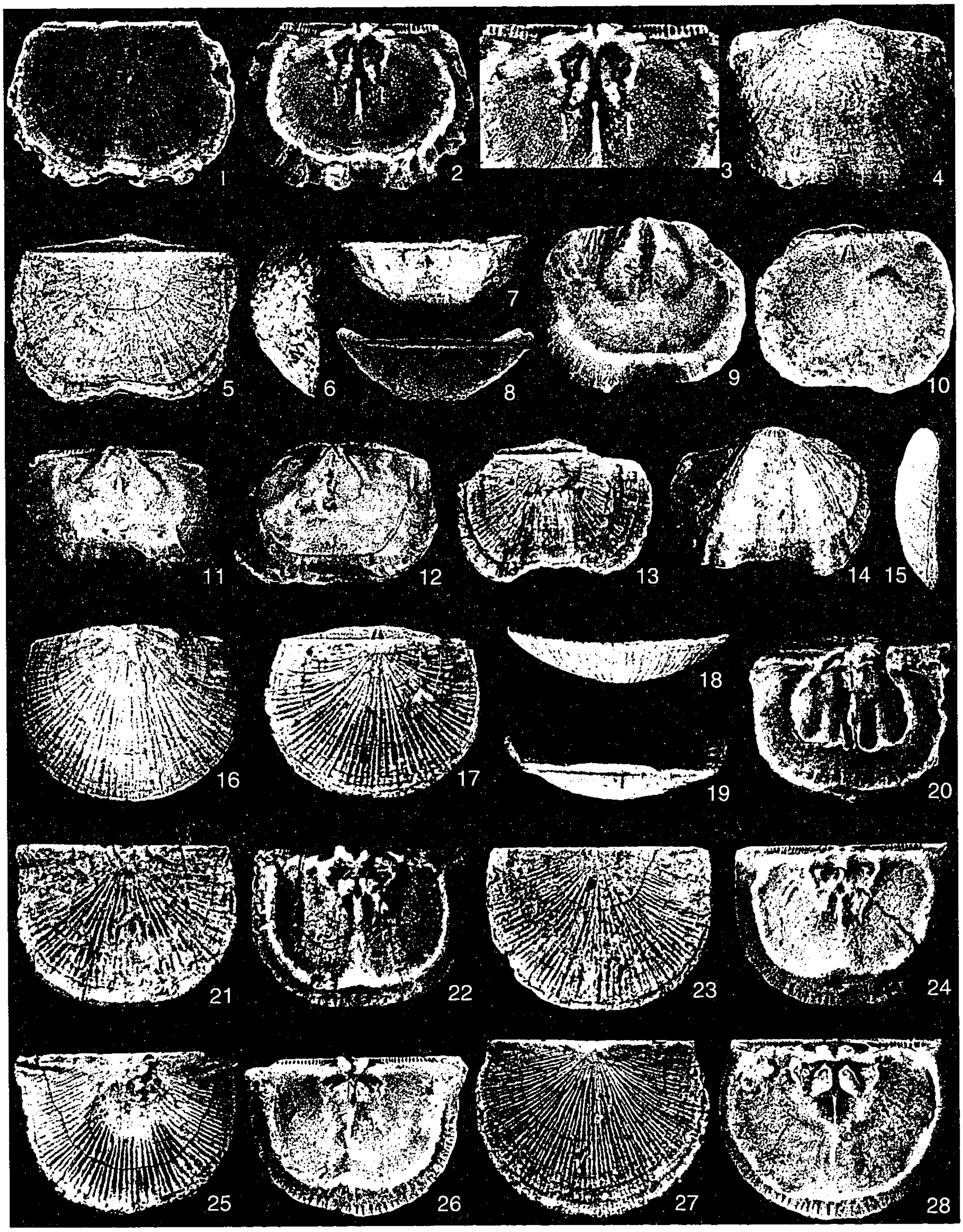
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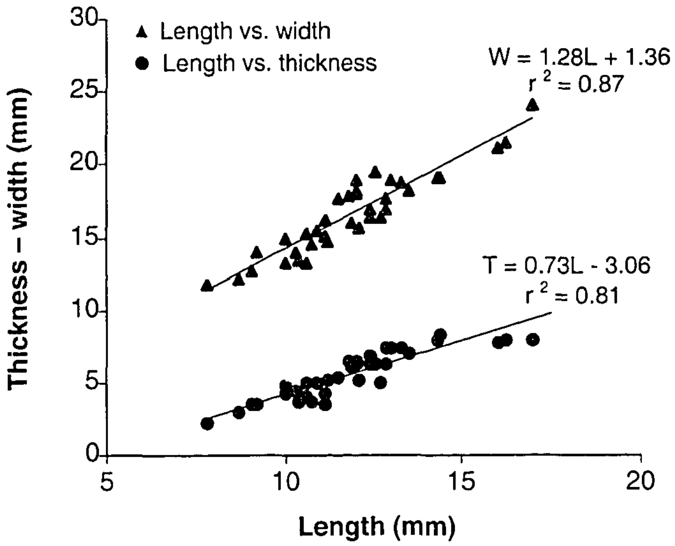

Figure 2.6--Length versus width and length versus thickness graphs for Borealistrophia rongi n. sp.

TABLE 2.1--Measurements of *Borealistrophia rongi* n. sp. (dimension in mm).

Section	81E-45 m	81H-183 m	NF-6	NF-7	Combined Data
Member	Norwegian Bay	Blubber Point	Baad Fiord	Baad Fiord	
Island	Ellesmere	North Kent	Devon Island	Devon Island	
No. measured	7	10	16	3	36
Length (L)	11.8 (12.8) 14.0*	7.8 (10.2) 11.5	10.3 (12.3) 17.0	12.8 (13.6) 14.4	7.8 (11.9) 17.0
Width (W)	17.0 (18.5) 19.6	11.8 (14.8) 19.0	13.3 (16.6) 24.1	17.6 (18.3) 19.2	11.8 (16.6) 24.1
Thickness (T)	6.2 (6.9) 7.9	2.3 (4.2) 6.4	3.5 (5.5) 8.0	7.0 (7.5) 8.3	2.3 (5.6) 8.3
L/W	0.64 (0.69) 0.74	0.63 (0.69) 0.77	0.69 (0.74) 0.80	0.73 (0.74) 0.75	0.63 (0.72) 0.80
T/L	0.52 (0.54) 0.57	0.29 (0.41) 0.53	0.32 (0.45) 0.51	0.52 (0.56) 0.58	0.29 (0.46) 0.58
T/W	0.32 (0.37) 0.40	0.19 (0.28) 0.35	0.22 (0.33) 0.38	0.38 (0.41) 0.43	0.19 (0.33) 0.43

*Data format: Minimum (Average) Maximum

?Subfamily PROTODOUVILLININAE Harper & Boucot, 1978

Genus ARCTICASTROPHIA new genus

Type species.--Arcticastrophia costellata n. sp. Monotype.

Diagnosis.--Medium sized, semi-circular, plano-convex Douvillinidae. Ventral muscle field strongly impressed, elevated, cordate, with high ridges laterally and anteriorly. Ventral myophragm prominent. Dorsal muscle field slightly elongate, with prominent ridges laterally and anteriorly. Socket ridges thin, separated from cardinal process and muscle bounding ridges, divergent at slight angle from hinge line. Transmuscle septa stout, confined by muscle bounding ridges. Dorsal median ridge short, narrow and low, extending to about two-thirds of shell length, not reaching well-developed subperipheral rim.

Etymology.--Combination of "arctic", where the new genus is found, and "-strophia", a suffix indicating Strophomenida.

Occurrence.—Baad Fiord Member, Bird Fiord Formation (late Early Devonian to Middle Devonian) in Arctic Canada (Figs. 2.1, 2.2). Found on Grinnell Peninsula, Devon Island (localities 81A, 81B, SWAF-2, SWAF-5, Fig. 2.1.4) and Bathurst Island (localities 80X, 80XI, Fig. 2.1.5).

Discussion.--The elevated ventral muscle field of the new genus indicates that it should be assigned to the subfamily Douvillininae Caster, 1939 in the family Douvillinidae. This is the only group that has an elevated ventral muscle field. The transmuscle septa and non-bifurcated dorsal median septum found in the new genus, however, preclude this assignment because the Douvillininae have a dorsal median septum that bifurcates anteriorly (Cocks and Rong, 2000, p. 266). The new genus is questionably assigned to the subfamily Protodouvillininae, even though the ventral muscle field of that subfamily is "not elevated" (Rong and Cocks, 1994; Cocks and Rong, 2000). A new subfamily may need to be established in the future to include genera that have an elevated ventral muscle field and a non-bifurcated dorsal median septum. Another alternative is to amend the definition of Protodouvillininae to "ventral muscle field elevated or not". If so, the distinction between Douvillininae and Protodouvillininae will then focus on the bifurcation of the dorsal median septum.

The stout transmuscle septa (cf. Rong and Cocks, 1994) of the new genus readily distinguish it from other genera (Fig. 2.3). *Megastrophiella* Harper and Boucot, 1978 and *Megastrophia* Caster, 1939 are the only other genera that have similar septa. They differ from the new genus, however, in their lateral profile and features of the ventral muscle field. These two genera have concavo-convex profiles, with strongly convex ventral valves (Harper and Boucot, 1978; Rong and Cocks, 1994; Cocks and Rong, 2000), whereas the new genus is plano-convex and has a gently convex ventral valve. The muscle bounding ridges around the ventral muscle field of *Megastrophiella* and *Megastrophia* are weak or even lacking (in *Megastrophia*) (Harper and Boucot, 1978; Rong and Cocks, 1994; Cocks and Rong, 2000), whereas they are high and prominent in *Arcticastrophia*.

Arcticastrophia can be distinguished from *Borealistrophia* n. gen. both externally and internally. Externally, *Arcticastrophia* has a gently convex ventral valve lacking sulcus, whereas *Borealistrophia* has a strongly convex ventral valve with a broad sulcus anteriorly. Internally, the pair of transmuscle septa of *Arcticastrophia* is different from the two pairs of side septa of *Borealistrophia*; the socket ridges of *Arcticastrophia* are less prominent than those of *Borealistrophia*; and the median septum of *Arcticastrophia* is much thinner than that of *Borealistrophia* (Fig. 2.3).

ARCTICASTROPHIA COSTELLATA new species

Figures 2.5.15-2.5.28, Figure 2.7.1-2.7.4

Diagnosis.--As for genus.

Description.--Shell medium sized, up to 22 mm wide (Table 2.2). Semi-circular with rounded cardinal extremities, plano-convex with ventral valve gently convex. Maximum width near midlength. Length about 80 percent of width, depth about 20 percent of width (Fig. 2.8; Table 2.2). Ventral interarea well-defined, apsacline; dorsal interarea catacline, about one-third high of ventral interarea. Delthyrium small, filled by psedodeltidium. Costellate.

Hinge line denticulate. Ventral process prominent. Ventral muscle field cordate, elevated, laterally and anteriorly bounded by prominent ridges. Two elliptical adductor scars locate anterior of ventral process with shallow groove between scars. Diductor scars bilobed, separated by prominent median ridge anterior to adductor scars. Regions between diductor muscle scar ridges and valve margin pustulose.

Cardinal process bilobed, well developed, supported by short myophragm, projecting posteroventrally. Socket ridges thin, separated from cardinal process and muscle bounding ridges, diverge at slight angle from hinge line. Dorsal muscle field elevated, slightly elongate, about one-third of valve length, with prominent bounding ridges laterally and anteriorly. Pair of stout transmuscle septa developed in dorsal muscle field, confined by muscle bounding ridges. Small, elongate central pit developed anterior to short myophragm. Narrow and low median septum developed immediately anterior to central pit, extending to about two-thirds of valve length, not reaching prominent subperipheral rim (Fig. 2.3).

Etymology.--From costellate, reflecting the costellate ornamentation of the species.

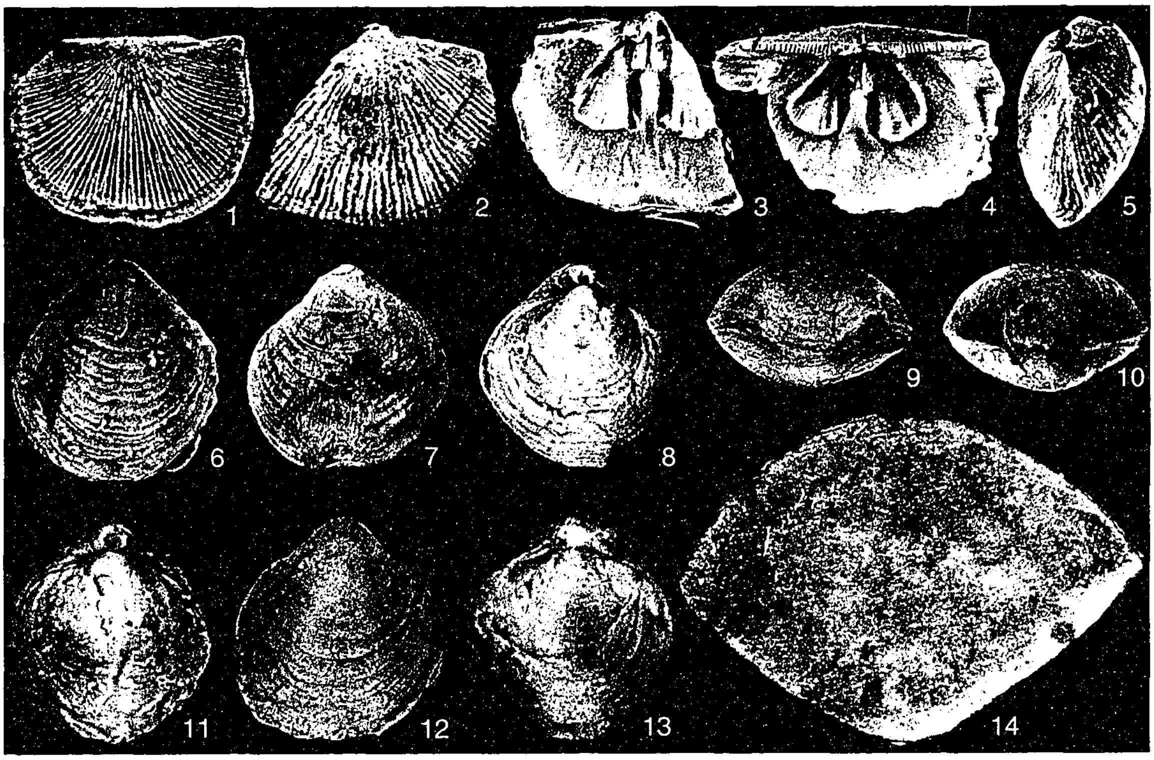

Figure 2.7.--1-4, *Arcticastrophia costellata* n. sp.; 1, paratype, dorsal view, X1.9, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA 12087; 2, 3, paratype, ventral view and ventral interior, X2.6, from Ensorcellement River (locality 81B), Grinnell Peninsula, Devon Island, UA 12088; 4, paratype, ventral interior, X2.6, from Ensorcellement River, Grinnell Peninsula, Devon Island, UA12089; 5-14, *Grinnellathyris alvarezis* n. sp.; 5, 7-10, holotype, lateral (5), ventral (7), dorsal (8), anterior (9), and posterior (10) views of same, X5.1, from Ensorcellement River (locality 81C1), Grinnell Peninsula, Devon Island, UA 12090; 6, 11, ventral and dorsal views of same, X2.6, from Ensorcellement River, Grinnell Peninsula, Devon Island, UA 12091; 12, 13, paratype, ventral and dorsal views of same, X2.6, from 20 kilometers west of Discovery Mountain (locality SWAF4-1), Arthur Fiord, Grinnell Peninsula, Devon Island, UA 12092; 14, paratype, transverse serial section at 6.3 mm from the ventral beak, showing spiralia and inverted U-shaped jugum, X10, from Half Moon Bay (locality 80X), Dundee Bight, Bathurst Island, UA 12093.

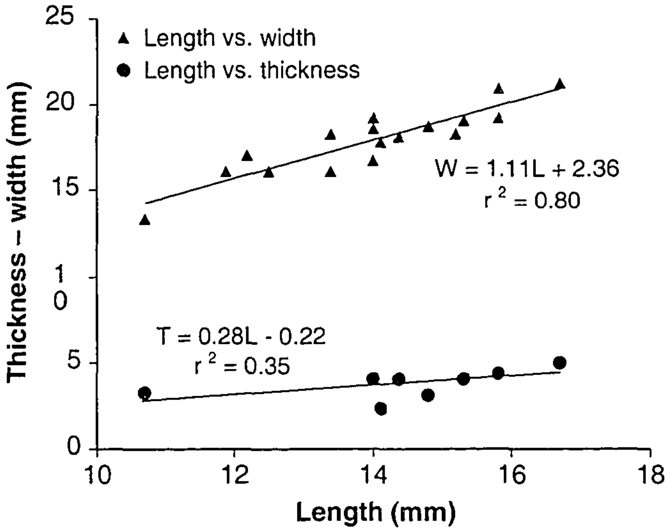

Figure 2.8--Length versus width and length versus thickness graphs for Arcticastrophia costellata n. sp.

TABLE 2.2--Measurements of Arcticastrophia costellata n. sp. (dimension in mm).

Not all parameters could be accurately measured because of damage to the specimens.

Section	80XI-0 m	81A-138.5 m	81A-224 m	81B-170 m	Combined Data
Member	Baad Fiord	Baad Fiord	Baad Fiord	Baad Fiord	
Island	Bathurst	Grinnell Peninsula	Grinnell Peninsula	Grinnell Peninsula	
No. measured	7	2	2	6	17
Length (L)	10.7 (13.5) 16.7*	13.4 (13.7) 14.0	13.4 (13.6) 14.0	12.5 (14.8) 15.8	10.7 (14.0) 16.7
Width (W)	13.3 (17.3) 21.3	18.4 (18.6) 18.7	16.1 (16.4) 16.7	16.2 (18.8) 19.2	13.3 (18.0) 21.3
Thickness (T)	2.4 (3.5) 5.0		4.0 (-) -	4.0 (4.2) 4.4	2.4 (3.8) 4.4
L/W	0.71 (0.77) 0.80	0.73 (0.74) 0.75	0.83 (0.84) 0.84	0.73 (0.78) 0.83	0.71 (0.78) 0.84
T/L	0.17 (0.25) 0.30		0.29 (-) -	0.26 (0.27) 0.28	0.17 (0.26) 0.30
T/W	0.13 (0.20) 0.24		0.24 (-) -	0.21 (0.22) 0.23	0.13 (0.21) 0.24

*Data format: Minimum (Average) Maximum

Types.--Holotype, UA12086 (locality 81B), paratypes, UA12081 (locality 81B), UA12082-12084 (locality 81A), UA12085 (locality 80XI), and UA12087-UA12088 (locality 81B) from Baad Fiord Member, Bird Fiord Formation.

Other material examined.-- 88 specimens, 12 with dorsal interior; four with ventral interior.

Occurrence.—As for genus.

Order ATHYRIDIDA Boucot, Johnson, and Staton, 1964

Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964

Superfamily ATHYRIDOIDEA Davidson, 1881

Family ATHYRIDIDAE Davidson, 1881

?Subfamily ATHYRIDINAE Davidson, 1881

Genus GRINNELLATHYRIS new genus

Type species.--Grinnellathyris alvarezis n. sp. Monotype.

Diagnosis.--Small, biconvex Athyrididae, elongate or rarely slightly transverse, with growth lines. Dental plates of medium length. Cardinal plate imperforate. Jugum in form of inverted U; lateral branches of jugum almost vertical, starting about mid-dorsal valve length; jugal saddle moderately developed; jugal stem lacking. Spiralia with 8-10 whorls.

Etymology.—After Grinnell Peninsula, Devon Island, where the type species of this genus comes from.

Occurrence.—Baad Fiord Member, Bird Fiord Formation (late Early Devonian to Middle Devonian) in Arctic Canada (Figs. 2.1, 2.2). Found on North Kent Island (locality WNK; Fig. 2.1.2), Grinnell Peninsula, Devon Island (localities 81A, 81AX, 81B, 81C1, SWAF4, SWAF5; Fig. 2.1.4), and Bathurst Island (localities 80-VIII, 80X, Fig. 2.1.5).

Discussion.--Grinnellathyris is internally similar to Johnsonathyris from Port Refugio Formation (Upper Devonian) of Alaska, in having imperforate cardinal plate and no jugal stem (Savage et al., 1978, p. 381, figs. 10, 11). They differ because Johnsonathyris is strongly globose with regularly developed fine costellae, whereas Grinnellathyris is less globose and lacks costellae. In addition, Grinnellathyris has a moderately developed jugal saddle whereas Johnsonathyris lacks such a structure. The similarities of Grinnellathyris and Johnsonathyris in shell size and internal structures may indicate that Johnsonathyris evolved from Grinnellathyris.

The new genus can be distinguished from most other genera in the family Athyrididae by its imperforate cardinal plate and lack of a jugal stem. Atrythyris Struve, 1965, from the Middle Devonian of Eifel region of Germany is another member of this family that has an imperforate cardinal plate (Struve, 1965, figs. 4-8). Atrythyris, however, is larger and has fine costellae.

In the classification of athyridid brachiopods, Alvarez et al. (1998) assigned the imperforated genera Johnsonathyris and Atrythyris along with other perforated ones to the subfamily Athyridinae. With the present discovery of the new imperforate genus Grinnellathyris, it may be advisable to establish a new subfamily (e.g., Johnsonathyridinae) to embrace the genera that have an imperforated cardinal plate. At present, the new genus is tentatively assigned to subfamily Athyridinae.

GRINNELLATHYRIS ALVAREZIS new species

Figures 2.7.5-2.7.14, Figure 2.10

Diagnosis.-- As for genus.

Description.-- Shell small, less than 15 mm wide (Table 2.3). Commonly elongate, rarely circular or transverse. Biconvex in lateral profile. Maximum width at about half shell length. Maximum thickness within posterior third of shell. Width/length ratio from 78 percent to 104 percent with average of 93 percent. Thickness/length ratio from 40 percent to 76 percent, with average of 59 percent (n=28) (Fig. 2.9). Adult anterior commissure uniplicate.

Ventral valve moderately convex with greatest convexity close to umbo. Beak prominent, recurved over cardinal area. Adult specimens with shallow sulcus originating at about mid length of valve. Dorsal valve slightly less convex than ventral one, greatest convexity in posterior third. Dorsal beak directed ventrally. Both valves with concentric growth lines, more obvious anteriorly.

Dental plates short, with narrow lateral apical cavities. Teeth small. Sockets bordered laterally by low inner and outer socket ridges. Cardinal plate subtriangular, slightly concave and apically imperforated. Lateral branches of jugum arise at about mid length of dorsal valve, forming inverted "U", perpendicular to commissure plane. Jugal saddle moderately developed. No jugal stem present. Spiralia with 8-10 whorls (Fig. 10).

Etymology.-- Species named after F. Alvarez of Universidad de Oviedo, Oviedo, Spain

Types.-- Holotype, UA12090, from Baad Fiord Member, Bird Fiord Formation, Ensorcellement River (locality 81C), Grinnell Peninsula, Devon Island. Paratypes, UA12091 (locality 81C1), UA12092 (locality SWAF4-1), and UA12093 (locality 80X) from Baad Fiord Member, Bird Fiord Formation.

Other material examined.-- 66 specimens.

Occurrence.--As for genus.

TABLE 2.3--Measurements of Grinnellathyris alvarezis n. sp. (dimension in mm).

Section Member Island	81AX-104 m Baad Fiord Devon	SWAF4-1 Baad Fiord Devon Island	Combined data
No. measured	15	13	28
Length (L)	5.8 (9.4) 13.0*	11.3 (13.4) 16.0	5.8 (10.7) 16.0
Width (W)	4.5 (8.5) 12.0	10.7 (12.7) 14.4	4.5 (10.0) 14.4
Thickness (T)	3.1 (5.5) 7.7	6.3 (8.0) 10.4	3.1 (6.4) 10.4
W/L	0.78 (0.91) 1.04	0.86 (0.95) 1.03	0.78 (0.93) 1.04
T/W	0.44 (0.64) 0.75	0.52 (0.63) 0.82	0.44 (0.64) 0.82
T/L	0.40 (0.58) 0.76	0.43 (0.60) 0.70	0.40 (0.59) 0.76

*Data format: Minimum (Average) Maximum

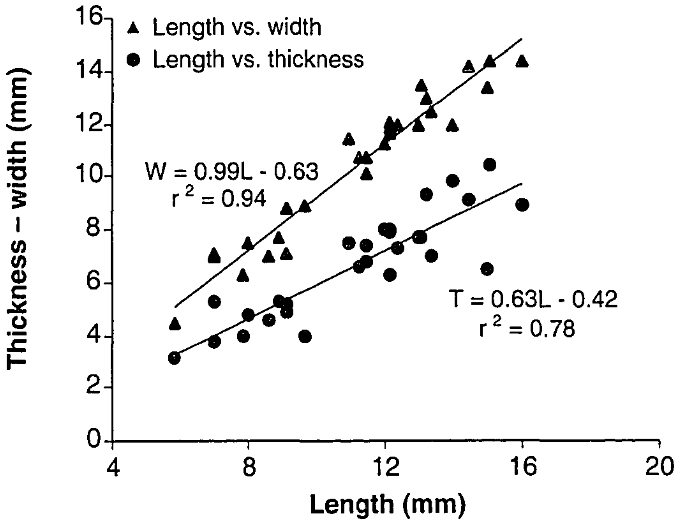

Figure 2.9--Length versus width and length versus thickness graphs for Grinnellathyris alvarezis n. sp.

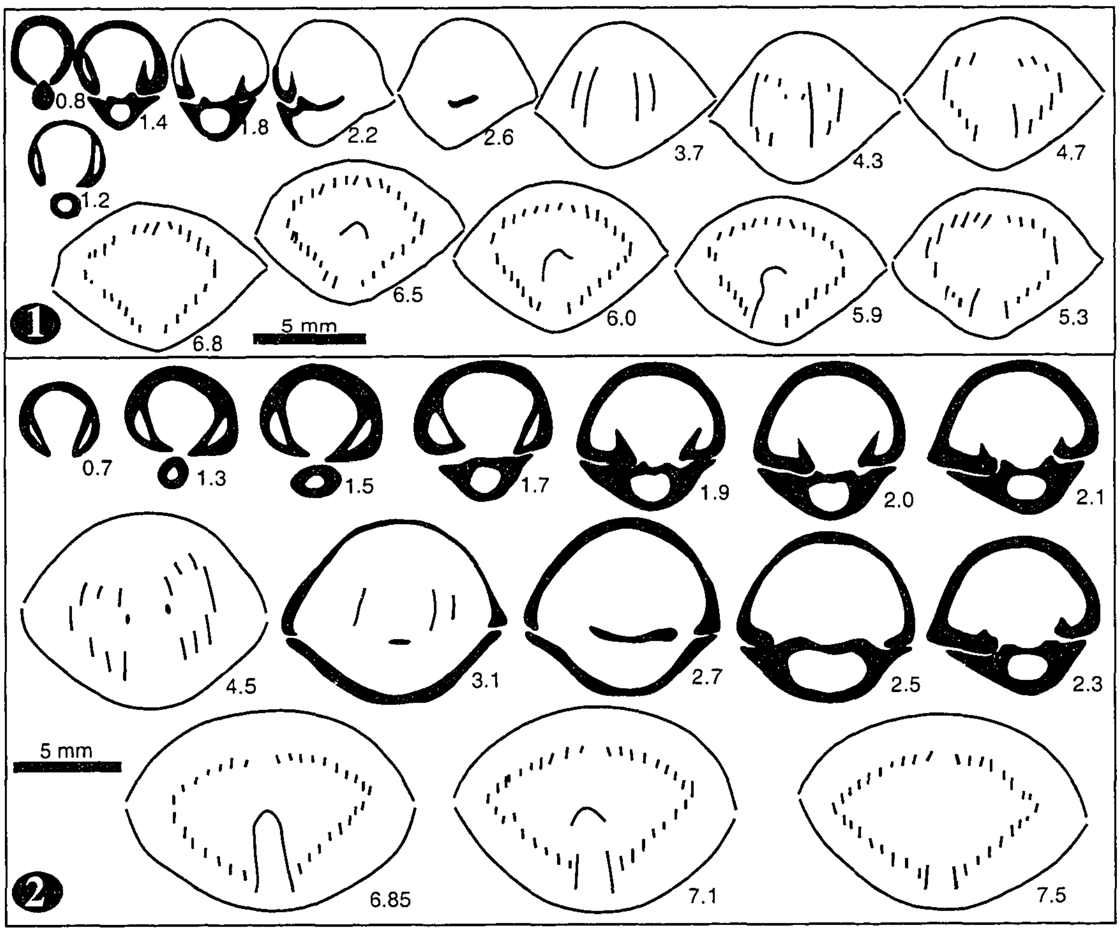

Figure 2.10--Selected transverse serial sections of *Grinnellathyris alvarezis* n. sp.;

(1) from locality 80X, Half Moon Bay, Dundee Bight, Bathurst Island (UA12093) (L=11.6 mm., W=10.4 mm., T=7.6 mm.);

(2) from locality SWAF 4, Arthur Fiord, Grinnell Peninsula, Devon Island (L=15.1 mm., W=14.4 mm., T=10.4 mm.). Distances in mm from posterior tip of ventral umbo.

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Chapter 3

Middle Devonian Brachiopods from Bird Fiord Formation, Arctic Canada*

INTRODUCTION

The upper Lower to Middle Devonian Bird Fiord Formation (Embry and Klovan, 1976; Goodbody, 1989) crops out on southwest Ellesmere Island, North Kent Island, northwest Devon Island, Bathurst Island, and parts of Cornwallis Island (Fig. 3.1). It varies from 465 m thick on eastern Grinnell Peninsula to more than 900 m on western Bathurst Island (Goodbody, 1989). This formation contains numerous brachiopods, mollusks, corals, trilobites, and sponges (Johnson and Perry, 1976; Goodbody, 1985). The brachiopods are common in the Baad Fiord, Blubber Point, Cardigan Strait, and Norwegian Bay members, and the carbonate equivalent of the Bird Fiord Formation (Fig. 3.2). Some of these brachiopods, collected from isolated localities, were described by Meyer (1913), Johnson and Perry (1976), Brice (1982), Jones (1982a, 1982b), and Jones and Boucot (1983).

Between 1979 and 1983, Q. H. Goodbody and B. Jones collected 47026 brachiopod specimens in 140 collections from 34 localities throughout the outcrop belt of this formation (Fig. 3.1). Goodbody (1985), however, only provided a brief overview of this fauna. This brachiopod biota, which consists of 22 species belonging to 21 genera, includes six new species. This paper focuses on those taxa that have not yet been systematically described (Table 3.1). Together with previous studies, it provides a comprehensive overview of an important Devonian biota from Arctic Canada.

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* This chapter is in press with the *Journal of Paleontology*, 77(2) (by Li and Jones, 2003)

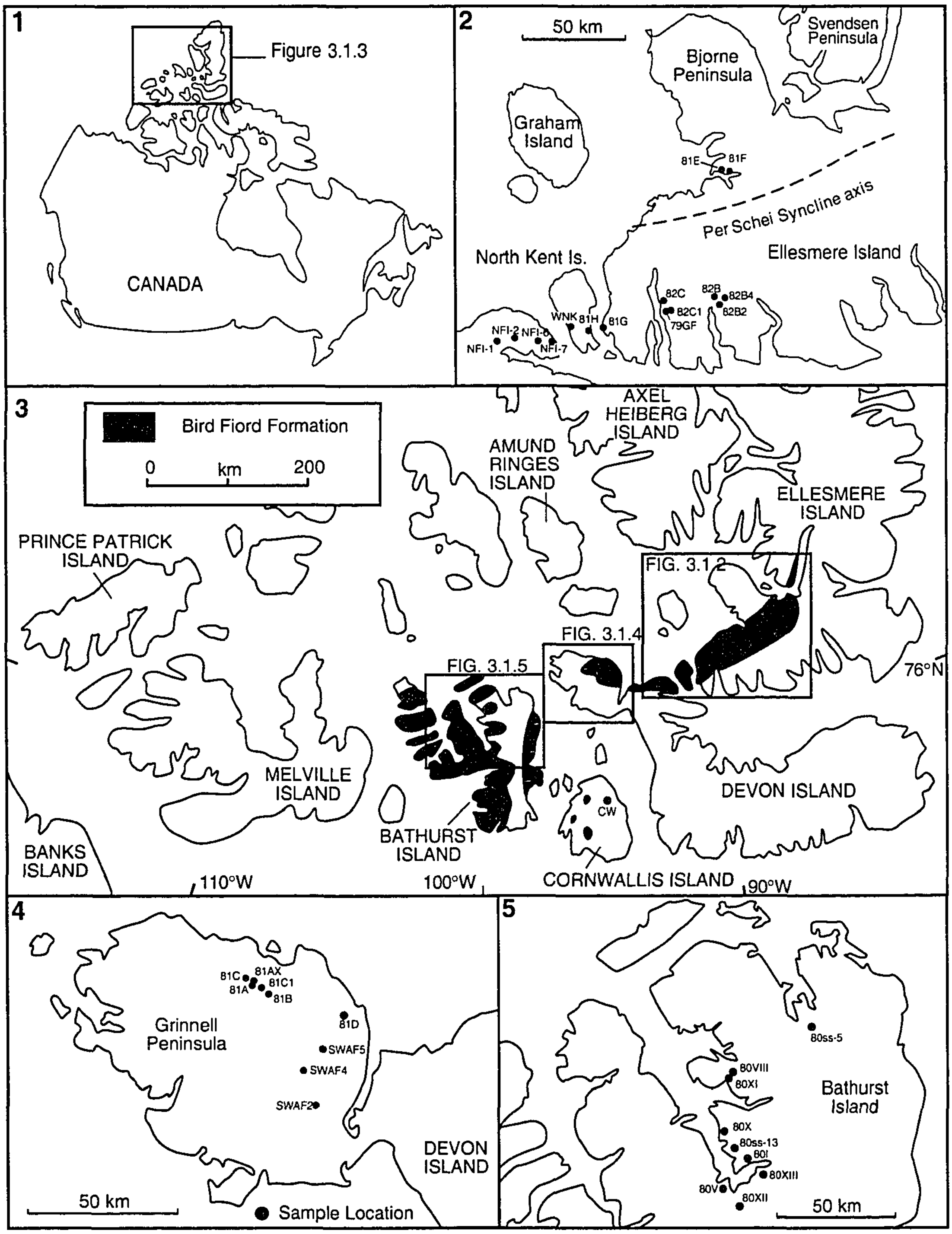

Figure 3.1--1, Map showing general location of study area; 2, location of measured sections on SW Ellesmere Island and North Kent Island; 3, distribution of the Bird Fiord Formation in the Arctic islands (modified from Goodbody, 1985); 4, location of measured sections on Grinnell Peninsula, Devon Island; 5, location of measured sections on Bathurst Island. Section numbers are the same as those used by Goodbody (1985).

TABLE 3.1—Brachiopods from the Bird Fiord Formation, Arctic Canada, source for their description, total number of specimens, and their paleobiogeographic affinity.

Species	Description	Total specimens	% of fauna	Endemic to Arctic
Arcticastrophia costellata	Li & Jones, 2002	87	0.19	Yes
Borealistrophia rongi	Li & Jones, 2002	179	0.38	Yes
Parapholidostrophia? sp.	This chapter	32	0.07	No
Spinulicosta sp.	This chapter	1392	2.96	No
Schizophoria sulcata	Johnson & Perry, 1976	3534	7.51	Yes
Gypidula mega n. sp.	This chapter	42	0.09	No
Ivdelinia grinnellensis	Brice, 1982	218	0.46	Yes
Cupularostrum repetitor	Johnson & Perry, 976 Brice, 1982	9114	19.38	Yes
Hypothyridina bifurcata	Brice, 1982	420	0.89	Yes
Spinatrypa (Iso.) parva n. sp.	This chapter	106	0.23	Yes
Spinatrypina borealis	This chapter	8178	17.39	No
Atrypa sp. B	Jones, 1982b	7669	16.31	No
Desquamatia (Ind.) fortis n. sp.	This chapter	8538	18.16	Yes
Grinnellathyris alvarezis	Li & Jones, 2002	100	0.21	Yes
Nucleospira lens	This chapter	645	1.37	No
Nucleospira stelcki n.sp.	This chapter	103	0.22	Yes
Emanuella bisinuata	Brice, 1982	1249	2.66	Yes
Elythyna sverdrupi	Brice, 1982	2505	5.33	Yes
Perryspirifer scheii	Jones & Boucot, 1983	647	1.38	Yes
Warrenella grinnellensis n. sp.	This chapter	1610	3.42	Yes
Costacranaena marlenae	Johnson & Perry, 1976	303	0.64	Yes
Cranaena briceae n. sp.	This chapter	355	0.75	Yes
Total		47026	100	

STRATIGRAPHIC SETTING

The Bird Fiord Formation is a carbonate-clastic succession that changes from marginal-marine carbonates in its lower part, to shelf, deltaic, and fluvial siliciclastics in its upper part (Goodbody in Mayr et al., 1994). Goodbody (1989) divided the formation into six members (Fig. 3.2). The Blubber Point, Baad Fiord, Norwegian Bay, and Cardigan Strait members, which are formed of sediments that accumulated on a shallow marine to shelf, contain brachiopods. The Cross Bay and Grise Fiord members, which are formed of sediments that accumulated in sabkha and delta plain settings, are devoid of brachiopods.

On Grinnell Peninsula and Bathurst Island, a carbonate unit directly under the Baad Fiord Member, is the time equivalent of the carbonate portion of the Bird Fiord Formation on Ellesmere Island. It has been variably referred to as the Blue Fiord Formation, a limestone member of the Disappointment Bay Formation (Smith, 1984), and an undifferentiated Devonian carbonate unit (Morrow and Kerr, 1977, Map 1421A, see Goodbody, 1985). Goodbody (1985), who termed it "the Bird Fiord Formation carbonate equivalent", suggested that this carbonate unit should be named as a new formation. The brachiopod fauna from this unit is similar to that found in other parts of the Bird Fiord Formation (Fig. 3.2); therefore, this unit is herein treated as part of the Bird Fiord Formation.

The Bird Fiord Formation ranges from late Early to Middle Devonian in age (late Emsian to late Eifelian). The basal (Cross Bay Member) and upper parts (Cardigan Strait Member) of the formation, which are the least fossiliferous, have not yielded conodonts diagnostic of a particular biozone (Freitas and Mayr, in Mayr et al., 1998). This makes it difficult to constrain the Bird Fiord Formation in terms of the established conodont zones. Conodonts indicative of the serotinus zone from the upper part of the Blue Fiord

Formation and conodonts of the inversus to serotinus zone from 173.8 m above the base of the Cross Bay Member indicates that the basal contact of the Cross Bay Member lies within the serotinus zone (Freitas and Mayr, in Mayr et al., 1998). Conodonts from strata below the base of Cardigan Strait Member belong to the australis zone. Spores from below the base of Cardigan Strait Member and from the overlying Strathcona Fiord Formation fall in the devonicus-naumovii palynomorph zone (late Eifelian). Thus, the upper contact of Cardigan Strait Member must lie in the ensensis conodont zone (Goodbody, 1989, fig.4; Freitas and Mayr, in Mayr et al., 1998, fig.4.2).

