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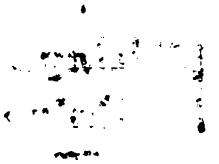

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GLOBAL BIOGEOGRAPHY, BIOSTRATIGRAPHY AND EVOLUTIONARY PATTERNS OF ORDOVICIAN AND SILURIAN BRYOZOA

By

Michael Edward Tuckey

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Geology

5179355X

ABSTRACT

GLOBAL BIOGEOGRAPHY, BIOSTRATIGRAPHY AND EVOLUTIONARY PATTERNS OR ORDOVICIAN AND SILURIAN BRYOZOA

By

Michael Edward Tuckey

The data for each of the chapters in this thesis was derived from a global bryozoan data base assembled for this project. The data base contains information on nearly all species of Ordovician and Silurian Bryozoa which have been described in the literature. The information recorded for each reported occurrence of a species includes: geographic locality, geologic formation, lithology of the formation, and colony morphology. Ages of formations were estimated from recently published stratigraphic charts. Taxonomy and synonymies of bryozoan clades were assembled with the advice of Dr. Robert Anstey. The bibliography of sources for the data base in contained in Appendix A.

Four independent problems were addressed in this thesis: 1) An investigation of the biogeography of Ordovician and Silurian Bryozoa revealed the existence of four major Ordovician bryozoans provinces: Baltic, North American, Siberian and Mediterranean. The Llandeilo-Caradoc was a period of high provinciality as all four provinces were in existence. Provinciality was reduced in the Ashgill, as the North American and Siberian and the Baltic and Mediterranean Provinces merged. In the Llandovery and Wenlock, the temperate latitude Mongolian Province existed on the northern portion of the Siberian plate. Silurian provinciality was reduced with the merging of the

North American-Siberian and Baltic Provinces in the Wenlock.

2) An investigation of Ordovician-Silurian radiations of the Bryozoa revealed that the major center of origin of bryozoan radiation in the Early Ordovician was the temperate latitude continent of Baltica. Within North America, bryozoan genera and families mad their first appearances in shallow water and reef environments along the continental margin, while speciation rates were highest in offshore areas of the craton.

3) The statistical technique of gradient analysis was found to be useful for stratigraphic correlation, and faunas from Poland and Burma were dated by this method.

4). The Late Ordovican mass extinction was found to be a composite of three separate extinction events. The major extinction occurred at the end of the Rawtheyan, and was associated with a marine regression which affected primarily species from terrigenous lithotopes.

DEDICATION

This thesis is dedicated to the numerous paleontologists and stratigraphers who have described the Ordovician and Silurian bryozoan faunas of the world. Their works are listed in Appendix A. A thesis of this sort would have been unthinkable without the years of effort and immense amounts of data generated by bryozoan specialists of the past. Bryozoan descriptive paleontology is approximately 100 years old, and over this time period four individuals stand out as being extraordinarily prolific in their description of Ordovician and Silurian faunas: G.G. Astrova, June Ross, E.O. Ulrich and R.S. Bassler. They are truly giants of paleontology.

ACKNOWLEDGEMENTS

I would like to acknowledge Dr. Robert Anstey for his advise and help in the formulation of the problem and for his taxonomic expertise. I would also like to thank Feng Bing-Cheng for his help in translating some of the Chinese literature.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE

BIOGEOGRAPHY OF ORDOVICIAN AND SILURIAN BRYOZOANS

INTRODUCTION

Ordovician and Silurian biogeographic histories have been compiled for a variety of marine invertebrates. Trilobite biogeography has been described by Whittington (1966, 1973) and Whittington and Hughes (1972, 1973). Jaanusson (1973), Sheehan (1979), Boucot and Johnson (1973) and Williams (1973) have described brachiopod biogeography. The biogeography of graptolites has been discussed by Skevington (1973) and Berry (1973, 1979). Other organisms such as corals (Kaljo and Klaaman, 1973), conodonts (Bergstrom, 1973 and Lindstrom, 1976), palynomorphs (Cramer and Diaz, 1974), echinoderms (Paul, 1976; Witzke, Frest and Strimple, 1979), molluscs (Pojeta, 1979; Rohr, 1979) and stromatoporoids (Webby, 1980) have also been subjects of biogeographic analysis. General reviews of Ordovician and Silurian biogeography have been provided by Ziegler et al. (1977), Jaanusson (1979), Boucot (1979), Burrett (1973) and Spjeldnaes (1981). Although each group of organisms has its own biogeographic history, similarities are evident in the patterns of distribution of all major groups.

The Ordovician can be characterized as a period of high provinciality, with biogeographic differentiation being greatest in the Lower to Lower Middle Ordovician. An abrupt change occurred in the Hirnantian (Latest Ashgill), and Silurian faunas are known to be highly cosmopolitan. For some organisms, a gradual decrease in provinciality became evident as early as

Caradoc time (Williams, 1973). These changes in provinciality are related to the changing positions of the continents, as the Iapetus Ocean was gradually closing through the Ordovician into the Silurian and the continent Baltica was moving from a temperate southerly latitude towards North America and the equator. This paper summarizes Ordovician biogeographic distributions for a number of marine invertebrates (Tables 1-3).

Bryozoan biogeography has not been studied in detail for the Ordovician and Silurian Periods. Ross (1985) published a short descriptive paper on Ordovician bryozoan biogeography, Anstey (1986) described Late Ordovician North American bryozoan biogeography and Astrova (1965) and Nekhorosheva (1976) described Ordovician bryozoan biogeography of the Soviet Arctic. The following analysis is an attempt at a detailed biogeographic history of the bryozoa, with an analysis of each stage of the Ordovician and Silurian, using quantitative techniques and data drawn from a global bryozoan data base of 495 sources newly compiled for this project.

METHODS

The multivariate statistical techniques of reciprocal averaging, detrended correspondence analysis and cluster analysis were used to quantitatively determine biogeographic associations. Gradient analysis methods, such as reciprocal averaging, have been used extensively in community ecology and

Table 1. Summary of Lower Ordovician biogeographic provinces.

Locality	1 Brachiopods	2 Brachiopods	2 Trilobites	3 Graptolites
NA. Midcontinent	Northern		Bathyurid	Pacific
NA. Geosyncline	Northern	Scoto-Appl.	Bathyurid	Pacific
Baltic Platform	Baltic	Baltic	Asaphid	Atlantic
Ural Geosyncline	Baltic		Asaphid	
Siberian Platform	Northern		Bathyurid	
Altai Sayan	Northern			
Northeast USSR	Northern	NE. USSR	Bathyurid	
Australia	Northern		Hung-Caly.	Pacific
Wales	Southern	Anglo-Frn.	Selenopel.	Atlantic
Montagne Noire	Southern	Anglo-Frn.	Selenopel.	
North Africa			Selenopel.	Atlantic
China	Northern		Hung-Caly.	Pacific

1. Jaanusson, 1973
2. Williams, 1973
3. Whittington, 1973
4. Skevington, 1973

Abbreviations: NA.=North America, Scoto-Appl.=Scoto-Appalachian Anglo-Frn.=Anglo-French, Selenopel.=Selenopeltis, Hung-Caly.= Hungaiid-Calymenid, NE.= Northeast

Table 2. Summary of Middle Ordovician biogeographic provinces.

Locality	1 Brachiopods	2 Brachiopods	3 Corals	4 Conodonts
NA Midcontinent	C. Northern	American	Amer-Sib.	NA Midcont.
NA Geosyncline	Scoto-Appl.	America	Amer-Sib.	European
Baltic platform	Baltic	Baltic	Euro-Asian	European
Ural Geosyncline	Scoto-Appl.			
Siberian Platform	C. Northern	American	Amer-Sib.	NA Midcont.
Altai Sayan	Scoto-Appl.		Euro-Asian	
Northeast USSR	Scoto-Appl.	American	Amer-Sib.	
Australia				Austral.
Wales	Southern	Anglo-Frn.	Euro-Asian	European
North Africa	Southern	Bohemian		
Southern Europe	Southern	Baltic		
Burma		Baltic		
Bohemia		Bohemia		

1. Jaanusson, 1973
2. Williams, 1973
3. Kaljo and Klaaman, 1973
4. Bergstrom, 1973

Abbreviations: NA.=North America, C.=Central, Scoto-Appl.= Scoto-Appalachian, Anglo-Frn.=Anglo-French, Amer-Sib.= American-Siberian, Austral.=Australian

Table 3. Summary of Upper Ordovician biogeographic provinces.

Locality	1 Brachiopods	2 Brachiopods	3 Trilobites	4 Corals
NA. Midcontinent	C. Northern	Mid-America	Mono-Remo.	Amer-Sib.
NA. App. Geosyn.	C. Northern	N. Europe	Mono-Remo.	
Baltic Platform	Hibern-Sal.	N. Europe	Mono-Remo.	Euro-Asian
Ural Geosyncline			Mono-Remo.	
Siberian Platform	C. Northern		Mono-Remo.	Amer-Sib.
Altai Sayan	Hibern-Sal.			Euro-Asian
Northeast USSR	Hibern-Sal.		Mono-Remo.	
Australia			Plio-Caly.	
Wales		N. Europe	Tri-Homal.	Euro-Asian
Montagne Noire			Tri-Homal.	
Ireland	Hibern-Sal.			
Anticosti	Hibern-Sal.	N. American		
Alaska	Hibern-Sal.			
Missouri	Hibern-Sal.			
North Africa		Bohemian	Tri-Homal.	
Bohemia		Bohemian		Euro-Asian
China			Plio-Caly.	

1. Jaanusson, 1973
2. Williams, 1973
3. Whittington, 1973
4. Kaljo and Klaaman, 1973

Abbreviations: NA.=North America, App. Geosyn.=Appalachian geosyncline, Hibern-Sal.=Hiberno-Salairian, C.=Central, N.= North, Tri-Homal.= Trinucleid-Homalonotid, Plio-Caly=Pliomerina-Calymenid, Mono-Remo.=Monorakid-Remopleuridid, Amer-Sib.= American-Siberian

are similar to factor analysis in that they reduce the dimensionality of the data matrix. The samples are ordinated along a gradient between two poles (the samples most distant from each other along the axis). Reciprocal averaging has been used by Cisne and Rabe (1978) and Anstey, Rabbio and Tuckey (1987a) in Ordovician paleoecological studies. Another gradient analysis method, polar ordination, was used by Raymond (1987) to define Devonian phytogeographic provinces and by Anstey, Rabbio and Tuckey (1987a) in paleoecological studies. Detrended correspondence analysis (hereafter called DCA) was used by Anstey, Rabbio and Tuckey (1987b) in a study of Late Ordovician paleocommunities. This method is an improvement on reciprocal averaging in that subsequent axes beyond the first axis are truly orthogonal, whereas in reciprocal averaging, the second, third and fourth axes are often correlated with the first axis. A summary of these techniques is provided in Gauch (1982).

In this study, DCA proved to be the most useful technique for distinguishing biogeographic units. The input data matrix for DCA was composed of the number of species per genus present at each locality. DCA was run with a separate data matrix for each stage of the Ordovician and Silurian. Localities of low diversity were not included in the analysis, with the minimum diversity being 5 to 8 genera, depending on the overall diversity of the stage. Because of the limited number of localities and overall low diversity of the Arenig, low diversity localities were included in that analysis.

Geographic patterns were generally distinguishable on plots of locality scores for DCA axes one vs. two. Occasionally biogeographic patterns were obscured by the effects of facies, so for the Caradoc, patterns were most easily distinguishable on plots of DCA axes one vs. three.

Cluster analysis was used by Williams (1973) to define Ordovician brachiopod provinces and by Raymond (1987) to help define Devonian phytogeographic provinces. Cluster analysis differs from gradient analysis in that it measures overall faunal similarity, and endemic genera, which may be characteristic of a particular province, have no special weight. In this study cluster analysis was used as a backup method to lend support to, or modify gradient analytic methods. The input data matrix for the cluster analysis consisted of a matrix of Simpson's indices of faunal similarity. Clustering was also done with data matrices of Jaccard coefficients; however Simpson's Index gave results more congruent with the gradient analysis methods. The clustering method used was the average linkage between group method. In keeping with previous Ordovician and Silurian biogeographic studies, the term, province, is used in this paper to refer to a biota characteristic of a particular continent, although present day provinces are often restricted to small portions of a continent. Geographic associations within continents, restricted to major lithotopes, are referred to as biomes, following Anstey (1986).

ARENIG

Except for one species (Ceramopora unapensis) described by Ross (1966a) from the Kindblade Formation (Late Tremadoc) of Oklahoma, bryozoa are first found in rocks of Arenigian age. However, a Tremadocian fauna from China is currently being decribed by Spjeldnaes and Hu (Taylor and Cope, 1987). The most diverse Arenig bryozoan fauna is found in Baltica in the B1 and B2 horizons of Estonia and Leningrad and in the Nelidov horizon of Novaya Zemlya. Less diverse faunas are found in North America in the Kanosh Shale in Utah, the Arenig-Llanvirn Oil Creek Formation in Oklahoma and the Late Arenig Shinbrook Formation in Maine. Faunas are also known in Central China and the North Urals. The species Sagenella vetera is known from Bohemia and Alwynopora orodamnus and a generically indeterminate species have been recorded from Ireland.

Baltic faunas are related by the common presence of Dianulites at all localities and the presence of Dittopora, Esthoniopora and Nicholsonella at two or more localities. Oklahoma, Utah and Maine are united by the common presence of Batostoma, which does not appear in Baltica. North American and Baltic Provinces are clearly distinguishable on a plot of locality scores for DCA axes one vs. two (Figure 1). China is allied faunistically with North America by the presence of Batostoma and is provisionally assigned to the North American Province (Figure 2).

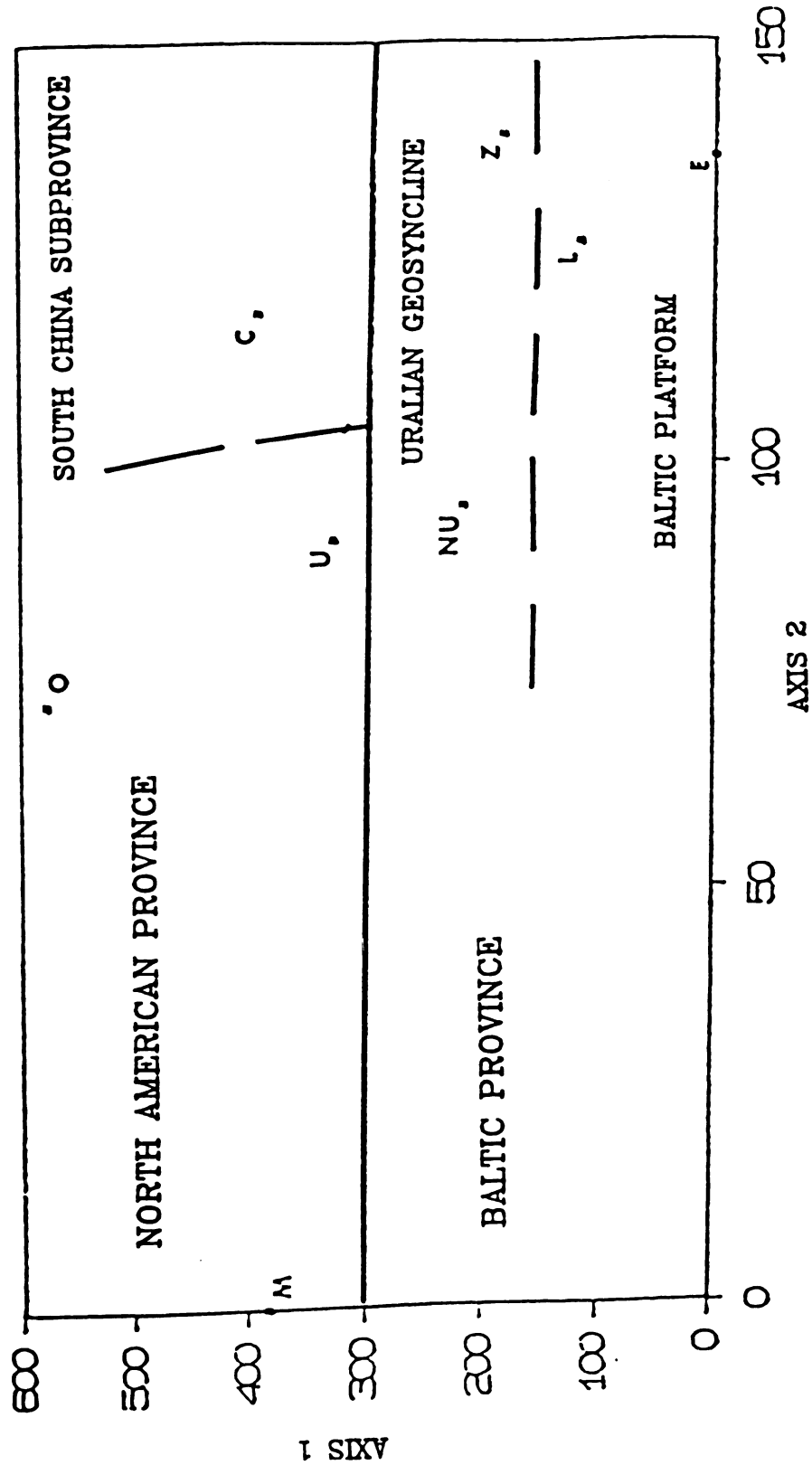


Figure 1. Arenig DCA axes 1 vs. 2. Symbols: C=South China, E=Estonia, L=Leningrad, M=Maine, NU=North Urals, O=Oklahoma, U=Utah, Z=Novaya Zemyla.