BRACHIOPOD FAUNA

The brachiopods previously described from the Bird Fiord Formation came from widely scattered localities. The lack of collections from all of the islands precluded an accurate assessment of the brachiopod biota. The present collection, with 22 species, includes most of the species described before and contains six new species: Gypidula mega n. sp, Spinatrypa (Isospinatrypa) parva n. sp, Desquamatia (Independatrypa) fortis n. sp., Nucleospira stelcki n. sp., Warrenella grinnellensis n. sp., Cranaena briceae n. sp. The genera/subgenus Gypidula, Spinatrypa (Isospinatrypa), Spinatrypina, Desquamatia, Warrenella, and Cranaena are reported from the Bird Fiord Formation for the first time. These taxa provide more information on the paleobiogeographic affinity of Arctic to other regions during Middle Devonian. The large collection of the brachiopods from numerous localities throughout the islands (Fig. 3.1) allows an accurate assessment of the biota in terms of its composition and distribution.

Collectively, the atrypids are most abundant, forming 52 percent of the collection, the rhynchonellids about 20 percent, spiriferids about 13 percent, orthids about eight percent, and productids about three percent. The terebratulids form slightly over one percent of the collection whereas strophomenids, pentamerids, and athyridids each form less than one percent (Table 3.1). Most of the species are found throughout the Bird Fiord Formation (except Cross Bay Member); only Parapholidostrophia? sp., Gypidula mega n. sp., Ivdelinia grinnellensis, and Spinatrypa (Isospinatrypa) parva n. sp, are confined to the lower part of the formation (Fig. 3. 2). There is no readily discernible relationship between individual taxa and the different members of the formation.

Biogeographically, the study area is in the Old World Realm as defined by Johnson and Boucot (1973) and Boucot (1988). The brachiopod fauna from the Bird Fiord Formation, however, is endemic in character. Arcticastrophia Li and Jones, Borealistrophia Li and Jones, Grinnellathyris Li and Jones, and Costacranaena Johnson and Perry are restricted to Arctic Canada. Sixteen species are limited to Arctic Canada (Table 3.1). The Old World Realm, with its numerous biogeographic divisions, is taxonomically more variable than other contemporary realms (Boucot, 1988, p. 218); therefore, the endemic character of the brachiopod fauna found in the Bird Fiord Formation is not surprising.

The presence of Nucleospira lens (Schnur) in the Bird Fiord Formation of Arctic Canada is of particular interest. This species has been reported from the Middle Devonian of Europe (Biernat, 1966; Ficner and Havlicek, 1978). Its appearance in Arctic Canada may indicate that there was some communication and faunal affinity between Arctic Canada and Europe. The presence of Spinatrypa (Isospinatrypa) in the Bird Fiord Formation of Arctic Canada may also indicate the communication and faunal affinity between the Canadian Arctic and Europe. According to Struve and Mohanti (1970), most of the European Spinatrypa species belong to S. (Isospinatrypa) whereas the North America specimens belong to S. (Spinatrypa). The Canadian Arctic specimens, however, show that the subgenus S. (Isospinatrypa) is also present in North America. Gypidula sp. from the upper Lower Devonian of Czechoslovakia is large (26.1 mm wide) (Havlicek and Kukal, 1990) and may prove to be G. mega n. sp. according to its size and external features. If this is the case, it may also indicate faunal affinity with Europe.

Ludvigsen and Perry (1975) recognized the franklinii lineage and occidentalis lineage among Middle Devonian Warrenella from northern Canada. The high triangular ventral interarea indicates that Warrenella grinnellensis n. sp. is part of the franklinii lineage. However, Warrenella grinnellensis n. sp. also processes some of the features of the occidentalis lineage; for example, its hinge line is not notably shorter than shell width. Ludvigsen and Perry (1975) suggested that there was faunal interchange between western North America and Europe based on different lineages of Warrenella in the Devonian of North America and Europe. The route of the exchange has been accepted to be via the Arctic Islands and Uralian Seaway. There was, however, no evidence to support this suggestion because knowledge of Warrenella in the Canadian Arctic Island was sparse. The presence of the Warrenella grinnellensis n. sp. in the Bird Fiord Formation on Grinnell Peninsula, Devon Island (Fig. 3.1), may confirm the faunal exchange originally suggested by Ludvigsen and Perry (1975).

SYSTEMATIC PALEONTOLOGY

Repository of illustrated specimens.-- All specimens are housed in the Paleontology Museum, Department of Earth and Atmospheric Sciences, University of Alberta (UA), Edmonton, Alberta, T6G 2E3, Canada.

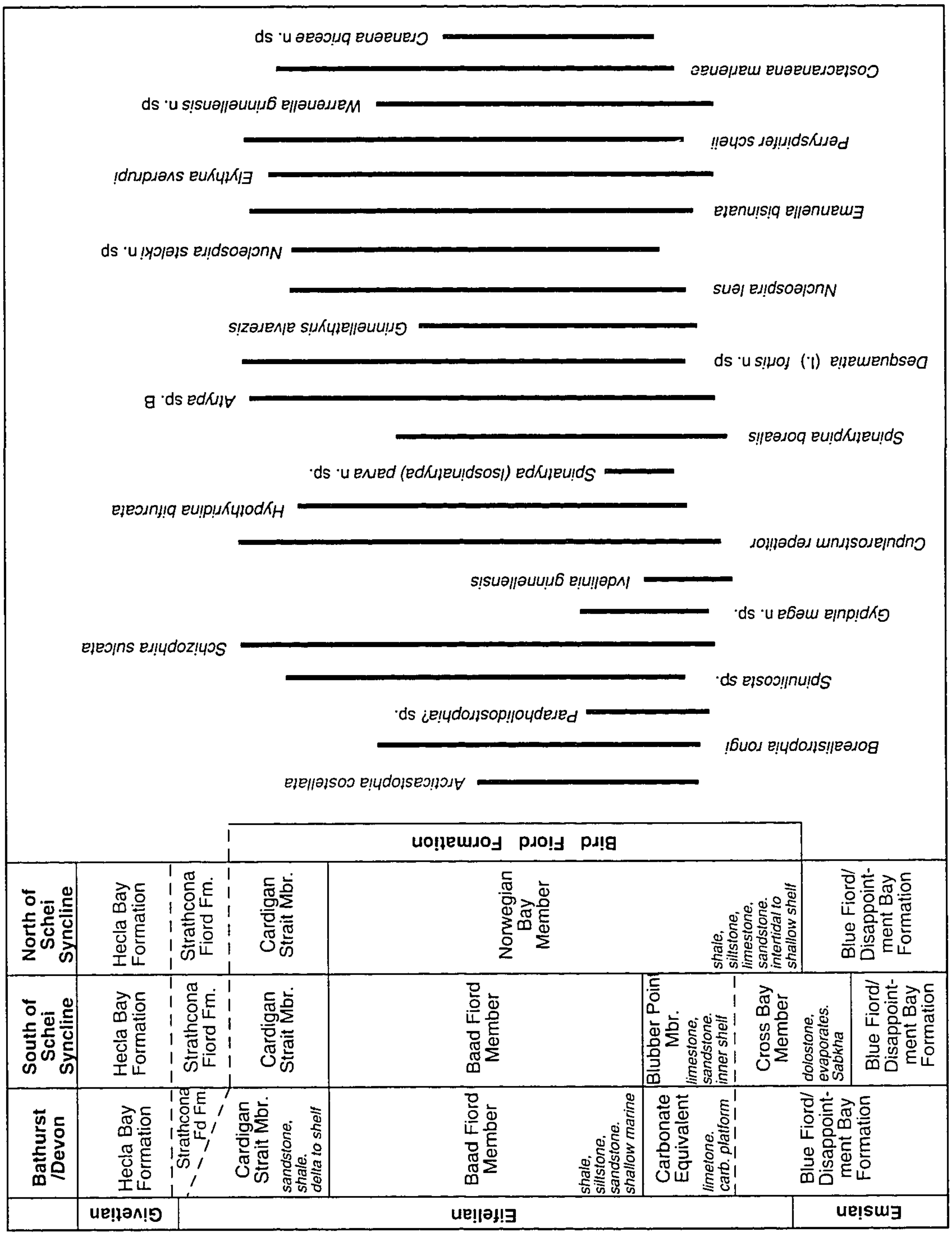

Figure 3.2--Correlation of members of Bird Fiord Formation (after Goodbody, 1985; 1989) and the distribution of brachiopod species. Solid horizontal lines indicate boundaries with biostratigraphic control; dash lines indicate inferred age boundaries. The Grise Fiord Member found on the extreme eastern part of Ellesmere Island, which is formed of sandstones that developed in a delta plain setting, is not shown in here because it does not contain brachiopods.

Order STROPHOMENIDA Öpik, 1934

Superfamily STROPHOMENOIDEA King, 1846

Family STROPHODONTIDAE Caster, 1939

Genus *PARAPHOLIDOSTROPHIA* Johnson, 1971

PARAPHOLIDOSTROPHIA? sp.

Figure 3.3.1-3.3.6

Description.--Shell medium sized, transverse to shield shaped. Strongly concavo-convex. Hinge line denticulate, cardinal extremities round, maximum width at or slightly anterior to hinge line. Ventral interarea low, orthocline to apsacline, dorsal interarea low, hypercline. Pseudodelthyrium filled. Unequal parvicostellate ornamentation. Ventral muscle field cordate, bilobed, about half of valve length, weak median myophragm.

Material examined.-- 30 complete or nearly complete specimens, 2 ventral interiors.

Occurrence.--Bird Fiord Formation carbonate equivalent and Baad Member, Grinnell Peninsula, Devon Island; Blubber Point Member, Devon and North Kent islands.

Discussion.—This taxon is distinguished from Borealistrophia Li and Jones, 2002, and Arcticastrophia Li and Jones, 2002, by its strong concavo-convex lateral profile. Its shape, lateral profile, ornamentation, and ventral muscle field are similar to Parapholidostrophia sorensis Jones (in Jones and Smith, 1980) and P. harperi Johnson, 1971, which came from the Lower Devonian Eids Formation of Arctic Canada (Jones and Smith, 1980; 1985). The tentative assignment to Parapholidostrophia? reflects the lack of information on the dorsal interior.

Order PRODUCTIDA Sarytcheva et Sokolskaya, 1959

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTOIDEA Gray, 1840

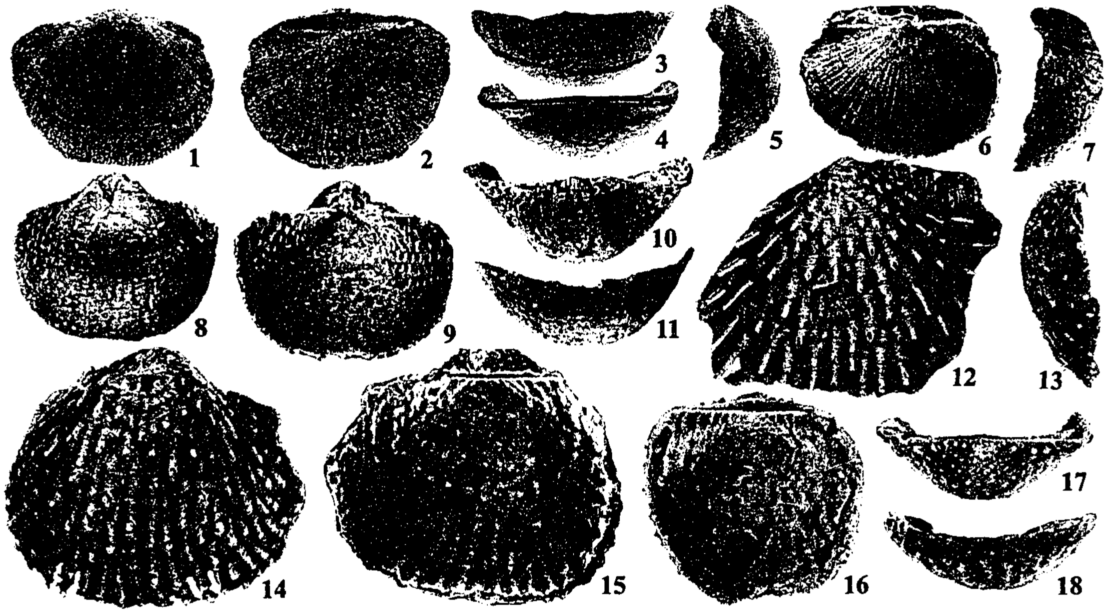

Figure 3.3—1-6, *Parapholidostrophia*? sp. 1-5, ventral (1), dorsal (2), anterior (3), posterior (4), and lateral (5) views, X0.9, from boundary of Blubber Point and Baad Fiord members, Norfolk Inlet (NFI-1), Devon Island, UA12927; 6, dorsal view, X1.2, from Bird Fiord Formation carbonate equivalent, 10 km west of Arthur Fiord (SWAF 2/1), Grinnell Peninsula, UA12928.

7-18, *Spinulicosta* sp. 7-11, lateral (7), ventral (8), dorsal (9), posterior (10), and anterior (11) views, X1.4, from Blubber Point Member, Blubber Point (81G), Simmons Peninsula, Ellesmere Island, UA12929; 12, ventral view, X3.8, from Baad Fiord Member, Ensorcellement River (81B), Grinnell Peninsula, UA12930; 13, 16-18, lateral (13), dorsal (16), posterior (17), and anterior (18) views, X2.2, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12931; 14, 15, ventral and dorsal views, X2.2, from Baad Fiord Member, 19 km west of Arthur Fiord (SWAF 5/4), Grinnell Peninsula, UA12932.

Family PRODUCTELLINDAE Schuchert, 1929

Subfamily PRODUCTELLINAE Schuchert, 1929

SPINULICOSTA Nalivkin, 1937

SPINULICOSTA sp.

Figure 3.3.7-3.3.18; Figure 3.4

Spinulicosta? sp. JONES, 1982b, pl. 2, figs. 31-33.

Description.--Small to medium sized, subrounded, strongly concavo-convex in profile. Corpus shallow. Hinge line straight, slightly less than maximum width. Ventral umbo curved. Ginglymus of both valves very low and linear. Cardinal extremities rounded, ears small. Spines long, projecting subparallel to shell surface, randomly placed on ventral valve. Weak concentric rugae variably developed, especially on large specimens. Dorsal valve with elongate dimples.

Cardinal process bilobed. Prominent alveolus under anteomedial portion of cardinal process, narrow, slightly elongated. Median septum initiated anterior to alveolus, with highest portion at mid-length, reaching to about two-thirds of the shell length (Fig. 3.4). Muscle scars not obvious.

Material examined.--1392 specimens, most incomplete.

Occurrence.-- Bird Fiord Formation carbonate equivalent, Baad Fiord, Cardigan Strait, Blubber Point, and Norwegian Bay members; Bathurst Island, Grinnell Peninsula, Devon, North Kent, and Ellesmere islands.

Discussion.-- On well-preserved shells, the spines are clearly evident and there is no evidence of costae. On poorly preserved shells, ventral valve surface seems to be costate, and therefore similar to Helaspis Imbrie, 1959. Spinulicosta and Chattertonia Johnson,

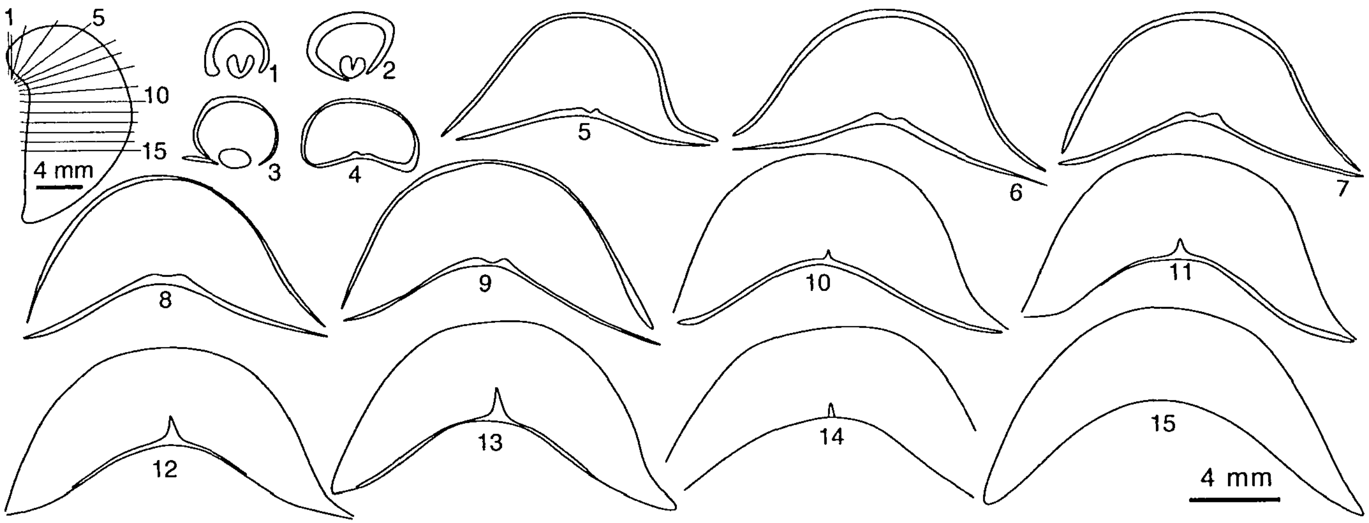

Figure 3.4--Selected transverse serial sections of Spinulicosta sp. Positions of sections are indicated on diagram in upper left corner of figure. Specimen from locality 81A-224 m, Baad Fiord Member, Ensorcellement River, Grinnell Peninsula.

1976, which are externally similar, can only be distinguished by the presence (Chattertonia) or absence/weakly developed (Spinulicosta) anderidia in the dorsal valve. Conversely, Spinulicosta has an alveolus (cf. Johnson, 1976) whereas Chattertonia does not. No anderidia were found in the three sectioned specimens; therefore, the specimens are assigned to Spinulicosta.

Most of the species previously assigned to Spinulicosta lack interior features. This, coupled with the fact that most of the specimens from the Bird Fiord Formation are embedded in the rock matrix means that assignment to a particular species is very difficult. S. stainbrooki Crickmay from Northwest Territories (Crickmay, 1960, p. 18-19, pl. 11, figs. 4-15) and S. muirwoodi Johnson from Nevada (Johnson, 1971, p. 311-312, pl. 41, figs. 5-14) have very prominent radial costae and therefore differ from Spinulicosta sp. which has weakly developed rugae. The weakly developed anderidia, greater density and length of the ventral spines, and a median septum that extends almost to the shell margin serve to distinguish S. prima Chatterton and Perry from northwest Canada (Chatterton and Perry, 1978, p. 34-35, pl. 1, figs. 1-10) from Spinulicosta sp.

Order PENTAMERIDA Schuchert et Cooper, 1931

Suborder PENTAMERIDINA Schuchert et Cooper, 1931

Superfamily GYPIDULOIDEA Schuchert et LeVene, 1929

Family GYPIDULIDAE Schuchert et LeVene, 1929

Subfamily GYPIDULINAE Schuchert et LeVene, 1929

Genus *GYPIDULA* Hall, 1867

Discussion.--Diagnostic features of the genus include its smooth or costate shell, with dorsal sulcus and ventral fold, and inner hinge plates convergent to valve floor that do not unite to form curalium. This genus excludes species with divergent inner hinge plates or cruralium (Jin et al., 1993).

Sapelnikov (1985) listed four subgenera of Gypidula but did not attempt to assign the 156 species he listed to those subgenera. Differences between the subgenera are extremely vague (Jin et al. 1993, Jin and Chatterton, 1997). Jin et al. (1993) and Jin and Chatterton (1997) therefore treated Gypidula as an undivided genus. This scheme is followed herein.

GYPIDULA MEGA new species

Figures 3.5.1-3.5.24, Figure 3.6

Gypidula? sp. HAVLICEK AND KUKAL, 1990, p. 142, pl. 5, fig. 6.

Diagnosis.-- Large gypidulid, outline roundly pentagonal, width and length subequal. Exterior smooth in young specimens, anteriorly plicated in adult specimens with 2-3 low rounded costae in sulcus and fold, 2-3 faint costae on each flank.

Description.--Shell up to 28 mm long and wide (Table 3.2). Outline roundly pentagonal, length and width subequal, ventri-biconvex in lateral profile. Hinge line curved, cardinal angle rounded. Anterior commissure sulcate. Ventral valve strongly convex, greatest thickness slightly anterior to mid-length. Ventral palintrope short, suberect. Fold obscure posteriorly, originating slightly anterior to umbo, becoming well-defined at anterior margin, flat-topped. Dorsal valve slightly convex, sulcus broad and shallow, beginning near beak, well developed in anterior half of shell. Shell surface smooth in young specimens. Adult specimens with low, rounded costae starting about mid-length, 2-3 costae in sulcus and fold, 2-3 faint costae on flanks.

Spondylium relatively large, wide. Median septum high. Teeth small. Inner hinge plates low, converging towards valve floor but not united to form cruralium. Outer hinge plates slightly longer than outer plates, divergent from each other ventrolaterally. Bases of crura merging smoothly with outer and inner hinge plates without forming carinae (Fig. 3.6).

Etymology.--Mega, Greek, large.

Types.--Holotype, UA12937 (Bird Fiord Formation carbonate equivalent, locality 80VIII); paratypes, UA12933 (Baad Fiord Member, locality 81A), UA12934, UA12935 (Bird Fiord Formation carbonate equivalent, locality 80XI and 80VIII respectively), UA12936, UA12938, and UA12939 (Bird Fiord Formation carbonate equivalent, all from locality 80X).

Other material examined.--42 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent, Baad Fiord Member; Bathurst Island and Grinnell Peninsula, Devon Island.

Discussion.--Many of the Eifelian Gypidula species are small (e.g., Veevers, 1959; Talent, 1963; Johnson and Reso, 1964; Biernat, 1966; Frost and Langenheim, 1966; Johnson, 1966; 1975; Boucot, 1973; Hou and Xian, 1975; Balinski, 1979; Smith, 1980; Savage, 1981; Cooper and Dutro, 1982; Chen, 1984; Perry, 1984; Lenz and Johnson, 1985; Wang and Rong, 1986; Rong et al., 1987; Sapelnikov et al., 1987; Soja, 1988; Farrell, 1992; Savage and Baxter, 1995; Norris, 1998). Gypidula cf. papyracea Belanski, 1928, from the Middle Devonian of Wisconsin is relatively large (12-21 mm long) (Griesemer, 1965). It differs from the new species by its very weak fold and sulcus and comparatively smooth flanks. Another large species, G. mansuyi Grabau, 1931, from Yunnan, China (Grabau, 1931) differs from G. mega n. sp. by its very strongly convex ventral valve and less prominent ventral beak and weakly developed fold and sulcus. Gypidula boucoti Lenz, 1977, a large species from the Lower Devonian of Yukon, differs from G. mega because its costae arise near the umbo and may increase in number by bifurcation.

TABLE 3.2-- Dimensions (mm) of 11 specimens of Gypidula mega n. sp. (*holotype)

UA No.	12933	12934	12935	12936	12937*	12938	12939				
Length	14.5	18.8	14.2	20.9	26.3	25.4	20.8	12.0	27.2	27.3	28.0
Width	15.1	19.4	14.0	24.7	26.8	26.0	19.7	12.5	26.1	23.5	28.1
Thickness	13.1	14.5	9.0	15.0	19.0	18.8	14.8	9.4	22.4	20.8	21.3

Figure 3.5---- *Gypidula* *mega* n. sp. *1*-*3*, Paratype, dorsal (*1*), ventral (*2*), and posterior (*3*) views, X2.2, from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula, UA12933; *4*, *9*-*11*, paratype, lateral (*4*), dorsal (*9*), posterior (*10*), and ventral (*11*) views, X1.8, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12934; *5*, paratype, dorsal view, X2.4, from Bird Fiord Formation carbonate equivalent, 1 km east of Half Moon Bay (80VIII), Dundee Bight, Bathurst Island, UA12935; *6*-*8*, paratype, anterior (*6*), dorsal (*7*), and transverse section at 4.1 mm from posterior tip (*8*) of sectioned specimen, 4, 6, X1.7, 10, X2, from Bird Fiord Formation carbonate equivalent, Half Moon Bay (80X), Dundee Bight, Bathurst Island, UA12936; *12*-*14*, *19*, *20*, holotype, dorsal (*12*), anterior (*13*), lateral (*14*), posterior (*19*), and ventral (*20*) views, X1.5, from Bird Fiord Formation carbonate equivalent, 1 km east of Half Moon Bay (80VIII), Dundee Bight, Bathurst Island, UA12937; *15*-*18*, paratype, dorsal (*15*), ventral (*16*), posterior (*17*), and anterior (*18*) views, X1.4, UA12938; *21*-*24*, paratype, posterior (*21*), ventral (*22*), lateral (*23*), and anterior (*24*) views, X1.7, UA12939. UA12938, UA12939 from Bird Fiord Formation carbonate equivalent, Half Moon Bay (80X), Dundee Bight, Bathurst Island.

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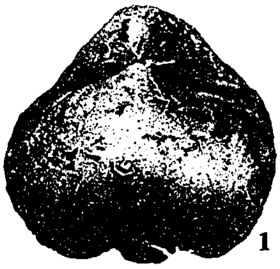
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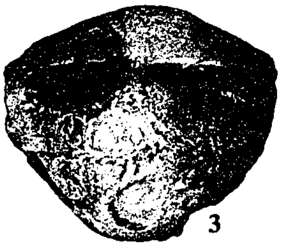
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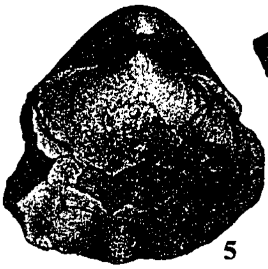
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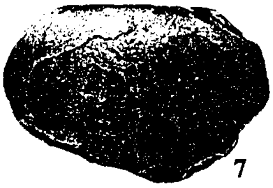
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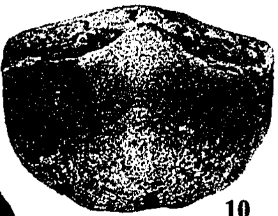
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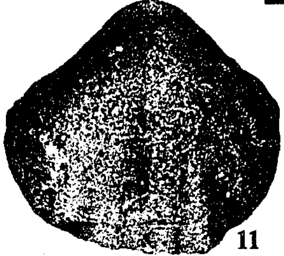
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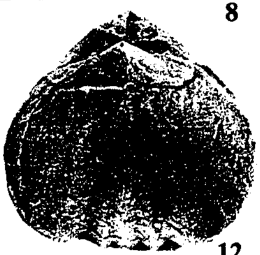
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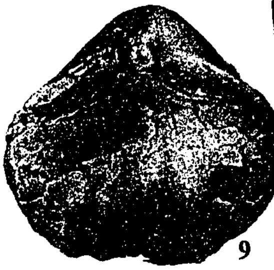
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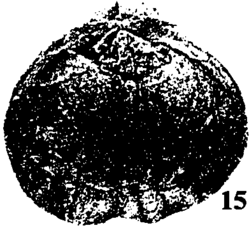
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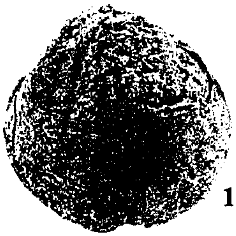
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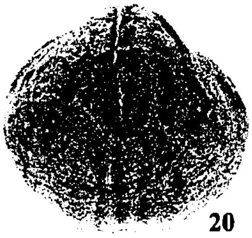
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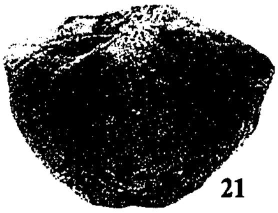
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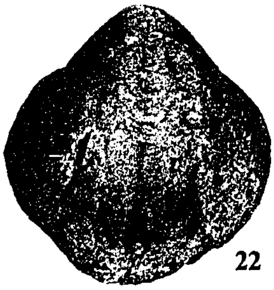
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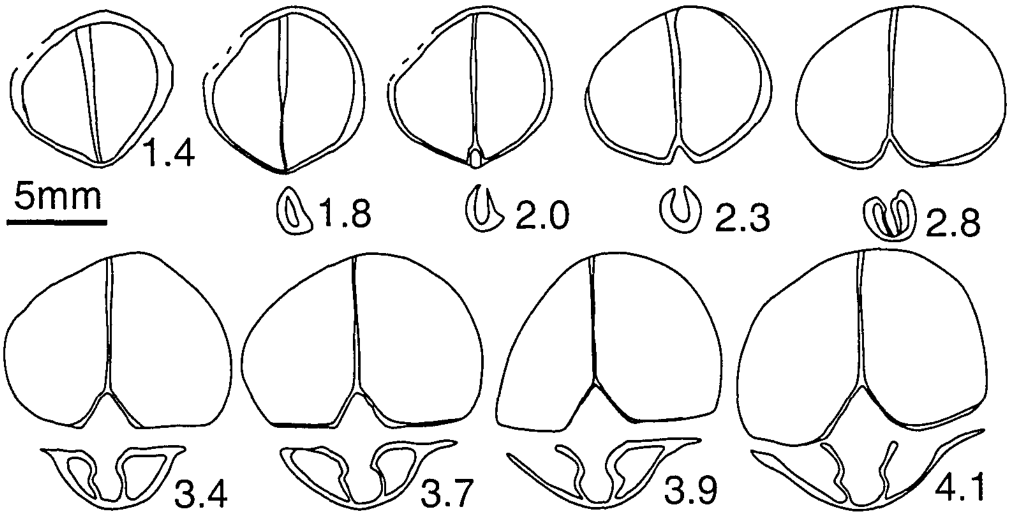

Figure 3.6--Selected transverse serial sections of Gypidula mega n. sp. Distances in mm from posterior tip of ventral umbo (specimen UA12936).

In addition to size differences, the well-developed fold and sulcus and the anterior costae also distinguish the new species from other congeneric species. Externally, *G*. cf. *loczyi* Grabau, 1931, from the Emsian of South China (Wang and Rong, 1986) is most similar to the new species. The absence of a medium septum in *G*. cf. *loczyi* (Wang and Rong, 1986, p. 128, fig. 43) serves to separate it from the new species. *Gypidula* *loczyi* was named by Grabau (1931) based on Loczy (1899)'s description and figures of *Pentamerus* *galeatus* (Middle Devonian, Sichuan). The figures of *G*. *loczyi* (Grabau, 1931, p. 75-77, text-fig. 4) show that it has stronger costae than those in *G*. *mega*, and its costae start near umbo region as oppose to mid-length in *G*. *mega*. Hou and Xian (1975) identified some Lower Devonian specimens from Guangxi as *G*. *loczyi*, which are externally similar to *G*. *mega*, but their specimens are generally smaller than *G*. *mega*.

Gypidula *mega* can be distinguished from *G*. *thorsteinssoni* Johnson, 1975, from the Lower Devonian of the Canadian Arctic Islands, because the latter has smooth flanks and its ventral fold splits to form a biplicate fold of variable strength, and a brachial sulcus with one median plication (Johnson, 1975). *G*. cf. *kayseri* (Peetz, 1901), also from the Lower Devonian of the Arctic Islands, has a ventral fold modified by a strong median furrow and a single pair of well-developed costae on the flanks (Johnson, 1975), which separate it from *G*. *mega*.

Gypidula sp. Havlicek and Kukal, 1990 from the upper Lower Devonian of Czechoslovakia is up to 26.1 mm wide, and may prove to be *G*. *mega*. The paucity of specimens, however, precludes a more confident assessment.

Order ATRYPIDA Rzhonsnitskaya, 1960

Superfamily ATRYPACEA Gill, 1871

Family ATRYPIDAE Gill 1871

Subfamily SPINATRYPINAE Copper, 1978

Genus *SPINATRYPA* Stainbrook, 1951

Discussion.--The spinose atrypids were originally named Hystricina when Stainbrook (1945) defined the genus. In 1951, Stainbrook renamed the genus as Spinatrypa because Hystricina was pre-occupied (Stainbrook, 1951). The original definition of the genus is still largely valid (Copper, 1967b). The difference between Spinatrypa and Spinatrypina Rzhonsnitskaya, 1964, however, seems to be subtle. According to Copper (1967a, 1967b), Spinatrypa differs from Spinatrypina because: 1) the ribs of the former are undulose instead of tubular-imbricated as on the latter; 2) the interarea and deltidial plates of Spinatrypa are relatively small; and 3) Spinatrypa has more prominent and abundant spines. In practice, it is not easy to determine if the interarea and deltidial plates are "relatively large", because these two features are small in atrypids. The development of spines may not always be apparent due to the style of preservation. The main difference between the two genera seems to be in the style of ribbing. In Spinatrypa, the ribs are not only undulose but also coarser, with the spacing between ribs being larger than that in Spinatrypina.

There are four subgenera belonging to Spinatrypa: Spinatrypa (Spinatrypa) Stainbrook, 1951; S. (Inveratrypa) Struve, 1961; S. (Isospinatrypa) Struve, 1966; and S. (Plicspinatrypa) Rzhonsnitskaya (in Rzhonsnitskaya et al., 1998). The recognition of these subgenera is mainly based on the lateral shell profile and the presence or absence of dental plates. Spinatrypa (Spinatrypa) is of medium to large size, with a pronouncedly dorsi-biconvex to ventri-resupinate (convexo-concave) profile. Spinatrypa (Isospinatrypa) has a small- to medium- sized shell, with an equi-biconvex to somewhat dorsi-biconvex profile. Spinatrypa (Inveratrypa) has a small or, at most, medium-sized shell, with a markedly to extremely ventri-biconvex or plano-convex profile, exceptionally faintly dorsi-resupinate (concave-convex) shell (Struve and Mohanti, 1970, p. 157-158). Spinatrypa (Plicspinatrypa) has distinctive dental plates (Rzhonsnitskaya et al., 1998), whereas the other subgenera do not.

SPINATRYPA (ISOSPINATRYPA) PARVA new species

Figures 3.7.1-3.7.18, Figure 3.8

Diagnosis.-- Equi-biconvex to slightly dorsi-biconvex, small Spinatrypa, length and width less than 15 mm, wider than long.

Description.-- Shell small, less than 15 mm long and wide, slightly dorsiconvex, subcircular in outline, maximum width near midlength of shell. Wider than long, rarely longer than wide, with average length/width ratio about 0.9, average thickness/width ratio about 0.5 (Table 3.3). Hinge line straight to slightly curved, about two-thirds of maximum width. Shell slightly uniplicate in anterior commissure due to a very shallow sulcus expanding anteriorly in ventral valve. Dorsal fold not developed. Ventral beak orthocline to weakly anacline, circular foramen in some specimens. Ventral interarea small, disjunct deltidial plates not seen. Dorsal beak and interarea obscured by incurvature against ventral interarea. Ornamentation of 7-17 coarse, strong radial costae, crossed by strong, concentric, regularly spaced lamellae, producing imbricate-like thickening over ribs. Costae increase anteriorly by bifurcation and implantation.

Prominent teeth pads without support of dental plates (Fig. 3.8). Spiralia not observed through serial sections of four specimens due to recrystallization.

Etymology.--from Latin, parva, small.

Types.--Holotype, UA12941 (Baad Fiord Member, locality 82B); paratypes, UA12940 (Baad Fiord Member, locality 82B), UA12942-12945 (Blubber Point Member, locality 82B)

Other material examined.--106 specimens.

TABLE 3.3--Dimensions (mm) of Spinatrypa (Isospinatrypa) parva n. sp.

Section	82B-ss1	82B-ss7	82B-ss5	
Member	Blubber Point	Baad Fiord	Baad Fiord	Data combined
Island	Ellesmere	Ellesmere	Ellesmere	
No. measured	34	36	4	74
Length(L)	5.2(8.8)12.0*	6.8(9.6)12.5	9.5(10.1)12.0	5.2(9.2)12.5
Width(W)	5.3(9.4)12.1	7(10.5)13.8	11.1(11.2)12.2	5.3(10.0)13.8
Thickness(T)	2.4(4.6)6.4	3(5.3)7.0	4.6(5.6)7.0	2.4(5.0)7.0
L/W	0.76(0.95)1.10	0.72(0.92)1.06	0.87(0.91)0.98	0.72(0.93)1.10
T/W	0.39(0.50)0.64	0.33(0.50)0.68	0.41(0.5)0.57	0.33(0.50)0.68
Anterior ribs	8(11.7)17	7(10.6)15	12(12.3)13	7(11.2)17

Data format: Minimum(Average)Maximum

Figure 3.7—*1*-*18*, *Spinatrypa* (*Isospinatrypa*) *parva* n. sp. *1*, *2*, paratype, dorsal and ventral views, X2.7, UA12940; *3*-*6*, *8* holotype, lateral (*3*), ventral (*4*), anterior (*5*), posterior (*6*), and dorsal (*8*) views, X2.7, UA12941; *7*, *9*, *10*, paratype, anterior (*7*), dorsal (*9*), and ventral (*10*) views, X2.7, UA12942; UA12940-12942 from Baad Fiord Member, 11 km north of head of Muskox Fiord (82B-SS7), Ellesmere Island; *11*, *13*, *14*, paratype, anterior (11), dorsal (*13*), and ventral (*14*) views, X2.7, UA12943; *12*, *15*, *18*, paratype, posterior (*12*), ventral (*15*), and dorsal (*18*) views, X3.3, UA12944; *16*, *17*, paratype, ventral and dorsal views, X3.3, UA12945; UA12943-12945 from Blubber Point Member, 11 km north of head of Muskox Fiord (82B-ss1), Ellesmere Island. *19*-*35*, *Spinatrypina* *borealis* (Warren), *19*, *24*, *33*, *35*, anterior (*19*), posterior (*24*), dorsal (*33*), and lateral (*35*) views, X1.9, from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula, UA12946; *20*, *22*, *25*, *26*, *30*, anterior (*20*), posterior (*22*), lateral (*25*), dorsal (*26*), and ventral (*30*) views, X1.7, from Baad Fiord Member, South end of Dundee Bight (80XII), Bathurst Island; UA12947; *21*, *23*, *27*, *31*, *32*, posterior (*21*), lateral (*23*), anterior (*27*), ventral (*31*), and dorsal (*32*) views, X1.7, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12948; *28*, *29*, ventral (*28*) and dorsal view showing part of spiralia (*29*), X1.7, UA12949; *34*, dorsal view showing part of spiralia, X1.7, UA12950; UA12949 and UA12950 from Baad Fiord Member, Ensorcellement River (81B), Grinnell Peninsula.

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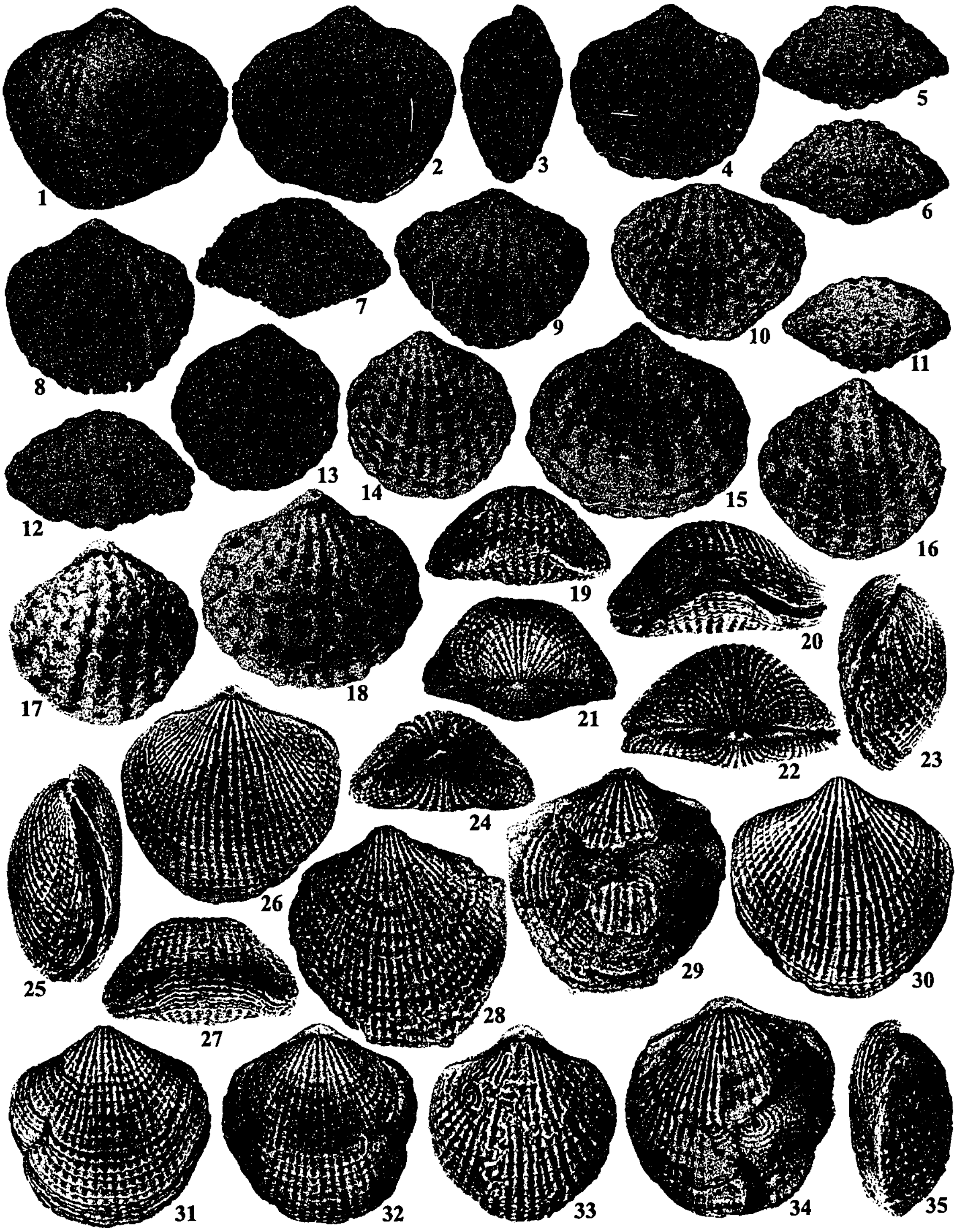
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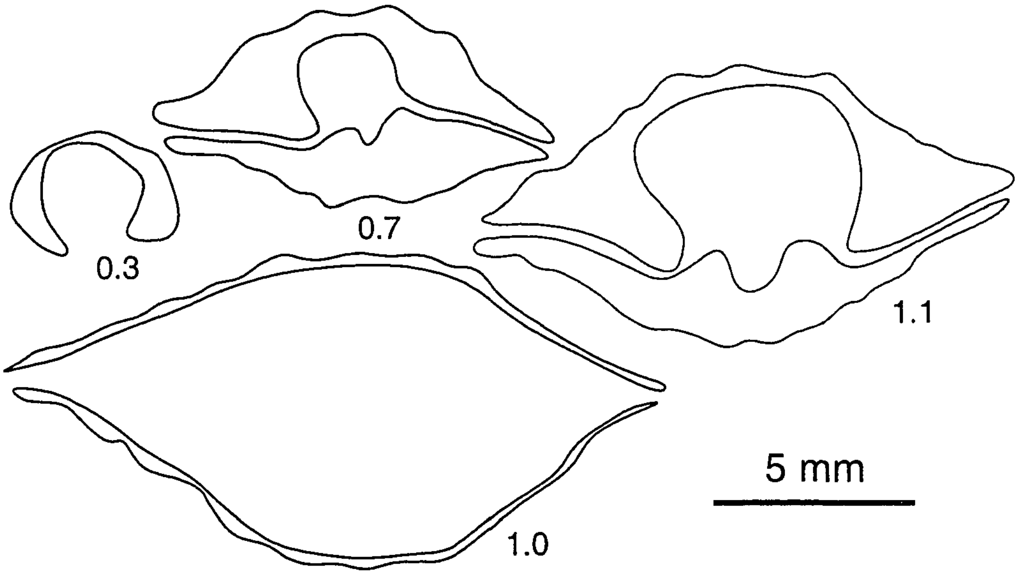

Figure 3.8--Selected transverse serial sections of Spinatrypa (Isospinatrypa) parva n. sp. Distances in mm from posterior tip of ventral umbo.

Occurrence.--Baad Fiord and Blubber Point members; Ellesmere Island.

Discussion.--These specimens are assigned to Spinatrypa mainly on the basis of their coarser, undulose ribs. The equi-biconvex to slightly dorsibiconvex lateral profile and small size indicates assignment to the subgenus S. (Isospinatrypa). According to Struve and Mohanti (1970), most of the European Spinatrypa species belongs to S. (Isospinatrypa) whereas the North America specimens belong to S. (Spinatrypa). The Arctic specimens, however, show that the subgenus S. (Isospinatrypa) is also present in North America.

The ribs of Spinatrypa (Isospinatrypa) parva n. sp. are coarser than those in Spinatrypina borealis (Fig.3. 9). The latter is also larger than the new species.

The new species is readily distinguished from other congeneric species by its small size (length and width less than 15mm) and slightly dorsi-biconvex shell profile. Spinatrypa coriacea Crickmay, 1960, from the Hume Formation in the North West Territories is much larger than the new species, with the holotype being 42 mm long and 44 mm wide (Crickmay, 1960, p. 14). S. globulina Copper, 1967b, and S. orthoclina Copper, 1967b, from Germany are medium to large-sized (18 to 25 mm), with equal length and width (Copper, 1967b, p. 506). Spinatrypa variaspina Copper, 1967b, from Germany can be distinguished from the new species because the length to width ratio of the former species varies from less than 1.0 to more than 1.0, and it developed a weak fold (Copper, 1967b, p. 495). The new species is similar in size and lateral profile to Spinatrypa tumuli Godefroid and Helsen, 1998, that is found in the upper Frasnian of south Belgium (Godefroid and Helsen, 1998, p. 245-248, figs. 4A-F, 5A.). They differ in that the growth lamellae of S. tumuli are neither as obvious nor as uniform as those in the new species. In addition, the shell material of the new species is raised where the ribs and growth lamellae meet.

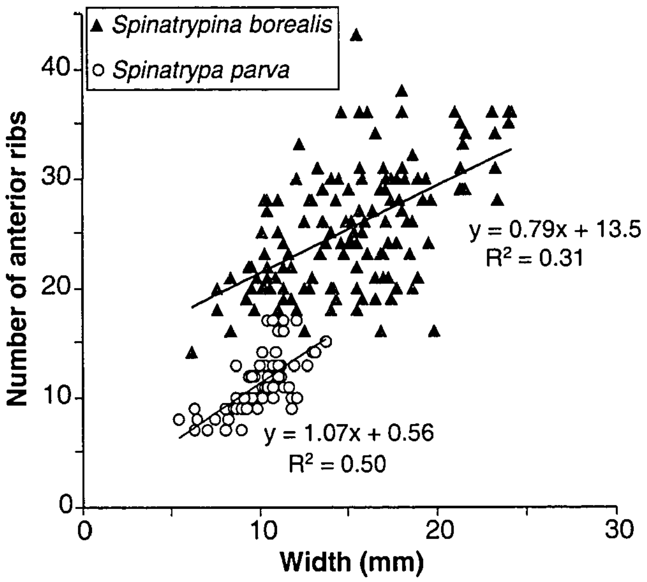

Figure 3.9--Number of anterior ribs of Spinatrypa (Isospinatrypa) parva n. sp. and Spinatrypina borealis (Warren) versus shell width.

The new species is similar in size to S. compacta Cooper and Dutro, 1982, and S. obsolescens Cooper and Dutro, 1982, from the Contadero Formation (late Frasnian), New Mexico. Spinatrypa compacta, however, is nearly square with small flattened ears, whereas the costae of S. obsolescens are vague or obsolescent anterior to the umbonal region (Cooper and Dutro, 1982, p. 89-90).

Genus *SPINATRYPINA* Rzhonsnitskaya, 1964

SPINATRYPINA BOREALIS (Warren), 1944

Figures 3.7.19-3.7.35, Figure 3.10

Atrypa borealis WARREN, 1944, p. 121, pl. 3, figs. 4-6; WARREN AND STELCK, 1956, pl. 3, figs. 5-6.

Spinatrypa borealis, MCLAREN, 1962, pl. 8, figs. 16-18.

Spinatrypa (Spinatrypa) borealis JOHNSON AND PERRY, 1976, p. 628-629, pl. 1, figs. 16-22.

Not Spinatrypa (Isospinatrypa) borealis, COPPER, 1978, p. 299, pl. 1, figs. 20-21, pl. 2, figs.1-5.

Description.--Shell less than 25 mm wide. Dorsi-biconvex in thicker specimens; gently and subequally biconvex in thinner ones. Subcircular in outline with maximum width near midlength of shell. Length/width ratio of 0.9-1.2 (average 1.0). Thickness/width ratio average 0.5 (Table 3.4). Hinge line straight to slightly curved, about two-thirds of maximum width. Very shallow sulcus expanded anteriorly in ventral valve, forming slightly uniplicate anterior commissure. Sulcus deflected dorsalward, more prominent in thicker specimens. Dorsal fold not developed.

Ventral beak low, suberect, open foramen in some specimens; ventral interarea minute, orthocline to weakly anacline; delthyrium with small disjunct deltidial plates. Dorsal beak and interarea obscured by incurvature against ventral interarea.

Both valves with 14 to 43 relatively fine, weakly imbricate, tubular costae (Fig. 3.9), separated by sloped interspaces. Costae increase anteriorly by bifurcation and implantation, crossed by concentric, fairly regularly spaced lamellae, producing thickenings over costae.

Teeth pads strong without support of dental plates. Prominent dental sockets between inner shell wall and extensions of hinge plates (Fig. 3.10). Spiralia directing dorso-medially with 7-12 loops.

Material examined.--8178 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent, Baad Fiord, Blubber Point, and Norwegian Bay members, Bathurst Island, Grinnell Peninsula, Ellesmere, and Cornwallis islands

Discussion.--The systematic position of Atrypa borealis Warren, 1944, in the spinatrypid was uncertain. Johnson (1970, p. 260) suggested that Atrypa borealis and A. borealis var. lata belong to Spinatrypina because of its narrow ribs and shell-hugging concentric lamellae. Johnson and Perry (1976, p. 629), however, assigned Atrypa borealis to Spinatrypa with reservation because the ornamentation is finer. The specimens of Atrypa borealis, illustrated in Warren (1944, pl. 3, figs. 4-6) and Warren and Stelck (1956, pl. 3, figs. 5-6), have tubular and fine costae. This indicates that Atrypa borealis (and A. borealis var. lata) belong to the genus Spinatrypina.

The Bird Fiord specimens are assigned to Spinatrypina based on their fine, weakly imbricate, tubular ribs. The total number of ribs on Bird Fiord specimens varies from 14 to 43 (Fig. 3.9), whereas the total number of ribs ranges from 10 to 20 in Spinatrypa as indicated in the original definition of the genus (e.g., ribs of Spinatrypa are coarser) (Stainbrook, 1945, p. 49).

TABLE 3.4—Dimensions (mm) of Spinatrypina borealis

Section	80I-819-825m	80XII-164m	81A-138.5m	81B-170m	Data
Member	Cardigan Strait	Baad Fiord	Baad Fiord	Baad Fiord	Combined
Island	Bathurst	Bathurst	Grinnell Peninsula	Grinnell Peninsula	
No. measured	72	48	38	38	196
Length (L)	6.1(13.7)19.8*	9.8(16.6)20.4	8.2(14.0)22.7	9.7(19.3)25.0	6.1(15.5)25.0
Width (W)	6.1(13.6)18.3	10.5(16.8)21.5	8.3(14.0)21.5	10.1(19.3)24.2	6.1(15.5)24.2
Thickness (T)	2.8(7.6)11.6	4.6(10.0)13.4	3.5(6.9)12.5	4.0(10.0)14.4	2.8(8.5)14.4
L/W	0.86(1.01)1.15	0.81(0.99)1.12	0.85(0.99)1.11	0.92(1.00)1.12	0.85(1.0)1.15
T/W	0.39(0.56)0.74	0.41(0.59)0.94	0.35(0.48)0.74	0.38(0.52)0.71	0.39(0.5)0.94
Anterior Ribs	14(27.7)43	16(22)30	16(24)33	18(30)36	14(25.5)43

*Data format: minimum (average) maximum

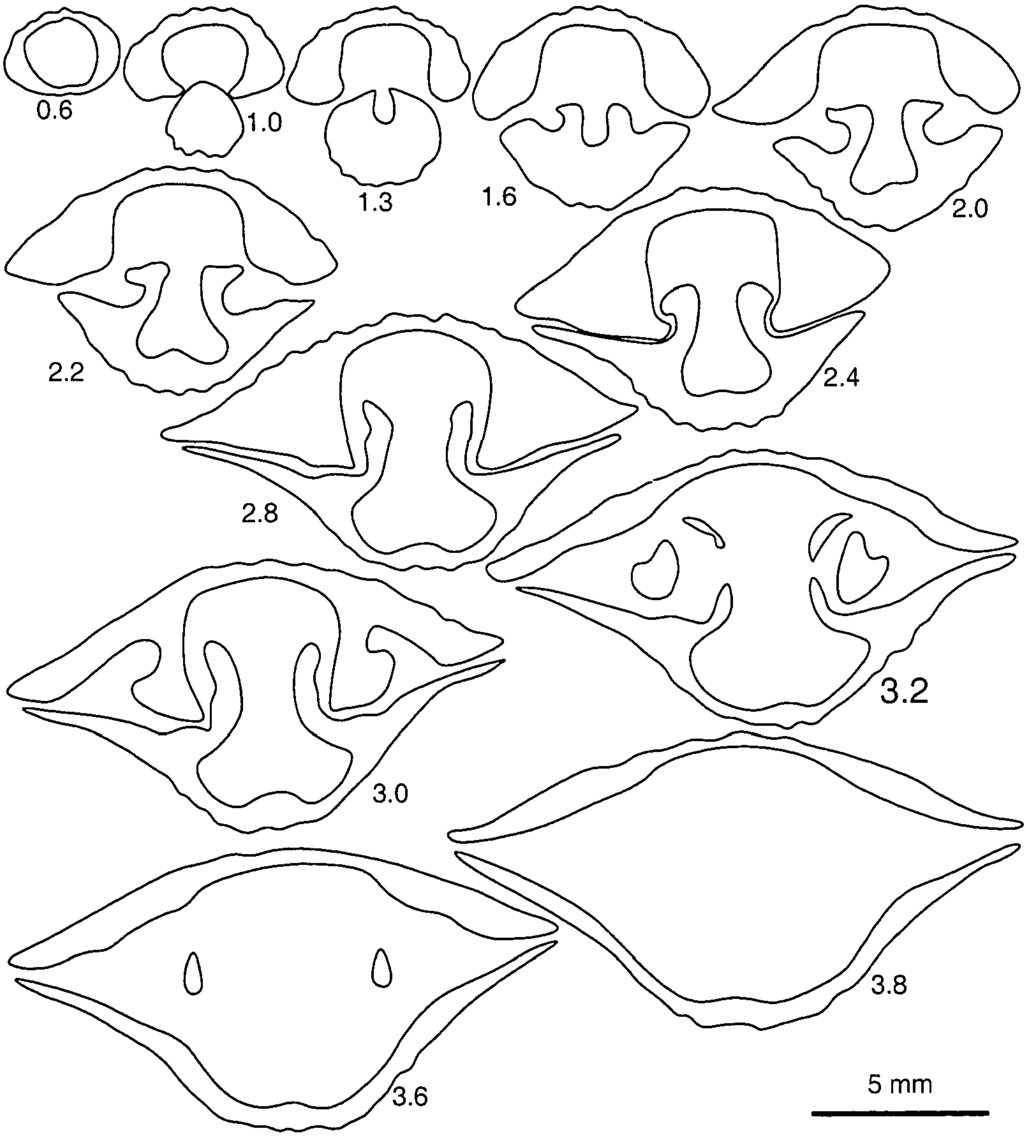

Figure 3.10--Selected transverse serial sections of Spinatrypina borealis (Warren). Distances in mm from posterior tip of ventral umbo.

The specimens illustrated as Spinatrypa (Isospinatrypa) borealis by Copper (1978, pl. 1, figs. 20-21; pl. 2, figs. 1-5) (Hume Formation, Powell Creek, west Canada) were correctly assigned to the genus Spinatrypa based on their coarse costae and prominent frills. That species, however, needs to be re-defined because the specimens are significantly different from Atrypa borealis Warren, 1944, in terms of costae and frills.

Subfamily VARIATRYPINAE Copper, 1978

Genus *DESQUAMATIA* Alekseeva, 1960

Subgenus *DESQUAMATIA (INDEPENDATRYPA)* Copper, 1973

DESQUAMATIA (INDEPENDATRYPA) FORTIS new species

Figures 3.11.1-3.11.26, Figure 3.12

Diagnosis.--Shell large, shield-shaped Desquamatia (Independatrypa); length to width ratio of 0.8-1.2, thickness to width ratio averages about 0.6; plications increase by implantation on dorsal valve and by bifurcation on ventral valve; 11-14 costae in 5 mm arc, 10 mm in front of beaks.

Description.--Shell up to 44 mm wide, dorsibiconvex to convexoplane, shield-shaped in outline, maximum width just anterior to hinge line. Length to width ratio of 0.8-1.2 (average 1.0), thickness/width ratio average 0.6 (Table 3.5). Hinge line long and straight, slightly shorter than maximum shell width. Anterior commissure slightly and broadly uniplicate in younger specimens, strongly so in adult specimens to form a U-shaped depression.

Ventral valve very gently convex, maximum convexity in umbonal region, gently arched transversely, flattened and recurved, becoming slightly concave laterally and anteriorly. Depressed anteriorly by sinus, broad and shallow in younger specimens, prominent and deep U-shaped in adult specimens. Beak small, interarea low, relatively narrow, round-edged laterally, orthocline to anacline. Delthyrium with two wedge-shaped deltidial plates. Foramen submesothyrid to mesothyrid.

Dorsal valve more strongly convex than ventral valve, strongly arched along midline from beak to anterior margin, highest near midlength. Beak completely concealed by opposite valve.

Both valves marked by fine radiating costae increasing by bifurcation on ventral valve and by implantation on dorsal valve. Eleven to 14 costae in an arc of 5 mm at 10 mm from beaks. Growth lines prominent, usually more prominent and closely spaced near lateral and anterior margins. Frills are not prominent possibly due to weathering or breakage on extraction from enclosing matrix.

Teeth strong, lateral cavity narrow. Dorsal interior with dental sockets between inner shell wall and extensions of hinge plates, low and short median ridge at posterior part (Fig. 3.12). Spiralia directing dorso-medially.

Etymology.--Latin fort-, strong, reflecting large and robust outline of the species.

Types.--Holotype, UA12956 (Bird Fiord Formation carbonate equivalent, locality 80X); paratypes, UA12951 and UA12957 (Baad Fiord Member, locality 81A), UA12953 (Baad Fiord Member, locality 81B), UA12952, UA12954, and UA12955 (Bird Fiord Formation carbonate equivalent, localities 80VIII, 80VIII, 80X respectively).

Other material examined.--8538 specimens.

Occurrence.-- Bird Fiord Formation carbonate equivalent, Baad Fiord and Blubber Point members; Grinnell Peninsula, Devon Island, Bathurst, North Kent, and Cornwallis islands.

Discussion.--The new species is similar to Variatrypa (Variatrypa) arctica (Warren, 1944, p. 120-121, pl. 3, figs. 19-21) in size, lateral profile, and shape. They can be distinguished by the multiple growth lamellae in Desquamatia (Independatrypa) fortis. According to Warren's (1944, p. 121) original description, Variatrypa (Variatrypa) *arctica* has a fold developed in its dorsal anterior region (especially sharply defined in strongly convex forms); the new species lacks such a fold.

The new species is similar to *Desquamatia* (*Independatrypa*) *independensis* (Webster, 1921) from the Waterways Formation, Peace River, Alberta (Norris and Uyeno, 1983, p. 24-25, pl. 5, figs. 14-33, pl. 8, figs. 5, 6) and from the Cedar Valley Formation of Iowa (Fenton and Fenton, 1935, p. 377, pl. 41, figs. 9-12; pl. 42, figs. 14-16; pl. 43. fig. 12; Stainbrook, 1938, p. 229, pl. 30, figs. 10, 15-16; Copper, 1973, p. 439, pl. 1 figs. 1-2, pl. 2, fig. 16). The new species can be distinguished from *D*. (*Independatrypa*) *independensis* by its length to width ratio and the style of plications – *D*. (*I*.) *independensis* is usually wider than long, and its plications increase by bifurcation on pedicle valve, by bifurcation and implantation on dorsal valve.

The new species differs from *D*. (*I*.) *scutifomis* (Stainbrook, 1938) described and illustrated by Stainbrook (1938, p. 234, pl. 31; figs. 15-16, 19-20); and Day and Cooper (1998, p. 159-160, fig. 3A-C, fig. 4C) in that length of *D*. (*I*.) *scutifomis* is slightly less than or equal to width and shell is less than 30 mm wide.

The new species differs from *D*. (*I*.) *randalia* (Stainbrook, 1938, p. 237-238, pl. 31, figs. 5, 7-9) from the Cedar Valley Formation of Iowa (also see Day and Copper, 1998, p. 160) because the latter has a subcircular outline, and the thickness/width ratio (0.6- 0.9 of the holotype and three paratypes) is larger than that of the new species.

The new species can be easily distinguished from *D*. (*I*.) *exila* Norris (*in* Norris et al., 1992, p. 52-54, pl. 5, figs. 14-39) from the uppermost Williams Formation (Middle Devonian) of Williams Island because the latter is thin and relatively small in size and has a suboval to subsemicircular outline. The thickness/width ratio (of the holotype and five paratypes) of *D*. (*I*.) *exila* is 0.3 to 0.5, and it is less than 25 mm. The number of costae in *D*. (*I*.) *exila* varies from 9-12 in 5 mm arc, 10 mm from the beaks.

TABLE 3.5—Dimensions (mm) of Desquamatia (Independatrypa) fortis n. sp.

Section	81A-281m	80X-88.8m	80VIIIB	81B-189m	81B-190m	
Horizon	Baad Fiord	Carb. Equiv	Carb. Equiv	Baad Fiord	Baad Fiord	Combined data
Island	Grinnell Penin.	Bathurst	Bathurst	Grinnell Penin.	Grinnell Penin	
No. measured	46	43	10	17	12	128
Length (L)	18.8(27.2)37.7*	21.2(31.9)39.7	19.7(30.6)35.4	25.3(31.3)36.4	21.1(28.9)34.9	18.8(29.7)39.7
Width (W)	20.0(28.4)35.7	23.7(34.5)43.5	20.8(32.3)37.7	25.0(33.1)39.5	21.0(29.9)34.8	20.8(31.5)43.5
Thickness(T)	8.9(15.3)20.4	10.8(18.9)24.3	8.8(16.9)21.0	15.1(18.0)21.4	10.4(16.0)20.7	8.8(17.1)21.4
L/W	0.92(1.05)1.16	0.78(0.92)1.23	0.93(0.95)1.00	0.84(0.95)1.03	0.87(0.97)1.03	0.78(0.98)1.23
T/W	0.41(0.54)0.68	0.45(0.55)0.69	0.42(0.52)0.60	0.47(0.55)0.73	0.43(0.53)0.66	0.41(0.54)0.73

*Minimum (Average) Maximum

Figure 3.11——Desquamatia (Independatrypa) fortis n. sp. 1-3, 5, 8, paratype, dorsal (1), anterior (2), posterior (3), ventral (5) and lateral (8) views, X1.2, from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula, UA12951; 4, 6, 9, 12, 16, paratype, lateral (4), dorsal (6), anterior (9), posterior (12), and ventral (16) views, X1.2, from Bird Fiord Fm. carbonate equivalent, 1 km east of Half Moon Bay (80VIII, PCC92170), Dundee Bight, Bathurst Island, UA12952; 7, paratype, dorsal view showing part of spiralia, X1.2, from Baad Fiord Member, Ensorcellement River (81B), Grinnell Peninsula., UA12953; 10, 11, 13, 19, 23, paratype, posterior (10), lateral (11), dorsal (13), anterior (19), and ventral (23) views, X1, from Bird Fiord Formation carbonate equivalent, 1 km east of Half Moon Bay (80VIII), Dundee Bight, Bathurst Island, UA12954; 14, 15, 17, 20, 24, holotype, lateral (14), dorsal (15), anterior (17), posterior (20), and ventral (24) views, X1, UA12955; 18, 22, 25, paratype, posterior (18), ventral (22), and anterior (25) views, X1, UA12956; UA12955 and UA12956 from Bird Fiord Formation carbonate equivalent, Half Moon Bay (80X), Dundee Bight, Bathurst Island; 21, 26, paratype, dorsal and ventral views, X1.2, from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula; UA12957.

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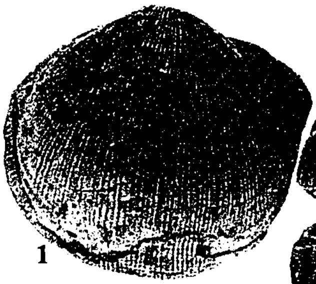
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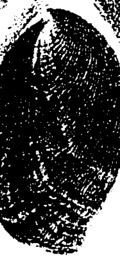
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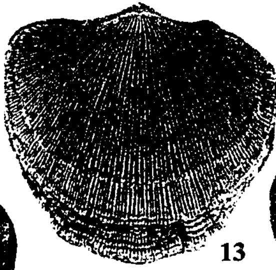
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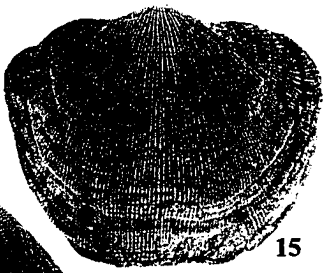
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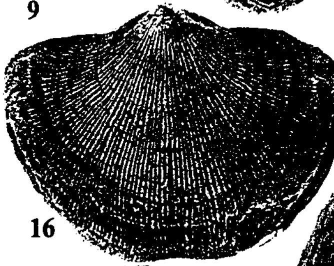
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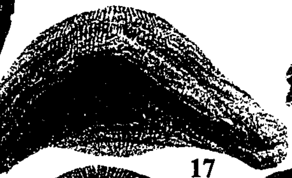
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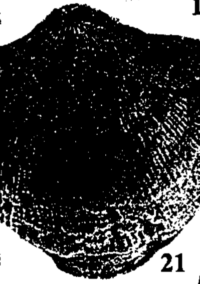
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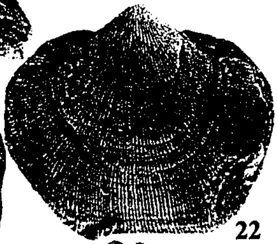
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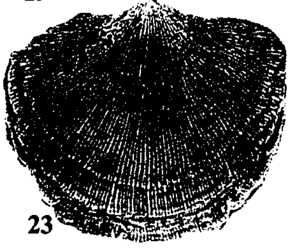
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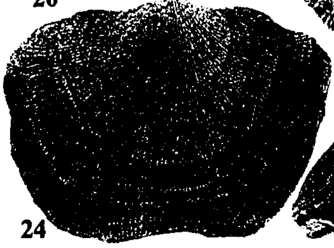
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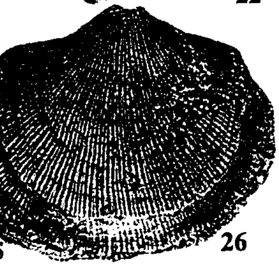
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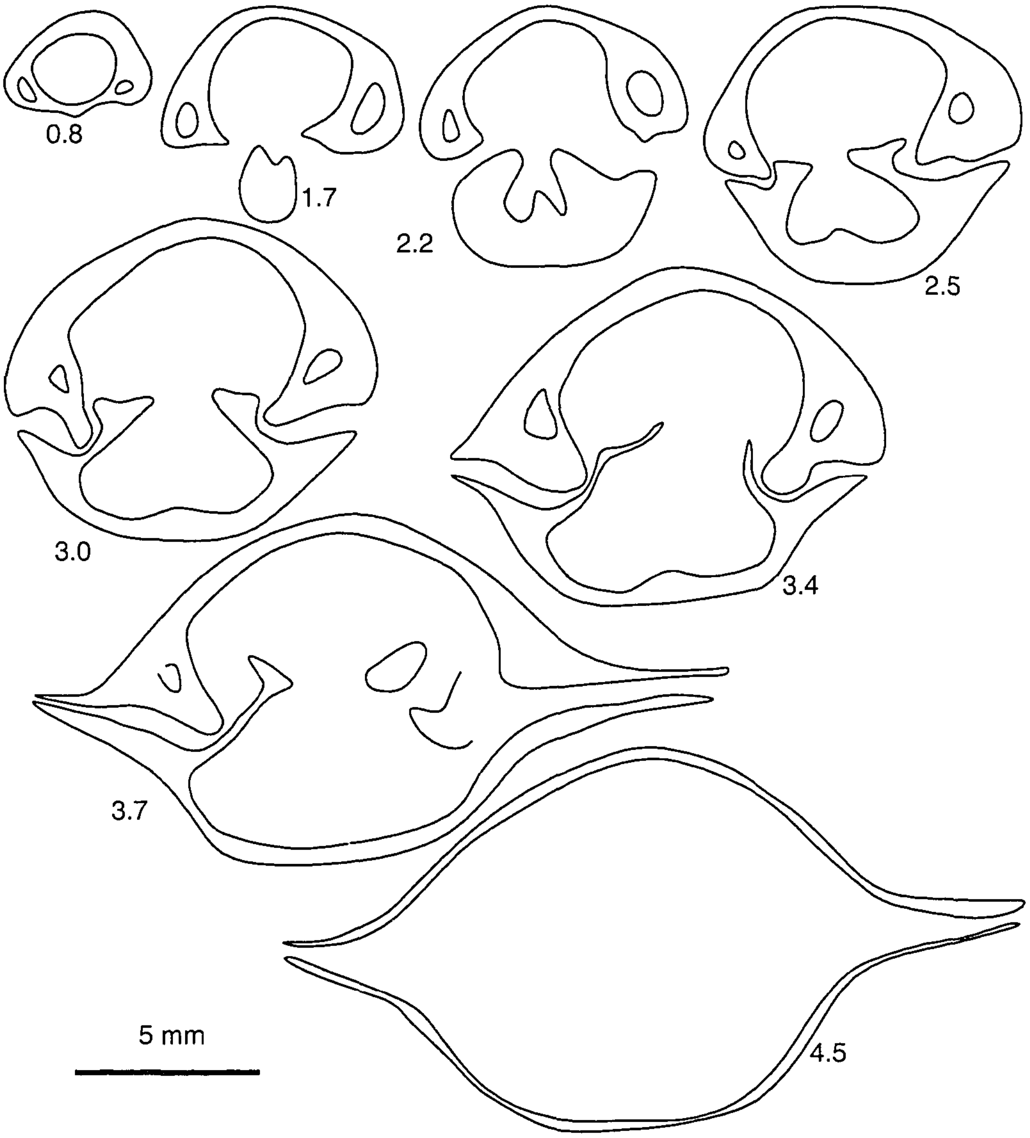

Figure 3.12--Selected transverse serial sections of Desquamatia (Independatrypa) fortis n. sp. Distances in mm from posterior tip of ventral umbo.

The new species differs from *D.* (*I.*) *sanfordi* Norris, 1993 (p. 31-34, pl. 2. figs. 16-40, pl. 3, fig. 1) from the lower shale member of Williams Island Formation of the Hudson Platform, northern Ontario and southern District of Keewatin because the latter has a subcircular outline, and the number of costae ranges from 7 to 12 in an arc of 5 mm at 10 mm from the beaks.

D. (*I.*) *fortis* is more transverse with finer ribs than illustrated specimens of the late Eifelian species *D.* (*I.*) *aperanta* (Crickmay, 1960) described from the Eifelian *adoceta* Zone in the lower part of the Hume Formation in the lower MacKenzie Valley (see Crickmay, 1960, p. 15, pl. 8, figs. 2-15; Caldwell, 1971, pl. 1, figs. 3a-d; illustrated as *Atrypa* cf. *A.* *aperanta* Crickmay in McLaren et al., 1962, p. 18, pl. 8, figs. 13-15). Crickmay (1957) also described a species of *Desquamatia* (*I.*) under *Atrypa* *perfimbriata* from the subsurface of northeastern Alberta (late Eifelian-early Givetian Methy Formation, see Norris, 1973, 1998). This species also has coarser ribs than *D.* (*I.*) *fortis*. Late Eifelian *Desquamatia* (*I.*) has also been recorded from the Rogers City Formation in the Michigan Basin (Koch and Day, 1996).

Order ATHYRIDIDA Boucot, Johnson, and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964
Superfamily NUCLEOSPIROIDEA Davidson, 1881
Family NUCLEOSPIRIDAE Davidson, 1881
Genus *NUCLEOSPIRA* Hall, 1859
NUCLEOSPIRA LENS (Schnur, 1851)
Figures 3.13.1-3.13.15, Figure 3.15

Spirifer *lens* SCHNUR, 1851, p. 12.

Nucleospira lens, SOBOLEV, 1904, p. 77, table 8, fig. 24; BIERNAT, 1966, p. 140-143, pl. 24, figs. 1-16, text-fig. 49; FICNER AND HAVLICEK, 1978, p. 80, pl. 5, fig. 21, pl. 16, fig. 1.

Nucleospira sp. JONES, 1982a, pl. 2, figs. 13-16; JONES, 1982b, pl. 2, figs. 34-37.

Description.-- Shell less than 17 mm long and wide, slightly transversely suboval in outline, hinge line curved, short, with rounded cardinal angles. Equally biconvex, both valves moderately convex. Ventral beak small, erect, commonly with a slight hook towards dorsal valve. Maximum width at mid-length, width/length ratio of 1.0-1.1 (average 1.0) (Fig. 3.14, Table 3.6). Faint, narrow, sulcus on some ventral valves, brachial valve without fold or sulcus. Concentric growth lines may be present anteriorly. Spinules not observed.

Teeth small, without dental plates. Dorsal interior with prominent cardinal flanges, extending ventro-posteriorly. Median ridge obsolescent, muscle scars slightly impressed. Spire, each with about 6-8 coils, directing laterally (Fig. 3.15).

Material examined.--645 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent; Baad Fiord, Blubber Point, and Norwegian Bay members, Bathurst, Devon, and Ellesmere islands.

Discussion.--Nucleospira lens, previously reported from the Middle Devonian of Europe (Biernat, 1966, Ficner and Havlicek, 1978), is difficult to distinguish from N. ventricosta which comes from the Lower Devonian of Oklahoma (Amsden, 1958) and the Lower to Middle Devonian of New York (Amsden, 1958, Feldman, 1985, 1994). However, N. ventricosta is more circular than N. lens, N. lens tends to be transversely ovate, and N. ventricosta has more pronounced growth lines and a ventral sulcus.

TABLE 3.6—Dimensions (mm) of Nucleospira lens

Section Member Island	81E-418.25m Norwegian Bay Ellesmere	81C-186m Baad Fiord Grinnell Peninsula	Data Combined
No. measured	20	36	56
Length (L)	7.5(12.0)15.8*	7.0(10.1)12.4	7.0(10.7)15.8
Width (W)	8.4(13.1)16.5	7.6(10.6)12.7	7.6(11.5)16.5
Thickness (T)	4.5(7.0)9.5	3.7(6.3)8.0	3.7(6.5)9.5
W/L	1.00(1.09)1.15	1.00(1.05)1.14	1.00(1.07)1.15
L/T	1.51(1.72)1.87	1.24(1.64)1.89	1.24.(1.67)1.89
W/T	1.72(1.87)2.16	1.24(1.73)2.05	1.24(1.79)2.16

*Minimum(Average)Maximum

Figure 3.13—1-15, *Nucleospira lens* (Schnur). 1, 2, 5, 11, 14, dorsal (1), ventral (2), lateral (5), anterior (11), and posterior (14) views, X2.7, UA12958; 3, 4, dorsal and ventral views, X2.3, UA12959; UA12958 and UA12959 from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula; 6, dorsal view, X2.7, from Baad Fiord Member, Ensorcellement River (81B), Grinnell Peninsula, UA12960; 7, 8, ventral and dorsal views , X3.3, from Baad Fiord Member, Ensorcellement River (81C), Grinnell Peninsula, UA12961; 9, 10, 12, 13, 15, lateral (9), dorsal (10), posterior (12), anterior (13), and ventral (15) views, X3.9, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island; UA12962. 16-27, *Nucleospira stelcki* n. sp. 16, 17, 19, paratype, ventral (16), dorsal (17), and lateral (19) views, X2.5, UA12963; 18, 20-23, paratype, dorsal (18), posterior (20), anterior (21), lateral (22), and ventral (23) views, X2.5, UA12964; UA12963 and UA12964 from Blubber Point Member, Blubber Point (81G), Simmons Peninsula, Ellesmere Island; 24, paratype, dorsal view showing part of spiralia, X2.5, from Cardigan Strait Member, 5 km east of north-central Goose Fiord (82C1), Ellesmere Isalnd, UA12965; 25-27, holotype, anterior (25), dorsal (26), and ventral (27) views, X2, from Baad Fiord Member, west North Kent Island (WNK), UA12966.