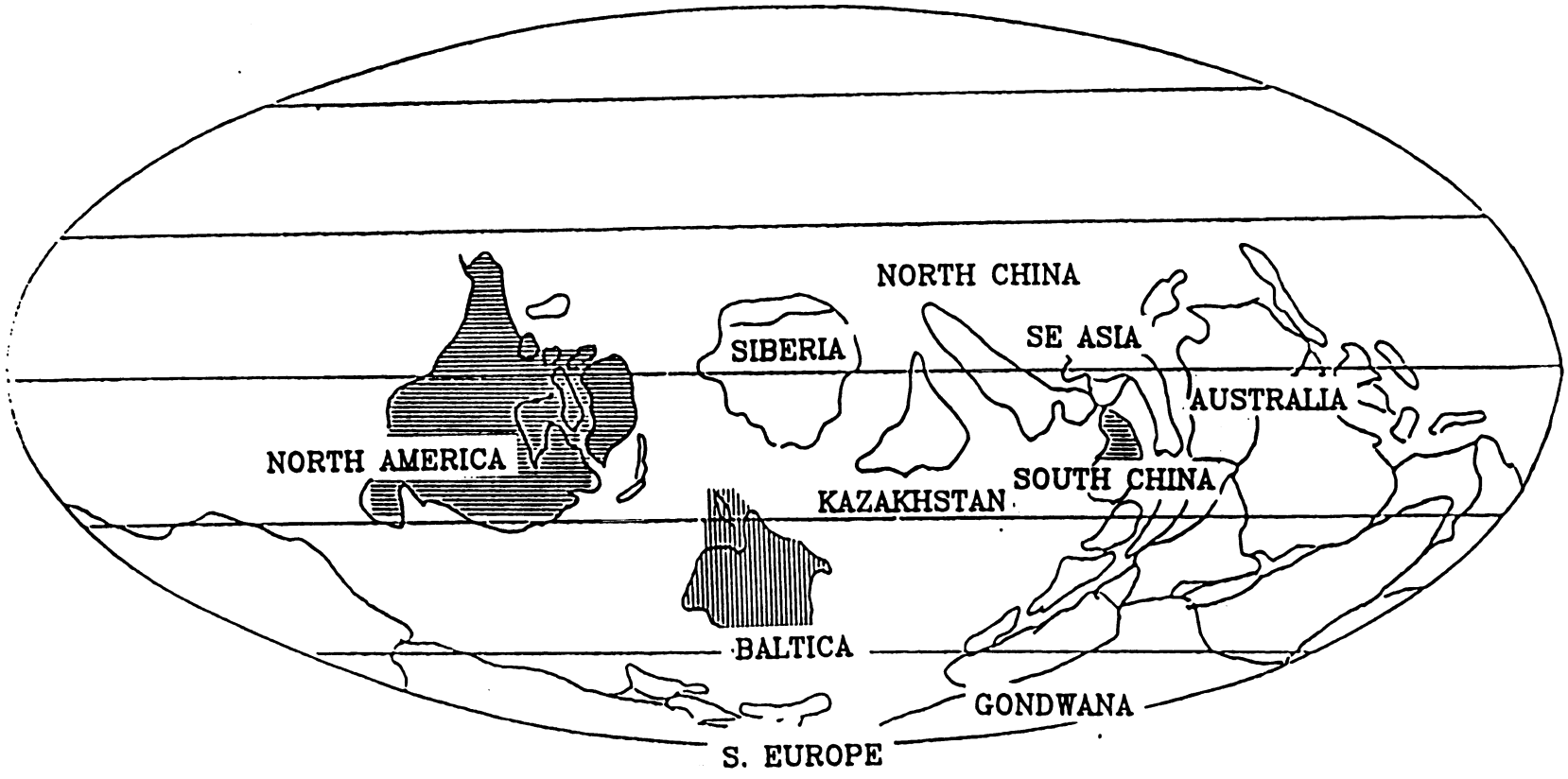


Figure 2. Arenig Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American Province

Baltic Province

LLANVIRN

During the Llanvirn, bryozoan faunas increased in both diversity and provinciality. The Baltic Province shows increased diversities of bryozoans from the B3, C1a and C1b horizons of Estonia and Leningrad, the Khydey Formation of the North Urals and the Yuno Yaga horizon in the Novaya Zemlya-Vaygach-Pay Khoy region. These faunas are characterized by Dianulites, Diplotrypa, Hemiphragma, Nicholsonella and Stictopora. The North American Province consists of bryozoans from the Oil Creek and McLish Formations of Oklahoma, the Chazyan Day Point and Lower Mingan Formations in the Lake Champlain and Mingan Island areas, and the Lower Lenoir Formation of Virginia. North American faunas are again characterized by the common presence of Batostoma at all localities. Other common North American genera are Phylloporina, Stictopora, Monotrypella, Chasmatopora, Nicholsonella and Eridotrypa. Bryozoans also appear in the Elgenchak and Labistakskaya Formations at Sette Daban on the Eastern Siberian margin. Provinces are defined on the plot of DCA axes one vs. two (Figure 3).

Along with provinciality, subprovinces or biomes (Anstey, 1986) can also be observed in the data. The Baltic Province can be subdivided into two different facies associations or biomes. Leningrad and Estonia occur in the Baltic Platform Biome and the North Urals and the Novaya Zemlya-Vaygach-Pay Khoy regions occur in the Uralian Geosynclinal Biome. Approximate positions of

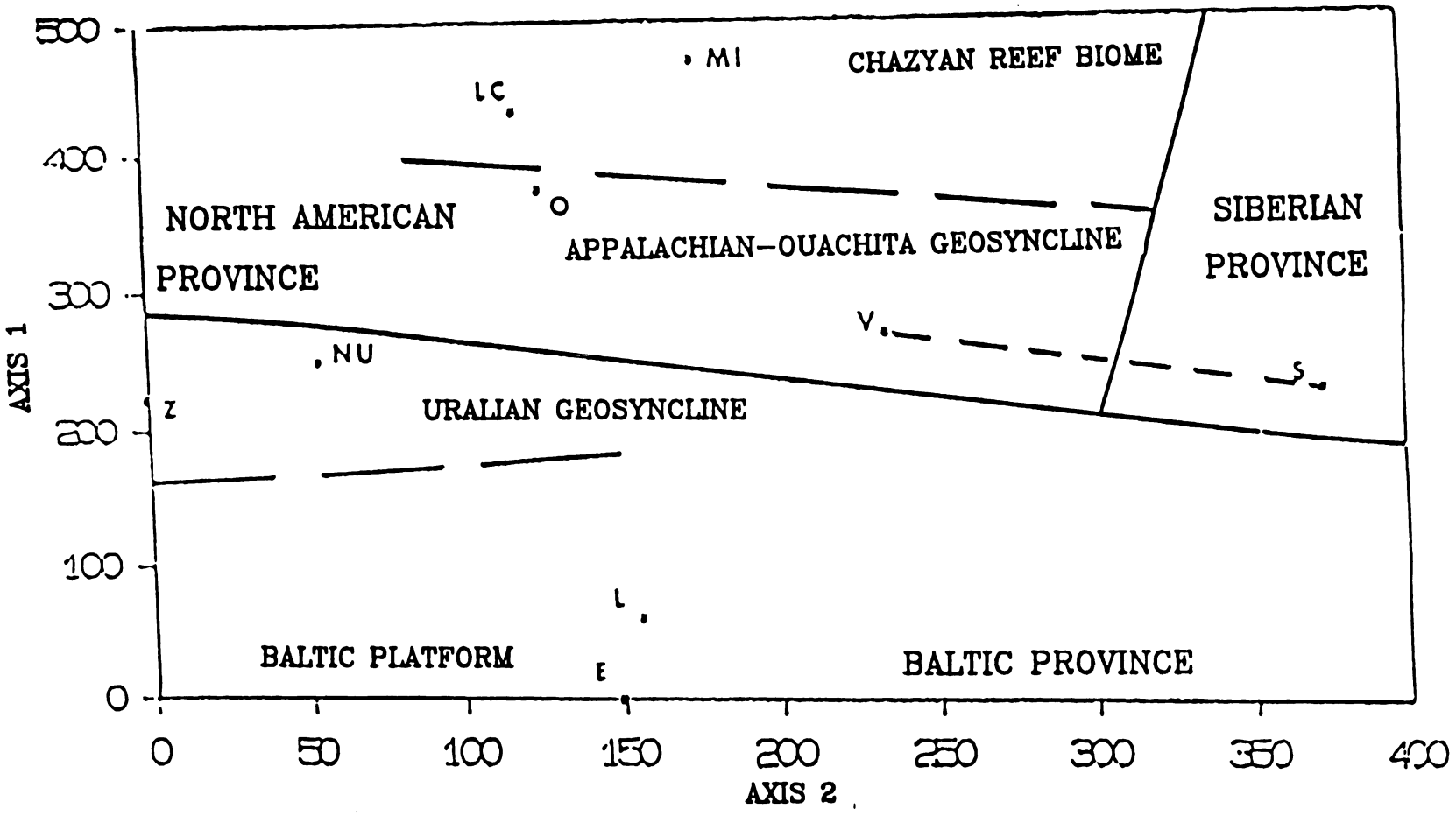


Figure 3. Llanvirn DCA axes 1 vs. 2. Symbols: E=Estonia, L=Leningrad, LC=Lake Champlain, MI=Mingan Island, NU=North Urals, O=Oklahoma, S=Sette Daban, V=Virginia Z=Novaya Zemyla-Vaygach-Pay Khoy. Dotted lines connecting localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.

geosynclinal and platform facies for the Ordovician, of Siberia, North America and Baltica, with the island of Novaya Zemlya observable in the northern part of the Uralian geosynclinal facies are shown in Figure 4. Virginia, as part of the Appalachian Geosynclinal Biome is distinguishable from other North American localities and shares common genera with both Baltica and Siberia. Its location on the North American continental margin apparently makes it a possible colonization site for migrants crossing the Iapetus Ocean. The genera Cyphotrypa and Monotrypa, which were endemic to Baltica in the Arenig, appear in Virginia in the Llanvirn. Conversely, Phyllodictya, which was endemic to Utah in the Arenig, appears in Estonia in the Llanvirn, indicating that a limited amount of migration across the Iapetus was occuring at this time. Provinces are plotted in their approximate paleogeographic positions in Figure 5.

A cluster analysis of Llanvirn localities, gave results similar to gradient analysis, as clusters representing the Chazyan Reef Biome, the Uralian Geosynclinal Biome and the Baltic Platform Biome appeared. Virginia clustered more closely with Sette Daban than with other North American localities. Its association with Sette Daban is represented by the dotted line connecting the two localities (Figure 3).

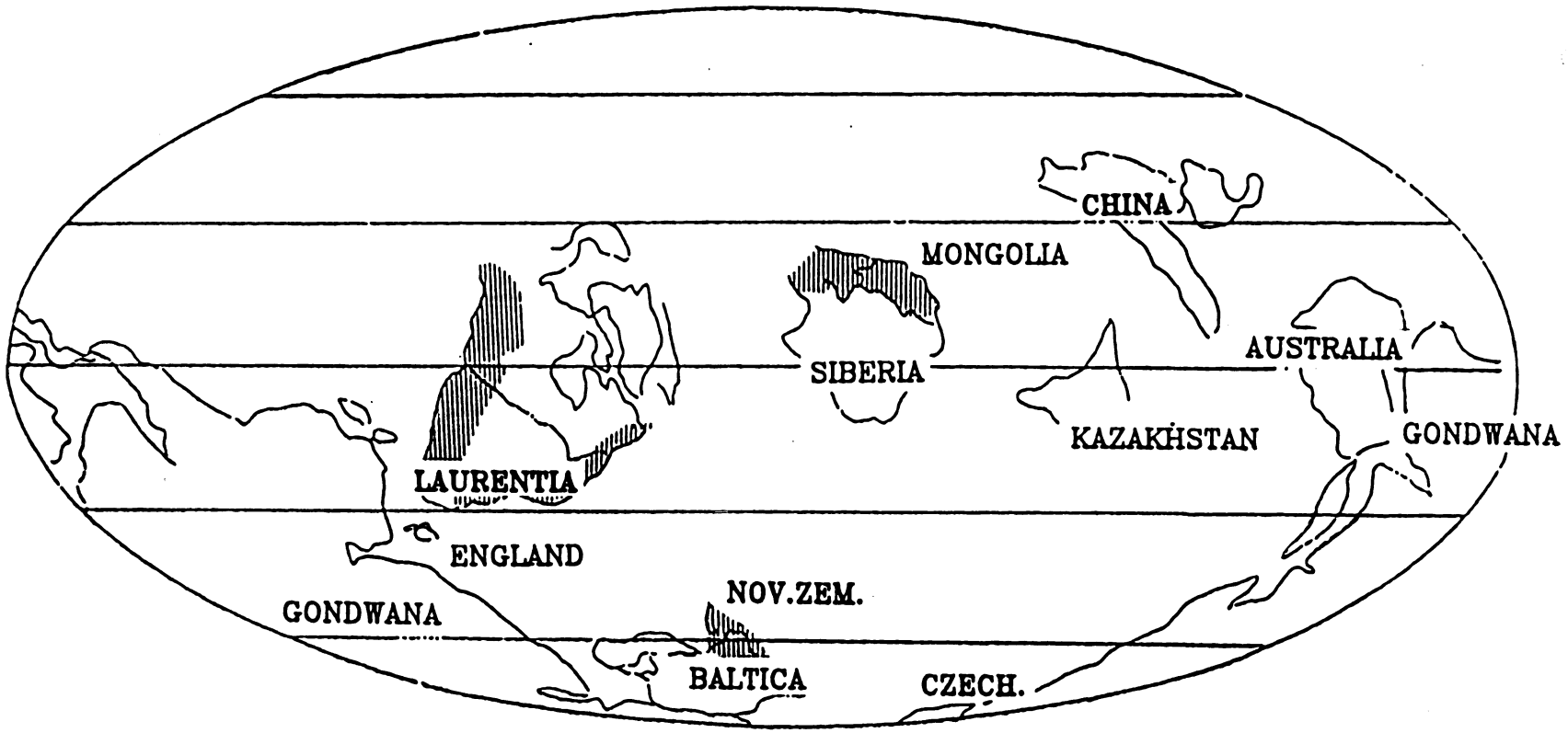


Figure 4. Ordovician geosynclinal facies map, modified from Williams (1973) and Scotese et al (1979).

Geosynclinal Facies

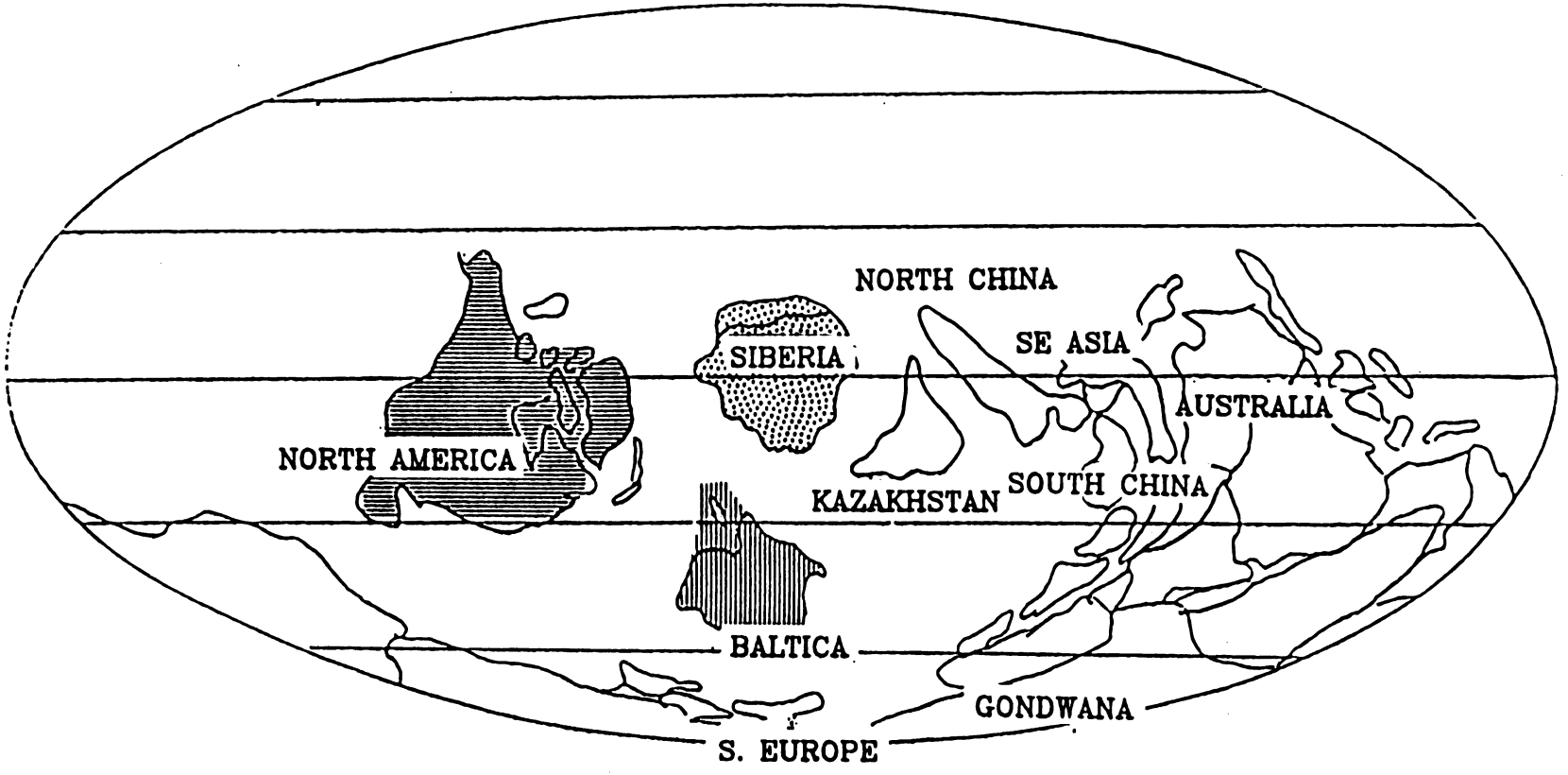


Figure 5. Llanvirn Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American Province

Baltic Province

Siberian Province

LLANDEILO

The provincial patterns of the Llanvirn carry through to the Llandeilo, although there is some blurring of provincial boundaries due to migration, and an increasing differention of North American faunas is seen. Provinces are defined on plots of DCA axes one vs. two (Figure 6). Localities in the Baltic Province cluster with high scores on axis one, with faunas occuring in the C1c and C2 horizons in Estonia and Leningrad, and in the Dyrovataya horizon in the Novaya Zemlya-Vaygach-Pay Khoy region. Leningrad, however, has a somewhat endemic fauna, with the endemic genera Scenellopora, Arthrostylus, and Hexaporites. Arenig-Llanvirn genera such as Dianulites, Diplotrypa, Esthoniopora and Hemiphragma continue to be common and new genera such as Pachydictya, Parvohallopora, Graptodictya and Mesotrypa appear. The Novaya Zemlya-Vaygach-Pay Khoy area shows an increasing faunal affinity with North America, particularly with Appalachian shelf localities. Faunal similarities between geosynclinal localities on widely separated continents reflect the presence of many cosmopolitan genera at these sites. Virginia, Novaya Zemlya and Alabama share the common genera Nicholsonella, Pachydictya, Parvohallopora, and Stictopora, indicating an increase in migration across a narrowing Iapetus Ocean. Alabama and Morocco were closely linked with Vaygach-Novaya Zemlya in the cluster analysis (dotted lines connect these localities in Figure 6).

The Siberian Province contains localities clustering with

Figure 6. Llandeilo DCA axes 1 vs. 2. Symbols: A=Alabama, E=Estonia, K=Kotel Island, L=Leningrad, LC=Lake Champlain, LR=Leni River, M=Morocco, MI=Mingan Island, O=Oklahoma, P=Podkammenaya Tunguska River, Q=Montreal, T=Taimir, V=Virginia, VR=Viluya River, Z=Novaya Zemyla-Vaygach-Paykhoy. Dotted lines connecting localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.

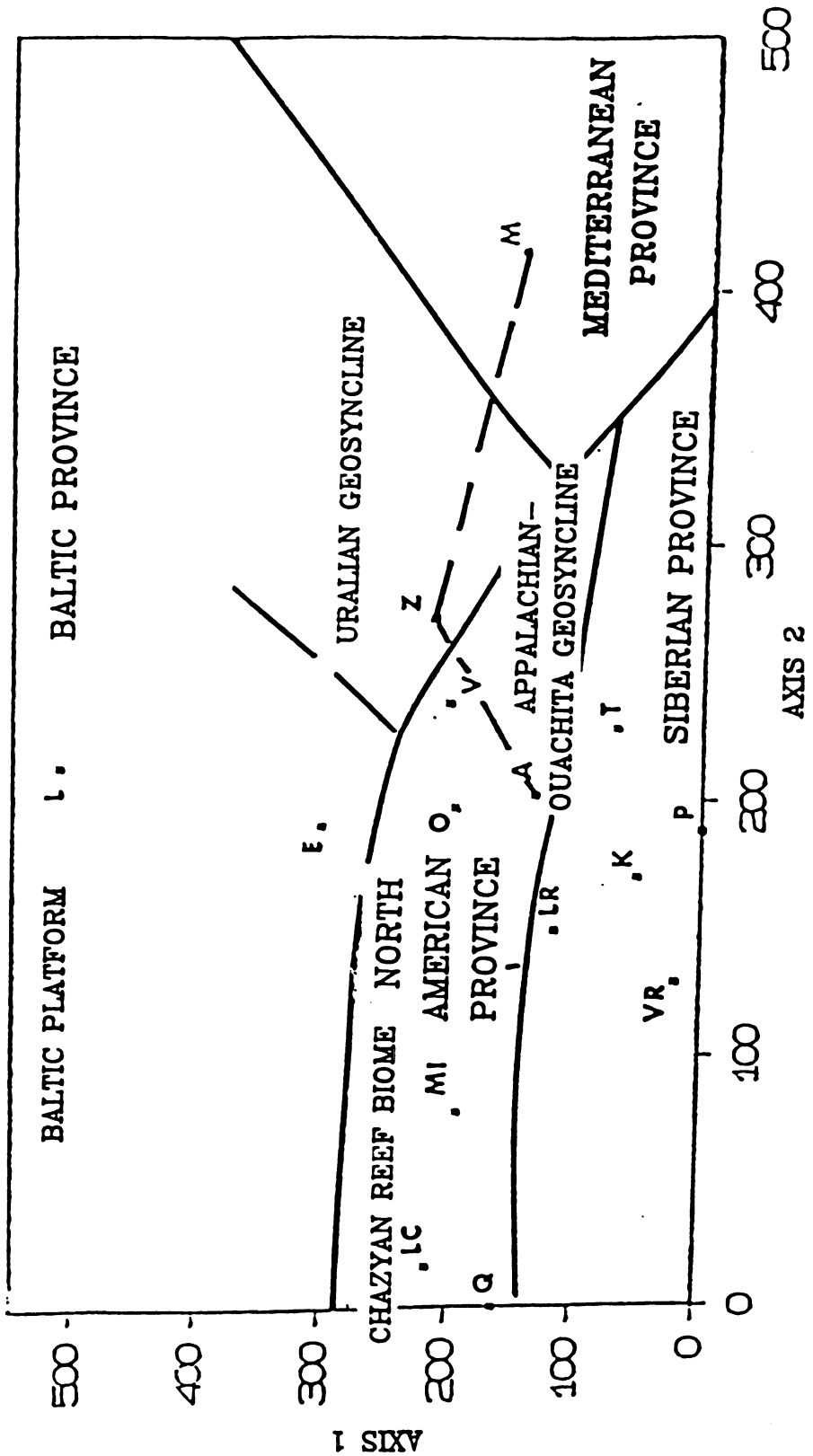

BALTIC PLATFORM
BALTIC PROVINCE
URALIAN GEOSYNCLINE
MEDITERRANEAN PROVINCE
APPALACHIAN-OUACHITA GEOSYNCLINE
SIBERIAN PROVINCE
CHAZYAN REEF BIOME
NORTH AMERICAN PROVINCE
L
E
Z
V
M
A
T
K
P
LC
MI
Q
LR
VR
AXIS 1
AXIS 2
0
100
200
300
400
500

Figure 6

low scores on DCA axis one. Faunas occur in the Krivolutski and Lower Mangazeyski stages in the Podkammenaya-Tunguska, Leni and Viluya River valleys on the Siberian Platform, the Engelgardt horizon on the Taimir Peninsula and in the Lower Malodiring horizon on Kotel Island. Common Siberian genera are Batostoma, Nicholsonella, Trigonodictya, Stictopora, Phaenoporella and Sibiredictya.

The North American Province consists of localities having intermediate scores on DCA axis one and is further differentiated into two subprovinces, or biomes on axis two. The Chazyan Reef Biome consists of faunas from the Crown Point and Lower Valcour Formations of the Champlain Basin, the Crown Point and Laval Formations at Montreal, Quebec, and the Upper Mingan Formation at Mingan Island. Common genera in this biome are cryptostomes such as Stictopora, Chasmatopora, Phylloporina and Pachydictya, and the trepostomes Monotrypella and Batostoma. The North American Geosynclinal Biome consists of faunas from the Upper Lenoir, Lower Effna, New Market and Lincolnshire Formations of the Appalachian shelf in Virginia and Alabama, and the Upper McLish and Tulip Creek Formations of the Simpson Group in the Arbuckle Mountains of Oklahoma. Ross (1976) stated that the Simpson Group strata were deposited in a rift zone or aulacogen, extending northward from the Ouachita continental margin. Faunal similarities between Oklahoma and the Appalachian shelf region may be explained by existence of a continuous Appalachian-Ouachita shelf biome.

These trends are similar to those which have been found in

the distributions of brachiopods and trilobites. The Scoto-Appalachian fauna, which is found in Scotland and in the Appalachians east of the Helena-Saltville Thrust, has an amphicratonic distribution, as a similar fauna has been reported from the west side of the craton, and a related fauna occurs in the Novaya Zemlya-Pay Khoy region (Jaanusson, 1979). This echoes the similarities between the bryozoan faunas of Virginia, Alabama and Novaya Zemlya.

A fourth faunal province, the Mediterranean Province, is represented by the Llandeilo faunas of Morocco. North Africa is placed at the approximate position of the South Pole in paleogeographic reconstructions (Figure 7), and its faunas have been linked to those of Southern Europe (Spjeldnaes, 1981). Spjeldnaes has suggested that Mediterranean and Baltic Provinces were separated by a climatic barrier rather than by a wide ocean. This is supported by the cluster linkage in Figure 6, in which Morocco is linked with Novaya Zemyla.

Migration patterns to the continents of North America, Baltica and Siberia during the Ordovician and Silurian were established by comparing estimated first appearances of genera on each continent (Figures 8-10). The Llandeilo is an epoch of high migration of genera into all three continents. Spjeldnaes (1981) identified this migration as the first major faunal exchange across the Iapetus Ocean. Migrations occurred in a variety of marine invertebrate groups including cephalopods, trilobites and brachiopods. Bryozoans seem have migrated in many directions, contrary to Spjeldnaes' assertion that the

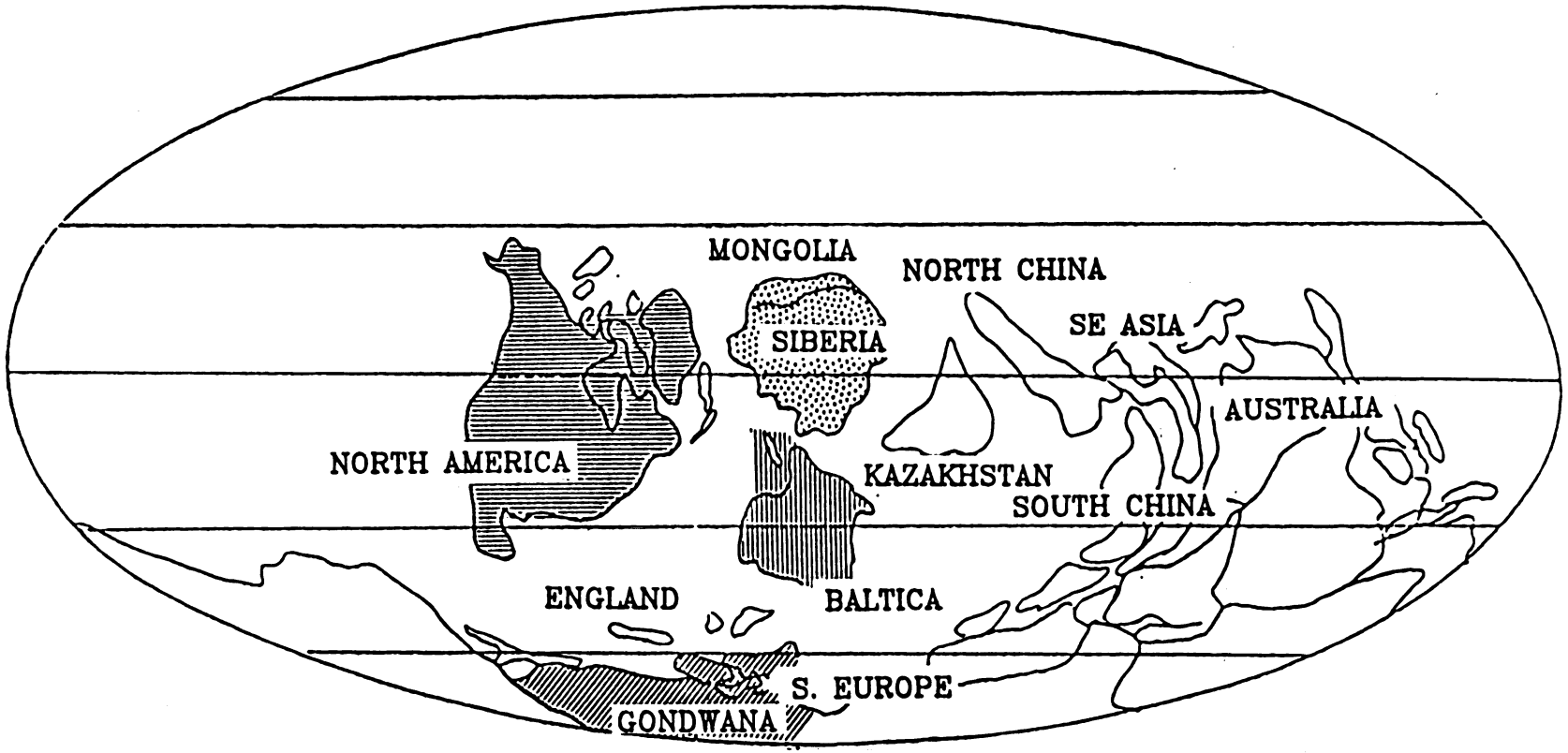


Figure 7. Llandeilo Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American Province

Siberian Province

Baltic Province

Mediterranean Province

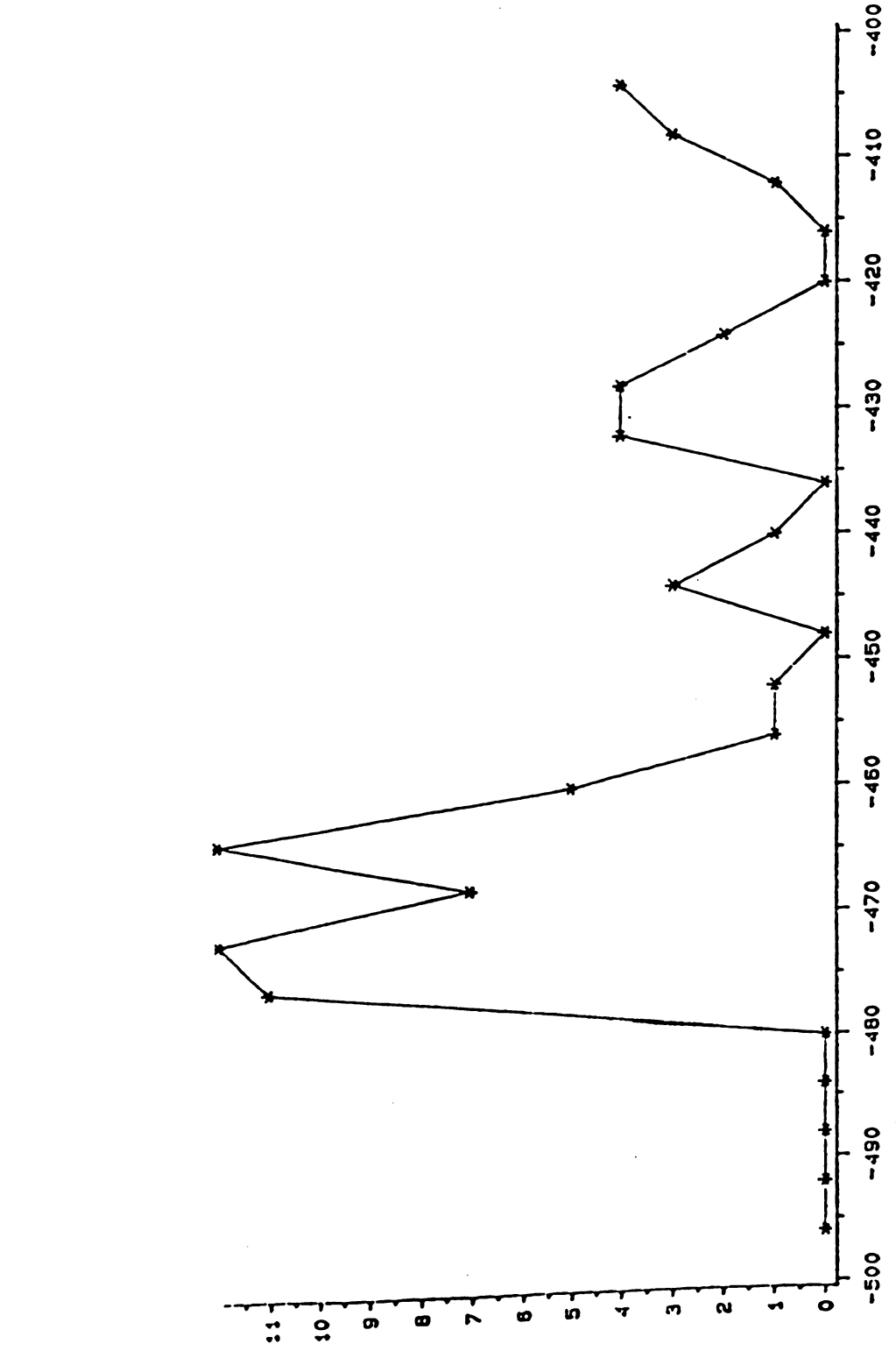


Figure 8. Ordovician and Silurian migrations of bryozoan genera to North America. Y axis = number of migrant genera.