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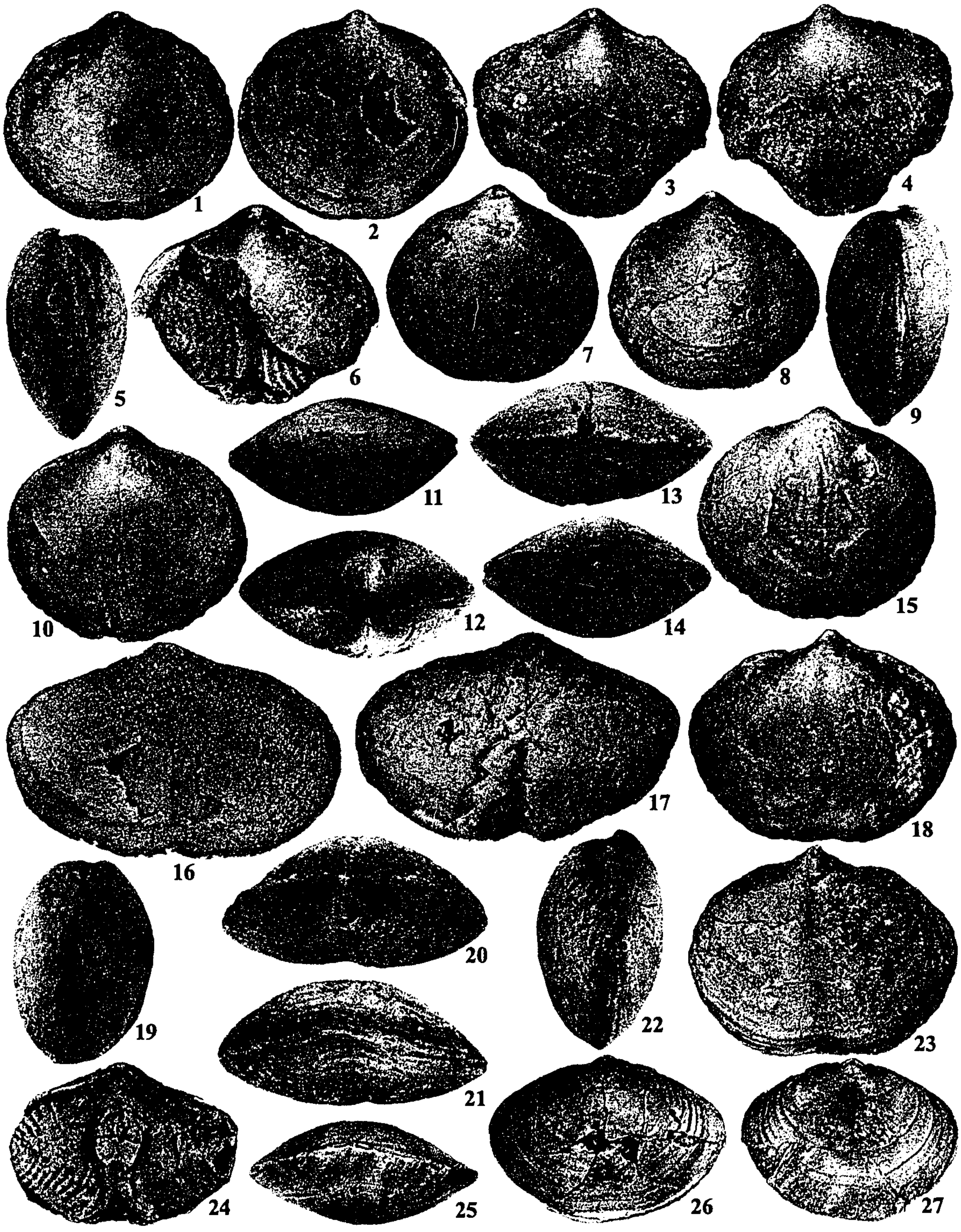
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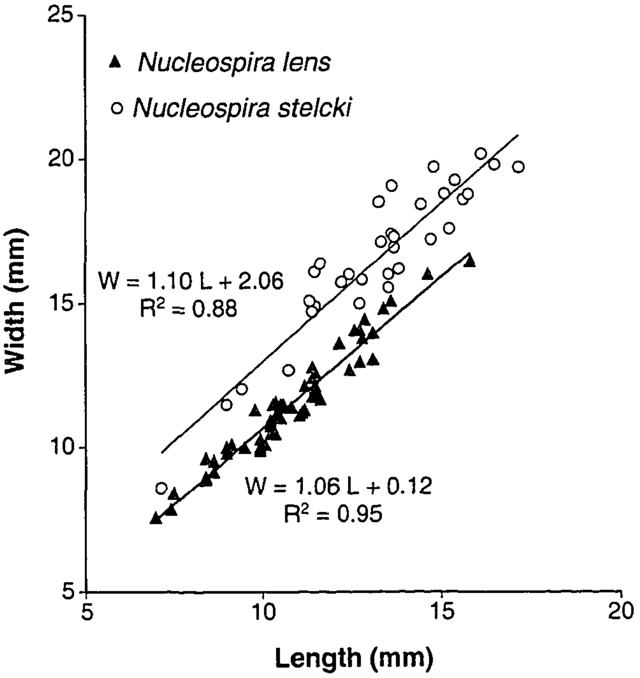

Figure 3.14--Length versus width graphs for Nucleospira lens (Schnur) and Nucleospira stelcki n. sp.

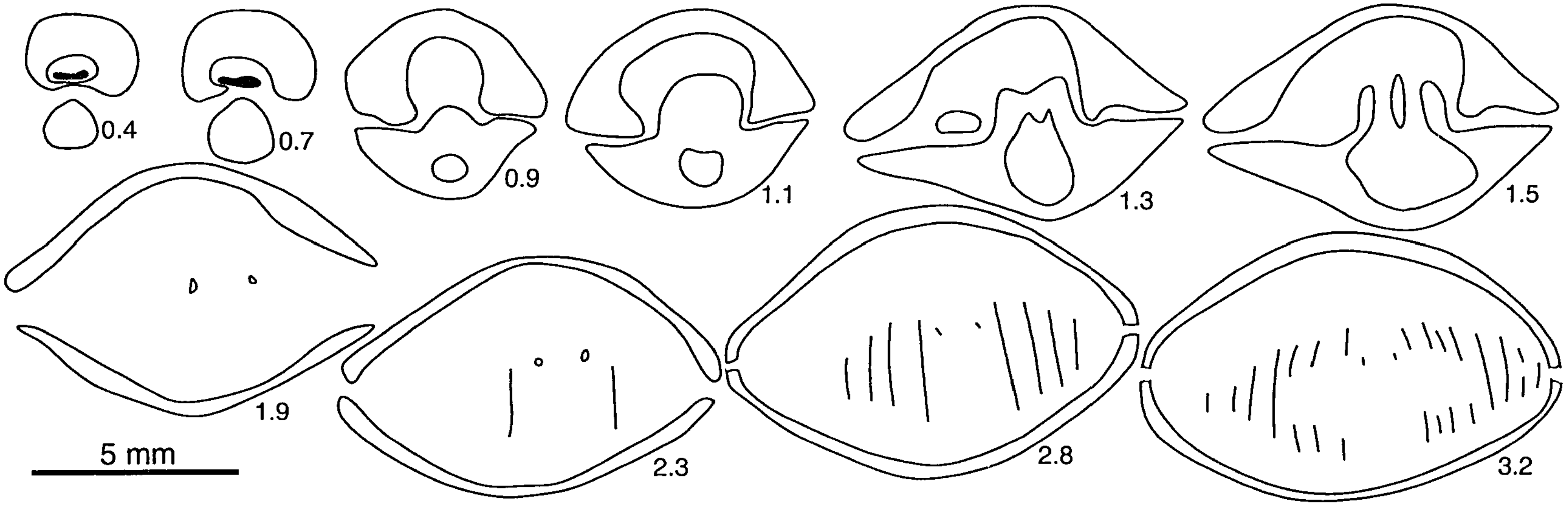

Figure 3.15--Selected transverse serial sections of Nucleospira lens (Schnur).
Distances in mm from posterior tip of ventral umbo.

Nucleospira lens differs from N. hecetensis Kirk and Amsden, 1952 from the Lower Devonian of Alaska because the latter has a longer and straight hinge line (Kirk and Amsden, 1952; Savage, 1981). Nucleospira subsphaerica Johnson, 1970 from the Lower Devonian of Nevada has a much more inflated lateral profile (Johnson, 1970) than N. lens. Nucleospira musculosa Hamada, 1971 from Lower Devonian of Xinjiang, China has a dorsal fold and its lateral profile is much thinner (Xu, 1991) than N. lens. Nucleospira bellornata Talent, 1963 from the Devonian of Victoria, Australia differs from N. lens by the virtual absence of any growth lines (Talent, 1963). Compared to N. lens, N. laevigata Lenz, 1977 from the Lower Devonian of the Yukon, Canada has less prominent growth lines which appear only in larger specimens, a ventral sulcus that is very weak or even absent, and a dorsal valve which may have a narrow, faint sulcus (Lenz, 1977).

NUCLEOSPIRA STELCKI new species

Figures 3.13.16-3.13.27, Figure 3.16

Diagnosis.--Small to moderate size, moderately biconvex, strongly transverse Nucleospira with ventral sulcus.

Description.--Shell up to 20 mm wide, equally biconvex, both valves moderately convex. Strongly transverse oval in outline, with width/length ratio of 1.2-1.4 (average 1.3) (Fig. 3.14, Table 3.7). Hinge line long, slightly curved. Maximum shell width at mid-length. Ventral beak moderate, erect. Ventral valve with narrow sulcus starting from umbo region. Very faint sulcus on some dorsal valves. Anterior commissure even to slightly sulcate. Both valves with concentric growth lines.

Ventral interior with strong teeth, no dental plates; median ridge low, extending to near anterior valve margin; muscle scar deeply impressed.

TABLE 3.7—Dimensions (mm) of Nucleopsira stelcki n. sp.

Section Member Island	81F-140m Norwegian Bay Ellesmere	81F-206m Norwegian Bay Ellesmere	81G-378m Baad Fiord Ellesmere	Data Combined
No. measured	11	8	15	34
Length (L)	9.0(13.7)17.4*	10.7(13.7)15.4	7.1(12.6)16.1	7.1(12.8)17.4
Width (W)	11.5(16.8)19.0	12.7(16.8)19.7	8.6(16.2)20.2	8.6(16.2)19.7
Thickness (T)	4.6(7.8)10.6	6.3(8.2)10.2	5.0(6.9)8.5	4.6(7.3)10.2
W/L	1.15(1.24)1.40	1.16(1.23)1.33	1.19(1.28)1.40	1.15(1.26)1.40
L/T	1.57(1.76)2.76	1.49(1.67)1.92	1.11(1.85)2.56	1.49.(1.78)2.76
W/T	1.86(2.19)3.26	1.73(2.06)2.26	1.34(2.38)3.22	1.34(2.26)3.26

*Minimum(Average)Maximum

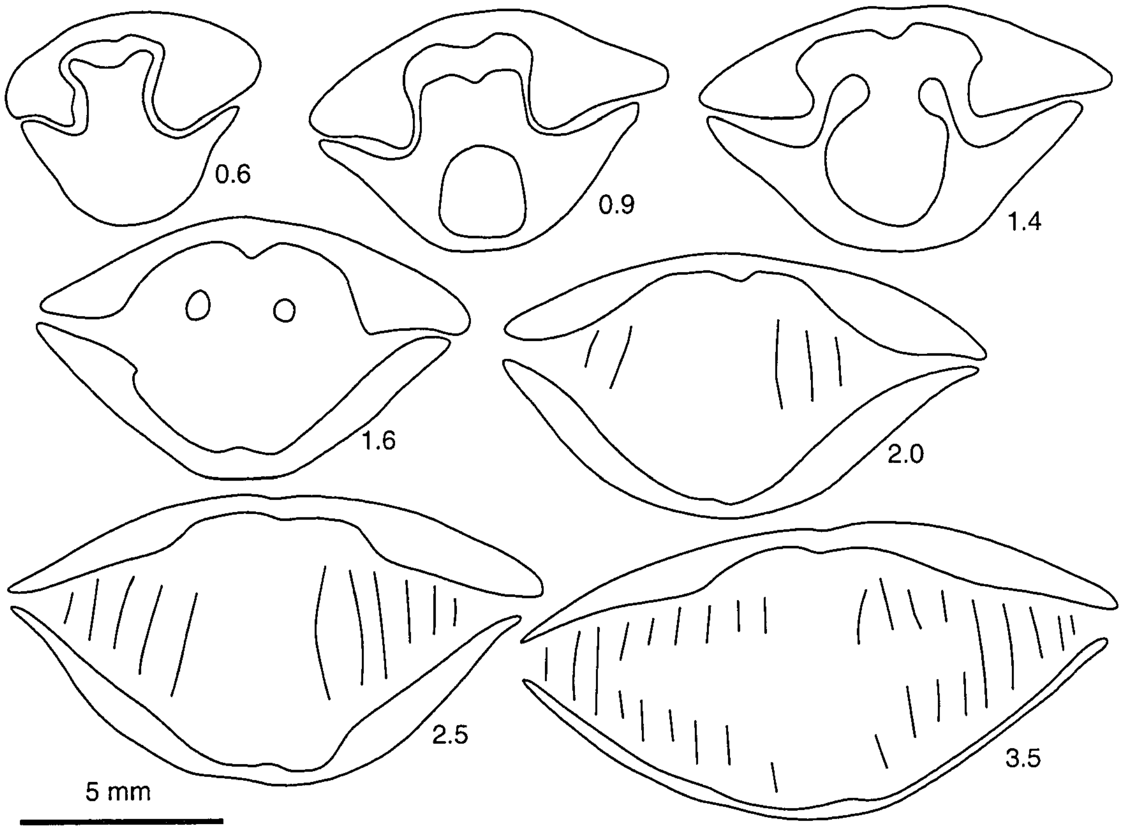

Figure 3.16--Selected transverse serial sections of Nucleospira stelcki n. sp. Distances in mm from posterior tip of ventral umbo.

Dorsal interior with pronounced cardinal flange, extending ventro-posteriorly; median ridge very low, weaker than ventral one; muscle scar slightly impressed; spire directing laterally, with about 10 coils on each side (Fig. 3.16).

Etymology.--After Dr. Charles Stelck.

Types.--Holotype, UA12966 (Baad Fiord Member, locality WNK); paratypes, UA12963 and UA12964 (Blubber Point Member, locality 81G), UA12965 (Cardigan Strait Member, locality 82C1).

Other material examined.--103 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent, Baad Fiord, Blubber Point, and Cardigan Strait members, Bathurst, Devon, North Kent, and Ellesmere islands.

Discussion.--The new species can be distinguished from Nucleospira lens and other species by its strongly transverse outline. The various species of Nucleospira are commonly similar externally and internally. Thus, as noted by Savage (1981, p. 366), species of Nucleospira have typically been defined on the basis of the differences in their external proportion such as width and thickness. The strongly transverse outline of the Canadian Arctic specimens defines them as a new species. Nucleospira stelcki and N. lens have not been found together in the same collection; thus, the difference in outline can not be attributed to morphological variation in a single population. A definite trend of gradual change of length/width ratio during growth has been noted in N. lens from Poland by Biernat (1966). Neither N. lens nor N. stelcki from the Bird Fiord Formation exhibits such a trend. Thus, the difference in the outline of the two species cannot be considered to be ontogenetic in nature.

Nucleospira robusta Kozlowski, 1929 is similar to N. stelcki because it is also wider than long, N. stelcki, however, is far more transverse than the specimens illustrated by Kozlowski (1929). Among 160 specimens of N. robusta measured by Kozlowski, 65.6

percent have the width/length ratio at 1.10, only one specimen reaches to 1.30 (Kozlowski, 1929, p. 218).

Order SPIRIFERIDA Waagen, 1883

Suborder DELTHYRIDINA Ivanova, 1972

Supper family DELTHYRIDOIDEA Phillips, 1841

Family RETICULARIIDAE Waggen, 1883

Genus *WARRENELLA* Crickmay, 1953

WARRENELLA GRINNELLENSIS new species

Figures 3.17.1-3.17.25, Figure 3.18

Diagnosis.--Large, elongate to transversely subheptagonal, evenly biconvex Warrenella. Conspicuous fold and sulcus originates from umbo. No furrow along midline of fold. Ventral interarea high, broadly triangular. Delthyrium of medium width, covered apically by small convex deltidium. Hinge line length about 70 percent of shell width.

Description.—Shell up to 42 mm wide. Outline varies from elongate to transversely subheptagonal, evenly biconvex. Maximum width near midlength, length/width ratio of 0.7-1.2 (average 0.9) (Table 3.8). Hinge line straight, ratio of hinge line length to shell width is 0.6-0.9, with average of 0.7. Anterior commissure uniplicate.

Pedicle valve moderately convex, highest at about one-third of length from umbo. Ventral beak incurved but not in contact with opposing valve. Interarea apsacline, high, broadly triangular with transverse striae. Delthyrium of medium width, covered apically by small, convex deltidium. Sulcus beginning immediately anterior to umbo, inconspicuous and shallow in posterior one-third, expanding and deepening anteriorly, forming a U-shaped tongue in opposite valve.

TABLE 3.8-- Dimensions (mm) of *Warrenalla grinnella* n. sp

Section	81C-186m	SWAF2/2	80X-117m	NFI-7	
Horizon	Baad Fiord Mbr.	Carb. Equv.	Carb. Equv.	Blubber Point	Combined Data
Island	Grinnell Peninsula	Grinnell Peninsula	Bathurst	Devon	
No. measured	44	44	14	19	121
Length (L)	14.9(23.6)30.1*	9.3(20.2)35.8	14(26.2)37.0	16.1(26.9)31.8	9.3(23.2)37.0
Width (W)	16.4(25.2)34.2	9.8(21.0)42.3	15.7(27.4)37.0	18.2(29.9)33.1	9.8(24.7)42.3
Thickness(T)	9.4(15.2)21.8	6.0(13.8)25.3	8.3(14.8)23.0	10.5(18.3)22.0	6.0(15.2)25.3
Hingeline Length (HL)	11.0(17.9)24.1	7.1(15.1)30.5	9.0(20.0)31.1	13.2(19.8)22.4	7.1(17.4)31.1
L/W	0.72(0.94)1.06	0.73(0.97)1.16	0.85(0.95)1.01	0.82(0.90)0.99	0.72(0.94)1.16
T/W	0.51(0.60)0.72	0.53(0.66)0.80	0.39(0.54)0.62	0.52(0.61)0.69	0.39(0.62)0.80
HL/W	0.62(0.71)0.84	0.63(0.71)0.82	0.57(0.72)0.85	0.57(0.66)0.73	0.57(0.71)0.85

*Minimum (Average) Maximum

Figure 3.17—*Warrenella grinnellensis* n. sp. 1. Paratype, ventral interior, X1.6, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12967; 2-6, paratype, dorsal (2), ventral (3), lateral (4), posterior (5), and anterior (6) views, X1.6, UA12968; 7-10, 13, paratype, posterior (7), lateral (8), dorsal (9), anterior (10), and ventral (13), views, X1.6, UA12969; UA12968 and UA12969 from Bird Fiord Formation carbonate equivalent, 10 km west of Arthur Fiord (SWAF2/2), Grinnell Peninsula; 11, 12, 14, 17, 24, holotype, posterior (11), anterior (12), dorsal (14), lateral (17), and ventral (24) views, X1.6, from Baad Fiord Member, Ensorcellement River (81C), Grinnell Peninsula, UA12970; 15, 20, paratype, ventral exterior and interior, X1.6, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12971; 16, paratype, ventral interior, X1.6, from Bird Fiord Formation Carbonate equivalent, Ensorcellement River (81B), Grinnell Peninsula, UA12972; 18, 19, 22, 23, paratype, lateral (18), dorsal (19), anterior (22), and ventral (23) views, Baad Fiord Member, Ensorcellement River (81C), Grinnell Peninsula; UA12973; 21, 25, paratype, ventral interior and exterior, X1.6, from Bird Fiord Formation carbonate equivalent, Stuart Bay (80XI), Bathurst Island, UA12974.

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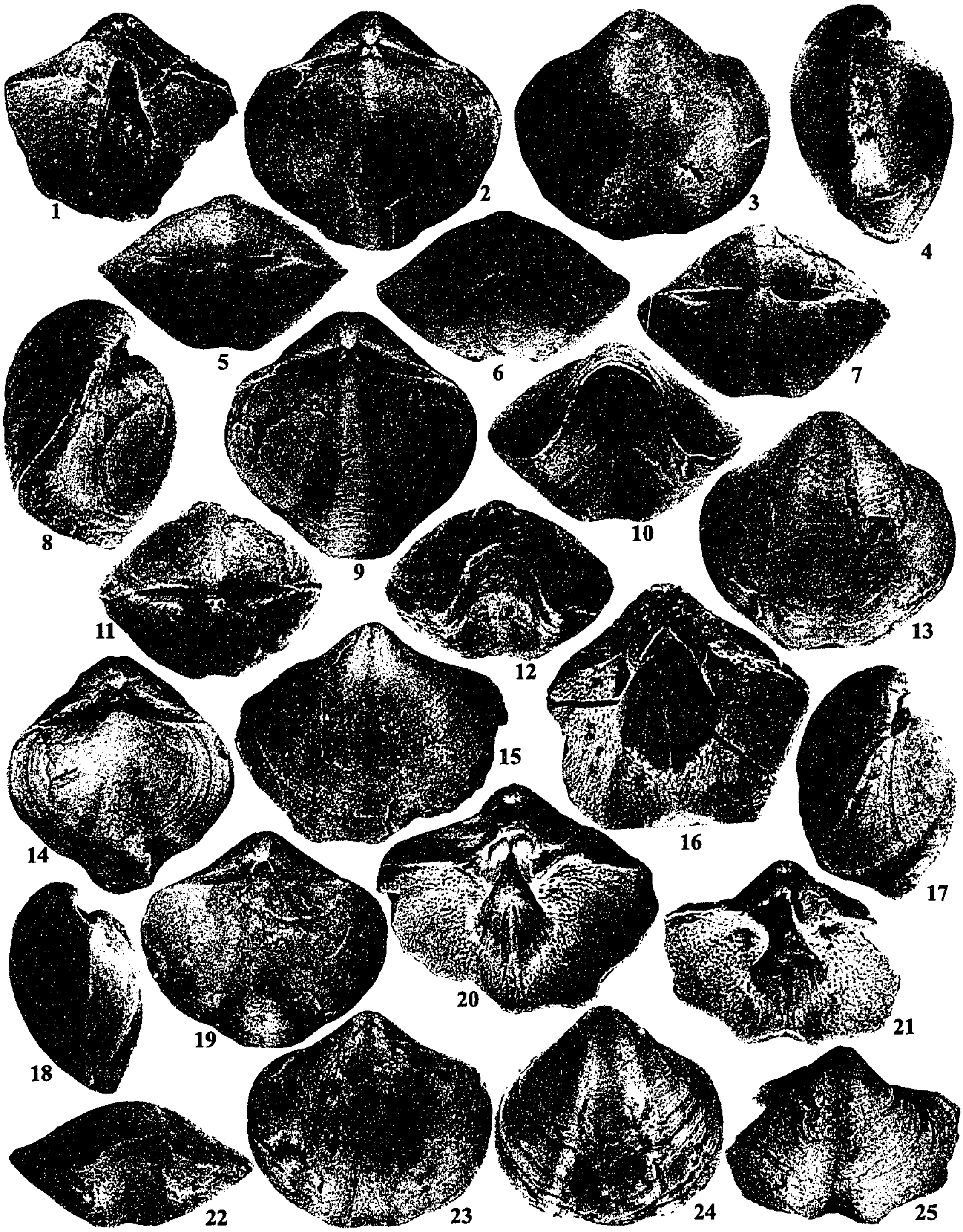
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Dorsal valve moderately convex, highest at midlength. Beak inturned and covered by opposing valve. Interarea very low and inconspicuous, linear, orthocline. Fold originating over umbo, low and narrow posteriorly, gradually widening and becoming conspicuous anteriorly.

Both valves with closely, regularly spaced, fine concentric growth lines. In well preserved specimens, very fine and closely spaced spinules present, making growth lines indented at their anterior margins. Recumbent spinules do not appear to project obliquely from shell surface as illustrated for Warrenella transversa Ludvigsen and Perry (1975, p. 73, text-figure 16). No other radial micro-ornament present.

Interior of ventral valve with thin and short dental plates, diverging anteriorly at about 30 degrees. Posterior parts of dental plates thickened. Hinge teeth small. Ventral muscle field subpyriform, deeply impressed, separated by low, indistinct myophragm along midline. Anterior edge of muscle field slightly elevated. Dorsal interior with divided hinge plates, supported by thin and short crural plates posteriorly; cardinal process comb-like, located at apex of notothyrial cavity. Spiralia directing laterally with about 10 cones (Fig. 3.18).

Etymology.--After Grinnell Peninsula where this new species is abundant.

Types.-- Holotype, UA12970 (Bird Fiord Formation carbonate equivalent, locality 81C); paratypes, UA12968 and UA12969 (locality SWAF 2/2), UA12970, UA12971, UA12973, UA12974, and UA12967 (all from locality 80XI), UA12972 (locality 81B), all from Bird Fiord Formation carbonate equivalent.

Other material examined.--1610 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent, Baad Fiord and Blubber Point members; Bathurst Island, Grinnell Peninsula, Devon, North Kent, and Ellesmere islands.

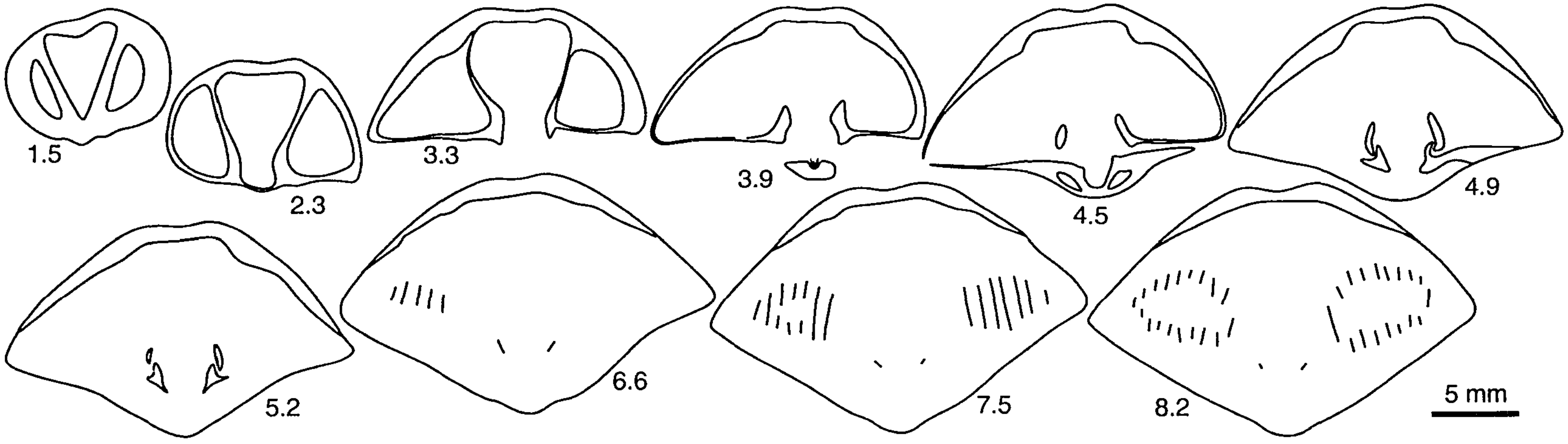

Figure 3.18--Selected transverse serial sections of Warrenella grinnellensis n. sp. Distances in mm from posterior tip of ventral umbo.

Discussion.--The recognition of species among Warrenella is mainly based on the characteristics of shell size, outline, lateral profile, ventral interarea, relative length of the hinge line to shell width, and the dorsal fold and ventral sulcus. For example, W. occidentalis (Merriam, 1940) is distinguished from the new species by its sulcus beginning more anteriorly from the umbo (see Johnson, 1974, p. 62). The new species can be easily distinguished from Warrenella plicata Johnson, 1974, because the latter has faintly developed anterior plications. Warrenella franklini (Meek, 1868), W. parafranklini Norris, 1998, W. kirki (Merriam, 1940), W. posteruskirki Norris, 1998, and W. whittakeri Norris, 1998, all have a median furrow on their folds.

Brice (1982) described some species of Warrenella from the Blue Fiord Formation of Arctic Islands, but none came from the Bird Fiord Formation. Warrenella disjuncta Brice, 1982, and W. pseudaequabilis Brice, 1982, from Blue Fiord Formation are more transverse than the new species. Brice also erected a new subgenus Warrenella (Warrenellina) that is characterized by 2-6 ribs on each flank. The smooth flanks of W. grinnellensis exclude it from this subgenus.

Order TEREBRATULIDA Waagen, 1883

Suborder TEREBRATULIDINA Waagen, 1883

Superfamily DIELASMATOIDEA Schuchert, 1913

Family CRANAENIDAE Cloud, 1942

Subfamily CRANAENINAE Cloud, 1942

Genus *CRANAENA* Hall et Clarke, 1893

CRANAENA BRICEAE new species.

Figures 3.19.1-3.19.16, Figure 3.20

Diagnosis.--Medium sized Cranaena, elongate, with average length/width ratio of 1.3. Loop about 35 percent of shell length, transverse band short, elevated, gently concave medially.

Description.--Shell up to 20 mm long. Elongate, subellipitical in outline, equally biconvex in lateral profile. Maximum width near mid-length, length/width ratio of 1.1-1.5 (average 1.3), thickness/width ratio of 0.5-0.7 (average 0.6) (Table 3.9). Both valves moderately convex. Shell smooth except for concentric growth lines developed anteriorly. Anterior commissure even, rectimarginate.

Ventral beak long, sub-erect to erect, pierced apically by mesothyrid foramen. Delthyrium small, flanked by deltidial plates. Palintropes gently concave, anterolaterally divergent. Dorsal beak covered by opposite valve.

Hinge teeth short, supported by short but prominent dental plates extending about 20 percent of shell length.

Dorsal interior with deep, narrow, anterolaterally divergent sockets. Cardinal plates free, slightly concave, posteriorly perforate. Crural bases diverge from cardinal plate at about 30 degrees. Loop about 35 percent of shell length. Transverse band of loop medially concave, elevated, very short, only about 5 percent of length of whole loop (Fig. 3.20).

Etymology.--After Dr. D. Brice.

Types.--Holotype, UA12976 (Baad Fiord Member, locality 81A); paratypes, UA12975, UA12977, and UA12978 (all from Baad Fiord Member, locality 81A).

Other material examined.--303 specimens.

Occurrence.--Bird Fiord Formation carbonate equivalent, Baad Fiord Member; Bathurst Island, and Grinnell Peninsula, Devon Island.

Discussion.--The characteristic short and elevated transverse band of the loop readily distinguishes the new species from other species. Cranaena cf. taxana from the Lower

Carboniferous Banff Formation of western Alberta is internally similar to the new species, but its transverse band of loop is highly arched like an inverted "V" (Carter, 1987).

Though the internal features of *Cranaena*? sp. and *C*?. *cryptonelloides* McLaren and Norris, 1964 from the District of Mackenzie (probable late Givetian) are not available, the very elongate outline of *Cranaena*? sp. (L/W ratio about 1.63) and the sub-circular outline of *C*.? *cryptonelloides* (L/W ratio about 1.10) (McLaren and Norris, 1964) distinguish them from the new species. *Canaena romingeri* (Hall) and *C*. *boucoti* Fagerstrom, 1971 from the Middle Devonian of Ontario (Fagerstrom, 1961, 1971) have permesothiridid foramen that distinguish them from the new species which has mesothyridid foramen. *Cranaena boucoti* is also smaller than *C. briceae*. Late Famennian *Cranaena lgaviensis* Biernat and Racki, 1986, from the Holy Cross Mountains (Poland) has a higher length/width ratio (up to 2.0) than the new species, and its cardinal plate is more distinctively concave medially than in the new species. Carboniferous *C*. *minuta* Lane, 1962, from Nevada is much smaller than *C*. *briceae* and its loop reaches to half shell length (Lane, 1962).

TABLE 3.9-- Dimensions (mm) of Cranaena briceae n. sp.

Section Member Island	81A-138.5m Baad Fiord Grinnell Pen.	81B-170m Baad Fiord Grinnell Penn.	SWAF 2/6 Cardigan Strait Grinnell Penn.	Combined Data
No. measured	46	11	20	77
Length (L)	6.6(13.5)17.7*	15.7(17.4)18.5	11.2(14.5)19.6	6.6(14.2)19.6
Width (W)	5.5(10.9)14.7	12.1(13.4)15.5	9.0(11.2)15.2	5.5(11.3)15.5
Thickness (T)	2.9(6.3)8.9	7.0(7.6)8.5	5.5(6.7)8.8	2.9(6.6)8.9
L/W	1.09(1.24)1.39	1.19(1.31)1.50	1.18(1.29)1.42	1.09(1.26)1.50
T/W	0.48(0.57)0.69	0.47(0.57)0.69	0.53(0.60)0.66	0.47(0.58)0.69
T/L	0.40(0.46)0.56	0.39(0.44)0.46	0.43(0.47)0.53	0.39(0.46)0.56

*Minimum(Average)Maximum

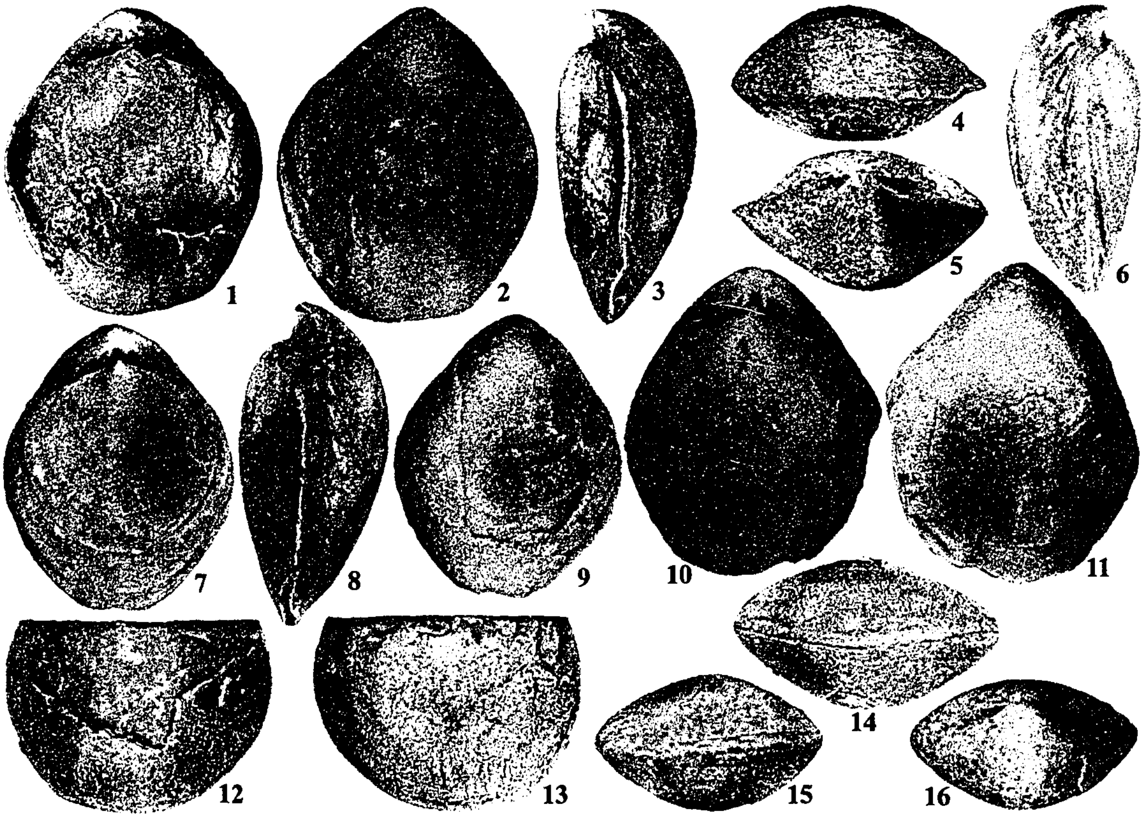

Figure 3.19--*Cranaena briceae* n. sp. 1-5, paratype, dorsal (1), ventral (2), lateral (3), anterior (4), and posterior (5) views, X2.5, UA12975; 6, 7, 9, 15, 16, holotype, lateral (6), dorsal (7), ventral (9), anterior (15), and posterior (16) views, X2.7, UA12976; 8, 10, 11, paratype, lateral (8), dorsal (10), and ventral (11) views, X3.3, UA12977; 12-14, paratype, dorsal (12), ventral (13), anterior (14) views of sectioned specimen, X2.5, UA12978; UA12975-12978 from Baad Fiord Member, Ensorcellement River (81A), Grinnell Peninsula.