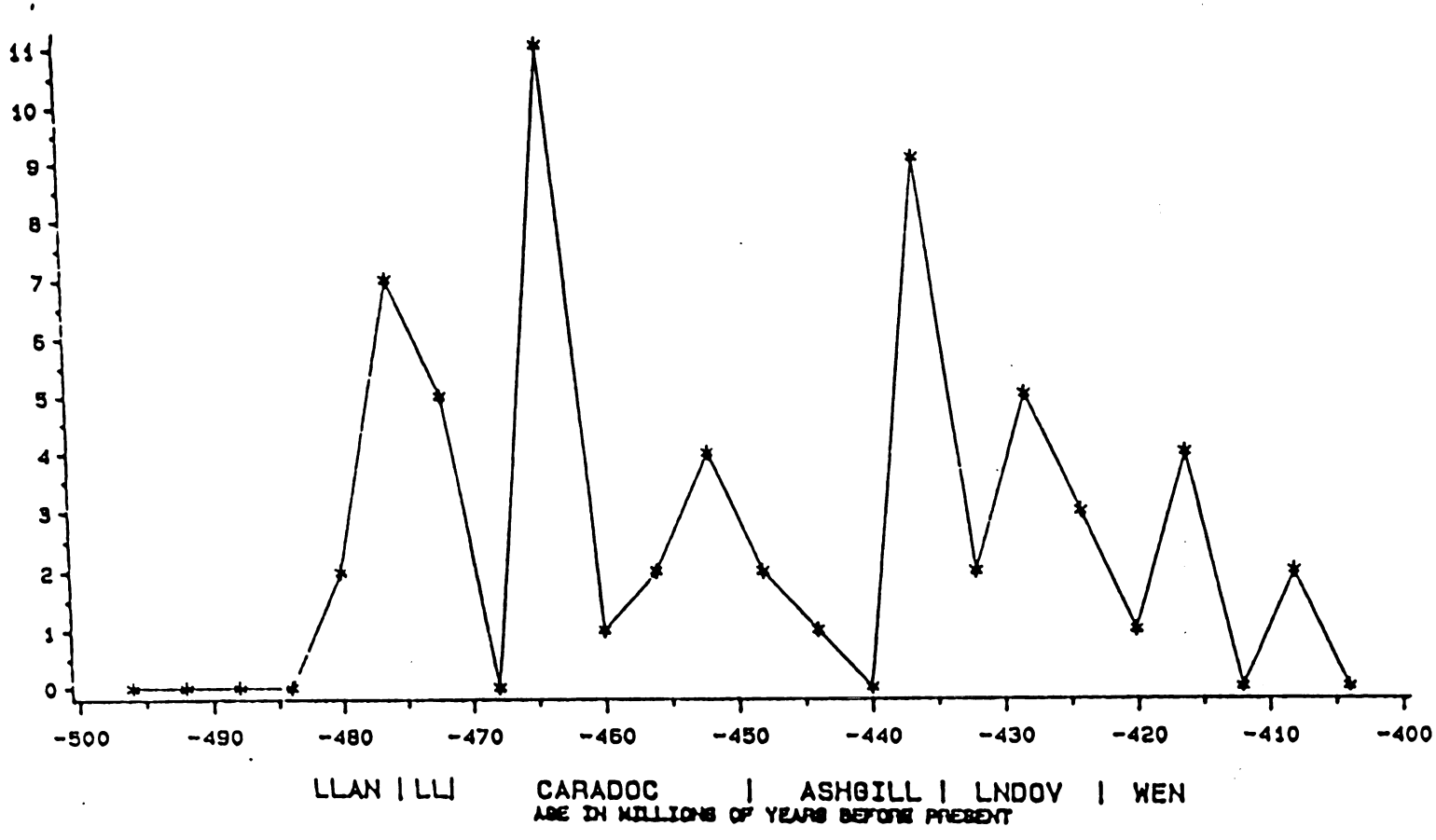


Figure 9. Ordovician and Silurian migrations of bryozoan genera to Baltica. Y axis = number of migrant genera.

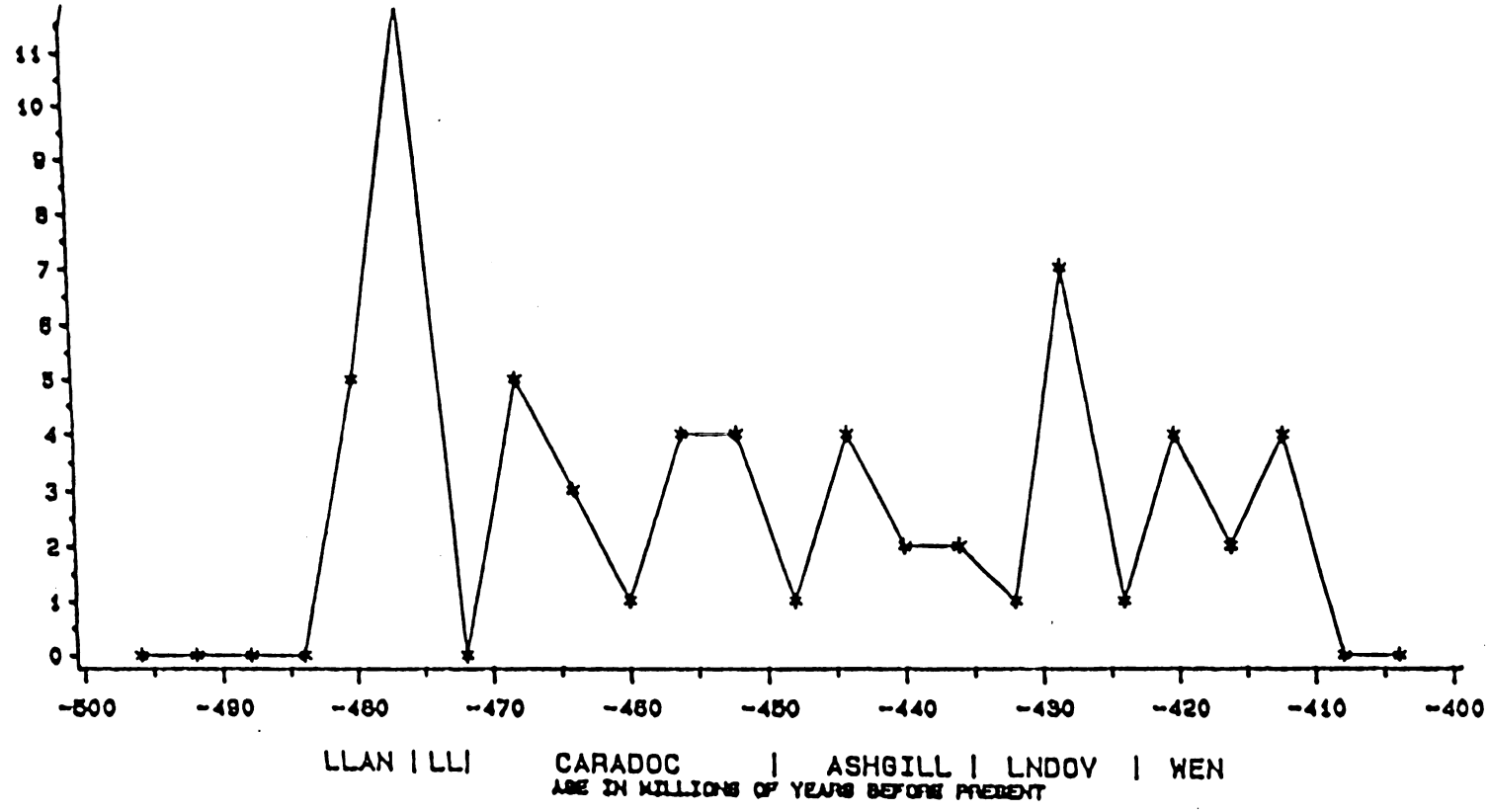


Figure 10. Ordovician and Silurian migrations of bryozoan genera to Siberia. Y axis = number of migrant genera.

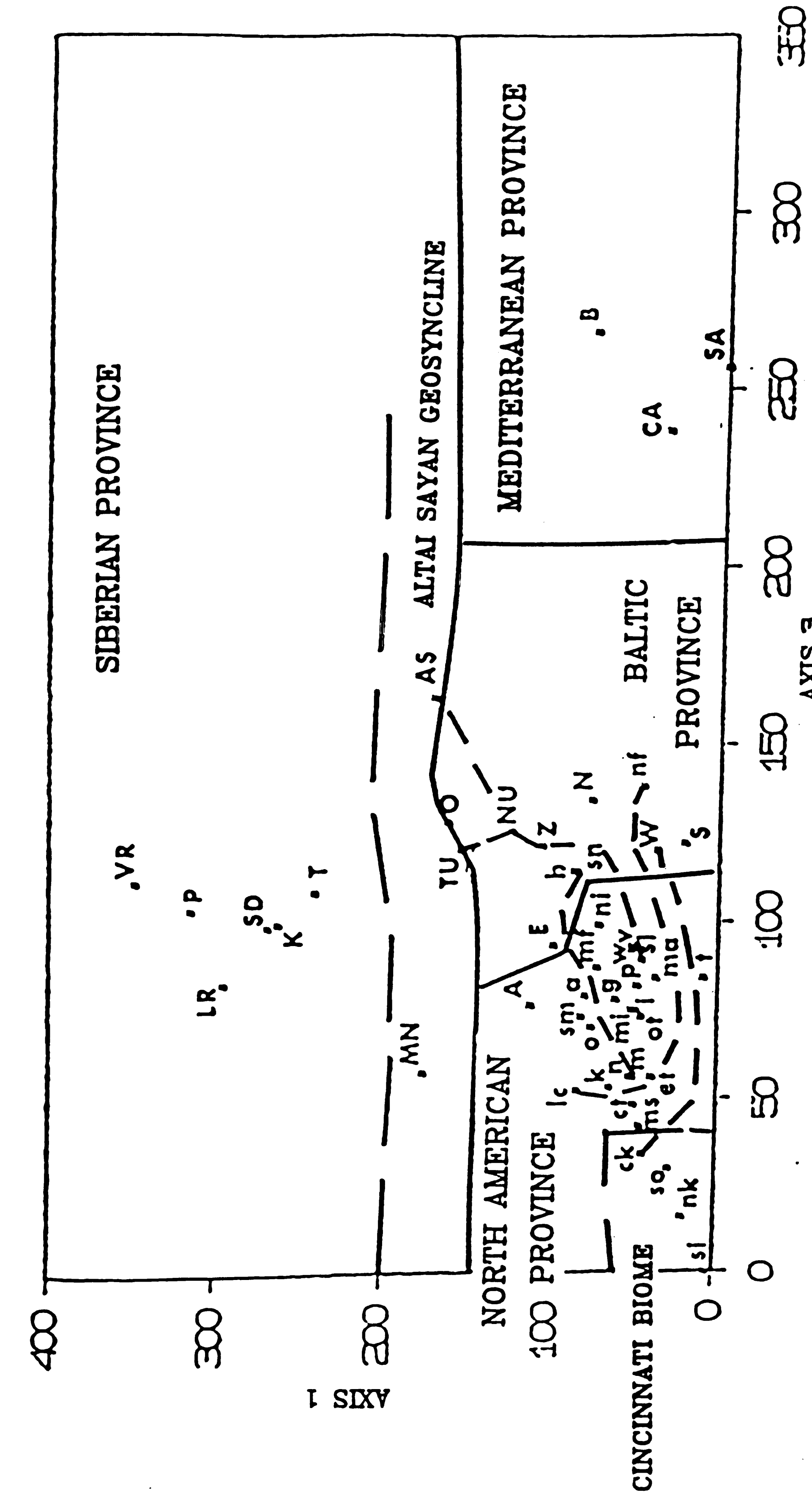
exchange was one-sided, with few Baltic forms appearing in North America.

CARADOC

The four Llandeilian provinces are again seen in the Caradoc (Figure 11). The Siberian Province consists of faunas from the Upper Mangazeyski and Dolborski horizons of the Siberian Platform, the Tolmachev horizon from Taimir, the Upper Malodiring horizon from Kotel Island and the Kulonskaya and Vodopadnenskaya horizons from Sette Daban. Also included in the Siberian Province are faunas from the geosynclinal regions of the Siberian plate in the Altai Sayan, Tuva and Manchuria. Cluster analysis also groups Siberian localities with the exception of the Altai Sayan and Tuva, which are linked with the St. Lawrence River Valley. These localities share the genera Batostoma, Ceramopora, Constellaria, Eridotrypa, Hemiphragma, Homotrypa, Nicholsonella and Parvohallopora. These localities also cluster closely with Uralian geosynclinal localities (North Urals and Novaya Zemyla-Vaygach), again emphasizing the similarity of shelf faunas from the three major plates. The Siberian province is characterized by endemic genera such as Insignia, Carinodictya, Phaenoporella, Sibiredictya and Ensipora.

The Mediterranean Province includes faunas from the Bohdalec Shales of Bohemia and from the Caradoc of Sardinia and the Carnic Alps. These localities have distinctive genera such as Monotrypella and the endemic Polyteichus.

Figure 11. Caradoc DCA axes 1 vs. 3. Symbols: A=Australia, a=Alabama, AS=Altai Sayan, B=Bohemia, b=Burma, CA=Carnic Alps, ck=Central Kentucky, ct=Central Tennessee, E=Estonia, et=East Tennessee, g=Georgia, i=Iowa, K=Kotel Island, k=Kansas, lc=Lake Champlain, LR=Leni River, m=Minnesota, ma=Maryland, mf=Meaford, mi=Manitoulin Island, MN=Manchuria, ms=Missouri, N=Norway, n=Central New York, nf=Newfoundland, ni=Northwest Illinois, nk=North Kentucky, NU=North Urals, O=Oeland, o=Oklahoma, ot=Ottawa, P=Podkammenaya Tunguska River, p=Pennsylvania, S=Sweden, SA=Sardinia, SD=Sette Daban, si=South Indiana, sl=St. Lawrence River Valley, sm=Southwest Mackenzie, sn=Southeast New York, so=South Ohio, T=Taimir, t=Toronto, TU=Tuva, v=Virginia, W=Wales-England, w=Wisconsin, VR=Viluya River, Z=Novaya Zemyla-Vaygach-Pay Khoy. Dotted lines connecting localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.



SIBERIAN PROVINCE
ALTAI SAYAN GEOSYNCLINE
MEDITERRANEAN PROVINCE
BALTIC PROVINCE
NORTH AMERICAN PROVINCE
CINCINNATI BIOME
AXIS 1
AXIS 3
0
50
100
150
200
250
300
350
400
VR
P
SD
K
T
LR
MN
TU
AS
NU
Z
N
nf
W
s
B
SA
CA
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A
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sn
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na
f
a
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Figure 11

The Baltic Province consists of faunas from Estonia, the North Urals, the Novaya Zemlya-Vaygach-Pay Khoy area, the Scandinavian island of Oeland, Sweden, Norway, England-Wales, Burma, Southeast New York and Newfoundland. The fauna from the Naungkangyi shales of Burma seems to have its greatest affinities with the Baltic Province. Williams (1973) also classified Burma with the Baltic Province on the basis of its brachiopods. Burma, as part of a Southeast Asian microcontinent, is geographically distant from Baltica (Figure 12).

Spjeldnaes (1981) raised the possibility of an "anti-boreal" fauna existing in the Northern Hemisphere resembling the south-temperate Baltic fauna of the Southern Hemisphere. Evidence for the existence of this fauna comes from the occurrence of brachipods with Baltic affinities in the Klamath Mountains of California and Alaska. The Baltic bryozoan species Parvohallopora tolli, native to Estonia, was reported from the Caradoc of the Inyo Mountains in California by Pestana (1960), and from the Caradoc of Gaspe, Quebec by Fritz (1941). The fauna from the Southwest McKenzie mountains in Western Canada also has Baltic affinities as indicated by the cluster analysis. Bergstrom (1973) reported that Ordovician conodonts in the Appalachians and in the western Cordilleran regions of North America also have Baltic affinities, differing from the North American midcontinent fauna. Bergstrom attributed these differences to climatic zonation, suggesting that the North American continent was rotated 90 degrees from its present position, with the equator running through the midcontinent and the west and east coasts situated in

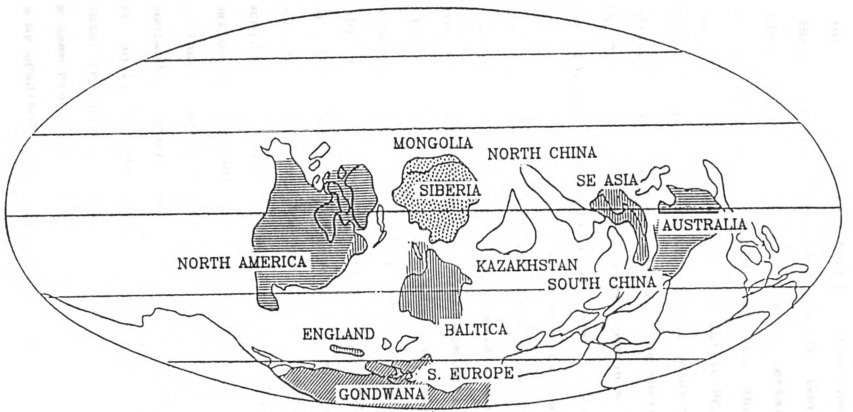


Figure 12. Caradoc Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American Province

Siberian Province

Baltic Province

Mediterranean Province

the north and south temperate zones, respectively. These findings appear to support the "anti-boreal" fauna hypothesis, however, most of these localities represent exotic terranes, and their Ordovician paleogeographic positions are uncertain.

Western Newfoundland, Southeast New York and Southern England-Wales are also included in the Baltic Province. The fauna from Newfoundland is from the autochthonous region of Western Newfoundland. This region was part of the North American plate and its Baltic affinities support Sheehan's (1975) contention that some Baltic brachiopods also lived in the open ocean and occupied habitats around the North American continental margin. The Southeastern New York fauna is also a continental margin fauna, which is found in the Balmville Limestone and the Rysedorph Hill Conglomerate. The Rysedorph Hill Conglomerate has been interpreted as an allochthonous outer shelf deposit, which was transported westward during the Taconic Orogeny (Vollmer and Bosworth, 1984). The existence of this "open-ocean fauna" may explain the recurrent faunal similarities between the geosynclinal localities in the Urals, the Altai Sayan and the Appalachians during the Ordovician. This may be a better explanation of why exotic terranes, such as Burma, have Baltic faunas. These shelf faunas also retain a local imprint, as Newfoundland is grouped most closely with Lake Champlain in the cluster analysis, and Southeast New York is linked with Minnesota. In general, shelf faunas have been grouped as a part of the same biogeographic province as their neighboring platform faunas by gradient analysis.

Southern England-Wales, located close to the North American plate (Figure 12), has a cosmopolitan bryozoan fauna which has affinities with both Baltica and North America. Seven of the nine genera present are shared with both Estonia and Northern Kentucky. Consequently England-Wales clusters closely with localities from the Cincinnati region in North America, but has been classified with the Baltic Province by DCA. Bergstrom (1973) also reported that Upper Middle Ordovician conodont faunas from Wales contained North American midcontinent elements that distinguished them from the rest of the Baltic Province.

In the North American Province, the Cincinnati Biome, previously recognized by Anstey (1986), can be distinguished. The Cincinnati Biome is composed of faunas from the Lower Kope Formation (Late Caradoc) of Southern Indiana, Southern Ohio and Central and Northern Kentucky. Anstey reported the Cincinnati Biome extended from Northern Kentucky to Southern Ontario in the Late Ordovician. However, in the Late Caradoc it is in its incipient stages of development and is geographically restricted to the Cincinnati area.

Australia is tentatively grouped with the North American province, but due to the low diversity of its fauna, its biogeographic affinities remain problematical.

Two waves of faunal migrations occurred during the Caradoc. An early Caradoc (Black River) migration event appears to have taken place in Baltica, North America and Siberia, while a smaller Late Caradoc migration event affected Siberia and Baltica (Figures 8-10). Spjeldnaes (1981) also recognized

the Late Caradoc event (which he termed the Vasalemma wave in reference to the Vasalemma beds in Estonia), as being characterized by a migration of American forms into Baltica.

ASHGILL

The Ashgill brought about a significant change in bryozoan faunas as a breakdown in Caradoc provinciality occurred and a more cosmopolitan fauna began to emerge. Ashgill provinces are delineated by DCA axes one vs. two (Figure 13). Two Ashgillian provinces are discernible: a North American-Siberian Province and a Baltic-Mediterranean Province.

The majority of Siberian localities are allied with North America during the Ashgill; however, the Taimir Peninsula, located on the southern tip of the Siberian plate was geographically adjacent to Baltica during the Ashgill (Figure 14), and its faunas from the Korotkin horizon have Baltic affinities . Although the width of the Iapetus ocean has narrowed considerably, the Baltic Province is still recognizable, as its faunas from Sweden, Norway, Wales, Estonia, Gotland and Novaya Zemlya-Vaygach-Pay Khoy are distinguishable from those of North America. Also included in the Baltic Province is the Ashgill fauna from Montagne Noire, southern France, which indicates that the Mediterranean and Baltic Provinces have merged. Sheehan (1979) noted that brachiopods from the Mediterranean Province became abundant in Sweden during the Ashgill. He believed that

Figure 13. Ashgill DCA axes 1 vs. 2. Symbols: a=Alabama, ai=Anticosti Island, AS=Altai Sayan, bi=Baffin Island, C=South China, ck=Central Kentucky, CM=Central Mongolia, ct=Central Tennessee, E=Estonia, ei=Northeast Illinois, G=Greenland, g=Georgia, GO=Gotland, I=Ireland, i=Iowa, mf=Meaford, mi=Manitoulin Island, MN=Montagne Noire, ms=Missouri, mt=Manitoba, N=Norway, n=New York, nk=North Kentucky, NM=Northwest Mongolia, S=Sweden, si=South Indiana, sl=St. Lawrence River Valley, SM=South Mongolia, so=South Ohio, T=Taimir, t=Toronto, TU=Tuva, up=Michigan Upper Peninsula, v=Virginia, W=Wales, w=Wisconsin, wt=West Texas, wy=Wyoming, Z=Novaya Zemyla-Vaygach-Pay Khoy. Dotted lines connecting localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.

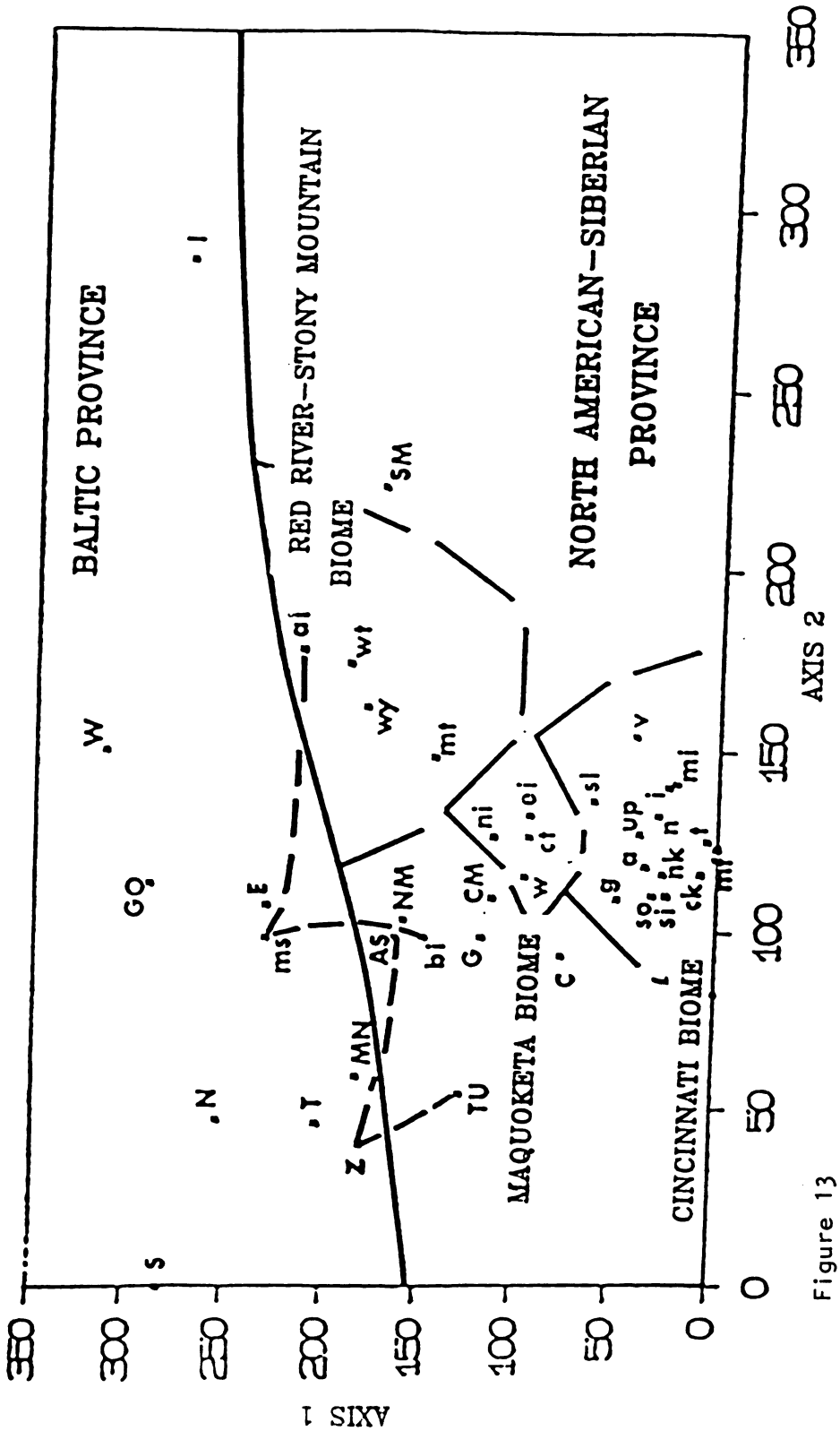

BALTIC PROVINCE
RED RIVER-STONY MOUNTAIN BIOME
NORTH AMERICAN-SIBERIAN PROVINCE
MAQUOKETA BIOME
CINCINNATI BIOME
AXIS 1
AXIS 2
0
50
100
150
200
250
300
350
W
I
N
T
Z
S
GO
E
MS
AS
NM
MN
TU
BI
G
CM
C
AI
WY
WT
SM
MI
NI
CT
OI
SL
V
MI
MF
SO
SI
HK
CK
A
UP
G

Figure 13

cold-water Mediterranean genera moved northward with cold water masses associated with the Ashgillian glaciation in North Africa. However, Whittington (1973) noted the appearance of Mediterranean type trilobites (Selenopeltis fauna) in Baltica as early as Caradoc time.

The fauna from the Portrane Limestone of Ireland is also grouped with the Baltic Province although this fauna is distinctive, as it includes the rare genera Discosparsa and Ichthyorachis. The Portrane Limestone is known to be an exotic terrane representing a volcanic island in the Iapetus Ocean (Neuman, 1984). Neuman has found that many brachiopod genera made their first appearances on oceanic islands.

Missouri-Southern Illinois clusters with the Baltic Province, and much of its fauna is from the Rawtheyan-Hirnantian age Girardeau Limestone. The Baltic Province conforms well with the Hiberno-Salarian fauna of Jaanusson (1973). This brachiopod fauna occurs in carbonate rocks in Sweden, Norway and Ireland and also in the Altai Sayan and in coastal North American localities such as Anticosti Island and Perce, Quebec, Alaska and California. A brachiopod fauna described by Amsden (1974) from the Noix limestone of Eastern Missouri and Western Illinois also has Hiberno-Salairian affinities (Jaanusson 1973). The existence of a Baltic fauna in the continental interior of the United States reflects the increasing cosmopolitanism of the Late Ashgill. The Hirnantian Stage (Latest Ashgill) is associated with a low diversity "Hirnantian fauna" characterized by the brachiopods Hirnantia and Dalmanella and the trilobite

Dalmanitina. The fauna, occurring in mudstones, is extremely widespread geographically and has been reported from Bohemia, Sweden, Ireland, England, Maine, Morocco, the Carnic Alps, Libya, Quebec, Kazakhstan, Scotland, China, Kolyma, and Anticosti Island (Rong 1984).

Ashgillian faunas from the Siberian localities of Tuva, the Altai Sayan, and Northern, Central and Southern Mongolia are grouped with those of North American localities by gradient analysis and particularly resemble faunas from the carbonate platform Red River-Stony Mountain Biome localities of Greenland, Baffin Island, Manitoba, Wyoming, Anticosti Island and West Texas. Distances between the Altai Sayan-Mongolia regions of the North Siberian plate and Canada and Greenland were not far (Figure 14) and oceanic currents (Figure 15) may have facilitated migration between the two areas. The Altai Sayan also shares faunal similarities with nearby Novaya Zemyla-Vaygach, as indicated in the cluster analysis. Kaljo and Klaaman (1973) also have recognized Late Ordovician North American-Siberian and European Provinces for fossil corals.

Also included in the North American-Siberian Province is a fauna from Southern China. Similarities between faunas from Southern China and North America-Siberia suggest an alternative paleogeographic reconstruction (Figure 16) may be more applicable. In this reconstruction the South China plate is positioned in the mid-Pacific, close to the western margin of North America.

Within the North American plate, the Late Ordovician biomes

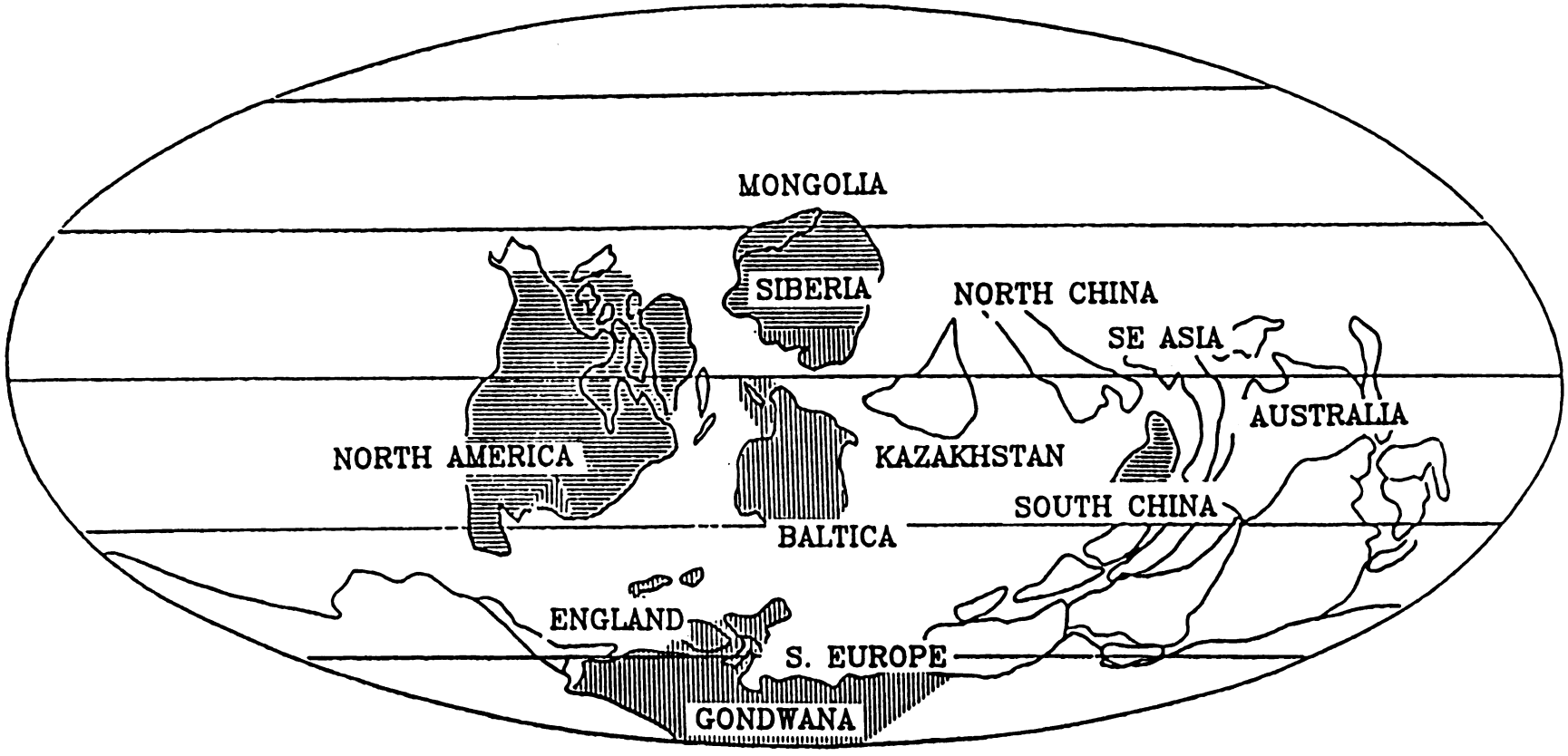


Figure 14. Ashgill Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American-Siberian Province

Baltic Province

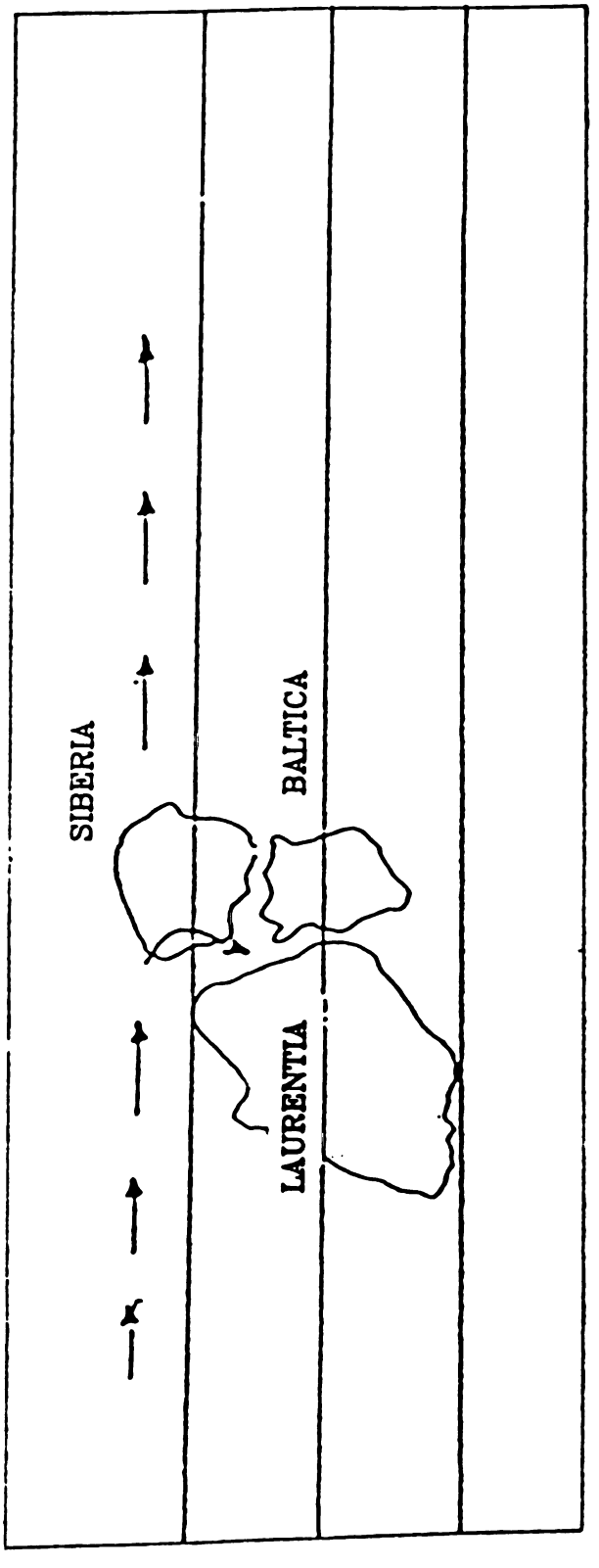


Figure 15. Oceanic Current Patterns for the Silurian, from Ziegler et al, 1981.