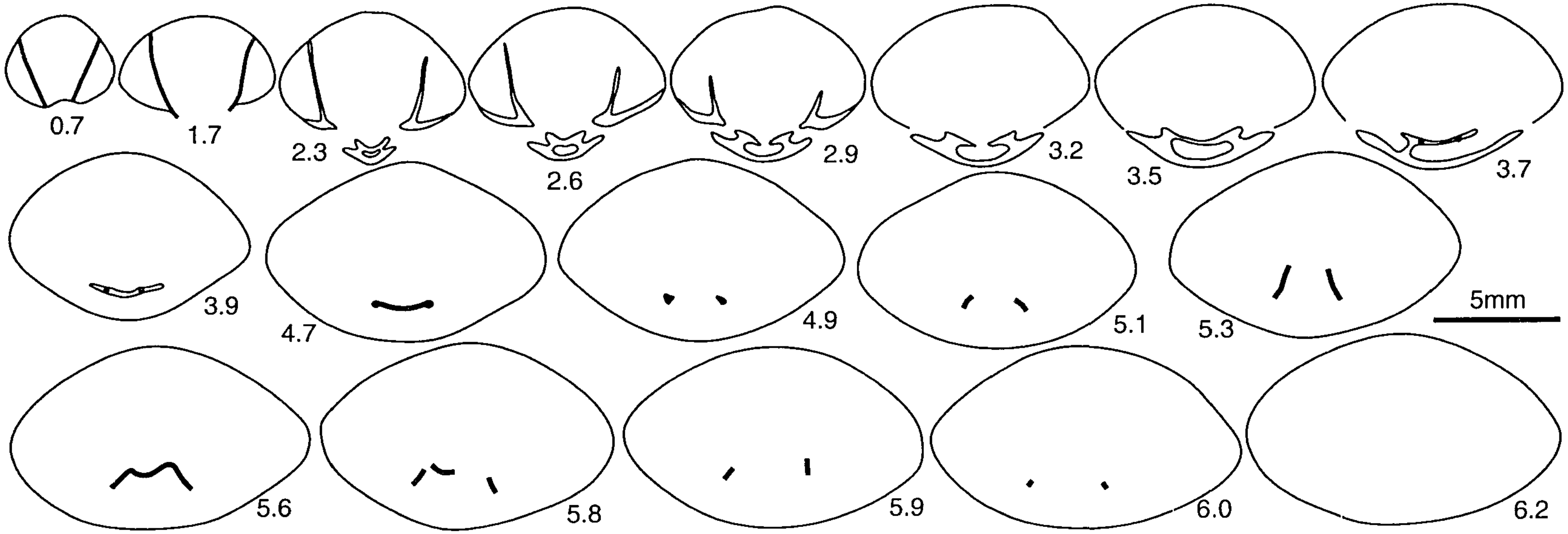

Figure 3.20--Selected transverse serial sections of Cranaena briceae n. sp.
Distances in mm from posterior tip of ventral umbo. (Specimen UA12978).

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Chapter 4

Communities and paleoecology of Eifelian (Mid-Devonian) brachiopods from the Bird Fiord Formation of Arctic Canada*

Introduction

The upper Lower to Middle Devonian Bird Fiord Formation of Arctic Canada (Embry and Klovan 1976; Goodbody 1989) is a carbonate-siliciclastic succession that outcrops widely on southwestern Ellesmere Island, North Kent Island, northwestern Devon Island, Bathurst Island, and parts of Cornwallis Island (Fig. 4.1). The formation, which ranges from 465 m thick on eastern Grinnell Peninsula to more than 900 m on western Bathurst Island, was initially divided into units A-F (Goodbody, 1985). Later, Goodbody (1989) formally named these units as the Cross Bay, Blubber Point, Baad Fiord, Norwegian Bay, Cardigan Strait, and Grise Fiord members (Fig. 4.2). On Bathurst Island, a 20 m thick unit of carbonates, named the "Blue Fiord" Formation by Goodbody (1989) [also referred to as the Blue Fiord Formation by Kerr (1974); the limestone member of the Disappointment Bay Formation by Smith (1984); and the "Bird Fiord Formation carbonate equivalent" by Goodbody (1985)] separates the Bird Fiord Formation from the underlying Eids Formation. The "Blue Fiord" Formation and the Baad Fiord Member, Blubber Point Member, Norwegian Bay Member, and Cardigan Strait Member of the Bird Fiord Formation contain an abundant, diverse fauna that is dominated by brachiopods along with fewer corals, mollusks, and trilobites.

Our brachiopod collection from the Bird Fiord Formation encompasses 22 species that belong to 21 genera (Table 4.1, Figs. 4.2–4). No taxon forms more than 20% of the total fauna. *Cupularostrum repititor*, *Spinatrypina borealis*, *Atrypa* sp. B, and

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* This chapter is in press with the *Canadian Journal of Earth Sciences* (by Li and Jones, 2002)

Desquamatia (*Independatrypa*) *fortis* each forms 15-20% of the total fauna (Table 1) whereas *Schizophoria sulcata* and *Elythyna sverdrupi* each forms 5-10% of the total fauna (Table 1). Members of the other 16 taxa are scarce, with each taxon forming < 5% of the total brachiopod fauna (Table 1). Individual collections are typically dominated by only one or two taxa. The collection of 4197 brachiopods from locality 80XII-99m, for example, includes 4145 specimens (98.76% of fauna) of *Cupularostrum repetitor*.

The brachiopods from the Bird Fiord Formation form distinct communities that are characterized by recurring associations of taxa (cf. Boucot 1975, 1981). Those communities that have taxa in common can be assigned to a Community Group (cf. Boucot 1975, 1981; Boucot and Perry, 1981; Soja 1988a, 1988b; Wang *et al.* 1987). Communities and community groups can be defined according to qualitative and quantitative criteria. Qualitative definitions are usually based on a worker's experience with the faunas and generally lack a statistical basis (e.g., Johnson 1974, 1990; Feldman 1980; Boucot and Perry 1981; Wang et al. 1987; Rong and Li 1999; Jin and Zhan 2001). This subjective approach, however, may cause problems because "...some of the communities may be difficult to understand for the workers unfamiliar with the examples" (Boucot and Perry 1981, p. 186). Accordingly, this study used quantitative methods (similarity index, cluster analysis) to define the brachiopod communities and community groups that are present in the Bird Fiord Formation.

The paleogeographic setting of the brachiopod communities and community groups is established by placing them in the sedimentological framework that was delineated by Goodbody (1985, 1989). These Eifelian brachiopods, which come from an outcrop belt of the Bird Fiord Formation that stretches for ~ 400 km, provide important insights into the factors that may have controlled their distribution. Potentially, these data are important for any future studies that consider the paleobiogeographic distribution of Eifelian brachiopods throughout North America and the rest of the world.

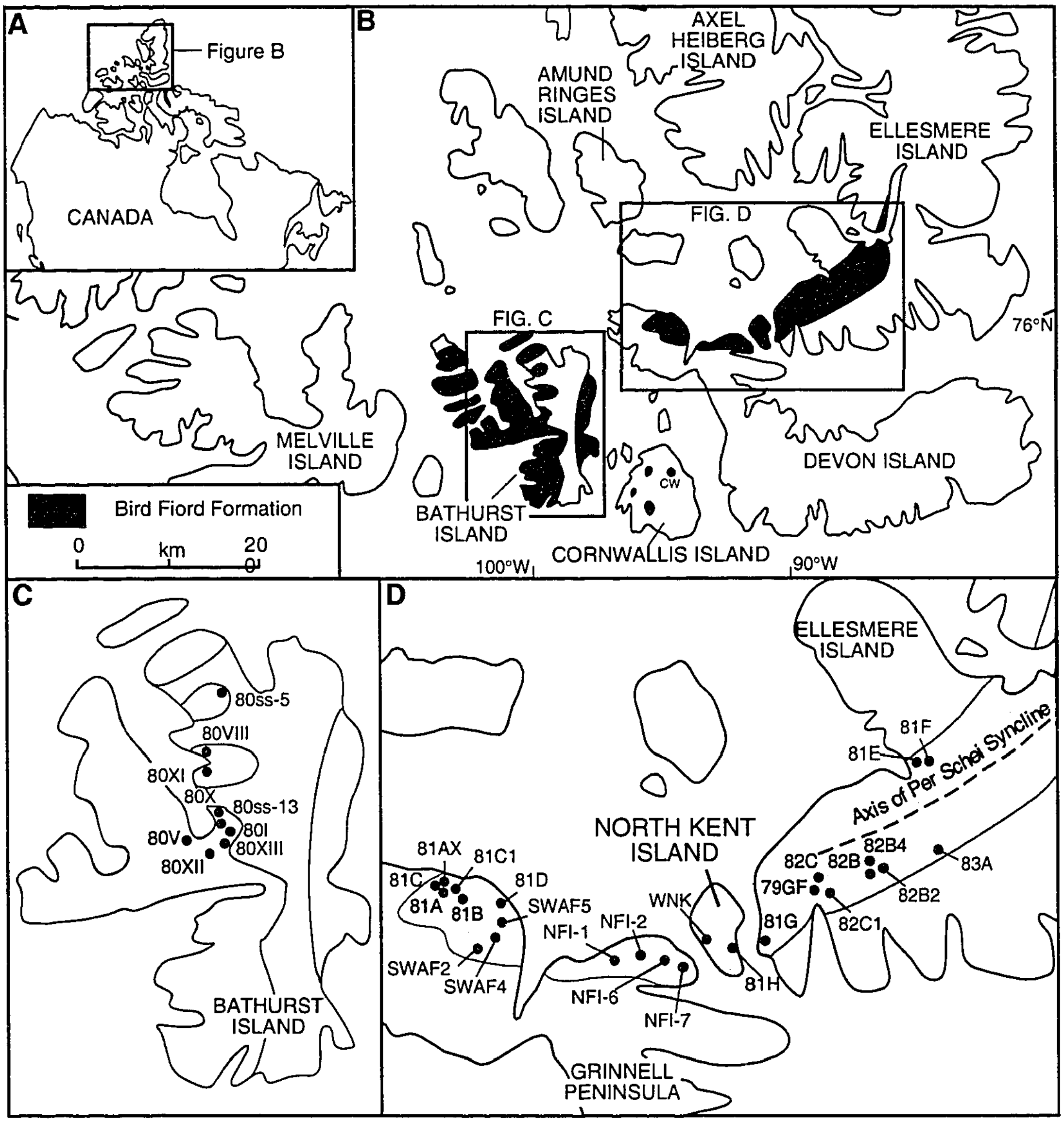

Figure 4.1--(A, B) Outcrops of Bird Fiord Formation in Arctic Canada.
(C, D) Location of sections and spot localities from which brachiopods were collected from the Bird Fiord Formation.

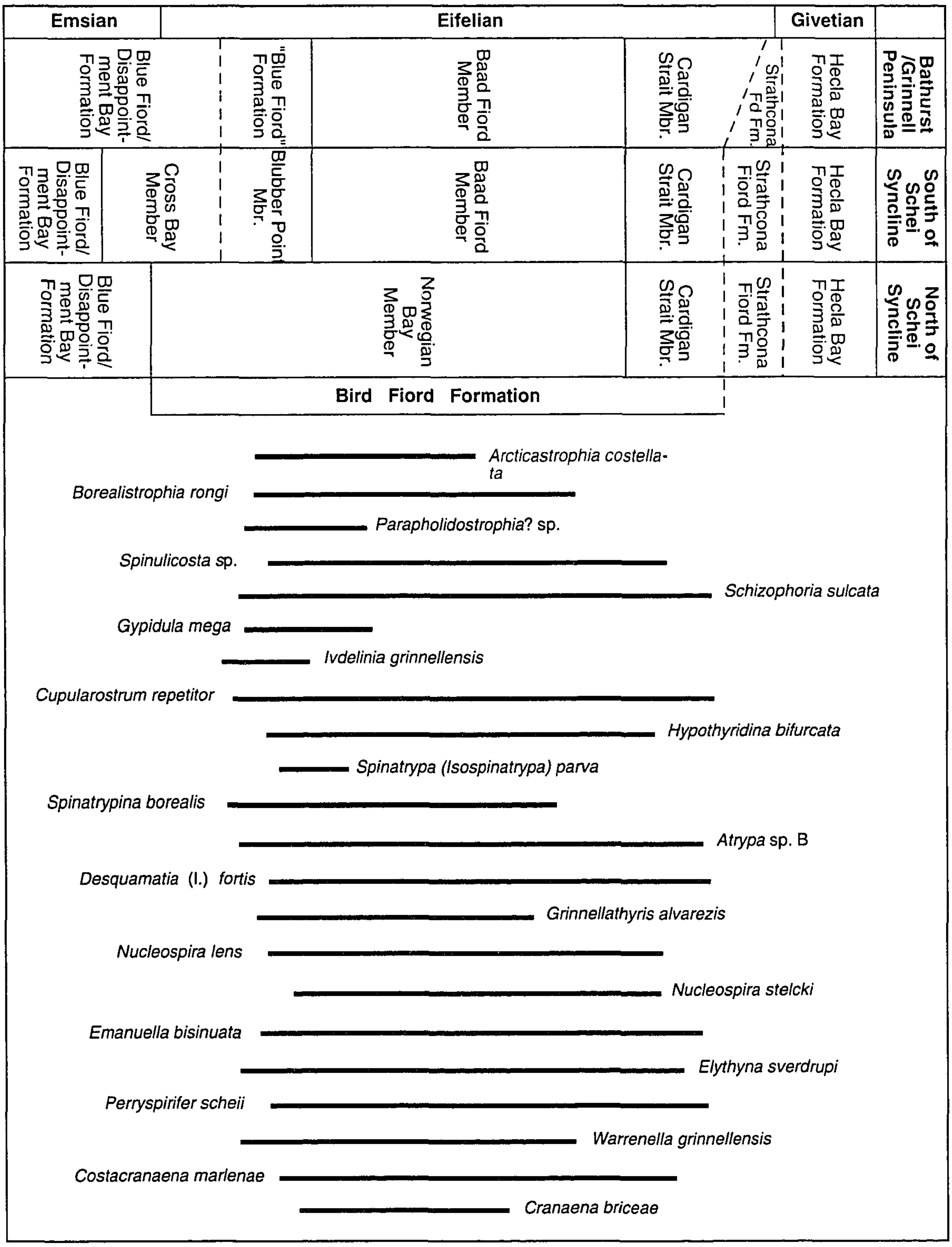

Figure 4.2--Stratigraphic ranges of brachiopod taxa found in the Bird Fiord Formation of Arctic Canada.

Table 4.1. - Brachiopods from the Bird Fiord Formation, Arctic Canada, source for their description, and total number of specimens collected form localities shown in Figure 1.

Species	Description	Total specimens	% of fauna
Arcticastrophia costellata	Li and Jones (2002)	87	0.19
Borealistrophia rongi	Li and Jones (2002)	179	0.39
Parapholidostrophia? sp.	Li and Jones (*in press*)	32	0.07
Spinulicosta sp.	Li and Jones (*in press*)	1392	3.00
Schizophoria sulcata	Johnson and Perry (1976)	3520	7.6
Gypidula mega	Li and Jones (*in press*)	42	0.09
Ivdelinia grinnellensis	Brice (1982)	218	0.47
Cupularostrum repetitor	Johnson and Perry (1976) Brice (1982)	9114	19.6
Hypothyridina bifurcata	Brice (1982)	420	0.9
Spinatrypa (Isospinatrypa) parva	Li and Jones (*in press*)	106	0.23
Spinatrypina borealis	Li and Jones (*in press*)	8178	17.63
Atrypa sp. B	Jones (1982)	7264	15.66
Desquamatia (Independatrypa) fortis	Li and Jones (*in press*)	8538	18.40
Grinnellathyris alvarezis	Li and Jones (2002)	100	0.22
Nucleospira lens	Li and Jones (*in press*)	645	1.39
Nucleospira stelcki	Li and Jones (*in press*)	103	0.22
Emanuella bisinuata	Brice (1982)	1099	2.37
Elythyna sverdrupi	Brice (1982)	2426	5.23
Perryspirifer scheii	Jones and Boucot (1983)	647	1.39
Warrenella grinnellensis	Li and Jones (*in press*)	1610	3.47
Costacranaena marlenae	Johnson and Perry (1976)	303	0.65
Cranaena briceae	Li and Jones (*in press*)	355	0.77
Total		46381	100

Figure 4.3. Nominal taxa of brachiopod communities in Bird Fiord Formation of Arctic Canada. **3.1-5,** *Atrypa* sp. B Jones, dorsal (1), ventral (2), anterior (3), posterior (4), and lateral (5) views, from Norwegian Bay Member, locality 81F, P951, ×2. **3.6-10,** *Elythyna sverdrupi* Brice, lateral (6), ventral (7), dorsal (8), anterior (9), and posterior (10) views, from Norwegian Bay Member, locality 81E, P952, ×1.7. **3.11-14, 27,** *Perryspirifer scheii* (Meyer), dorsal (11), ventral (12), posterior (13), anterior (14), and lateral (27) views, from boundary of Blubber Point and Baad Fiord members, locality NFI-1, P953, ×1. **3.15, 16, 20, 21, 28,** *Spinatrypina borealis* (Warren), dorsal (15), ventral (16), posterior (20), lateral (21), and anterior (28) views, Baad Fiord Member, locality 81A, UA12974, ×2. **3.17-19, 25, 26,** *Desquamatia (Independatrypa) fortis* Li et Jones, lateral (17), anterior (18), posterior (19), ventral (25), and dorsal (26) views, Baad Fiord Member, locality 81A, UA12951, ×1.3. **3.22-24,** *Cranaena briceae* Li and Jones, lateral (22), ventral (23), and dorsal (24) views, Baad Fiord Member, locality 81A, UA12976, ×2.8. All the specimens are stored in the Paleontology museum, Department of Earth and Atmospheric Sciences, University of Alberta.

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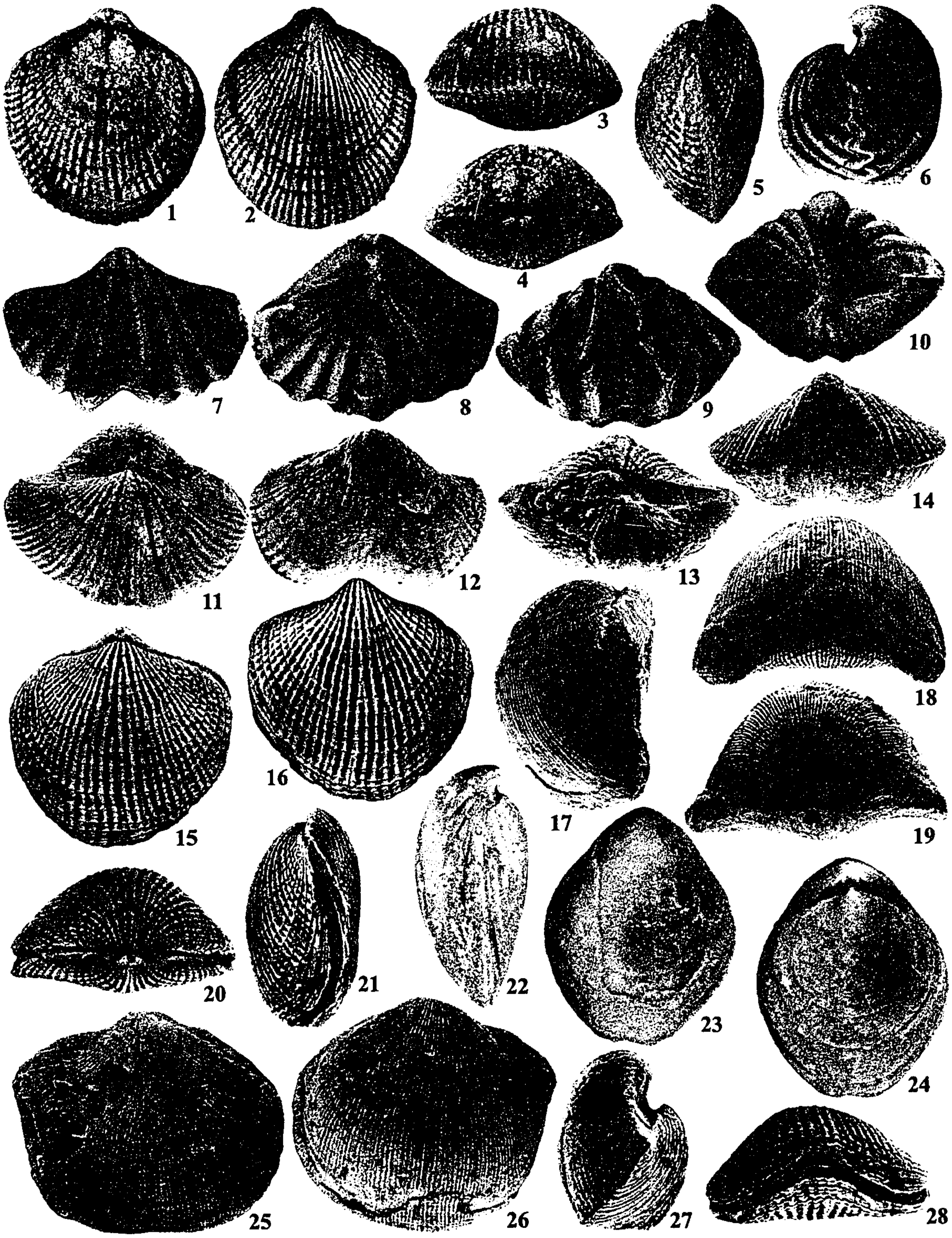
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Figure 4.4. Common taxa in brachiopod communities from Bird Fiord Formation of Arctic Canada. **4.1-5, 9, 14,** *Schizophoria sulcata* Johnson et Perry, 4.1-4, 14, ventral (1), dorsal (2), anterior (3), posterior (4), and lateral (14) views, from Baad Fiord Member, locality 80XII, P954, ×1.3; 4.5, 9, ventral exterior (5) and interior (9) views, "Blue Fiord" Formation, locality 80VIIIA, P955, ×1.8. **4.6-8, 10, 11,** *Ivdelinia grinnellensis* Brice, ventral (6), dorsal (7), lateral (8), anterior (10), and posterior (11) views, "Blue Fiord" Formation, locality SWAF2, P956, ×1.4. **4.12, 13, 15-17,** *Cupularostrum repetitor* Johnson et Perry, lateral (12), ventral (13), posterior (15), anterior (16), and dorsal (17) views, Norwegian Bay Member, locality 81F, P957, ×2.9. **4.18-21,** *Hypothyridina bifurcata* Brice, ventral (18), anterior (19), lateral (20), and dorsal (21) views, "Blue Fiord" Formation, locality 81B, P958, ×2. **4.22-26, 31,** *Emanuella bisinuata* Brice, 22, ventral view showing part of spiralia, Baad Fiord Member, locality SWAF5, P959, ×3.7; 23-26, 31, lateral (23), posterior (24), anterior (25), dorsal (26), and ventral (31) views, Baad Fiord Member, locality 82B, P960, ×3.7. **4.27-30, 32,** *Costacranaena marlenae* Johnson et Perry, 27-30, lateral (27), ventral (28), dorsal (29), anterior (30) views, Cornwallis Island (locality CW), P961, ×1.8; 32, dorsal view showing part of loop, Baad Fiord Member, locality 80XII, P962, ×2.6.

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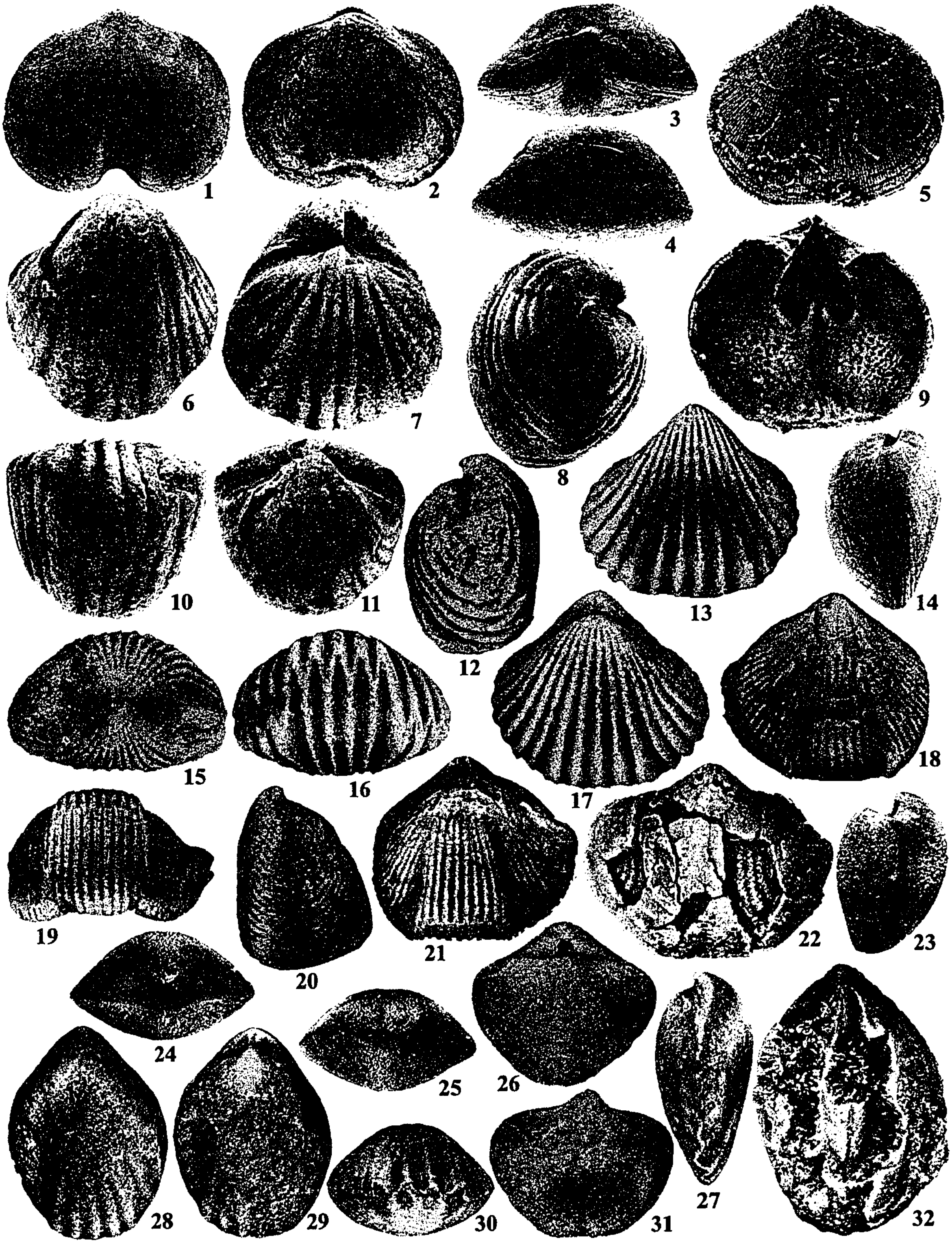
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Methods

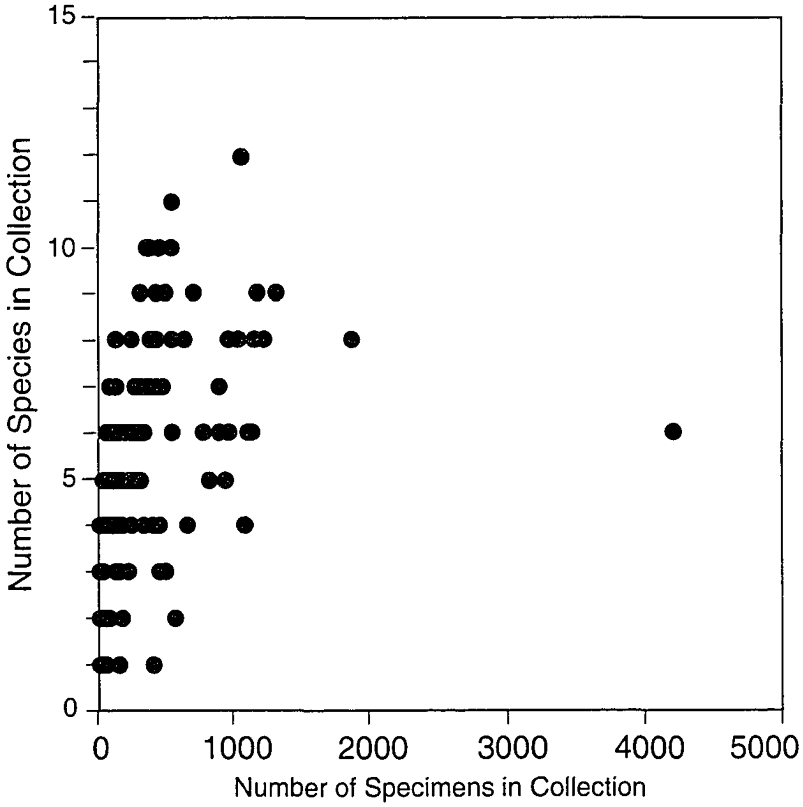
This study is based on 46,381 brachiopods collected from 126 sites at 35 localities throughout the outcrop belt of the Bird Fiord Formation (Fig. 4.1, Appendix 1). Some collections came from different stratigraphic levels in continuous sections whereas others came from isolated outcrops. Most of the brachiopods are articulated and the lack of abrasion indicates that they underwent little or no transport after their death. Following Jones and Smith (1980, 1985) and Jones (1991), the total number of specimens of each species is calculated as the total number of articulated individuals and the larger number of either the dorsal or ventral valves.

Cluster analysis is commonly used to quantitatively delineate communities (e.g. Keyser 1977; Ludvigsen and Westrop, 1983; Jones and Smith 1985; Lespérance and Sheehan 1988; Soja, 1988*a*, 1988*b*; Jones, 1988, 1991; Kovach, 1989; Kovach and Batten, 1994; Patzkowsky, 1995; Budd *et al.,* 1999; Etter, 1999; Smith, 1999; Watkins *et al.,* 2000; Zhan *et al.,* 2002). In this study, cluster analyses were done using ClustanGraphics 5.0 (Wishart 1999). R-mode and Q-mode analyses of the raw data (absolute numbers) produced chained clusters whereas analyses based on percentages produced good clusters for localities but chained clusters for the taxa. Such analyses were deemed unacceptable because of the chaining effect (cf. Jones 1988). Q-mode and R-mode cluster analysis based on binary data (i.e., presence or absence of a taxon), however, produced very good clusters that facilitated definition of the brachiopod communities. For these analyses, the Jaccard Coefficient of similarity and Ward's Method (=Minimum Variance or Increase in Sum of Square) of clustering were used. The Jaccard coefficient is expressed as:

$$Jd=C/(N_A+N_B-C)$$

Where C is the total joint occurrences of taxa A and B in the collections, and $N_A(N_B)$ is the total presences of taxon A (B) in the collections. The simple matching coefficient was not used because it is based on the mutual presence and absence of a taxon (cf. Keyser 1977, p. 188). With this index, there is the possibility that a high coefficient may be more reflective of mutual absences than mutual presences. The Jaccard Coefficient avoids this problem and is one of the reasons why it has been widely used, in conjunction with Ward's Method of clustering, for delineating communities (e.g., Keyser 1977; Jones and Smith 1985; Jones 1988, 1991; Lespérance and Sheehan 1988; Soja, 1988*a*, 1988*b*).

Our samples should be statistically reliable given the size of the total collection, the number of brachiopods in individual collections (up to 4197), and the manner in which the samples were collected. Two to four people collected as many brachiopods as possible from each site with special attention being paid to the acquisition of specimens of all sizes. Small specimens are, for example, well represented throughout the collections. The collection from 81AX-104m (Devon Island), for example, contains numerous *Grinnellathyris alvarezis* that are less than 5 mm wide (Li and Jones, 2002, table 3). Thus, we are confident that there is little or no size bias in these collections. The overall integrity of the samples is further supported by the fact that virtually almost all of the brachiopod taxa previously reported from the Bird Fiord Formation by Johnson and Perry (1976), Brice (1982), Jones (1982), and Jones and Boucot (1983) are present. Nevertheless, the rarefaction curve does not show the classic pattern of progressively decreasing number of species with increasing sample size (Fig. 4.5). For this set of samples, the number of species does not always correlate with sample size. The 4197 brachiopods in sample 80XII-99m, for example, only include six species whereas the 1842 brachiopods in sample 80I-659m include eight species. The poor correlation between the sample size and the species diversity probably reflects the fact that most of the collections are dominated by only one or two species.



Fiure 4.5--Rarefraction plot comparing number of species and number of specimens in individual brachiopod collections from the Bird Fiord Formation.

Sedimentological Regimes

The Bird Fiord Formation is part of the Devonian succession that accumulated in the Franklinian Mobile Belt (Goodbody 1989, fig. 2). During the Eifelian, a broad shelf stretched from northern Ellesmere Island, through Grinnell Peninsula (Devon Island), to Bathurst Island and Cornwallis Island (Fig. 4.6). That shelf was bound to the east and south by land and to the northwest by a deep oceanic basin (Fig. 4.6). The Bird Fiord Formation, which is transitional between an underlying carbonate shelf/argillaceous basin regime and an overlying siliciclastic regime, records the westerly advance of siliciclastic sediments, derived from the land masses to east and south, over a carbonate platform (Embry and Klovan 1976; Goodbody 1985, 1989). Goodbody (1985, 1989) showed that the Bird Fiord Formation encompasses a broad array of depositional regimes. The following summary, which provides an overview of the facies that are considered representative of each stratigraphic unit, is based on the descriptions given by Goodbody (1985, 1989).

Near Bird Fiord, Ellesmere Island, the Bird Fiord Formation is divided into the Norwegian Bay Member and the Cardigan Strait Member (Fig. 4.2). The Norwegian Bay Member (583 m thick), which is confined to the north axis of the Schei Syncline, encompasses a diverse array of facies. Goodbody (1989) divided this member into units 1 (basal) to 5 (top):

- Unit 1 (232 m) – interbedded bioclastic limestones/calcareous siltstone and shale;
- Unit 2 (26 m) – interbedded shale and rubbly bedded siltstone or cryptalgal laminite, with scattered stromatolites;
- Unit 3 (90 m) – coarsening upward cycles that grade upward from shale into calcareous rubbly sandstone;
- Unit 4 (115 m) – coarsening upward cycles that grade from shale to argillaceous siltstone to cross-bedded, bioturbated calcareous sandstones;

- Unit 5 (120 m) – interbedded bioclastic, calcareous sandstones and shale.

The Norwegian Bay Member encompasses facies that formed in an intertidal to shallow shelf setting (Goodbody 1985).

The Cardigan Strait Member, which overlies the Norwegian Bay Member in the Bird Fiord area, is 230 m thick (Goodbody, 1989). This member is formed of planar and cross-bedded noncalcareous sandstone that commonly contains crinoids, brachiopods, bivalves, and plant fragments (Fig.4.7). These successions formed as deltas advanced onto the shelf.

The Grise Fiord Formation, which is only found in the eastern most part of the outcrop belt, underlies the upper tongue of the Strathcona Formation (Goodbody 1989). This succession (~ 100 m thick), formed of orange-brown noncalcareous, fine-medium grained, mica-rich subarkosic sandstones with lesser amounts of argillaceous siltstone, shale, and calcareous shale, formed in a non-marine, delta plain setting (Goodbody 1985).

On the south limb of the Schei Syncline, the Bird Fiord Formation is divided into the Cross Bay Member, the Blubber Point Member, the Baad Fiord Member, and the Cardigan Strait Member (Fig. 4.2). The upper part of the Cross Bay, Blubber Point, and Baad Fiord members are equivalent to the Norwegian Bay Member (Fig. 4.2).

The Cross Bay Member, ~ 300 m thick, is formed of interbedded dolostones, limestones, siltstone, shale, and evaporites. The succession encompasses 2-6 m thick cycles that grade up from basal shale into silty dolostone and, in some areas, gypsum. Planar laminations, wrinkly laminations, stromatolitic laminae, fenestrae, mudcracks, scours, vugs, and intraclastic layers are common (Fig. 4.7). Few fossils are found in this member. The lithologies and sedimentary structures are indicative of sediments that accumulated in a sabkha setting.

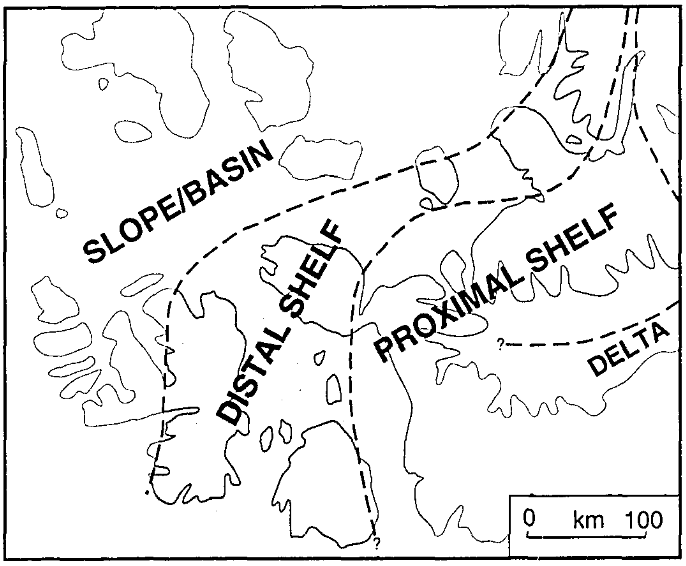


Figure 4.6--Middle Devonian paleogeography of the Arctic Canada (modified from Goodbody, 1985).

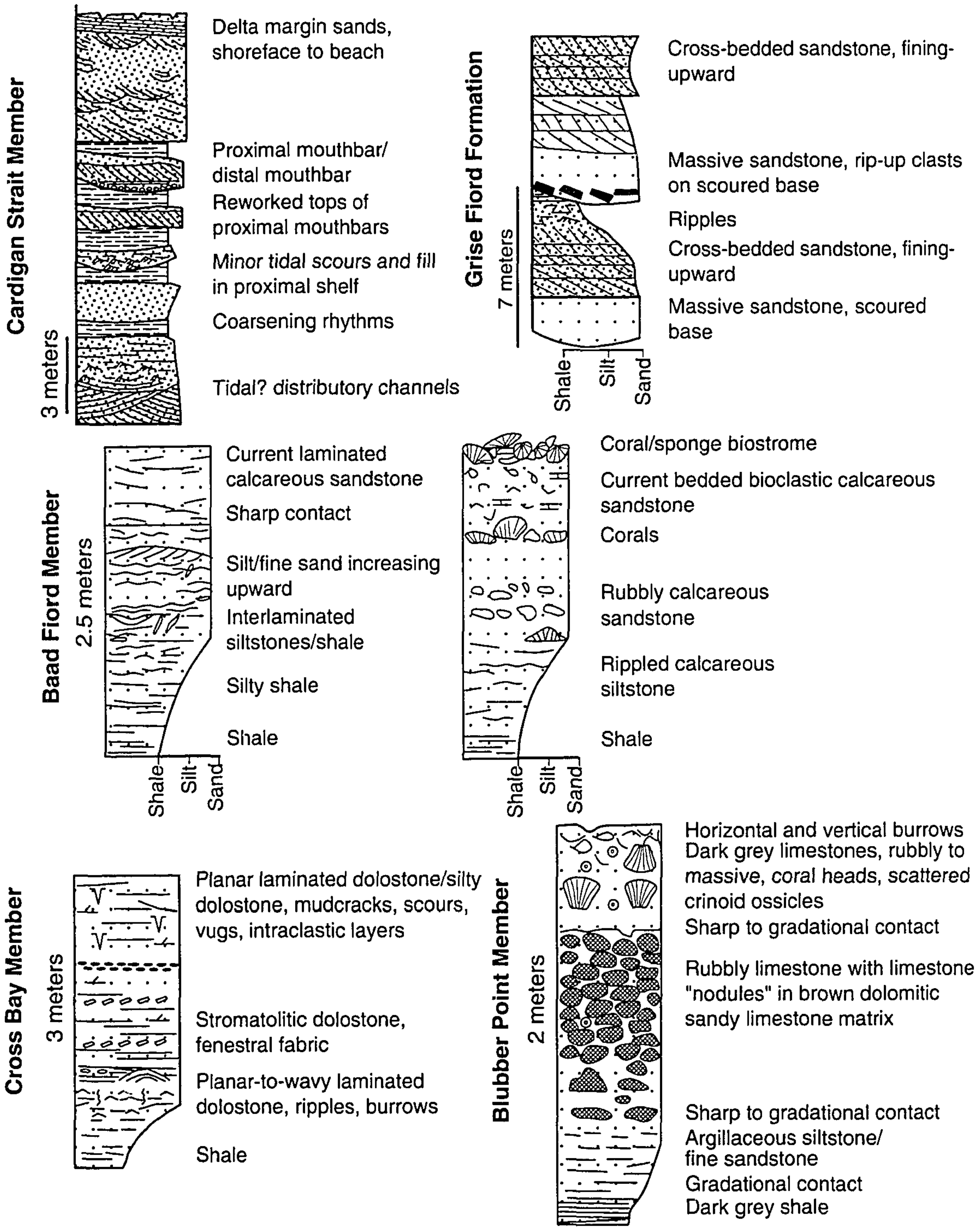


Figure 4.7. Schematic diagrams showing facies succession and characteristics of typical cycles in the Cross Bay Member, Blubber Point Member, Baad Fiord Member, and Cardigan Strait Member. All diagrams modified from Goodbody (1989, figs. 8, 13, 15, and 18).