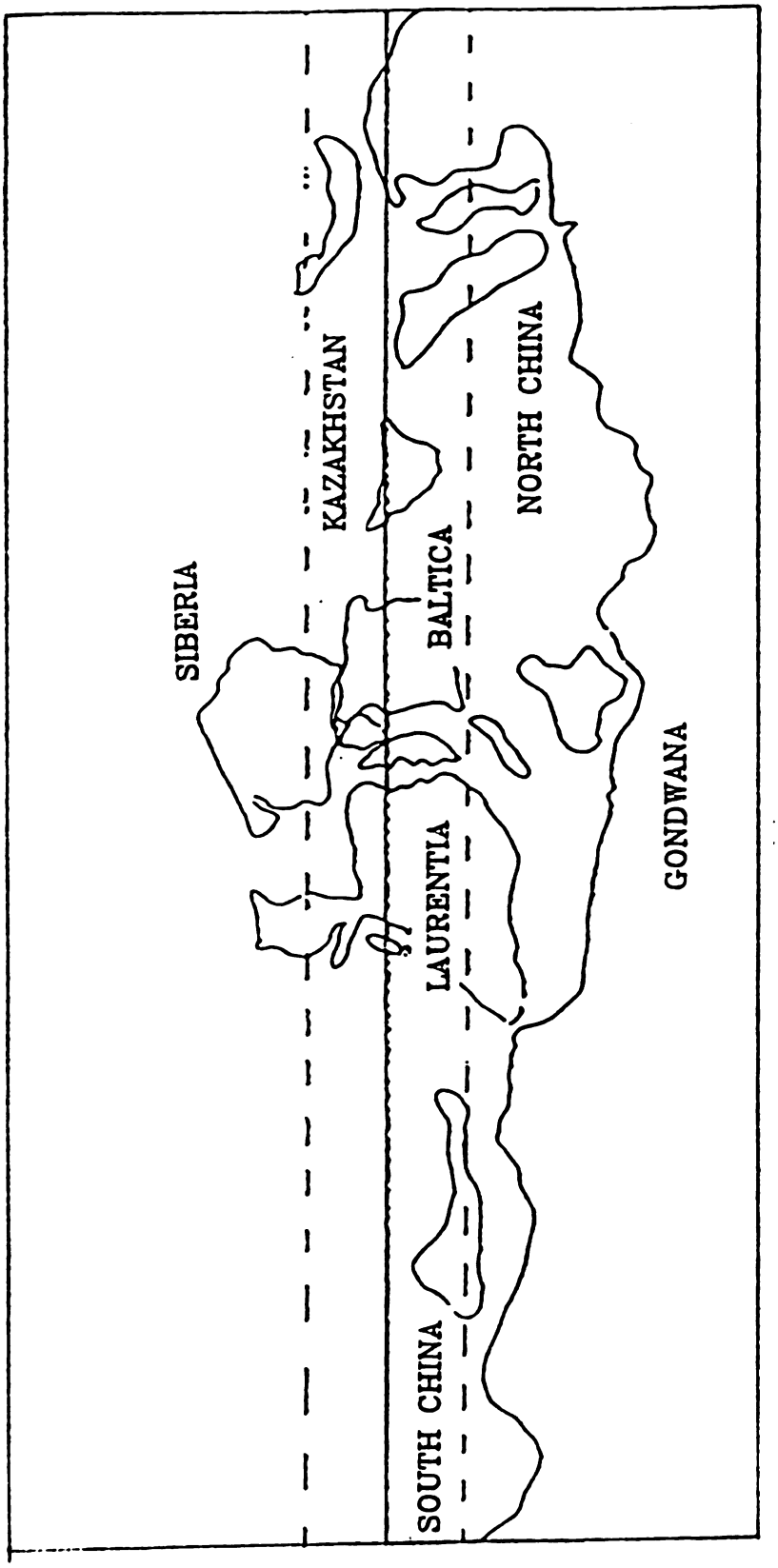


Figure 16. Silurian paleogeographic reconstruction of Ziegler et al, 1977 showing South China plate located off west coast of North America.

of Anstey (1986) can be recognized. The carbonate platform Red River-Stony Mountain Biome is represented by the closely grouped localities of Anticosti Island, West Texas, Wyoming, and Manitoba (Figure 13). Anticosti Island and nearby Baffin Island have been grouped with the Baltic Province by the cluster analysis as many of the localities in the Red River-Stony Mountain Biome have typical Baltic genera. The Maquoketa Biome is represented by the grouping of Wisconsin, Northwestern Illinois, Northeastern Illinois and Central Tennessee, and was recognized as a subunit of the Red River-Stony Mountain Biome by Anstey (1986). The terrigenous Cincinnati Biome has expanded in size since the Caradoc and now includes Georgia, Alabama, the St. Lawrence River Valley, Virginia, Iowa, New York, Manitoulin Island, the Upper Peninsula of Michigan, Toronto and Meaford Ontario, Southern Ohio, Southern Indiana and Central and Northern Kentucky. These localities conform remarkably well to the terrigenous areas of the Upper Ordovician lithofacies map (Figure 17).

A migration wave of largely North American genera into Baltica took place during the Hirnantian (Figures 8-10). Spjeldnaes (1981) has recognized this event as the "Porkuni wave" in reference to the Porkuni Stage (Hirnantian) of Estonia. This wave of migration probably contributed to the increasing cosmopolitanism of Hirnantian faunas.

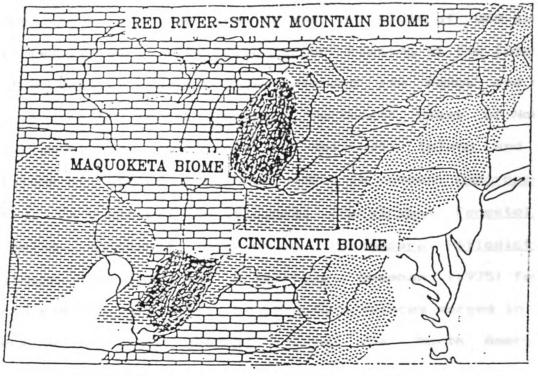


Figure 17. Late Ordovician lithofacies, midcontinental United States, adapted from Frey, 1987.

BASINS

CARBONATE PLATFORMS

MUD–BOTTOM SHELVES

FLUVIAL–DELTAIC PLAINS

LLANDOVERY

Although still faunally distinct, the North American-Siberian and Baltic Provinces have begun to merge during the Llandovery. Faunal provinces are defined on plots of DCA axes one vs. two (Figure 18). With further closing of the Iapetus Ocean, the Baltic province has extended its range and now includes Anticosti Island, on the Northeast coast of North America. Llandoverian formations of Anticosti Island and the Baltic Island of Gotland have these genera in common: Asperopora, Ceramopora, Corynotrypa, Cuneatopora, Cyphotrypa, Fenestella, Glauconomella, Hallopora, Nematopora, Phaenopora, Ptilodictya, Semicoscinium, Thamniscus and Eridotrypa. Sheehan (1975) found that North American and Baltic brachiopod provinces merged in the Llandovery when Baltic genera invaded the North American continent following the Late Ordovician extinctions. North America, Baltica and Siberia all received relatively large numbers of immigrants during the Llandovery (Figures 8-10). Eight genera from the Ashgill of Baltica, Asperopora, Clathropora, Cheilotrypa, Eridotrypella, Fistulipora, Hennigopora, Rhinopora and Thamniscus newly appear on the North American continent during the Llandovery. Three of these genera, Asperopora, Cheilotrypa and Thamniscus newly appear at Anticosti Island, giving the fauna a Baltic aspect.

The North American-Siberian Province includes localities from the Podkammenaya-Tunguska and Viluya River Valleys of the

Figure 18. Llandovery DCA axes 1 vs. 2. Symbols: ai=Anticosti Island, C=Central China, ck=Central Kentucky, E=Estonia, GO=Gotland, mf=Meaford, N=Norway, n=New York, nf=Ontario-Niagara Falls Region, nk=North Kentucky, NM=Northwest Mongolia, o=Oklahoma, P=Podkammenaya Tunguska River, PO=Podolia, si=South Indiana, so=South Ohio, t=Toronto te=Tennessee. TU=Tuva, up=Michigan Upper Peninsula VR=Viluya River. Dotted lines between localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.

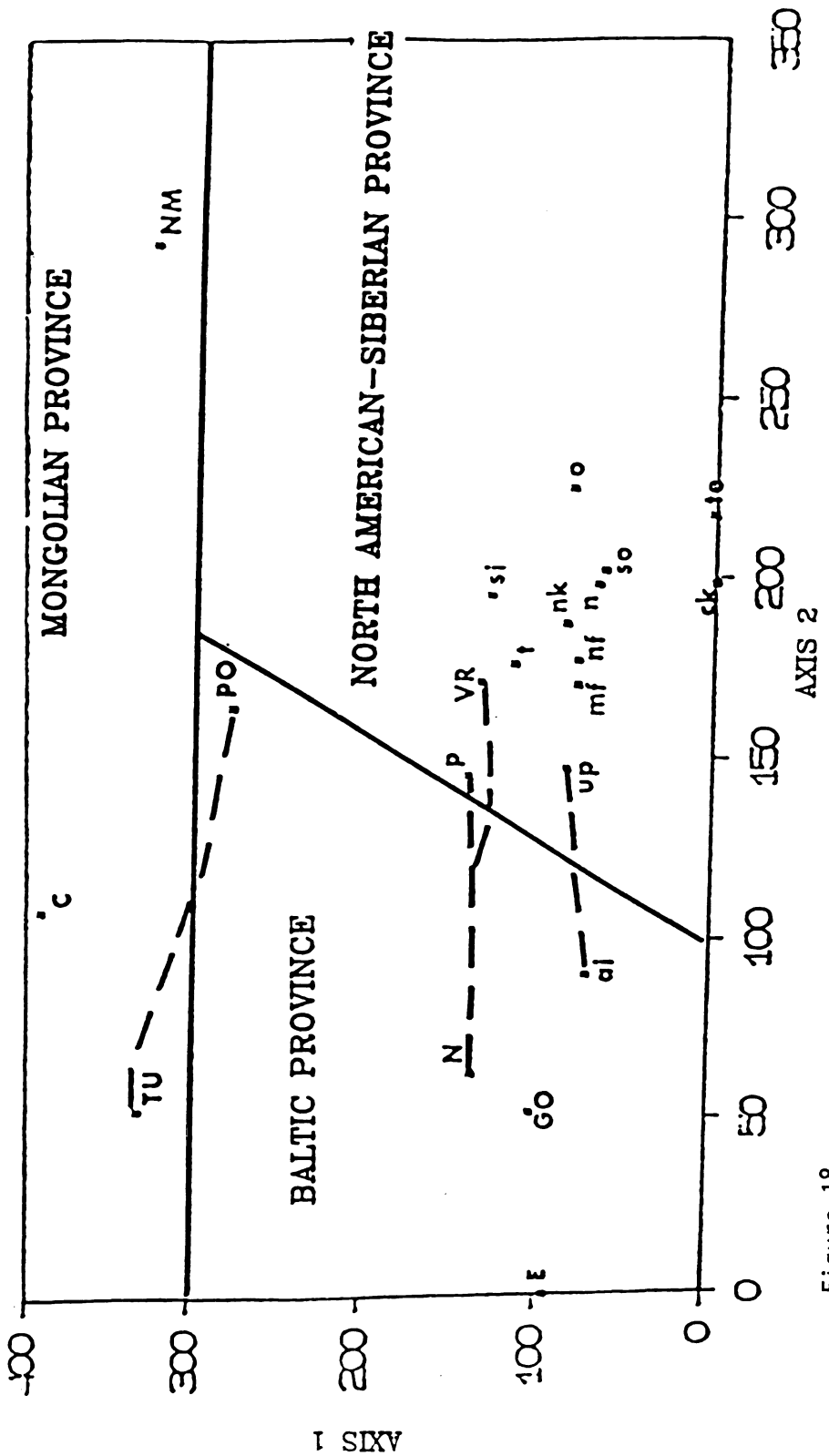

MONGOLIAN PROVINCE
NORTH AMERICAN-SIBERIAN PROVINCE
BALTIC PROVINCE
NM
C
PO
TU
VR
P
N
GO
E
si
nk
mf
nf
so
up
ai
ck
AXIS 1
AXIS 2
-100
300
200
100
0
0
50
100
150
200
250
300
350

Figure 18

Siberian Platform, and the midcontinent regions of North America. The biome partitioning evident in the Ordovician of the North American continent is not present in the Llandovery, as all North American localities were former members of the Ashgillian Cincinnati Biome. The only North American locality remaining from the Ashgillian Red River-Stony Mountain Biome is Anticosti Island. A lack of faunas from other localities within the Red River-Stony Mountain Biome leaves the question as to whether the entire Red River-Stony Mountain Biome took on a Baltic aspect in the Llandovery, subject to additional analysis. The cluster analysis grouped Siberian Platform localities with the Baltic Province, as indicated by the dotted lines. The Podkammenaya-Tunguska River Valley locality shares 5 of its 7 genera with Norway, however it also shares 5 genera with Meaford, Ontario. This reflects the cosmopolitanism of many genera in the Llandovery. Appearing in the Llandovery is a third faunal province, the Mongolian Province, which contains faunas from Tuva, Northwestern Mongolia and Central China. Podolia was linked with this province by the cluster analysis. Tuva and Northwestern Mongolia were situated on the northern portion of the Siberian plate, while Central China rests on the South China plate. Faunal provinces of the Llandovery are plotted on the Silurian paleocontinental reconstruction (Figure 19). Silurian brachiopods show a similar provincialism in this region as Boucot and Johnson (1973) described a provincial Tuvaella Community fauna from the Late Llandovery-Wenlock of Southeast Kazakhstan, Tuva, the Altai Mountains, Mongolia and Manchuria. Ziegler et al

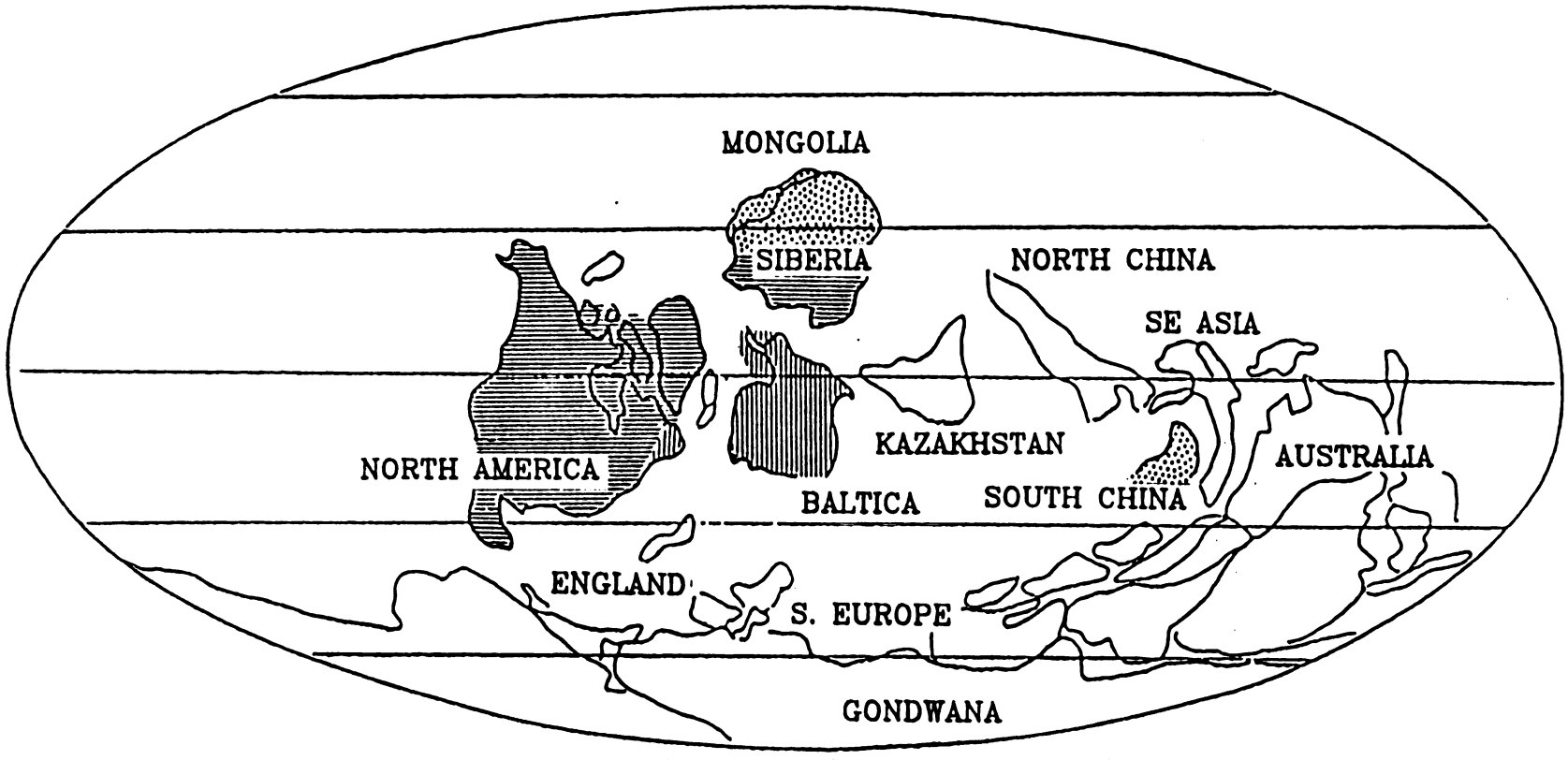


Figure 19. Llandovery Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American-Siberian Province  Mongolian Province 

Baltic Province 

(1977) believe that Silurian provinciality was caused by climatic zonation, with the Mongolian region situated in the north temperate realm. A comparison of paleocontinental reconstructions for the Ashgill and Llandovery (Figs. 14 and 19) reveals that the Siberian continent moved northward during this time interval and provinciality may have developed as the northern portion of the Siberian plate moved into north temperate realms in the Late Llandovery.

The fauna from central China is a low diversity fauna of 5 genera from the Late Llandovery Cuijiago and Lojoping Formations of Northern Sichuan and Southern Shaanxi provinces. Because of its low diversity, biogeographic conclusions are tentative. However, its affinities with the Mongolian Province in the Llandovery, and also in the Wenlock may indicate that the South China plate was also in a north temperate latitude at this time. Scotese (1986) positioned South China near the equator, in accordance with Early Cambrian and Permian paleomagnetic data. South China's faunal similarity with Mongolia in the Llandovery and Wenlock suggest that it may have drifted northward in the Ordovician-Silurian and returned to an equatorial latitude by the Permian.

Podolia (West Ukraine) is regarded as belonging to the Baltic province, although it shares two genera in common with Central China, Fistulipora and Hennigopora. Podolia was located on the southern portion of the Baltic plate at this time and the faunal affinities between Podolia and the Mongolian province can perhaps be explained by the similar Late Llandovery ages of their

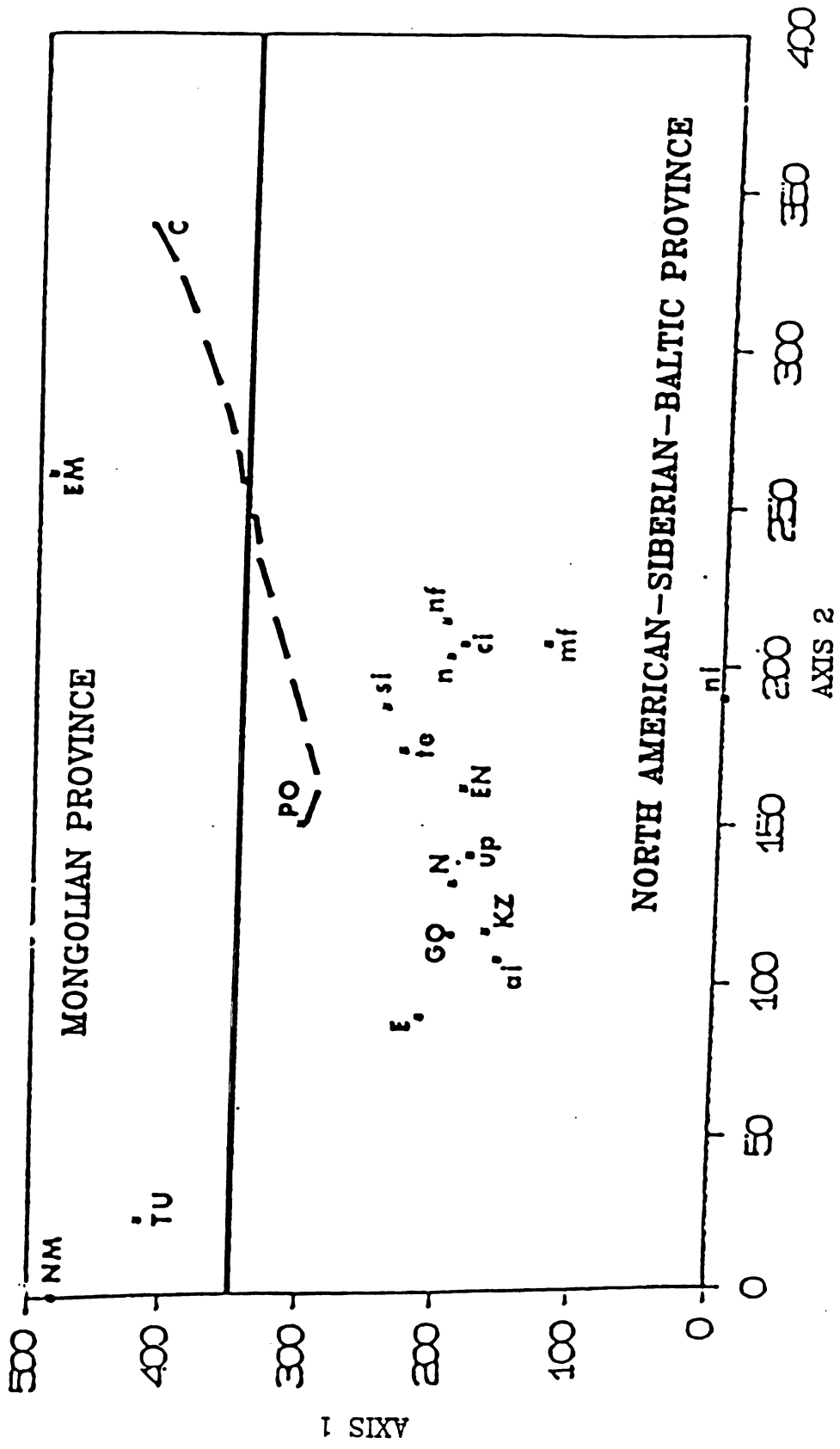
faunas rather than by geographic proximity.

WENLOCK

During the Wenlock, the merging of the Baltic and North American-Siberian Provinces was completed. All Baltic and North American localities group as a single cluster (Figure 20). Also included in the Baltic-North American-Siberian Province is a fauna from the Wenlock of Kazakhstan. Kazakhstan is pictured as a separate continent located in the tropical climatic zone east of Baltica and North America (Figure 21). Baltic and North American localities share a number of common genera in the Wenlock, among them: Asperopora, Ceramopora, Corynotrypa, Fenestella, Fistulipora, Hallopora, Monotrypa, Ptilodictya and Sagenella. A somewhat unusual fauna was described from Northwest Illinois by Grubbs (1939). This fauna occurred in the Niagaran reefs of the Racine Dolomite, of Wenlock-Ludlow age, and included endemic genera such as Pholidopora and Arthrostylus.

Also reappearing in the Wenlock is the Mongolian faunal province from the northern Siberian plate. The province is composed of faunas from the Wenlock of Northwest Mongolia, Tuva, East Mongolia and Central China. There appears to have been some longitudinal zonation in this province, as Tuva and Northwest Mongolia, on the northeastern side of the Siberian plate have

Figure 20. Wenlock DCA axes 1 vs. 2. Symbols: ai=Anticosti Island, C=Central China, ci=Central Indiana, E=Estonia, EM=East Mongolia, EN=England, GO=Gotland, KZ=Kazakhstan, mf=Meaford, N=Norway, n=Western New York, nf=Ontario-Niagara Falls Area, ni=Northwest Illinois, NM=Northwest Mongolia, PO=Podolia, si=South Indiana, te=Tennessee, TU=Tuva, up=Michigan Upper Peninsula. Dotted lines connecting localities across provincial boundaries indicate additional faunal similarities detected by cluster analysis.


MONGOLIAN PROVINCE
NORTH AMERICAN–SIBERIAN–BALTIC PROVINCE
NM
TU
EM
C
PO
SI
IO
NF
CI
MF
NI
E
GO
N
UP
EN
AI
KZ
AXIS 1
AXIS 2
500
400
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200
100
0
0
50
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150
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250
300
350
400

Figure 20

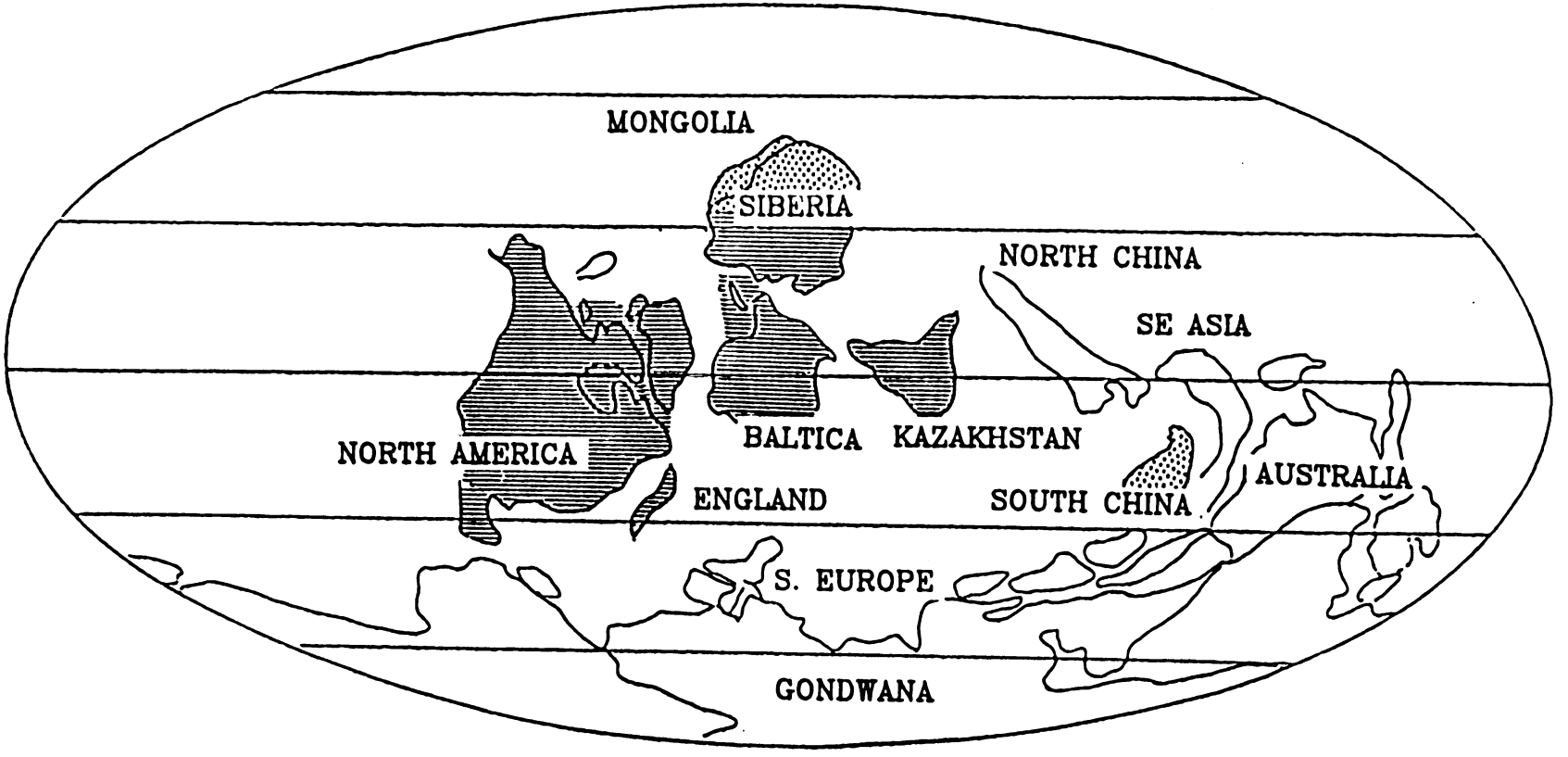

Figure 21. Wenlock Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American-Siberian-Baltic Province

Mongolian Province

faunal similarities, while East Mongolia, on the northwest side of the Siberian plate has greater faunal affinities with Central China, which suggests a paleogeographic position for South China as indicated in Figure 16, although at a more northerly latitude. Podolia was again linked with the Mongolian Province in the cluster analysis.

The complete merging of the North American and Baltic Provinces in the Wenlock slightly preceded closing of the Iapetus Ocean, as Late Silurian folding in Scotland and Norway suggests that the Northern Iapetus had closed by Ludlow or Pridoli time (Cocks and McKerrow, 1973).

LUDLOW

The Ludlow was a time of cosmopolitanism among the Bryozoa. The Mongolian Province of Llandovery-Wenlock time has disappeared as faunas from Mongolia and Tuva now show high faunal similarities with European and American faunas (Figure 22). Distinctive faunas again occur in the Niagaran reefs of Northwest Illinois, and also in the Quganhebu and Xibiehu Formations of Inner Mongolia. Ludlovian faunal gradients are controlled by the presence of distinctive faunas at single localities rather than by provinciality. The fauna from Inner Mongolia was located on the North China plate, and contains the genera Anaphragma,

Figure 22. Ludlow DCA axes 1 vs. 2. Symbols: A=Australia, B=Bohemia, ca=Canadian Arctic, d=Dolgiy Island, E=Estonia, EN=England, GO=Gotland, i=North Indiana, IM=Inner Mongolia, MN=Montagne Noire, mv=Moldavia, ni=Northwest Illinois, NM=Northwest Mongolia, PO=Podolia, S=Sweden, SM=South Mongolia, te=Tennessee, TU=Tuva, w=Wisconsin, Z=Novaya Zemyla-Vaygach-Pay Khoy..

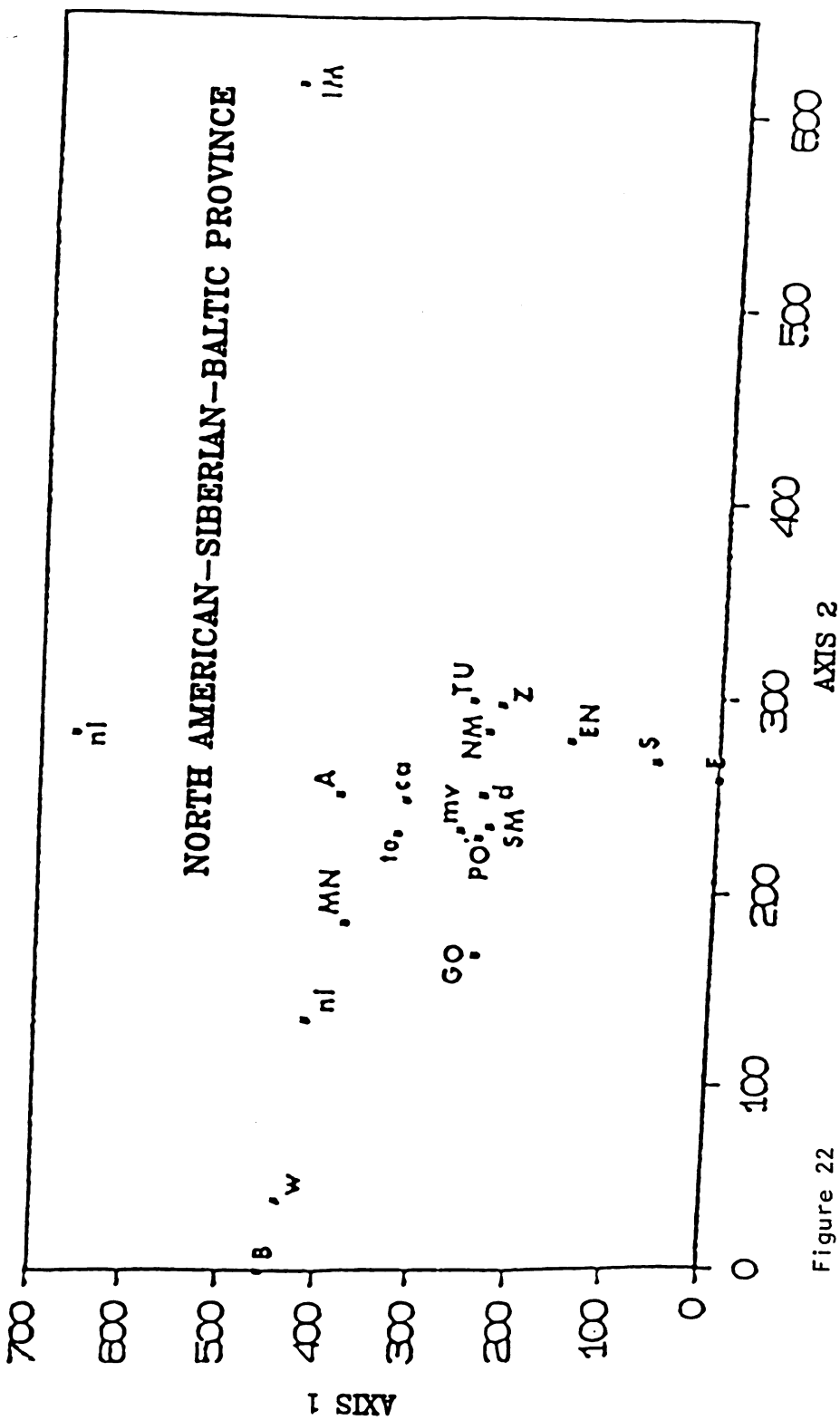
NORTH AMERICAN–SIBERIAN–BALTIC PROVINCE
AXIS 1
AXIS 2
0
100
200
300
400
500
600
700
B
W
MN
A
GO
PO
SM
NM
TU
Z
EN
S
E

Figure 22

Eridotrypa, Homotrypa, Paralioclema and Stictopora. Although Llandoverian-Wenlock faunas from the South China plate had faunal similarities with the Mongolia-Tuva region, this fauna from the North China plate is distinctive in nature.