The Blubber Point Member on southwest Ellesmere Island (south of Schei Syncline axis), North Kent Island, and northern Devon Island (excluding Grinnell Peninsula), typically ~ 60 m thick, is formed of resistant, cliff-forming limestone, and calcareous sandstone and some shale. Cycles consist of dark grey-green shale that grades upwards into argillaceous siltstone/fine-grained sandstone, to grey-green rubbly bedded sandy, fossiliferous micrite and/or calcareous sandstone (Fig. 4.7). Horizontal trace fossils are common in the micrite. The sandstone is characterized by current lineations, planar laminations, cross-laminations, and in some areas, large channels. Fossils include brachiopods, crinoid ossicles, corals and sponges, tentaculites, gastropods, and fish bones. Goodbody (1985, fig. 5.21) suggested that these facies represent sediments that were deposited in a shallow, proximal shelf setting.

The Baad Fiord Member, usually ~ 60 m thick, is formed of intercalated dark grey shale, dark grey-brown argillaceous siltstone, and variable fossiliferous mica-rich, subarkosic sandstones. Coral-sponge biostromes are scattered throughout the member. Like the Blubber Point and Cross Bay members, most of the Baad Fiord Member is characterized by repetitive coarsening-upward cycles (shale to sandstone) that are typically ~ 3 m thick (Fig. 4.7). There are, however, variations in the cycles from area to area. Thus, in some areas the upper sandstones are characterized by planar laminae and cross-bedding (Fig. 4.7). Elsewhere, the upper parts of the cycles are characterized by variable amounts of bioclastic material with coral-sponge biostromes being present in some areas (Fig. 4.7). Goodbody (1985, figs. 5.21, 9.8) suggested that this sequence of facies represents deposition on a shallow, proximal shelf. The dominance of clastic material over coral-bearing limestone in the Baad Fiord Member suggests that these sediments may have accumulated in a shallower, more landward setting than the sediments in the Blubber Point Member.

On Grinnell Peninsula (Devon Island) and Bathurst Island, the Bird Fiord Formation is divided into the Baad Fiord Member and the Cardigan Strait Member (Fig.4. 2). In those areas, the Baad Fiord Member is underlain by the "Blue Fiord" Formation, which probably represents deposition on a carbonate platform.

The Baad Fiord Member on Grinnell Peninsula and Bathurst Island is divided Unit 1, which is dominated by cycles that grade from a basal silty shale into very silty limestones, and Unit 2, which is formed of cycles that grade upward from shale to argillaceous siltstone to silty sandstone to fine-grained sandstone. The argillaceous content of these rocks decreases up section. Goodbody (1985, fig. 9.8) suggested that these successions developed in distal shelf (Unit 1) and mid-shelf (Unit 2) settings. The higher shale and argillaceous content in the Baad Fiord Member on Grinnell Peninsula and Bathurst Island indicates that the water in this area was deeper than that in the southwest Ellesmere Island - North Kent Island - northern Devon Island area.

Sedimentological analysis indicates that the southwest Ellesmere Island - North Kent Island - northern Devon Island (excluding Grinnell Peninsula) region was the site of deposition on a shallow, proximal shelf whereas the Grinnell Peninsula – Bathurst Island region was characterized by deeper water sedimentation in a more offshore position.

Brachiopod Communities

Cluster analysis divides the localities into groups A and B that are characterized by significantly different brachiopod faunas (Fig. 4.8). *Spinatrypina* and *Desquamatia* are present at virtually every locality in Group A whereas *Atrypa* and *Elythyna* are usually present at each locality in Group B (Fig. 4.8). Other common genera present in Group A include *Spinulicosta, Schizophoria,* and *Cupularostrum* whereas *Spinulicosta, Schizophoria,* and *Borealistrophia* are found in Group B (Fig. 4.8). *Spinatrypina* and *Desquamatia* are generally present at each locality in Group A but are rarely present at localities in Group B. Conversely, *Atrypa* and *Elythyna* are generally present at each locality in Group B but are rarely found at localities in Group A (Fig. 4.8). Collectively, these comparisons define the *Spinatrypina-Desquamatia* Community Group (Group A) and the *Atrypa-Elythyna* Community Group (Group B) (Fig. 4.8).

Primarily on the basis of the presence/absence of *Cranaena* and/or *Arcticastrophia*, the *Spinatrypina-Desquamatia* Community Group is divided into the *Spinatrypina-Desquamatia* (A1 – Fig. 4.8) and *Spinatrypina-Desquamatia-Cranaena* (A2 – Fig. 4.8) communities. *Emanuella* and *Costacranaena* are less common in the *Spinatrypina-Desquamatia* Community than in the *Spinatrypina-Desquamatia-Cranaena* Community (Fig. 4.8). The diversity of the former (~ 7) is slightly lower than that of the latter (~ 9).

The presence/absence of *Perryspirifer* is the main basis for dividing the *Atrypa-Elythyna* Community Group into the *Atrypa-Elythyna-Perryspirifer* (B1 – Fig. 4.8) and *Atrypa-Elythyna* (B2 – Fig. 4.8, Table 4.2) communities. *Nucleospira stelcki* and *Cupularostrum* are present in the *Atrypa-Elythyna-Perryspirifer* but generally absent in the *Atrypa-Elythyna* Community (Fig. 4.8). The diversity of the *Atrypa-Elythyna-Perryspirifer* Community (~ 9) is higher than that of *Atrypa-Elythyna* Community (~ 5). In the *Atrypa-Elythyna-Perryspirifer* Community, the percentage of *Atrypa* is typically higher than that of *Elythyna.* Conversely, the percentage of *Elythyna* tends to be higher than the percentage of *Atrypa* in the *Atrypa-Elythyna* Community (Table 4.2).

Potentially, each of the four communities can be divided into smaller units according to the hierarchical structure of the dendrogram (Fig. 4.8). The smaller divisions, however, would primarily reflect differences in the taxa that are relatively minor components of each fauna. For example, the *Spinatrypina-Desquamatia* Community could be divided according to the presence/absence of *Warrenella* (Fig.4. 8). In most cases, however, the further division of the four communities is not warranted and serves to confuse rather than clarify the paleoecological framework.

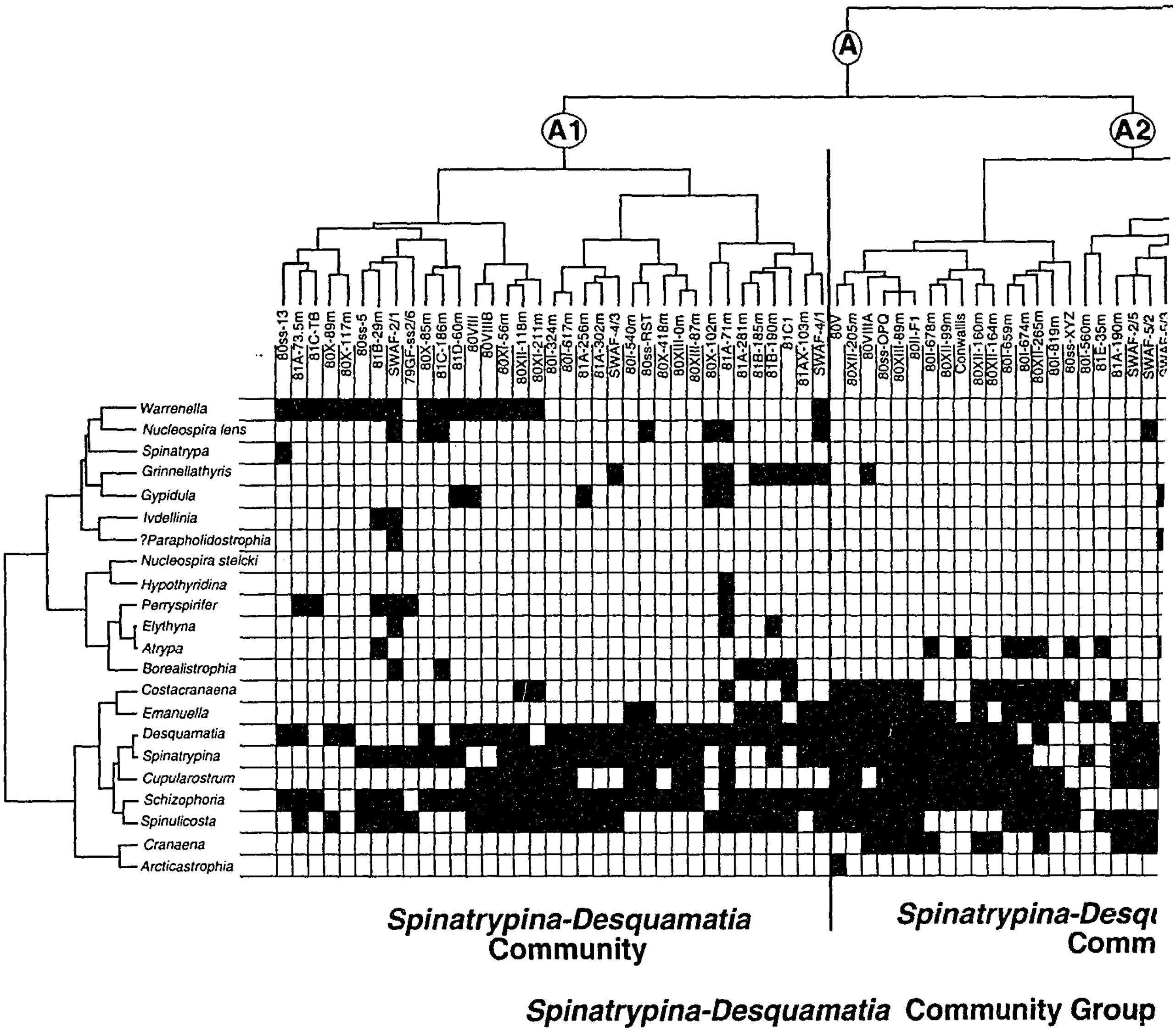
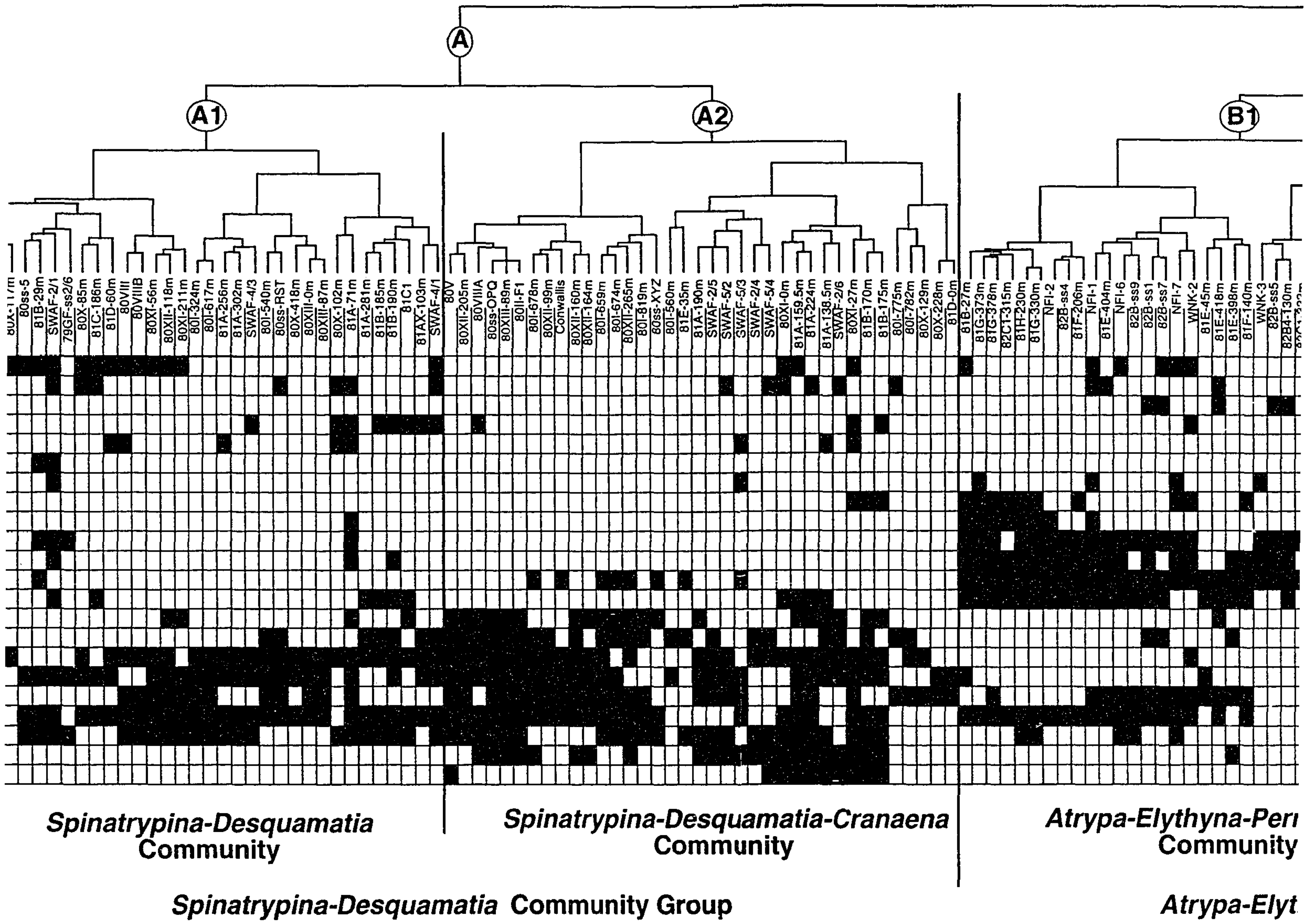


Figure 4.8--Delineation of brachiopod community groups and communities based on distribution of brachiopod species (black indicates presence) throughout the Bird Fiord Formatio of Arctic Canada. The dendrograms, which dictate the ordering of the localities and species, are based on the Jaccard Similarity Coefficient and Ward's Method of Clustering.



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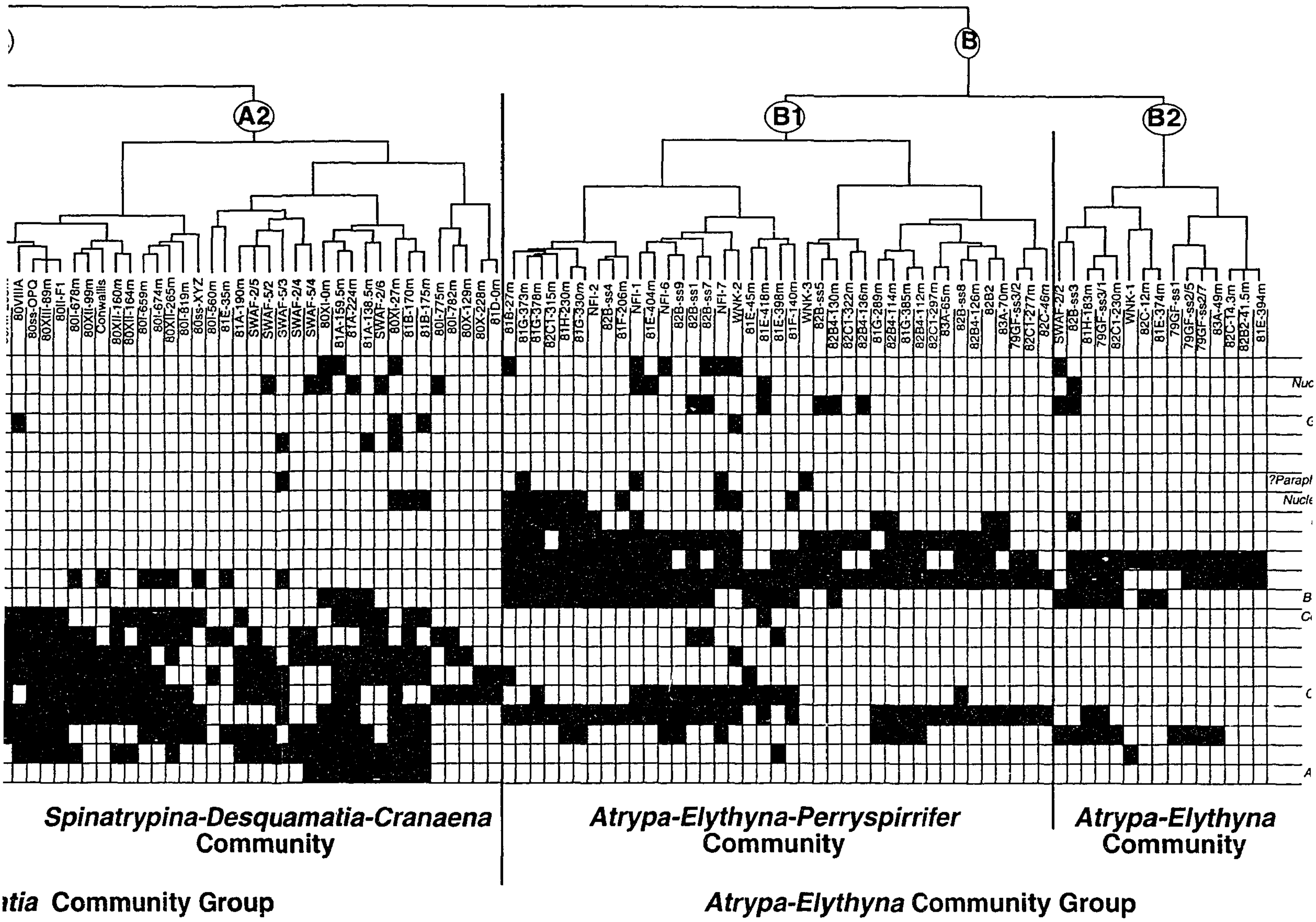

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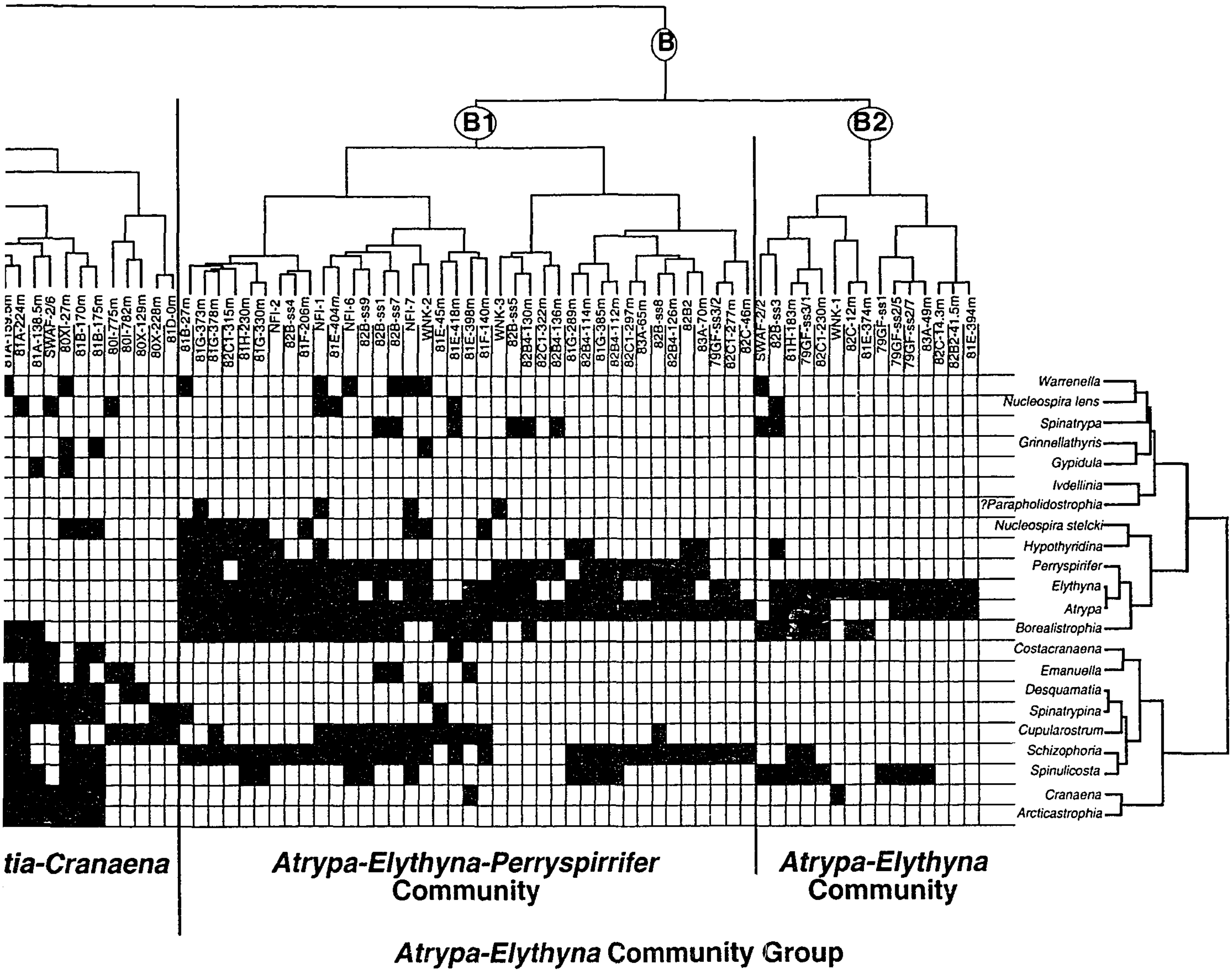
B
B1
B2
81A-224m
81A-138.5m
SWAF-2/6
80XI-27m
81B-170m
81B-175m
80I-775m
80I-782m
80X-129m
80X-228m
81D-0m
81B-27m
81G-373m
81G-378m
82C1-315m
81H-230m
81G-330m
NFI-2
82B-ss4
81F-206m
NFI-1
81E-404m
NFI-6
82B-ss9
82B-ss1
82B-ss7
NFI-7
WNK-2
81E-45m
81E-418m
81E-398m
81F-140m
WNK-3
82B-ss5
82B4-130m
82C1-322m
82B4-136m
81G-289m
82B4-114m
81G-385m
82B4-112m
82C1-297m
83A-65m
82B-ss8
82B4-126m
82B2
83A-70m
79GF-ss3/2
82C1-277m
82C-46m
SWAF-2/2
82B-ss3
81H-183m
79GF-ss3/1
82C1-230m
WNK-1
82C-12m
81E-374m
79GF-ss1
79GF-ss2/5
79GF-ss2/7
83A-49m
82C-14.3m
82B2-41.5m
81E-394m
Warrenella
Nucleospira lens
Spinatrypa
Grinnellathyris
Gypidula
Ivdellinia
?Parapholidostrophia
Nucleospira stelcki
Hypothyridina
Perryspirifer
Elythyna
Atrypa
Borealistrophia
Costacranaena
Emanuella
Desquamatia
Spinatrypina
Cupularostrum
Schizophoria
Spinulicosta
Cranaena
Arcticastrophia
tia-Cranaena
Atrypa-Elythyna-Perryspirrifer Community
Atrypa-Elythyna Community
Atrypa-Elythyna Community Group

Table 4.2. Distribution of brachiopod species in the brachiopod communities of the Bird Fiord Formation of Arctic Canada.

Community	**Nominal Taxa (% of fauna)**	**Associated Taxa**
Atrypa-Elythyna –Perryspirifer	*Atrypa* (50-70%) *Elythyna* (5-20%) *Perryspirifer* (5-20%)	*Spinulicosta, Schizophoria, Cupularostrum, Emanuella, Borealistrophia, Hypothyridina, ?Parapholidostrophia, Nucleospira lens, N. stelcki, Spinatrypa, Warrenella*
Atrypa-Elythyna	*Atrypa* (5-45%) *Elythyna* (50-95%)	*Spinulicosta, Schizophoria, Borealistrophia, Spinatrypa*
Spinatrypina - Desquamatia	*Spinatrypina* (5-55%) *Desquamatia* (5-85%)	*Spinulicosta, Schizophoria, Cupularostrum, Emanuella, Costacranaena, Borealistrophia, Ivdelinia, Gypidula, Grinnellathyris,* *Nucleospira lens, Warrenella*
Spinatrypina – Desquamatia - Cranaena	*Spinatrypina* (5-55%) *Desquamatia* (10-55%) *Cranaena* (1-15%)	*Spinulicosta, Schizophoria, Cupularostrum, Arcticastrophia, Emanuella, Costacranaena, Borealistrophia, Gypidula, Grinnellathyris, Atrypa,Nucleospira lens, N. stelcki, Warrenella*

Distribution of Brachiopod Communities

The *Atrypa-Elythyna* Community Group is found on the northern part of Devon Island (excluding Grinnell Peninsula), North Kent Island, and Ellesmere Island (Fig. 4.9). Conversely, the *Spinatrypina-Dequamatia* Community Group is found on Grinnell Peninsula, Bathurst Island, and Cornwallis Island (Fig. 4.10).

From a stratigraphic perspective, the *Atrypa-Elythyna* Community is generally restricted to the Blubber Point Member whereas the *Atrypa-Elythyna-Perryspirifer* Community is typically found in the Baad Fiord Member (Fig. 4.9). The *Spinatrypina-Desquamatia* Community is found in the "Blue Fiord" Formation and Unit 2 of the Baad Fiord Member, whereas the *Spinatrypina-Desquamatia-Cranaena* Community is largely restricted to Unit 1 of the Baad Fiord Member (Fig. 4.10).

The high degree of organization in the geographic and stratigraphic distribution of the four communities clearly indicates that environmental conditions must have exerted a significant control over their distributions. Among the collections examined, there are only a few that are exceptions to these well defined geographic (e.g., 81B-27m, 81E-35m, SWAF2/2, and 79GF-ss2/6) and stratigraphic (e.g., 83A-49m, 81C-186m, 80XI-56m, 80I-560m, 80XII-118m) distribution patterns.

Benthic Assemblages

Boucot (1975) suggested that the Silurian and Devonian benthic biota can be divided into five Benthic Assemblages (BA) that were fundamentally related to water depth. Thus, BA1 developed in near shore, shallow water settings whereas BA5 was present in distal, deep-water settings. Each BA encompassed many different communities that developed in response to local environmental conditions.

Previous studies of *Elythyna-* and *Atrypa*-dominated communities have shown that they are part of BA3 that developed in a shallow, moderately quiet marine environment (e.g., Boucot and Perry 1981; Wang et al. 1987). Boucot and Perry (1981), for example, assigned a BA3 position to the Early Devonian *Elythyna* community that had originally been defined by Johnson and Kendall (1976). *Atrypa*, which is the dominant element in many *Atrypa*-bearing communities, usually appears in BA3. Such communities include the *Atrypa* Community of Boucot (1975) that spans BA3-5; the *Carinagypa-Atrypa* Community and *Brachyspirifer-Atrypa* Community of Johnson (1977) and Niebuhr (1977) that are part of BA3 (Boucot and Perry 1981); and the Emsian *Acrospirifer-Atrypa* Community and the Eifelian *Atrypa-Xystostrophia* Community that was placed in BA3 by Wang et al. (1987). Comparisons with communities like these indicate that the *Atrypa-Elythyna-Perryspirifer* Community and the *Atrypa-Elythyna* Community in the Bird Fiord Formation should also be considered part of BA3 (Fig. 4.11).

The Middle Devonian *Spinatrypina asymmetrica* Community of Johnson (1990) [formerly named *Spinatrypina-Thamnopora* Community by Johnson and Flory (1972)] probably inhabited a quiet water biotope landward of the shelf edge (Johnson and Flory 1972). Boucot and Perry (1981) assigned this community to BA3 or 4. With similar diversity and dominant taxa, a BA4 position is proposed for the *Spinatrypina-Desquamatia* Community and the *Spinatrypina-Desquamatia-Cranaena* Community that are found in the Bird Fiord Formation (Fig. 4.11).

Correlation between brachiopod communities and sedimentological regimes

There is a strong correlation between the distribution of the brachiopod communities and the depositional framework, as determined by sedimentological analysis (Fig. 4.11). Brachiopods are absent from the Cross Bay Member that is formed of sediments that accumulated in a sabkha setting and from the Grise Bay Member that represents deposition on a delta plain. Brachiopods are found throughout the members that include sediments that accumulated on a shelf in open marine conditions.

The *Atrypa-Elythyna* community, which is common in the Blubber Point Member (Fig. 9), lived in a proximal shelf setting. The *Atrypa-Elythyna-Perryspirifer* Community, found in the Baad Fiord Member (Fig. 9), also lived in a proximal shelf setting but in a slightly shallower setting than that of the *Atrypa-Elythyna* community (Fig. 4.11).

The *Spinatrypina-Desquamatia-Cranaena* Community, found in Unit 1 of the Baad Fiord Member (Fig. 4.10), lived in a distal shelf environment (Fig. 4.11). The *Spinatrypina-Desquamatia* Community, found in Unit 2 of the Baad Fiord Member (Fig. 4.10), probably lived in a mid-shelf environment (Fig. 4.11).

The distribution patterns indicate that parameters related to water depth exerted a primary control over the distribution of the brachiopod communities. The fact that the same brachiopod community is found in limestone, shale, siltstone, and sandstone indicates that the substrate did not play a major role in the distribution of these communities. The paleogeographic boundary between proximal and distal shelf, established on sedimentological criteria (Fig. 4.6), also separates the *Atrypa-Elythyna* Community Group on Ellesmere Island, North Kent Island, and north Devon Island from the *Spinatrypina-Desquamatia* Community Group that is found on Grinnell Peninsula, Cornwallis Island, and Bathurst Island (Fig. 4.12). This spatial correlation supports the notion that environmental parameters related to water depth were responsible for their distribution (Fig. 4.11).

On southwest Ellesmere Island, North Kent Island, and north Devon Island, the sedimentological change from the Blubber Point Member to the Baad Fiord Member has been attributed to a regressive cycle (Goodbody 1985). The change in the lithologies between these members is matched by a change from the *Atrypa-Elythyna* Community in the Blubber Point Member to the *Atrypa-Elythyna-Perryspirifer* Community in the Baad Fiord Member. This correlation supports the notion that parameters related to water depth exerted a primary control over the distribution of the brachiopod communities. In this case, the *Atrypa-Elythyna-Perryspirifer* Community lived in shallower water than the *Atrypa-Elythyna* Community (Fig. 4.11). A parallel situation is also found in the Baad Fiord Member on Grinnell Peninsula, Cornwallis Island, and Bathurst Island. At those localities, the change from Unit 1 to Unit 2, which resulted from a regressive cycle, is matched by a change from the *Spinatrypina-Desquamatia-Cranaena* Community in Unit 1 to the *Spinatrypina-Desquamatia* Community in Unit 2. The change in brachiopod communities appears to have been related to depth-related environmental parameters (Fig. 4.11).

The change from the *Spinatrypina-Desquamatia* Community in the "Blue Fiord" Formation to the *Spinatrypina-Desquamatia-Cranaena* Community in the overlying Baad Fiord Member (Unit 1) probably resulted from a short-lived transgression.

Discussion

The composition and paleoecology of Early Devonian brachiopod communities are relatively well known from studies such as those by Johnson (1974, 1977, 1990), Boucot (1975), Johnson and Kendall (1976), Niebuhr (1977), Boucot and Perry (1981), Jones and Smith (1985), Wang et al. (1987), Jones (1991), Hiller and Theron (1988), Soja (1988*a*, 1988*b*), and Lespérance and Sheehan (1988). Although Middle Devonian brachiopod communities have been described from various parts of the world (e.g., Johnson and Flory 1972; Savage and Boucot 1978; Feldman 1980; Wang et al. 1987; Brower et al. 1988; Johnson 1990; Brower and Nye 1991; McCollum 1991), they are generally not as well known as the Early Devonian communities.

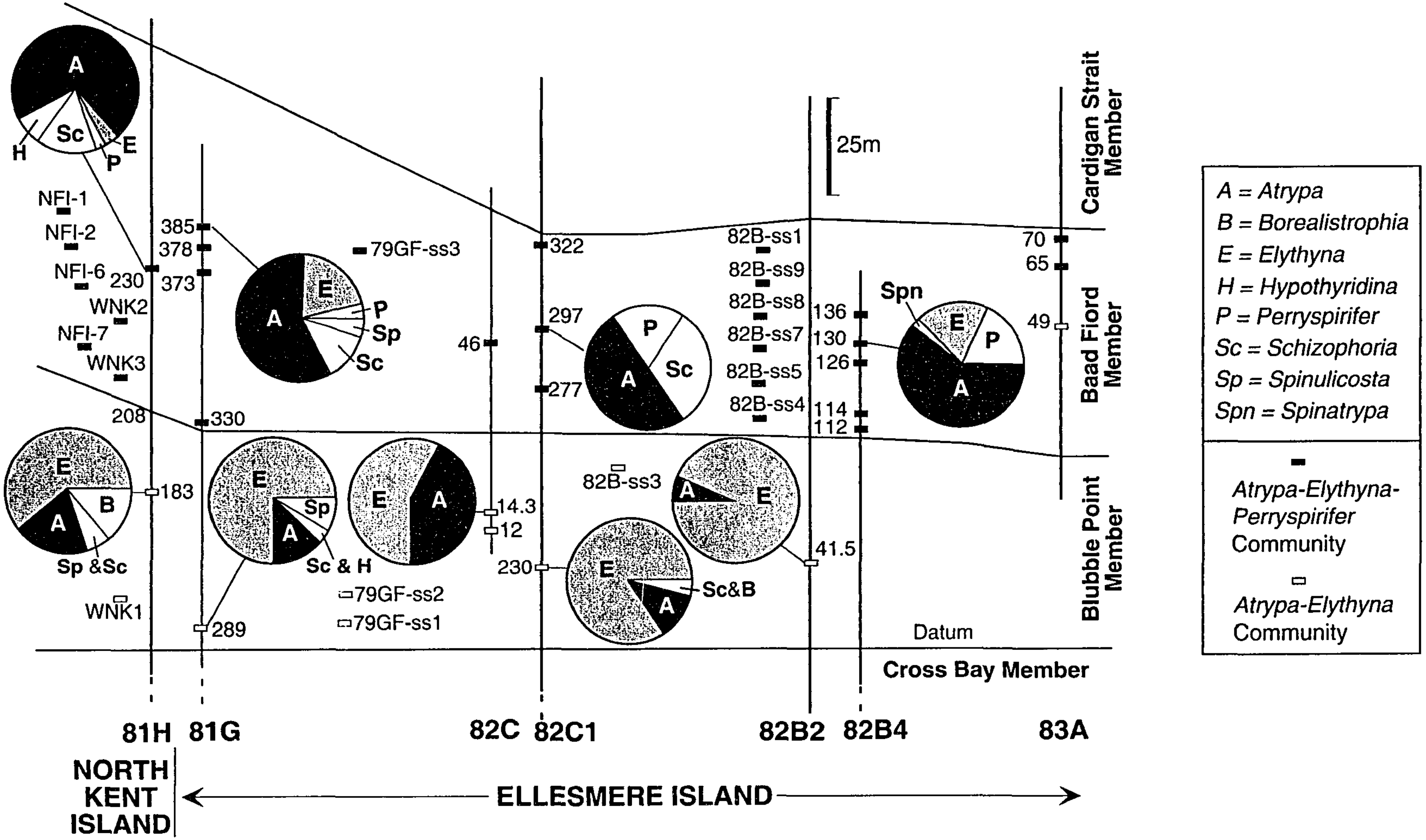

Figure 4.9--Distribution of the *Atrypa-Elythyna-Perryspirifer* Community and the *Atrypa-Elythyna* Community in the Bird Fiord Formation on Ellesmere Island and North Kent Island. Selected pie diagrams are included to illustrate the percentage of brachiopod fauna formed by constituent taxa. Numbers on section indicate meters above base of measured section.

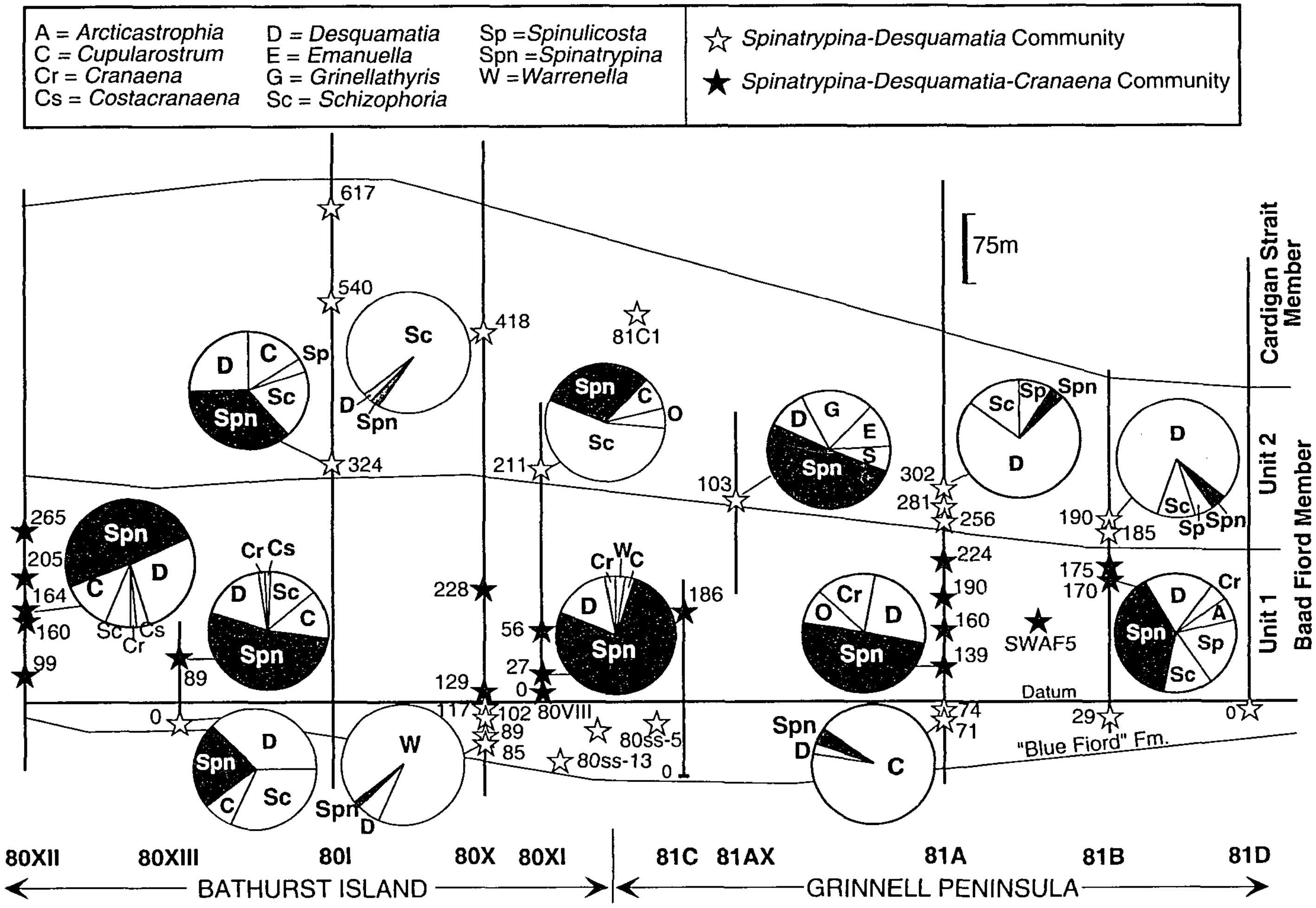

Figure 4.10--Distribution of the *Spinatrypina-Desquamatia* Community and the *Spinatrypina-Desquamatia-Cranaena* Community in the Bird Fiord Formation on Grinnell Peninsula and Bathurst Island. Selected pie diagrams are included to illustrate the percentage of brachiopod fauna formed by constituent taxa. Numbers on section indicate meters above base of measured section. Correlation modified from Goodbody (1985).

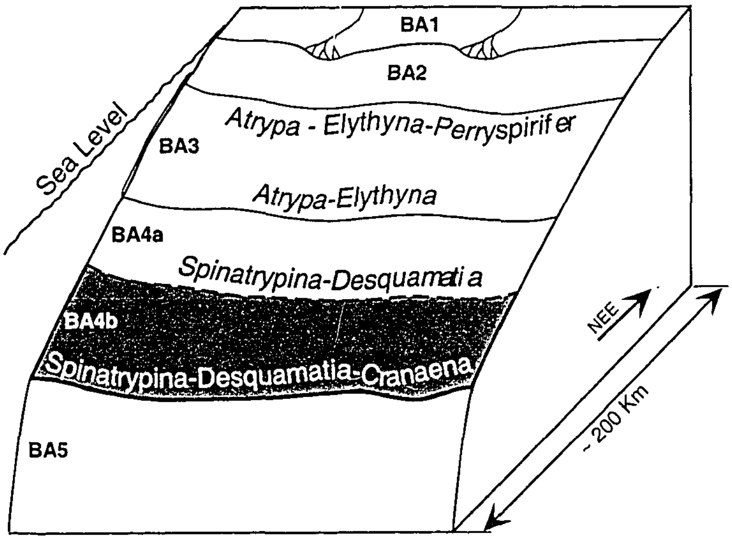

Figure 4.11--Positions of brachiopod communities in the Bird Fiord Formation of Arctic Canada relative to sea level and Benthic Assemblages as defined by Boucot (1975).

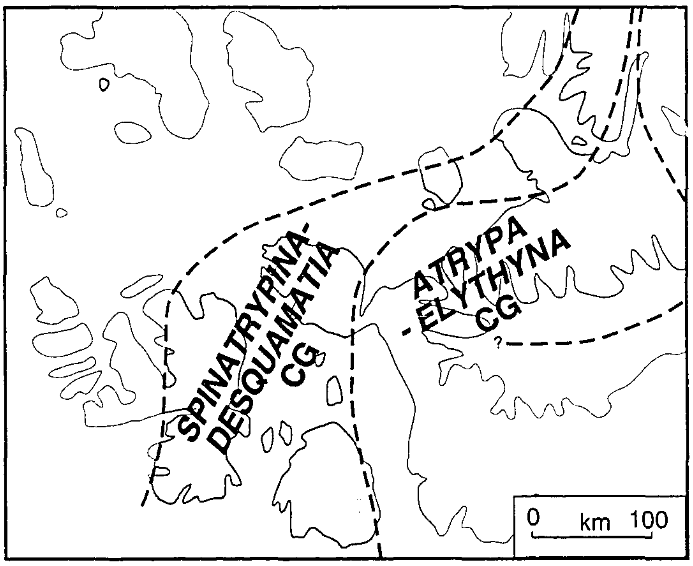

Figure 4.12--Distribution of the *Atrypa-Elythyna* and *Spinatrypina-Desquamatia* community groups relative to paleogeographic framework (from Fig. 6).

The *Atrypa-Elythyna-Perryspirifer* Community in the Bird Fiord Formation is similar to the Early Devonian *Atrypa-Schizophoria-Perryspirifer* Community from southwest Ellesmere Island, as defined by Jones and Smith (1985). *Atrypa* dominates both, *Perryspirifer scheii* is common to both, and *Schizophoria, Nucleospira,* and *Warrenella* are present in both. The two communities differ because the *Atrypa-Schizophoria-Perryspirifer* Community lacks *Elythyna, Spinulicosta, Cupularostrum, Hypothyridina,* and *Borealistrophia.* Conversely, *Cymostrophia, Carinagypa, Cortezorthis,* and *Parapholidostrophia* are present in the *Atrypa-Schizophoria-Perryspirifer* Community, but absent from the *Atrypa-Elythyna-Perryspirifer* Community. The similarities between these two communities may indicate that the Middle Devonian *Atrypa-Elythyna-Perryspirifer* Community may have replaced the Early Devonian *Atrypa-Schizophoria-Perryspirifer* Community. This suggestion is realistic given that both communities had similar geographic and environmental constraints. The *Atrypa-Schizophoria-Perryspirifer* Community can therefore be assigned to *Atrypa-Elythyna* Community Group.

Communities belonging to Benthic Assemblage 1 or 2 have not been recognized among the brachiopod collections from the Bird Fiord Formation. The absence of such communities may reflect the fact that they (1) were not recognized, (2) are not present in the Bird Fiord Formation but may be present in time-equivalent formations that were not examined in this study, or (3) were in strata that are not exposed or have been removed by erosion.

The brachiopod communities found in the Middle Devonian strata of Arctic Canada are taxonomically different from Middle Devonian communities found in New York (Feldman 1980; Brower et al. 1988; Brower and Nye 1991; McCollum 1991), Nevada (Johnson and Flory 1972; Johnson 1990), northern California (Savage and Boucot 1978) and South China (Wang et al. 1987). Biogeographically, the Middle Devonian fauna from New York belongs to the Eastern Americas Realm, whereas the Arctic Canada fauna falls into the Old World Realm (Johnson and Boucot 1973; Boucot 1988). The lack of similarity between the brachiopod faunas of Arctic Canada and other areas is perhaps not surprising given that some elements of the Arctic brachiopod fauna are endemic (cf. Brice 1982; Li and Jones 2002, *in press*). The endemism of these genera/species probably explains, at least in part, why the brachiopod communities are not comparable to those found in Nevada, Northern California, and South China even though they were all part of the Old World Realm during the Middle Devonian (Wang et al. 1987; Boucot 1988; Johnson 1990).

The distribution of the brachiopod communities in the Bird Fiord Formation of Arctic Canada was primarily determined by ecological controls that were related to water depth (Figs. 4.11, 4.12). This is the fundamental reason for the differences between the brachiopod faunas found in the Ellesmere Island – North Kent Island and the Grinnell Peninsula – Bathurst Island regions. Clearly, this ecological control will have to be factored into any biostratigraphic zonation scheme that is based on the brachiopods. Furthermore, biogeographic comparisons between Arctic Canada and other parts of the world must be based on comparisons of faunas from similar water depth. Such comparisons, for example, will be invalid if they are based on comparison of a brachiopod community that belonged to Benthic Assemblage 1-2 with a brachiopod community that belonged to BA3-4.

Conclusions

The analysis of the brachiopod faunas from the Bird Fiord Formation has demonstrated the following points:

- Two community groups and four brachiopod communities are present in the fauna,

- The *Atrypa-Elythyna-Perryspirifer* and *Atrypa-Elythyna* communities, which belong to Benthic Assemblage 3, probably lived in a shallow, proximal shelf environment,
- The *Atrypa-Elythyna-Perryspirifer* Community lived in shallower water than the *Atrypa-Elythyna* Community,
- The *Spinatrypina-Desquamatia* and *Spinatrypina-Desquamatia-Cranaena* communities, which belong to Benthic Assemblage 4, probably lived in a deeper, distal shelf environment,
- The *Spinatrypina-Desquamatia* Community lived in shallower water than the *Spinatrypina-Desquamatia-Cranaena* Community,
- The *Atrypa-Elythyna-Perryspirifer* Community may have developed from the Early Devonian *Atrypa-Schizophoria-Perryspirifer* Community of Jones and Smith (1985) from southwest Ellesmere Island.
- The distribution of the brachiopod communities appears to have been primarily related to water depth or factors that were controlled by water depth.

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Chapter 5

Eifelian (Mid-Devonian) Brachiopod Biogeography: A Quantitative Assessment*

1. Introduction

Biogeographically, the Devonian was a unique period because the high provincialism that was established during the Early Devonian was replaced by a very cosmopolitan biota during the Late Devonian (Boucot, 1988). Numerous worldwide and regional studies of Devonian biotas (e.g. Boucot et al., 1967, 1969; Johnson, 1971, 1979; Johnson and Boucot, 1973; Boucot, 1975; Oliver, 1976; Oliver and Pedder, 1979; Savage et al., 1979; Koch, 1981; Wang et al., 1984; Wang and Rong, 1986; Boucot, 1988; Blodgett et al., 1990; Zhao in Yin, 1994; Koch and Day, 1996; Talent et al., 2000) led to the qualitatively defined Old World, Eastern Americas (=Appalachian), and Malvinokaffric Realms. The Old World Realm consists of Western and Arctic America, Europe, Asia, Australia, and North Africa whereas the Eastern Americas Realm encompasses Eastern North America and northern South America, and the Malvinokaffric Realm includes southern South America, southern Africa, and Antarctica (Boucot et al., 1967, 1969; Johnson, 1971, 1979; Johnson and Boucot, 1973; Boucot, 1975; 1988; Oliver and Pedder, 1979; Savage et al., 1979; Koch, 1981; Blodgett et al., 1990). The qualitative studies also suggested that the Old World Realm existed throughout much of the Devonian, whereas the Malvinokaffric Realm disappeared near the Eifelian-Givetian boundary and the Eastern Americas Realm vanished during late (but not the latest) Givetian (see Boucot, 1988).

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The worldwide Devonian biogeographic divisions have been established largely through qualitative analyses that rely entirely on subjective comparisons of biotas from different regions of the world. This study re-assesses the Eifelian biogeographic framework by using three different quantitative methods to define the realms, subrealms, and regions. The database (Appendix II) incorporated newly acquired data from Arctic Canada (Li and Jones, 2002, in press) with published data from many other parts of the world. Specifically, this paper (1) tests the validity of the Eifelian biogeographic framework, (2) delineates the faunal subrealms and regions in the Old World Realm, and (3) assesses the timing of and cause for the disappearance of the Eastern Americas Realm in eastern North America by comparing the biogeographic patterns established during the Emsian and Eifelian.

2. Data

A presence/absence database of 309 Eifelian brachiopod genera from 14 regions is the database for this study (Appendix II). The regions examined are Arctic Canada (27 genera), Western Canada (33 genera), Nevada (38 genera), Michigan Basin (56 genera), Appalachian Basin (68 genera), Bohemia (48 genera), Ural (73 genera), Germany-Belgium-North France (52 genera), northwest Spain (40 genera), South China (84 genera), Burma (31 genera), Inner Mongolia (45 genera), Algerian Sahara (31 genera), and South Africa (30 genera). Some other biogeographically important regions such as Moroco, Central and South America, Antarctica, and Australia have not been included because there are no Eifelian brachiopods recorded or the documented record is sparse. The record of Eifelian brachiopods from Australia, Victoria, Tasmania, New Zealand, and Antarctica, for example, is poor (Talent et al., 2000) because of the erosion or non-deposition of Eifelian strata during the Taberabberan Event (Blodgett et al., 1990; Talent et al., 2000). At the end of the Early Devonian, a major orogeny took place in the Middle or Middle to Late Devonian that terminated marine deposition in Australia, Victoria, Tasmania, New Zealand, and Antarctica (Brown et al., 1982). The Eifelian Australian brachiopods, known only from the Sedgeford Formation at Alpha, central Queensland, include *Desquamatia, Atryparia, Cydimia, Howellella, Howittia,* and *Cyrtina* (Henderson et al., 1995). The lack of comprehensive data for Eifelian brachiopods from Australia precludes quantitative comparison with other regions.

In compiling the database, we examined available published literatures on Eifelian brachiopods and updated the age determinations of those records where possible. The taxonomy was also updated to reflect the latest developments in Devonian brachiopod taxonomy. Nevertheless, some synonyms may still exist due to the fact that it is impossible to completely re-evaluate all 309 genera based solely on published descriptions and/or figures. In some cases, even the original identifications were questioned. Under such circumstances, the original description/illustrations were checked and compared to the same taxa from other regions to determine if the particular taxon should be included or discarded from the database. To avoid any potential bias of the data, we adopted the quantitative methods that are the least affected by sampling. We agree with Shen and Shi's (2000, p. 300) opinion that the fossil records of species are too imperfect to use for large-scale paleobiogeographic analysis, that they are more sensitive to local environments, and that family-level taxa are too broad to reveal detailed paleogeographic structure. Thus, generic level data were used in the quantitative analyses.

The paleobiogeographic analysis should also take into account the paleoecology of the organism under study. Ideally, only those taxa that had similar distributions in terms of Benthic Assemblage (BA) (cf. Boucot, 1975) should be included in the database. Otherwise, comparisons between regions with taxa adapted to different BA may skew the results. If, for example, a region characterized by BA1 taxa is compared to another region with BA5 taxa, the difference between them represents ecological factors rather than biogeographic differences. The problem is further compounded by the fact that paleoecology information is not given for many regions. To minimize the possible effect of local ecology on biogeographic analysis, as many localities as possible in each region have been sampled in order to embrace all brachiopod communities from various substrates and water depths. This sampling strategy, proposed by Shi and Archbold (1993) and used by Shi and Archbold (1993), Yin (1994), and Shen and Shi (2000), is practical and effective.

The number of genera found in each region ranges from 27 to 84 with a standard deviation of 17.8. The difference in these numbers may represent the biotic diversity of the region or may be affected by factors such as area of, and/or thickness of the Eifelian strata and the completeness of the collecting/taxonomic study. Most regions considered in this paper have a long history of investigation and are therefore relatively well known. Although we consider the fossil records from these regions to be reasonably complete and therefore acceptable, it is still possible that further collecting will yield new taxa. Thus, only those statistical approaches that are least affected by sampling and sample size were used. The integrity of the database was tested by randomly deleting some of the presence/absence data and re-running the analyses. This had little or no affect on the results and thereby further validated the reliability of the database.

3. Methodology

Three methods of quantitative analysis were employed: 1) similarity analysis, using a similarity index/coefficient such as the Jaccard and Dice indices; 2) probabilistic analysis, which is an alternative statistical method to similarity measures (Raup and Crick, 1979); and 3) parsimony analysis of endemicity (PAE) as developed by Rosen and Smith (1988) and Rosen (1988, 1992). Cluster analysis was used with methods 1 and 2 to group the regions based on the similarity/probabilistic indices using the software PAST (version 0.78) (Hammer et al., 2001). PAUP 3.1 (Swofford, 1993) was used to construct the cladograms of the regions in PAE analysis.

3.1. Similarity method

Various binary similarity indices have been adopted for calculating the biotic similarity between regions and degree of association between taxa. Nevertheless, Cheetham and Hazel (1969), Shi (1993a, b), and Rong et al. (1995) showed that the Jaccard and Dice indices are consistent indices that are the least susceptible to sampling biases or inefficiencies. Accordingly, these two indices were used in this study.

3.2. Probabilistic method

Many similarity indices emphasize the joint presence of taxa in two faunas. These indices, however, have not been tied to clearly defined null hypotheses. Thus, it is impossible to tell whether the similarity between two faunas is reliable at the 95% level of confidence (Raup and Crick, 1979). Assuming that the taxa were distributed randomly, Raup and Crick (1979), proposed a measure of similarity that compared the observed number of taxa common to two faunas (C_{obs}) against the probability distribution of the expected number of common taxa (C_{exp}). Thus, the probabilistic index is the probability that C_{obs} will be less than or equal to C_{exp} (Raup and Crick, 1979). This index uses a randomization procedure, comparing the observed number of taxa common to both faunas with the distribution of co-occurrence from many random replications. Raup and Crick (1979) showed that this index allows a rigorous assessment of statistical confidence and is more effective than similarity indices. This index has been used in the study of Permian brachiopod biogeography (Hanger, 1996). The implementation of Raup and Crick's probabilistic index in the program PAST (Hammer et al., 2001) (up to 200 random replications) made the current analysis possible.

3.3. Parsimony analysis of endemicity (PAE)

PAE, an alternative method of analyzing taxonomic distributions, was devised to overcome some of the difficulties associated with the similarity method (Rosen, 1988; 1992; Rosen and Smith, 1988). PAE uses the same basic analytical method of cladistics (the most parsimonious distribution of shared characters of taxa), but the 'taxa' in PAE are the regions, and the 'characters' the absence or presence of the taxa in particular regions. Like multivariate analysis, the method proceeds by organizing the presence/absence data matrix for a set of sample regions and a particular group of organism. This assumes that the presence of a taxon is 'derived' and absence is 'primitive', and that the 'ancestral' area is one in which none of the sample set of taxa exist (Rosen, 1988, 1992; Rosen and Smith, 1988). Therefore, in the data matrix each taxon present in a region is 1 and the absence is 0. As in cladistics, the most widespread 'characters' (i.e. cosmopolitan elements) are the least informative, and the least widespread 'characters' (i.e. endemic elements) are the most informative. In PAE, therefore, the cosmopolitan presences are treated like symplesiomorphies and the endemic presences like synapomorphies (Rosen and Smith, 1988; Rosen, 1992). The data matrix (when in NEXUS format) then can be analysed using PAUP 3.1 (Swofford, 1993) to construct cladogram(s) showing the relationship among these regions. Lundberg rooting in PAUP is recommended to root the cladograms (Rosen, 1988; 1992; Rosen and Smith, 1988).

Smith (1992) compared the biogeographic results from PAE and similarity analysis for the same Cenomanian echinoid data set. He found a surprisingly good correspondence between the similarity analysis and PAE. Hanger (1996) showed that the results of PAE analysis of Permian brachiopod palaeobiogeography of South America are broadly congruent with those based on similarity and probabilistic indices. It seems that with good data sets (i.e. large number of taxa in relation to the number of regions, and the numbers of taxa from different regions do not differ significantly), PAE and similarity and probabilistic methods should give similar results.

4. Eifelian Biogeography

4.1. Framework

The hierarchy of the biogeographic units in the following discussion follows the scheme of Realm-Subrealm-region-Province-Subprovince recommended by Westermann (2000a, b), although the 'region' is suggested for informal use (Westermann, 2000a,b).

The dendrograms derived from the UPGMA (unweighted pair-group method using arithmetic averaging) cluster analysis of both the Dice index (Fig. 5.1A) and Jaccard index (Fig. 5.1B) yielded identical clusters. Hierarchically, South Africa is distinguished as a separate cluster (cluster I) from all the other regions (cluster II). In cluster II, the following second order clusters (IIA and IIB) can be further recognized at similarity level of ~0.2 of Dice index and ~0.1 of Jaccard index: cluster IIA, includes Inner Mongolia, Burma, Northwest Spain, Germany-Belgium-Northern France, Algeria, Bohemia, and the Uralian area; whereas cluster IIB encompasses South China, Michigan Basin, the Appalachian Basin, Western Canada, Nevada, and Arctic Canada (Fig. 5.1). The same patterns of first order clusters and second order clusters are also evident in the dendrograms derived from the UPGMA cluster analysis based on the Raup and Crick Index (Fig. 5.2). There is a close affinity, as revealed by similarity and probabilistic indices, between Germany-Belgium-North France and Algeria, Michigan and Appalachian basins, and among Nevada and Arctic and Western Canada (Figs. 5.1, 5.2). Thus, third order clusters among IIA and IIB are divided into the following third order clusters (Fig. 5.1):

- IIA1-Inner Mongolia,
- IIA2-Burma and Northwest Spain,

- IIA3-Germany-Belgium-Northern France and Algeria,
- IIA4-Bohemia, IIA5-Ural;
- IIB1-South China,
- IIB2-Michigan and Appalachian Basins, and
- IIB3-Western-Canada-Nevada-Arctic Canada.

The similarity analysis indicates that Burma is akin to Northwest Spain whereas the probabilistic analysis (Fig. 5.2) indicates that it is closely related to Inner Mongolia. The reason for this discrepancy is not known.

The single cladogram from the PAE based on Heuristic search and Lundberg rooting has a tree length of 480 and a high consistency index (CI) of 0.65 (Fig. 5.3). The tree, which is fairly congruent with the results from cluster analyses (Figs. 5.1, 5. 2), shows that: Arctic and Western Canada, Michigan and Appalachian basins, Nevada, and South China (corresponding to cluster IIB in Figs. 5.1, 5.2) form a sister group with Inner Mongolia, Ural, Bohemia, Northwest Spain, Burma, Germany-Belgium-Northern France, and Algeria (corresponding to cluster IIA in Figs. 5.1 and 5.2). All of these regions (corresponding to cluster II in Figs. 5.1 and 5.2) form a sister group with South Africa (cluster I of Figs. 5.1, 5. 2).

From a biogeographic perspective, the first order clusters can be regarded as Realms, the second order clusters as Subrealms, and the third order clusters as Regions. South Africa, therefore, corresponds to the Malvinokaffric Realm as recognized by previous qualitative analysis. Interestingly, the Michigan and Appalachian basins, previously included in the Eastern Americas Realm (e.g. Oliver and Pedder, 1979; Koch, 1981) are

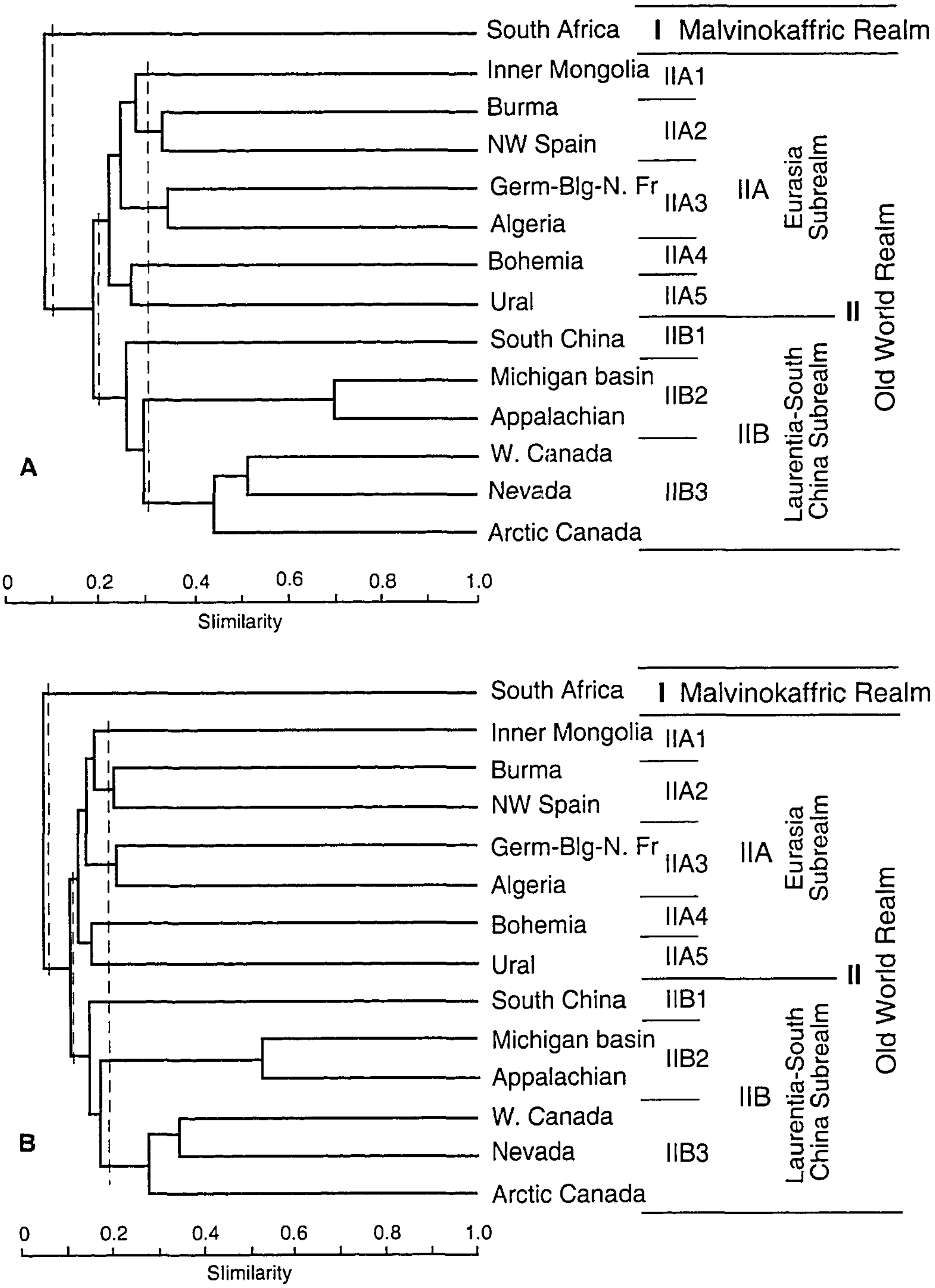

Figure 5.1--Dendrograms of Eifelian brachiopods derived from UPGMA cluster analysis based on Dice (A) and Jaccard (B) indexes.

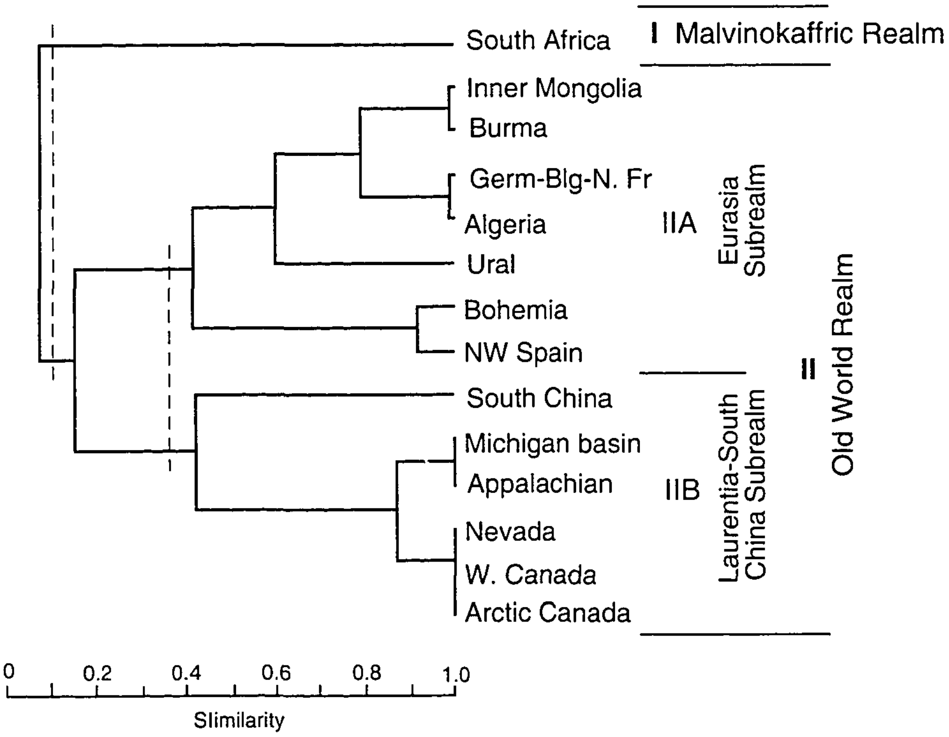

Figure 5.2--Dendrograms of Eifelian brachiopods derived from UPGMA cluster analysis based on Raup and Crick probabilistic index.

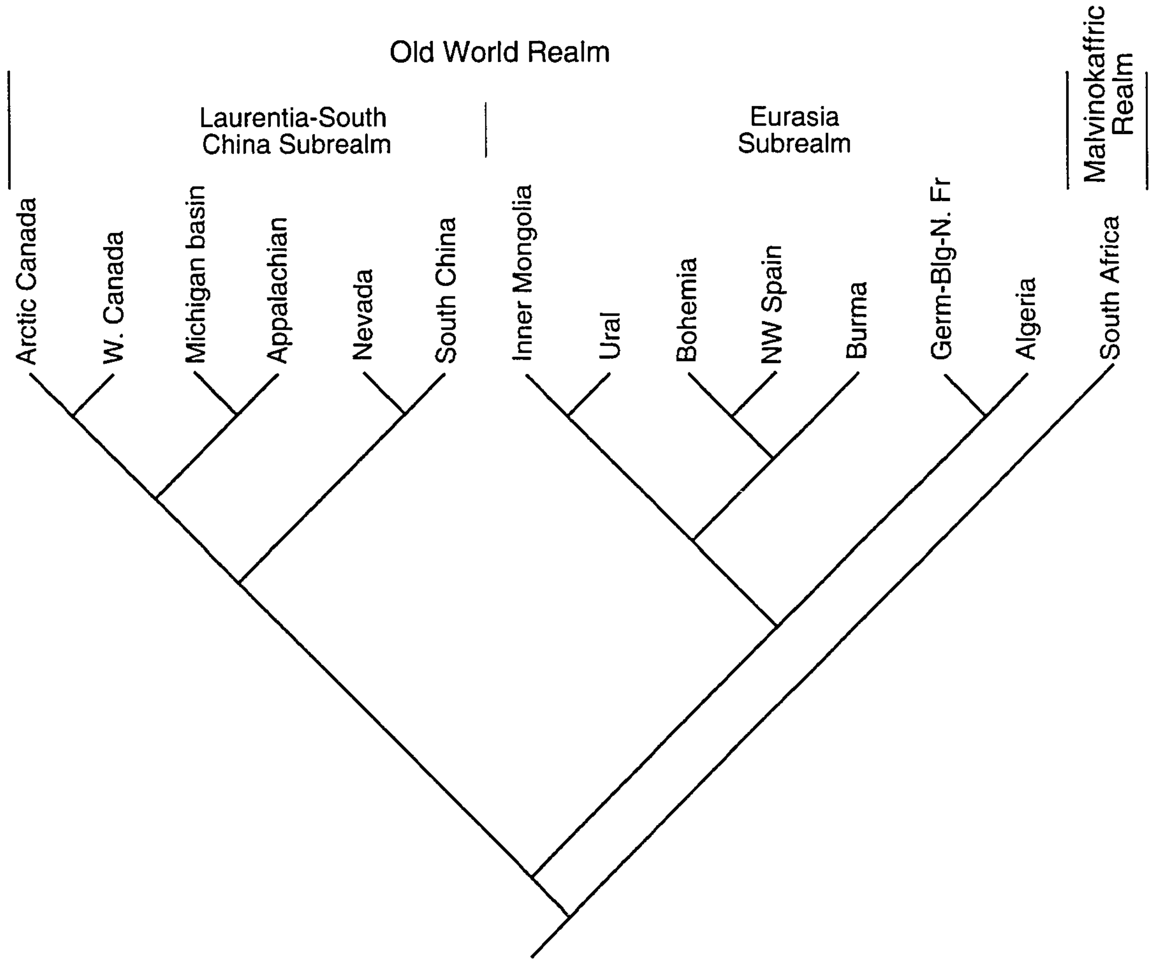

Figure 5.3--Single cladogram derived from parsimony analysis of endemicity of Eifelian brachiopods using PAUP 3.1. Treelength=480, CI=0.65.

clustered into the same first order cluster as Western and Arctic Canada, Nevada, South China and other regions (i.e. in cluster II) (Figs. 5.1, 5.2, 5.3) that, based on qualitative analysis, belong to the Old World Realm. The difference between the Michigan-Appalachian basins and other regions of the Old World Realm is not significant enough to separate them into different realms. The difference between the Michigan-Appalachian basins and Western-Arctic Canada, for example, is even less than that between Bohemia and the Uralian area (Figs. 5.1, 5.2). Thus, it seems inadvisable to exclude these basins from the Old World Realm. These two basins together with other regions in cluster II (Figs. 5.1, 5.2, 5.3) are, therefore, regarded as the Old World Realm. In the Old World Realm, the regions represented by the second order clusters IIA and IIB are herein defined as the Eurasia Subrealm and Laurentia-South China Subrealm, respectively. The Eurasia Subrealm includes Europe and most parts of Asia, whereas the Laurentia-South China Subrealm encompasses North America and South China. In the Eurasia Subrealm, the third order clusters IIA1-5 and IIB1-3 are equated to regions (Fig. 5.1).

4.2. Comments

The results from the three different biogeographic quantitative analyses produced the same conclusions. First, South Africa was a distinct region during the Eifelian and that the Malvinokaffric Realm status, originally based on qualitative analysis, is confirmed. Second, the Michigan and Appalachian basins, previously recognized as the Eastern Americas Realm, should be included in the Old World Realm. Third, the Old World Realm is divided into the Eurasia and Laurentia-South China Subrealms that can be further divided into regions.

No subrealm level biogeographic units were recognized in the qualitative analysis by Boucot et al. (1967, 1969), Johnson and Boucot (1973), and Boucot (1988). The results from three different quantitative methods consistently show the same pattern of two groups in the Old World Realm (Figs. 5.1, 5.2, 5.3) that are herein named the Eurasia and Laurentia-South China subrealms. Their development may be related to the plate tectonics. The Caledonian (=Scandian) Orogeny during Late Silurian led to closure of the northern Iapetus between Laurentia and Baltica/Avalonia; however, the southern part of the Iapetus remained open until the late Early Devonian by the Acadian Orogeny (see Scotese and McKerrow, 1990). The faunal interchange between Laurentia and Baltic/Avalonia, therefore, may have still existed via the southern part of the Iapetus before late Early Devonian. This may explain why the Eurasia and Laurentia-South China Subrealms are not recognizable during theEmsian. After the Acadian Orogeny, the high mountain belt between Laurentia and Baltica/Avalonia served as a barrier that separated the benthos and resulted in the development of the Eurasia and Laurentia-South China Subrealms during the Eifelian. South China was a separate block during the Devonian and its faunal affinity to Laurentia might have been caused by oceanic current circulation.

The division of the Old World Realm into regions, as reflected by the third order clusters (Figs. 5.1, 5.2), is broadly consistent with the results from qualitative analysis (Boucot, 1988, p. 212, p. 218-219). The Uralian, South China, and Cordilleran regions (represented by Nevada, Arctic and Western Canada in Figs. 5.1, 5.2) recognized by qualitative approaches are also recognized by the quantitative methods used herein. Conversely, the Rhenish-Bohemia region defined by the qualitative approach may, on the basis of quantitative analysis, be split into the Rhenish and Bohemia regions. Algeria, North Africa may belong to Rhenish region. Based on the quantitative results, Inner Mongolia may be regarded as a region. Northwest Spain, previously assigned to the Rhenish-Bohemian region (Boucot et al., 1967), showed close affinity with Burma in similarity analysis (Fig. 5.1) but a close relation to Bohemia in probabilistic analysis (Fig 5.2). The biogeographic assignment of Burma and NW Spain needs further study.

The previous definition of worldwide Devonian biogeography framework was based mainly on the distribution of certain critical genera (e.g. Boucot et al., 1967, p. 1239). The qualitative recognition of the formal Eastern Americas Realm during the Eifelian, for example, was mainly based on the endemic taxa such as *Coelospira, Levenea, Protoleptostrophia, 'Leptocoelia', Longispina, Megakozlowskiella, Elytha, Pentagonia,* and *Centronella* (Boucot et al., 1967, p. 1249). The endemic status of these genera is still valid (Appendix II). As noted by Kauffman (1973), however, the percentage of the endemic genera in the fauna should also be taken into account in any definition of any biogeographic unit. Every region may develop some endemic elements due to ecological and/or biogeographical factors; thus, the degree of endemism is more critical than the presence of endemism for recognizing different biogeographic units. The percentage of endemic genera from the regions studied decreases from South Africa (63.3%), to South China (42.9%), Michigan-Appalachian basins (40.2%), NW Spain (35%), Ural (31.5%), Bohemia (29.2%), Nevada-Arctic and Western Canada (27.6%), Inner Mongolia (24.4%), Algeria (22.6%), Burma (16.1%), Germany-Belgium-Northern France (13.5%) (Appendix II). The highest level of endemism in South Africa makes it a distinct Realm. The fact that the endemism level of Michigan-Appalachian basins is less than that of South China further supports the notion that they should not be segregated from the Old World Realm.

5. Disappearance of Eastern Americas Realm in eastern North America

5.1. Timing

To assess the timing of the disappearance of the Eastern Americas Realm in eastern North America, Emsian brachiopod data compiled by Wang and Rong (1986) were analysed using the same quantitative methods. A total of 357 Emsian brachiopod genera were recorded from the Appalachian Basin (92 genera), Nevada (76 genera), Ural (76 genera), Altai-Sayan (94 genera), Western Canada (86 genera), South China (83 genera), Arctic Canada (67 genera), Central Europe-North Africa (168 genera), and Eastern Australia (69 genera) by Wang and Rong (1986). The brachiopod data for Eastern Inner Mongolia-Less Khingan (Wang and Rong, 1986) were not included in the analysis because the area has not been extensively studied. This may also explain why Wang and Rong (1986) found it difficult to account for the faunal affinity of this region to other regions.

The dendrograms derived from Dice and Jaccard indices, which are identical (Fig. 5.4), show the Appalachian Basin as a distinct cluster and the other regions as another cluster. Biogeographically, such patterns indicate a division of Eastern Americas Realm (represented by Appalachian basin) and Old World Realm (represented by other regions) during the Emsian.

The dendrogram derived from the Raup and Crick Index is different from those based on Dice and Jaccard indices because Central Europe forms a distinct cluster (Fig. 5.5). This may be caused by its much higher number of genera (168) and the large variation of the genera numbers among the regions. The standard deviation of the genera numbers in Emsian regions (STDEV=30.7) is much higher than that of Eifelian regions (STDEV=17.4).

Two trees were found by Heuristic search in PAUP 3.1 when running PAE analysis; both have tree lengths of 518 and a consistency index of 0.68. According to Rosen (1992), PAE and similarity methods should give similar dendrograms; therefore, we adopted the one that is consistent with the cluster analysis (Fig. 5.6). The tree shows the Appalachian Basin as a distinct unit, confirming its status as Eastern Americas Realm

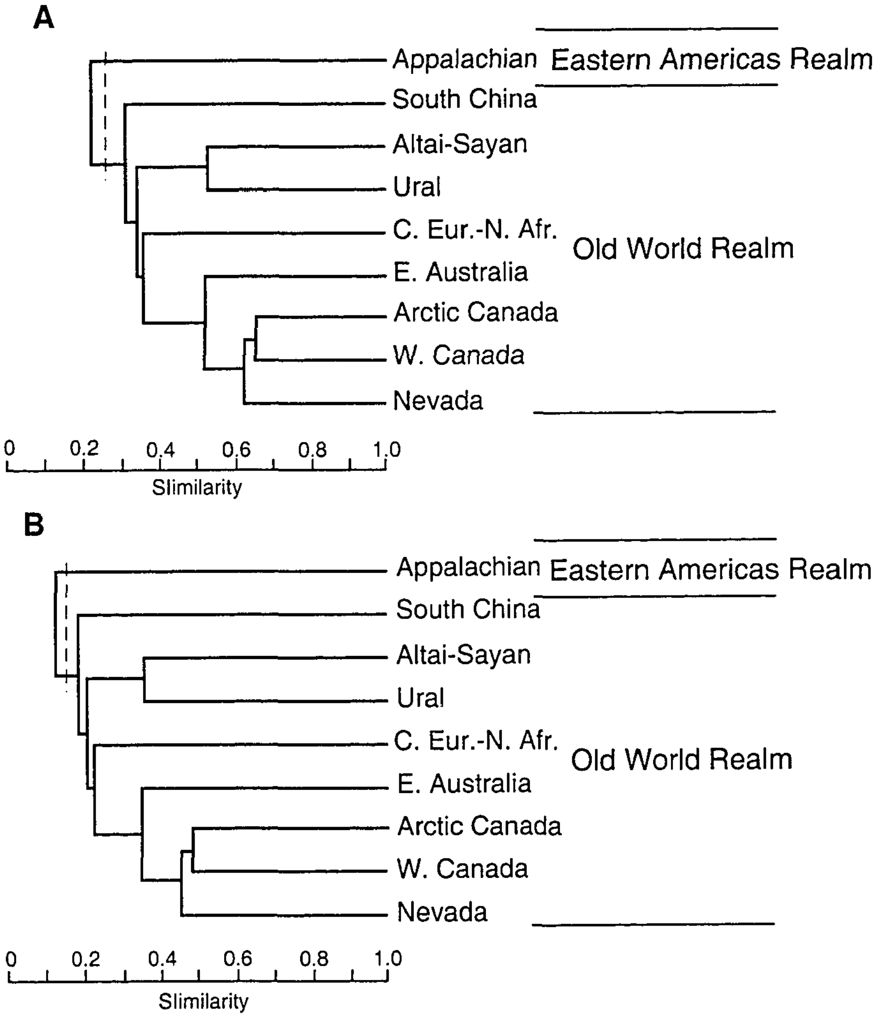

Figure 5.4--Dendrograms of Emsian brachiopods derived from UPGMA cluster analysis based on Dice (A) and Jaccard (B) indexes. Data from Wang and Rong (1986 and the references therein).

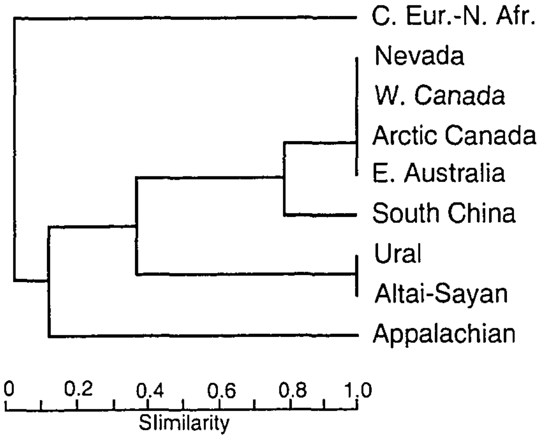

Figure 5.5--Dendrograms of Emsian brachiopods derived from UPGMA cluster analysis based on Raup and Crick probabilistic index. Data from Wang and Rong (1986, and the references therein).

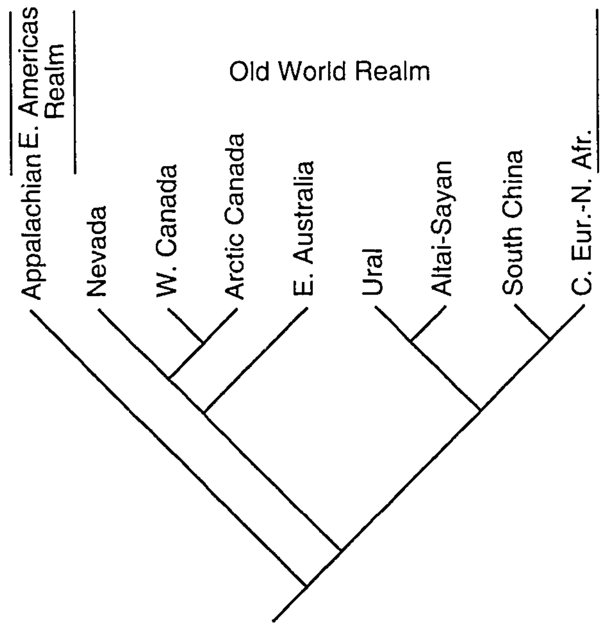

Figure 5.6--One of the two cladograms derived from parsimony analysis of endemicity of Emsian brachiopods using PAUP 3.1. Treelength=518, CI=0.68. Data from Wang and Rong (1986, and the references therein).

during the Emsian. The results from cluster analysis based on Dice and Jaccard indices and PAE show that the Eastern Americas Realm, as represented by the Appalachian Basin, is readily identifiable during the Emsian. The fact that the Eastern Americas Realm is recognizable during Emsian but unrecognizable during Eifelian indicates that it may have disappeared during the late Emsian to early Eifelian in eastern North America.

The dendrograms for the Emsian regions did not show two groups in the Old World realm (Figs. 5.4, 5.5). Thus, no subrealms can be recognized during this time period. The open southern part of the Iapetus during Emsian made the faunal interchange between Laurentia and Baltic/Avalonia possible, such communication may have prevented the development of different subrealms.

5.2. Possible cause for the disappearance

The disappearance of the Eastern Americas Realm in eastern America during the late Emsian to early Eifelian may have begun with the invasion of elements of the Old World Realm into the Eastern Americas Realm. The mixture of biogeographic realm affinities of the Old World Realm and Eastern Americas Realm during the Eifelian was recognized in the Michigan Basin on the basis of gastropods (Blodgett et al., 1990, p. 280). A distinct brachiopod fauna, composed of a mixture of Cordilleran Old World Realm endemic genera, cosmopolitan and formerly endemic genera of the Eastern Americas Realm was recognized in central and eastern North America during the late Eifelian (Koch and Day, 1996). Koch and Day (1996) pointed out that such a mixture was caused by the sea level rise associated with the Devonian Transgression-Regression (T-R) Cycle 1e of Johnson et al. (1985) and Johnson and Klapper (1992), which was sufficient to breach barriers of benthic migrations and resulted in a breakdown of Middle Devonian brachiopod provincialism. The major sea level rise started from late Emsian to early Eifelian (T-R Cycle Ic), followed by a transgression during middle and late Eifelian (T-R Cycle Id), and a further onlap and deepening associated with T-R Cycle Ie during late

Eifelian (Johnson et al., 1985; Johnson and Sandberg, 1988; Johnson and Klapper, 1992). Thus, it is reasonable to assume that the biogeographic pattern in North America may have been affected by the late Emsian to early Eifelian transgression (T-R Cycle Ic). The timing of the T-R Cycle Ic is consistent with the timing of the disappearance of the Eastern Americas Realm in eastern North America based on our quantitative analysis; therefore, it may have been this transgression that destroyed the provincialism at realm level during late Emsian to early Eifelian.

5. Summary and conclusions

1) Three quantitative methods, including similarity analysis, probabilistic analysis, and parsimony analysis of endemicity (PAE) were adopted to analyse the 309 Eifelian brachiopod genera from Arctic Canada, Western Canada, Nevada, Michigan basin, Appalachian basin, Bohemia, Ural, Burma, South China, Inner Mongolia, Algerian Sahara, Germany-Belgium-Northern France, northwestern Spain, and South Africa. The results from different methods are identical.
2) The Old World Realm and Malvinokaffric Realm can be readily recognized on the basis of the results from the three methods. During the Eifelian, the Michigan and Appalachian basins belong to the Old World Realm.
3) In the Old World Realm, the Eurasia and Laurentia-South China Subrealms can be defined by cluster analysis and PAE. The mountain belts between Laurentia and Baltic/Avalonia formed by Caledonian Orogeny and Acadian Orogeny may have served as barrier and led to the development of these subrealms during the Eifelian.
4) In the Old World Realm, the Uralian, South China, and Cordilleran Regions recognized by qualitative approach are also recognized by the quantitative methods, whereas the Rhenish-Bohemia region distinguished by qualitative approach may be split into Rhenish and Bohemia regions based on cluster analysis. Algeria, North

Africa may belong to Rhenish region. Inner Mongolia may be regarded as a region based on the quantitative results.

5) The fact that the Eastern Americas Realm is recognizable during the Emsian but not during the Eifelian in the eastern North America may indicate that this Realm began to disappear during late Emsian to early Eifelian starting from eastern North America.
6) The timing of the disappearance of the Eastern Americas Realm in eastern North America is consistent with the late Emsian to early Eifelian (T-R Cycles Ic) transgression in North America. The sea level rises represented by T-R Cycles Ic, Id, Ie may have overcome the barrier separating the western (Old World Realm) and eastern America, and eventually caused the demise of the Eastern Americas Realm.

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Chapter 6.

Conclusions

Brachiopods are common in the upper Lower to Middle Devonian Bird Fiord Formation that is a carbonate-clastic transition succession found in Arctic Canada. A collection of 47,026 brachiopods, which came from 140 collections made at 34 locations throughout the outcrop belt of the Bird Fiord Formation from Ellesmere Island to Bathurst Island, contains 22 species of brachiopods that belong to 21 genera. This biota includes three new genera: *Borealistrophia, Arcticastrophia,* and *Grinnellathyris*, and nine new species: *Borealistrophia rongi, Arcticastrophia costellata, Gypidula mega*, *Grinnellathyris alvarezis, Spinatrypa* (*Isospinatrypa*) *parva*, *Desquamatia* (*Independatrypa*) *fortis*, *Nucleospira stelcki, Warrenella grinnellensis*, and *Cranaena briceae*. Among the new genera, the strophomenid *Borealistrophia,* which is found in the Baad Fiord, Blubber Point, and Norwegian members on Bathurst, Devon, North Kent, and Ellesmere islands, is characterized by two pairs of straight side septa, prominent and thick socket ridges, a thick but short median septum, and a cordate ventral muscle field. The strophomenid *Arcticastrophia*, which is found in the Baad Fiord Member on Bathurst and Devon islands, is distinctive because of its stout transmuscle septa, its narrow and low medium septum, and elevated ventral muscle field. The athyridid *Grinnellathyris*, which is found in the Baad Fiord Member on Bathurst, North Kent, and Devon islands, is characterized by an imperforated cardinal plate and inverted U-shaped jugum. The similarities between *Grinnellathyris* and *Johnsonathyris* Savage, Eberlein, and Churkin, 1978, in terms of their shell size and internal structures, may indicate that the latter evolved from the former.

Cluster analysis, based on binary data, shows that the brachiopods belong to the *Atrypa-Elythyna* Community Group and the *Spinatrypina-Desquamatia* Community

Group. The former encompasses the *Atrypa-Elythyna* and *Atrypa-Elythyna-Perryspirifer* communities whereas the latter includes the *Spinatrypina-Desquamatia* and *Spinatrypina-Desquamatia-Cranaena* communities. The distribution of these communities was fundamentally controlled by water depth. Thus, the *Atrypa-Elythyna* Community Group, which belongs to Benthic Assemblage 3, lived in a shallow, near shore shelf environment. The *Spinatrypina-Desquamatia* Community Group, which belongs to Benthic Assemblage 4, lived in a deeper, distal shelf environment. Within the community groups, the *Atrypa-Elythyna-Perryspirifer* Community lived in shallower water than the *Atrypa-Elythyna* Community, and the *Spinatrypina-Desquamatia* Community lived in shallower water than the *Spinatrypina-Desquamatia-Cranaena* Community. The *Atrypa-Elythyna-Perryspirifer* Community may have evolved from the Early Devonian *Atrypa-Schizophoria-Perryspirifer* Community of Jones and Smith (1985) from Southwest Ellesmere Island.

Three quantitative approaches, including similarity analysis, probabilistic analysis, and parsimony analysis of endemicity (PAE), were used to analyse the presence/absence database of 310 Eifelian brachiopod genera from Arctic Canada, Western Canada, Nevada, Michigan basin, Appalachian basin, Bohemia, Ural, Burma, South China, Inner Mongolia, Algerian Sahara, Germany-Belgium-Northern France, Northwestern Spain, and South Africa. The results from different methods are congruent. On a regional scale, the quantitative results from similarity analysis, probabilistic analysis, and PAE analysis consistently show that the brachiopods from the Arctic Canada are closely related to those from Western Canada and Nevada, and that biogeographically they can be assigned to the Cordilleran Region of the Old Word Realm. On a worldwide scale, the Old World Realm and Malvinokaffric Realm can be readily recognized during Eifelian. Within the Old World Realm, the Eurasia and Laurentia-South China Subrealms are recognized based on the consistent pattern revealed by cluster analysis and PAE. The mountain belts between Laurentia and Baltic/Avalonia formed by Caledonian Orogeny and Acadian Orogeny may have served as barrier that led to the development of these subrealms during Eifelian. The Michigan and Appalachian basins (previously assigned to the Eastern Americas Realm), did not show enough difference when compared to other regions of North America, Eurasia, and North Africa of the Old World Realm, they, therefore, should not hold a different Realm status. The Michigan-Appalachian region in the Old World Realm and Laurentia-South China Subrealm is proposed for their biogeographic status during Eifelian. In the Old World Realm, the Uralian, South China, and Cordilleran regions recognized by qualitative approach are also recognized by quantitative methods. The Rhenish-Bohemia region distinguished by qualitative approach may be split into Rhenish and Bohemia regions based on quantitative results. The analysis of Emsian brachiopod data showed the existence of the Eastern Americas Realm during Emsian. The disappearance of the Eastern Americas Realm in eastern North America may have taken place during late Emsian or early Eifelian. The timing of the disappearance is consistent with the late Emsian to early Eifelian transgression (T-R Cycles Ic) in North America. The sea level rises represented by T-R Cycles Ic and following Id and Ie may have overcome the barrier separating the western (Old World Realm) and eastern America, and eventually caused the demise of the Eastern Americas Realm.

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Appendix 1. Data of brachiopods from Bird Fiord Formation for cluster analysis (references in Chapter 3).

T1=*Arcticastrophia costella* Li & Jones, 2002; T2=*Borealistrophia rongi* Li & Jones, 2002; T3=?*Parapholidostrophia* sp.; T4=*Spinulicosta* sp.; T5=*Schizophoria sulcata* Johnson & Perry, 1976; T6=*Gypidula mega* Li & Jones, *in press;* T7=*Ivdelinia grinnellensis* Brice, 1982; T8=*Cupularostrum repetitor* Johnson & Perry, 1976; T9=*Hypothyridina bifurcata* Brice, 1982; T10=*Atrypa* sp. B; T11=*Spinatrypa (Isospinatrypa) parva* Li & Jones, *in press*; T12=*Spinatrypina borealis* (Warren, 1944); T13=*Desquamatia (Independatrypa) fortis* Li & Jones, *in press*; T14=*Grinnellathyris alvarezis* Li & Jones, 2002; T15=*Nuclesospira lens* (Schnur, 1851); T16=*Nucleospira stelcki* Li & Jones, *in press*; T17=*Emanuella bisinuata* Brice, 1982; T18=*Elythyna sverdrupi* Brice, 1982; T19=*Perrysperifer scheii* (Meyer, 1913); T20=*Warrenella grinnellensis* Li & Jones, *in press*; T21=*Costacranaena marlenae* Johnson & Perry, 1976; T22=*Cranaena briceae* Li & Jones, *in press.*

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	Total
80SS-13					3						2		2							2			9
80SS-5				16	7							3								112			138
80V	1			14	58			54				476	317				4				15		939
80I-324m				2	10			11				22	15										60
80I-540m					2			6				2	1				200						211
80I-560m												1					160						161
80I-617m				3	206			1				11	17										238
80I-659m				31	303			479		5		279	602				120				23		1842
80I-674m				1	21			315		21		26					33				2		419
80I-678m					9			27		1		8	30				2				2		79
80I-775m								1							150		300						451
80I-782m								49					7				69						125
80I-819m				14	83			49									8				12		166
80X-85m					1							1	23		1					233			259
80X-89m				38									438							4			480
80X-102m				1		31							2	1	1								36
80X-117m													13							42			55
80X-129m								42					1										43
80X-228m								18				3											21
80X-418m					118							2	2										122
80VIII				1	7	3		128					77							30			246
80VIIIA				4	105							185	32	2			12				8	16	364
80VIIIB				4	3			1					63							8			79
80XI-0m	11	1		5								293	17		17					48		2	394
80XI-27m	1			6	7	1		11				411	83	1		2				10		1	534
80XI-56m				11	5			7				3	21							8			55

80XI-211m				1	38			5				25								3	1		73
80XII-99m					30			4145				3	3				15				1		4197
80XII-118m				1	11			1				16	80							1	1		111
80XII-160m					54			84				141	69				8				6	2	364
80XII-164m					50			99				374	215								23	9	770
80XII-205m				1	68			364				342	107				1				1		884
80XII-265m				2	56			653		56			372				15				38	17	1209
80SS-XYZ				1	54					5											6		66
80SS-OPQ				3	87			65				255	99				9				19	5	542
80SS-RST					85			436				428	135		1		2						1087
80XIII-0m					32			8				23	38										101
80XIII-87m					69			66				471	457										1063
80XIII-89m				4	158			144				602	206				1				13	7	1135
80II-F1				33	158			135				502	143				27				14	4	1016
81A-71m				8	10	1		950	1			15	8	2	8			1	1		28		1033
81A-73.5m				1	15								1						1	11			29
81A-138m	10	3		132		2						629	294				3				25	190	1288
81A-159m	2	1		56	17			1				125	233							1	6	5	447
81A-190m				4				3				331	525								2	8	873
81A-224m	8	1		19	60			7				293	115		12						7	17	539
81A-256m				19	34	1						1	155										210
81A-281m		1		33	69								710				1						814
81A-302m				32	51							5	317										405
81C1		6		39	148								896	12							8		1109
81AX-103m					6							70	13	26			17						132
81B-27m		11			131				100	414		496				1		6	1	6			1166
81B-29m				9	46		79			51		10							22	33			250
81B-170m	21			94	60							189	94			2	1				6	19	486
81B-175m	7			117	33							199	49	2		1					4	11	423

81B-185m		1		10	9								211	1			4						236
81B-190m		3		12	29							1	314	1			7	1					368
81C-TB					1														1	15			17
81C-186m		2			9							20			336					563			930
81D-0m								8				3											11
81D-60m					1	3						4	3							2			13
SWAF-2/1		2	1	6	64		139					54			8			8	2	59			343
SWAF-2/2		1		8											5					318			332
SWAF-2/4				69									86				6					4	165
SWAF-2/5				24				35				6	107				1					1	174
SWAF-2/6	7											230	25		1		2				12	23	300
SWAF-4/1				10	52							4	324	17	1		2			16			426
SWAF-4/3				5	81							3	146	33									268
SWAF-5/2				3				527				1	2		2							1	536
SWAF-5/3			2	283				2		3		48		1								1	340
SWAF-5/4	19			86									202		5		11					12	335
NFI-1		1	2		42			1	5	243					2			22	32	28			378
NFI-2		8			33				28	105								4	3				181
NFI-6		23		3	60			2		116								28	1	4			237
NFI-7			6	1	94			1		488						4		8	47	48			697
WNK-1																		566			1		567
WNK-2					96			3		186			3	1		3		4	8	4			308
WNK-3			12							68								10	17				107
81H-183m		24		9	1					34								104					172
81H-230m		5		3	49				20	270						3		14	9				373
81G-289m				10	2				1	15								87					115
81G-330m		3		12	10				4	76						4		9	6				124
81G-373m		1	9		88				31	981						2		24	62				1198
81G-378m		2			21			13	223	344						16		7	1				627

81G-385m				5	13					63								22	4				107
82GF-SS1				5														33					38
82GF-SS2/5				4						6								10					20
82GF-SS2/6				1								1							1				3
82GF-SS2/7				1						22								87					110
82GF-SS3/1		5		8	21					244								34					312
82GF-SS3/2					5					32								1					38
82C-12m		5																26					31
82C-14.3m										24								32					56
82C-46m					5					70													75
82C1-230m		2		7						26								189					224
82C1-277m					11					198								4					213
82C1-297m					3					5									2				10
82C1-315m		1			16				3	70						1		2					93
82C1-322m										42									17				59
82B2-41m										3								58					61
82B-SS1		1			5			6		35	35						2	9	14				107
82B-SS3		7		2					1	18	21				1			68					118
82B-SS4		1			30					27								1	66				125
82B-SS5										18	5							1	1				25
82B-SS7		1			2			4		73	40						1		5	1			127
82B-SS8					32			2		192								3	4				233
82B-SS9		2		3	4			4		280									5				298
82B2					2				1	48								17	6				74
82B4-112m				1	1					38								80	8				128
82B4-114m				1	7				1	70								40	27				146
82B4-126m					10					62								2	21				95
82B4-130m		1								53	2							16	16				88
82B4-136m										13	1								1				15

83A-49m				1						16								51					68
83A-65m					3					136									11				150
83A-70m					10				1	360									69				440
81E-35m				39						35							53						127
81E-45m		9						31		588		20											648
81E-374m		12																67					79
81E-394m										1								127					128
81E-398m		7						15		6							2	200			2		232
81E-404m		2			1			4		152					1			116	2				278
81E-418.3m		13			4			21		3		330			93						2		466
81F-140m		4			3			10		40						44		171					272
81F-206m		6			3					703						20		56	153				941
Conwallis					12			60		10		182	18								15		297
Total	87	179	32	1392	3520	42	218	9114	420	7264	106	8178	8538	100	645	103	1099	2426	647	1610	303	355	46381

Appendix II. Data of Eifelian Brachiopods [Endemic genera (E) are indicated with *. References cited are listed in Chapter 5]

1. Arctic Canada (27 genera, E=6, E%=22.2)(data from Johnson and Perry, 1976; Brice, 1982; Jones, 1982; Racheboeuf, 1987; Li and Jones, 2002, Li and Jones, in press): *Anatrypa, Arcticastrophia**, *Atrypa, Borealistrophia**, *Carinagypa, Costacranaena**, *Cranaena, Cupularostrum, Dagnachonetes**, *Desquamatia, Emanuella, Elythyna, Eoschuchertella, Grinnellathyris**, *Gypidula, Hypothyridina, Ivdelinia, Megastrophia, Nucleospira, Parapholidostrophia?, Perryspirifer/Fimbrispirifer*[†], *Schizophoria, Spinatrypa, Spinatrypina, Spinulicosta, ?Spurispirifer**, *Warrenella.* [[†]Jones and Boucot (1983) re-assigned *Fimbrispirifer* from Arctic Canada to a newly defined genus *Perryspirifer.* The main difference between *Perryspirifer* and *Fimbrispirifer,* lies in that the latter has minute, anteriorly directed spines fringing growth lamellae, whereas *Perryspirifer* does not. Due to the lack of information on the spines in *Fimbrispirifer* from other regions, and considering the possible preservation bias towards the spines, we treated *Perryspirifer* and *Fimbrispirifer* undifferentiatedly in the database].

2. Western Canada (33 genera, E=3, E%=9.1)(data from Crickmay, 1960; McLaren, 1962; McLaren et al., 1962; Norris, 1965, 1973, 1998; Craig et al., 1967; Caldwell, 1971; Pedder, 1975; Chatterton and Perry, 1978; Koch, 1981; Norris et al., 1982; Koch and Day, 1996): *Ambocoelia, Anatrypa, Atrypa, ?Barroisella**, *Carinatrypa, Cassidirostrum, Chonetes?, Cupularostrum, Cymostrophia, Cyrtina, Desquamatia, Devonoproductus, Elita, Emanuella, Eoschuchertella, Fimbrispirifer, Gypidula, Ivdelinia, Leiorhynchus, Meristina, Nucleospira?, Pentamerella, "Plectospirifer"**, *Productella, Rhyssochonetes**, *Schizophoria, Schuchertella, Spinatrypa, Spinatrypina, Spinulicosta, Stringocephalus, Variatrypa, Warrenella.*

3. Nevada (38 genera, E=5, E%=13.2)(data from Johnson, 1966, 1970, 1990; Johnson and Flory, 1972; Johnson et al., 1980): *"Productella", Ambocoelia, Atrypa,* *Cassidirostrum, "Chonetes", Cranaena, Crurithyris, Cryptatrypa, Cyrtina, Davidsonia, Delthyris, Desatrypa*, Echinocoelia, Emanuella, Eoschuchertella, Gypidula, Gypidulina*, Hadrorhynchia*, Leiorhynchus, Leptathyris, Mucroclipeus*, Nucleospira, Parapholidostrophia, Pentamerella, Quadrithyris, Rensselandia, Rhipidothyris, Schizophoria, Spinatrypa, Spinatrypina, Spinulicosta, Stringocephalus, Subrensselandia*, Teichertina, Vagrania, Vallomyonia, Variatrypa, Warrenella.*

4. South China (84 genera, E=36, E%=42.9)(data from Wang et al., 1974; Hou and Xian, 1975; Xu, 1979; Wang and Zhu, 1979; Vogel et al., 1989; Sun, 1992): *Acrospirifer, Alatiformia, Ambocoelia, Amboglossa*, Amoenospirifer, Athyrisina*, Atrypa, Changtangella*, Chonetes, Costanoplia*, Cranaena, Craniops*, Crurithyris, Cryptatrypa, Cyrtina, Dalejina?, Dalmanellopsis*, Davidsonia, Desquamatia, Devonalosia*, Devonoproductus, Douvillina, Dushanirhynchia*, Echinocoelia, Eifelatrypa*, Emanuella, Eospriferina*, Euryspirifer, Guicyrtia*, Gypidula, Hercostrophia*, Holynatrypa, Hypsomyonia*, Ilmenia, Ilmenispina*, Kaplex, Kayserella, Kwangsia*, Leiorhynchus, Longdongshuia*, Luofuia*, Megachonetes*, Megastrophia, Mendacella*, Muriferella*, Nabiaoia*, Nadiastrophia*, Nucleospira, Orbiculoidea, Otospirifer*, Paracostanoplia*, Paraplicanoplia*, Paucistrophia*, Pentamerella, Perichonetes*, ?Phragmophora*, Planatrypa*, Plectodonta, Plectospira, Prokopia, Rensselandia, Reticulariopsis, Rhipidothyris, Rhynchospirifer, Rostrospirifer*, Salopina, Schizophoria, Schuchertella, Septatrypa*, Skenidioides, Spinatrypa, Spinocyrtia, Spinulicosta, Steinhagella*, Stringocephalus, Strophodonta, Strophochonetes*, Tangxiangia*, Uncinulus, Vallomyonia, Warrenella, Xenospirifer*, Zdimir, Zlichorrhychus*.*

5. Appalachian Basin/New York (68 genera, E=15, E%=22.1) (data from Oliver, 1954; Feldman, 1980, 1985, 1994; Koch, 1981; Racheboeuf and Feldman, 1990; Linsley, 1994; Koch and Day, 1996): *Acrospirifer, Alatiformia, Ambocoelia, Amphigenia,* *Atlanticocoelia*, Athyris, Atribonium, Atrypa, Brachyprion*, Camarotoechia, Camarospira, Centronella*, Charionoides*, Chonetes, Chonostrophia*, Coelospira*, Costistrophonella, Cranaena, Cryptonella, Cupularostrum, Cymostrophia, Cyrtina, Dalejina, Discomyorthris*, Duryeella, Elita, Elytha, Elythyna, Emanuella, Eodevonaria, Eoschuchertella, Fimbrispirifer, Gypidula, Hallinetes*, Isorthis, Kayserella, Kozlowskiella*, Leptaena, Leptocoelina*, Levenea, Longispina, Machaeraria, Mediospirifer, Megakozlowskiella, Megastrophia, Meristella, Meristina, Mesodouvillina, Mucrospirifer, Nucleospira, Pacificocoelia*, Paraspirifer, Pentagonia*, Pentamerella, Pholidostrophia, Plicoplasia, Plicostropheodonta*, Protoleptostrophia, Pseudoatrypa, Rhynchospirifer, Schizophoria, Schuchertella, Spinatrypa, Spinulicosta, Strophodonta, Trematospira*, Truncalosia*, Variatrypa.*

6. Michigan Basin (56 genera, E=5, E%=8.9) (data from Fagerstrom, 1961a, 1961b, 1971; Koch, 1981; Koch and Day, 1996): *"Schuchertella", "Spirifer", Acrospirifer, Ambocoelia?, Amphigenia, Athyris, Atribonium, Atrypa, Brachyspirifer?, Brevispirifer*, Camarospira, Camarotoechia?, Chonetes, Costistrophonella, Cranaena, Crurithyris, Cryptonella, Cupularostrum, Cymostrophia, Cyrtina, Dalejina, Duryeella, Elytha, Emanuella, Fimbrispirrifer, Gypidula?, Howellella?, Isorthis, Leptaena, Longispina, Machaeraria, Mediospirifer, Megakozlowskiella, Megastrophia, Meristella?, Meristina, Meristospira, Mesodouvillina, Metaplasia, Mucrospirifer, Nucleospira, Orthospirifer*, Paraspirifer, Pentamerella, Pholidostrophia, Protodouvillina*, Protoleptostrophia, Prosserella*, Pseudoatrypa, Rhipidomella*, Rhytistrophia, Schizophoria, Spinatrypa, Spinulicosta, Stenoscisma*, Strophodonta.*

7. Ural (73 genera, E=23, E%=31.5) (data from Khodalevich et al., 1959; Breivel et al., 1967; Kondiain et al., 1967; Sapelnikov and Mizens, 1984, 1985, 2000; Yudina, 1989): *Anatrypa, Athyris, Atrypa, Atryparia, Barbarothyris*, Beckmannia*, Biarea*, Biseptum*, Bornhardtina*, Brachythyris*, Camerotoechia, Camerophorina*,* *Carinatina, Chascothyris*, Clorinda, Conchidiella*, Corvinopugnax, Cryptonella, Cyrtina, Dentatrypa*, Desquamatia, Elythyna, Emanuella, Eoreticularia, Eospirifer*, Glosshypothyridina*, Gruenewaldtia*, Gypidula, Gypidulella*, Holynatrypa, Hypothyridina, Ilmenia, Isopoma*, Ivdelinia, Karpinskia*, Kosirium, Kransia, Lazutkinia*, Leiorhynchus, Leptostrophia, Megastrophia, Merista, Meristella, Mimatrypa*, Nymphorhynchia, Parachonetes*, Pentamerella, Peratos*, Pholidostrophia, Plectatrypa*, Plectospira, Productella, Pugnax, Punctatrypa, Pyramidalia, Quadrithyrina, Radiomena, Rensselandia, Rhenothyris, Rhynchospirifer, Rhytistrophia, Schnurella, Septalaria, Sibirirhynchia*, Spinatrypa, Totia*, Uncinulus, Undispirifer, Vagrania, Variatrypa, Warrenella, Wilsoniella, Wyella.*

8. Bohemia (48 genera, E=14, E=29.2) (data from Havlícék, 1959; 1961; 1967; 1977; 1987; Biernat, 1966; Ficner and Havlícék, 1978; Havlícék and Kukal, 1990): *Ambocoelia, Amissopecten*, Amoenospirifer, Astutorhyncha*, Carinatina, Cerberatrypa*, Cingulodermis, Clorinda, Corvinopugnax, Cyrtina, Delthyris, Desquamatia, Emanuella, Eomartiniopsis*, Eoreticularia, Glossinotoechia*, Howellella, Iridistrophia, Kaplex, Karbous, Kosirium, Kransia, Leptathyris, Markitoechia, Merista, Nemesa, Notothyris*, Nymphorhynchia, Obesaria*, Pinguispirifer, Plectodontella, Plectospira, Prodavidsonia, Quadrithyrina, Quasidavisonia, Quasimartinia*, Radimatrypa*, Rhynchatrypa*, Rochtex*, Septalaria, Skenidioides, Spinatrypa, Stringocephalus, Telaeoshaleria, Trigonatrypa*, Uncinulus, Undispirifer, Xenomartinia*.*

9. Inner Mongolia (45 genera, E=11, E%=24.4)(data from Su, 1976; Zhang, 1981, 1985): *Acrospirifer, Apicilirella*, Athyris, Aulacella, Carinatina, Chonetes, Coelospirella*, Cymostrophia, Cyrtina, Dalejina, Desquamatia, Douvillina, Fimbrispirifer, Gypidula, Howellella, Ivdelinia, Kayseria*, Kozlowskiellina*, Leiorhynchus, Leptaena, Leptaenopyxis*, Leptostrophia, Levenea, Lissatrypa*,* *Lissostrophia, Malurostrophia*, Merista, Minutostropheodonta*, Paraspirifer, Plectospira, Pseudochonetes*, Quadrithyris, Reticulariopsis, Rhytistrophia, Schizophoria, Skenidium*, Spinatrypa, Spinatrypina, Spinocyrtia, Teichertina, Tridensilis*, Uncinulus, Undispirifer, Wilsoniella, Wyella.*

10. Burma (31 genera, E=5, E%=16.1) (data from Anderson et al., 1969): *Alatiformia?, Athyris, Atrypa, Aulacella, Cimicinoides*, Cyrtina, Desquamatia, Devonaria, Emanuella, Indospirifer*, Kayserella, Laptaena, Leptodontella*, Leptostrophia, Markitoechia?, Merista, Mesodouvillina, Mystrophora*, Nucleospira, Plectospira, Productella?, Radiomena, Reticulariopsis, Schizophoria, Schnurella, Septalaria?, Sieberella, Spinatrypa, Telaeoshaleria, Uncinulus, Xystostrophia*.*

11. NW Spain (40 genera, E=14, E%=35) (data from Struve and Mohanti, 1970; Arbizu et al., 1979; Alvarez, 1990; Garcia-Alcalde et al., 1990): *Alatiformia, Ambocoelia, Anathyris*, Arduspirifer*, Athyris, Atrypa, Bifida*, Camarotoechia, Chlupacina*, Cingulodermis, Cyrtina, Dalejodiscus*, Desquamatia, Devonaria, Euryspirifer, Hexarhytis*, Holynetes*, Imatrypa*, Iridistrophia, Karbous, Leptostrophia, Luanquella*, Nemesa. Paraspirifer, Peridalejina*, Plectospira, Plicathyris*, Prodavisonia, Prokopia, Pyramidalia, Quasidavisonia, Resserella*, Schizophoria, Spinatrypa, Spinatrypina, Teichostrophia*, Telaeoshaleria, Tyersella*, Uncinulus, Zdimir.*

12. Germany-Belgium-Nothern France (52 genera, E=7, E%=13.5)(data from Struve, 1963, 1964a, b, 1965a, b, 1966, 1970, 1976, 1978, 1981; Copper, 1966, 1967; Erben and Zagora, 1967; Lecompte, 1967; Copper and Rachebouef, 1985; Godefroid, 1995): *Acrospirifer, Alatiformia, Ambocoelia, Amoenospirifer, Athyris, Atrypa, Atryparia, Atrythyris*, Auchmerella*, Brachyspirifer, Carinatina, Crurithyris, Dalmanella, Delthyris, Desquamatia, Devonaria, Dicamara, Douvillina, Eodevonania, Eoreticularia, Euryspirifer, Fimbrisprifer, Gypidula, Ivanothyris*, Hypothyridina, Hysterolites,* *Meristella, Paraspirifer, Pinguispirifer, Prodavidsonia, Productella, Pugnax, Punctatrypa, Pyramidalia, Quadrithyris, Reticulariopsis, Retzia*, Rhenothyris, Rhipidomella, Schizophoria, Schuchertellopsis*, Septalaria, Spinella*, Spinatrypa, Spinatrypina, Spinocyrtia, "Spirifer", Strophodonta, Tingella*, Uncinulus, Undispirifer, Vagrania.*

13. Algerian Sahara (31 genera, E=7, E%=22.6) (data from Legrand, 1967): *Acrospirifer, Brachyspirifer, "Camarotoechia", Chonetes, Cyrtina, Cyrtinopsis*, Dalmanella, Dicamara, Gypidula, Hysterolites, Janius*, Mediospirifer, Mucrospirifer, Paraspirifer, Pholidostrophia, Platyorthyris*, Productella, Quadrithis, Reticularia*, Retichonetes*, Rhipidomella, Septalaria, Schellwienella, Schizophoria, Sieberella, Spinocyrtia, "Spirifer", Strophodonta, "Terebratula"*, Trigeria*, Uncinulus.*

14. South Africa (30 genera, E=19, E%=63.3) (data from Du Toit, 1954; Haughton, 1969; Oosthuizen, 1984; Hiller and Theron, 1988): *Acrospirifer, Ambocoelia, Australocoelia*, Australospirifer*, Australostrophia*, Austronopolia*, Chonetes, Cryptonella, Derbyina*, Leptocoelia*, Metaplasia*, Meristella, Meristelloides*, Mutationella*, Notiochonetes*, Orbiculoidea, Pleurochonetes*, Pleurothyrella*, Plicoplasia, Pustulatia*, Rensselaeria*, Rhynchonella*, Salopina, Scaphiocoelia*, Schellwienella*, Schuchertella, Spirifer, Strophodonta,Tropidoleptus*, Vitulina*.*