The cosmopolitan Baltic-North American-Siberian Province consists of faunas from Southern and Northwest Mongolia, Tuva, Gotland, Novaya Zemlya-Vaygach-Pay Khoy, Podolia, Sweden, Estonia, Moldavia, England, Tennessee, Arctic Canada, Australia, Wisconsin, Northern Indiana, Northwest Illinois, Bohemia and Montagne Noire (Figure 23). These localities show a high degree of similarity to one another and contain common Late Silurian genera such as Fistulipora, Fenestella, Hallopora and Monotrypa.

PRIDOLI

The cosmopolitanism of the Ludlow continued into the Pridoli. There is little biogeographic differentiation into provinces among faunas from Estonia, Podolia, Gotland, Northwest Mongolia, South Mongolia, Pennsylvania, Maryland, West Virginia, New York, Oklahoma and Tuva (Figure 24). The fauna from the Taugantelyski Formation of Tuva shows a high degree of dissimilarity with other faunas. It is a low diversity fauna of 5 genera: Amplexopora, Eridotrypella, Eridotrypa, Heterotrypa and Stigmatella. This fauna has a distinctly Ordovician aspect to it

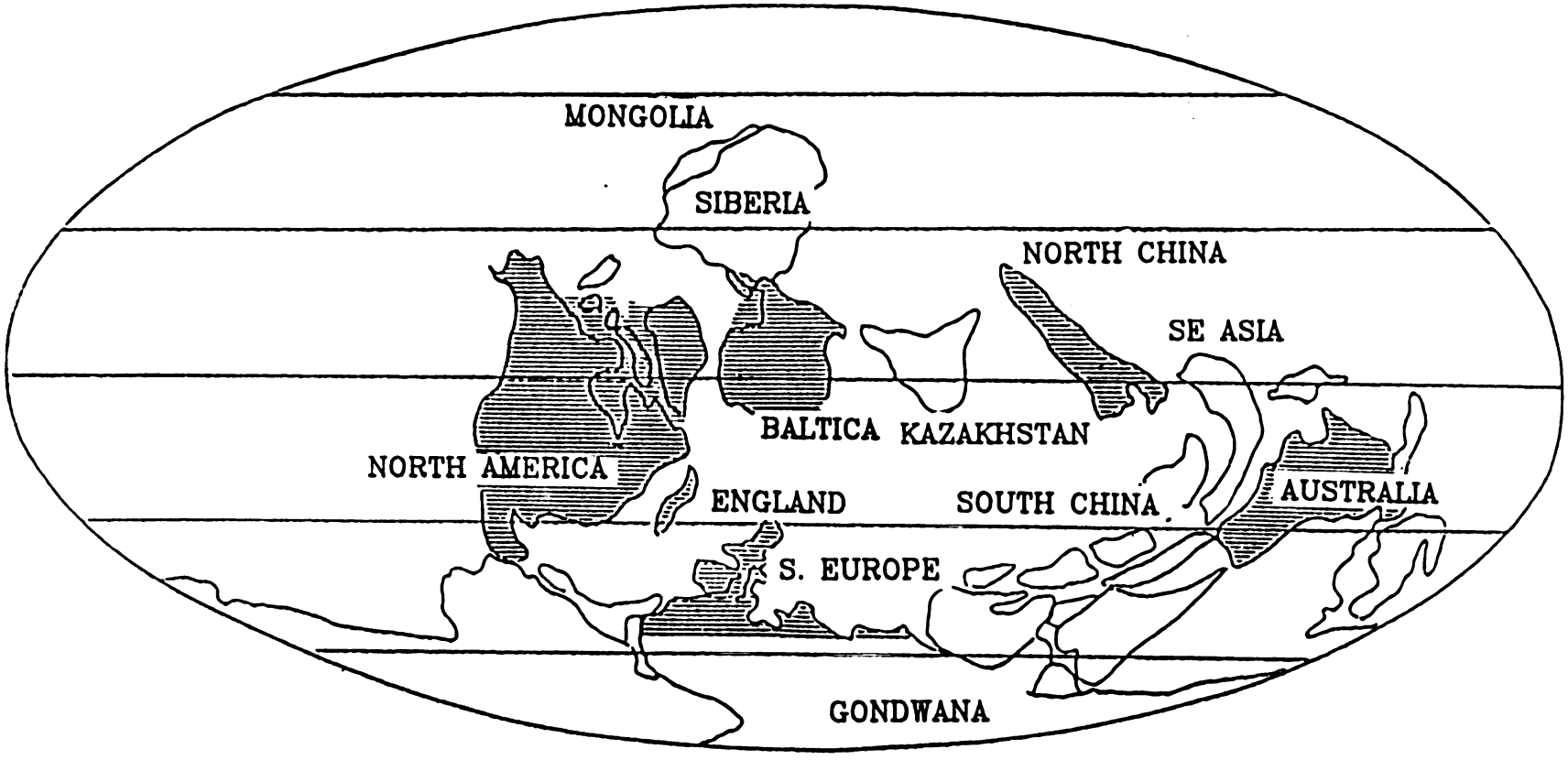

Figure 23. Ludlow Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North America-Siberian-Baltic Province

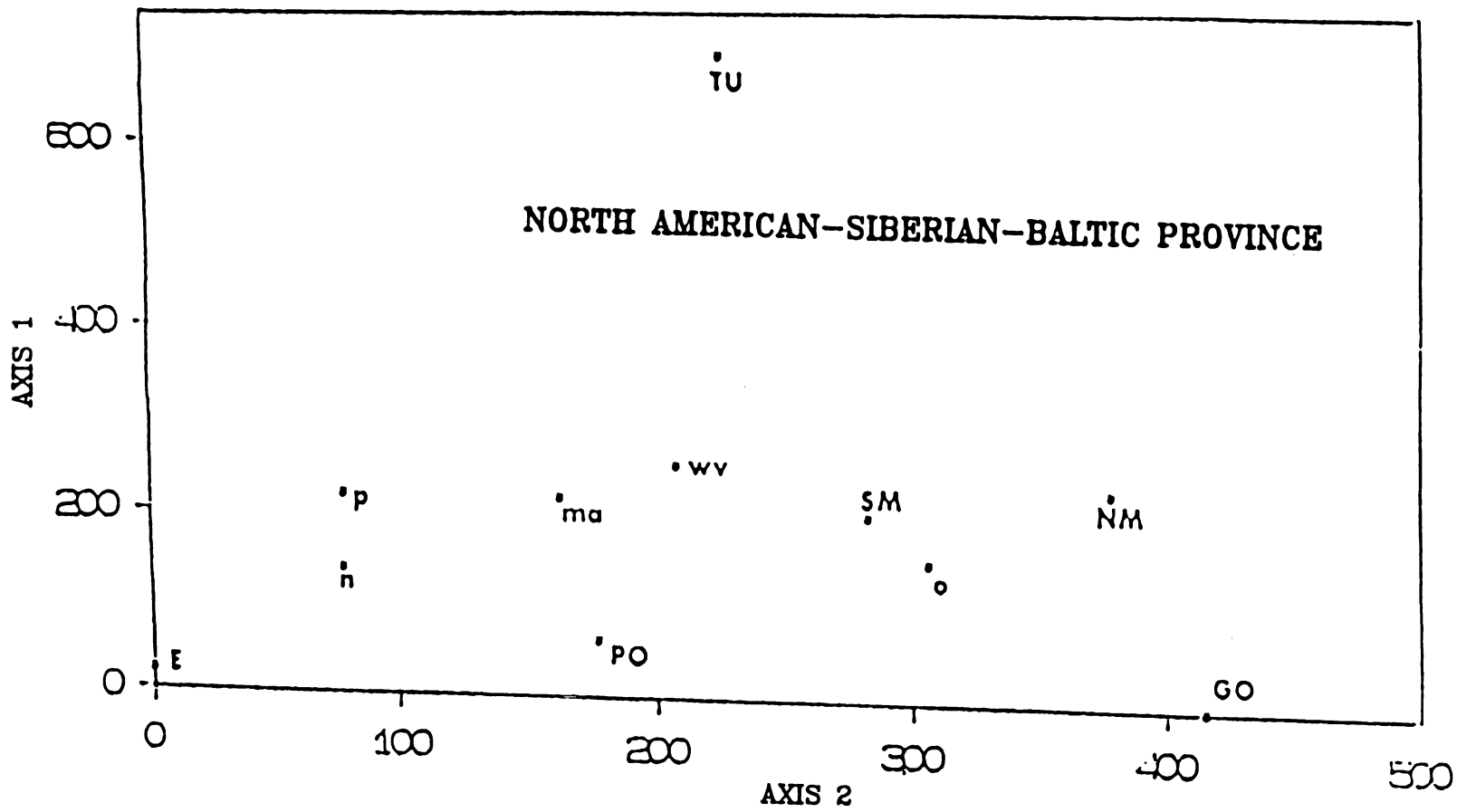

Figure 24. Pridoli DCA axes 1 vs. 2. Symbols: E=Estonia, GO=Gotland, ma=Maryland, n=New York, NM=Northwest Mongolia, o=Oklahoma, p=Pennsylvania, PO=Podolia, SM=South Mongolia, TU=Tuva, wv=West Virginia.

as most of these genera were abundant in the Caradoc and Ashgill. However, Ludlovian faunas from Tuva also contain these "Ordovician" genera along with more typical Silurian genera such as Fistulipora, Hallopora and Lioclema.

Another highly endemic fauna is found in the reef community of the Hamra Formation in Gotland. Along with Fenestella and Fistulipora are found the endemic genera Saffordotaxis, Flabellotrypa and Sagenella. These faunas from Tuva and Gotland are interpreted to be communities within the cosmopolitan Baltic-North American-Siberian Province. Pridoli faunal provinces are shown in Figure 25.

DISCUSSION

Patterns in the biogeographic distribution of the bryozoa are generally consistent with those found in other fossil groups and can be explained by continental convergence and latitudinal climatic gradients. However many interesting questions are raised by anomalous patterns of distribution, such as the presence of a Baltic fauna in the Ashgill of Missouri, and the presence of Baltic faunas on both the east and west coasts of North America and in Burma.

Spjeldnaes (1981) and Bergstrom (1973) explained the presence of Baltic brachiopod and conodont faunas on the west coast of North America by hypothesizing that the west coast of

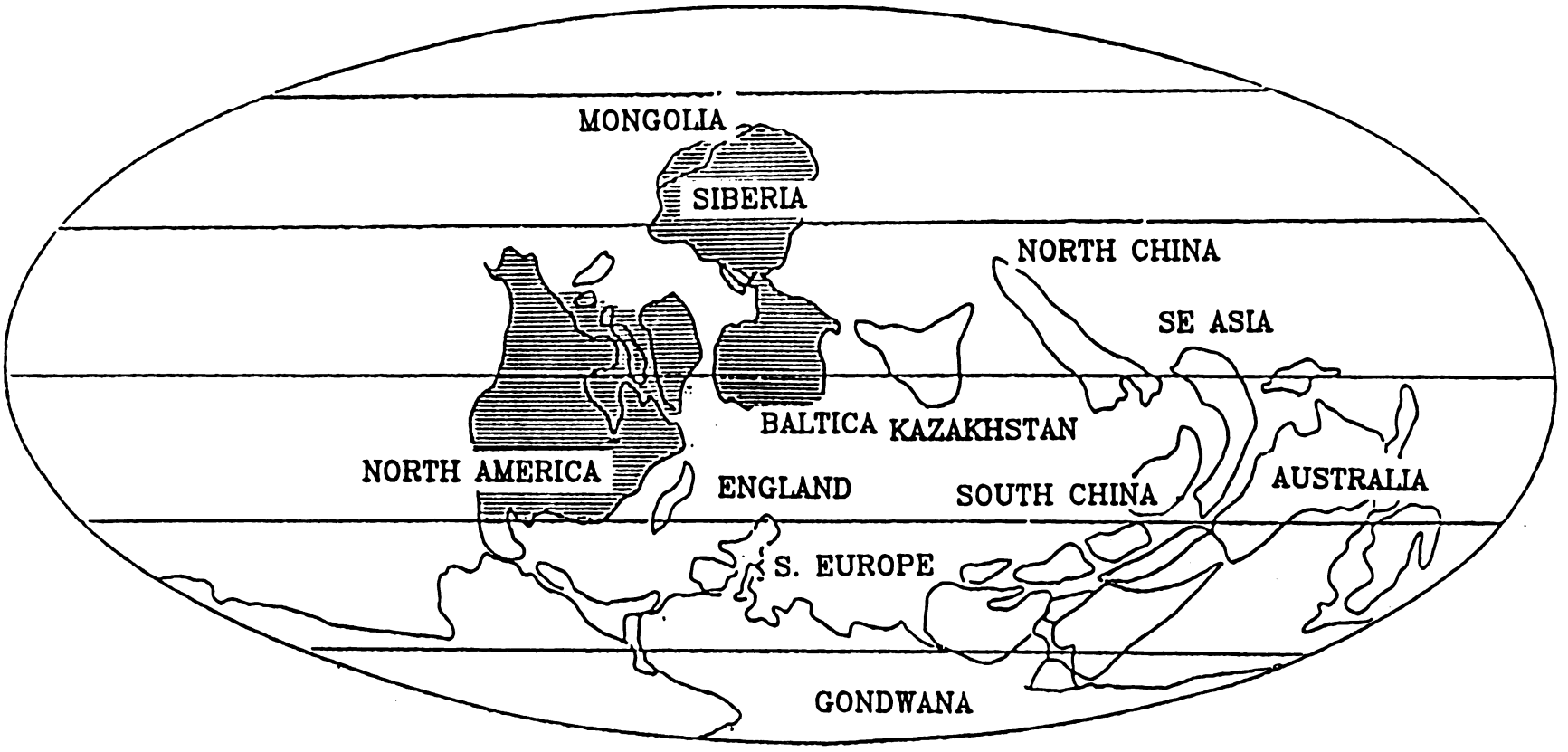

Figure 25. Pridoli Faunal Provinces. Paleogeographic reconstruction from Scotese, 1986.

North American-Siberian-Baltic Province

North America was above the equator in the north temperate zone. The coastal faunas were believed to be temperate (antiboreal) faunas, which mirrored the south-temperate (boreal) Baltic faunas. This idea is not supported by the continental reconstructions of Scotese (1986), however, as the west coast of North America is projected to be lying in equatorial latitudes through the Ordovician and Silurian Periods. Also, many of the fossiliferous localities on the west coast are believed to be exotic terranes. The Klamath Mountain region, where a Baltic brachiopod fauna has been found, has been interpreted to be the remnants of an island arc, which was separated from the continent by a marginal basin (Potter et al., 1977). Nur and Ben Avraham (1977) suggested that allochthonous terranes in Western North America are remnants of a microcontinent called Pacifica originally located near Australia. Other island arc faunas, such as those of the Portrane Limestone, have also been classified as being of Baltic affinity. Faunas from Newfoundland, Southeast New York and Anticosti Island, on the North American east coast, have also been linked with Baltica. Mitchell (1986) stated that the Shan Plateau area of Burma was part of a Western Southeast Asia microcontinent island arc system which collided with Eastern Southeast Asia in the Triassic. Thus it appears that the Baltic fauna was an open ocean fauna inhabiting islands and continental margin localities, as well as the Baltic platform, as Sheehan (1975) stated for brachiopods, and was not confined to temperate latitudes.

The Baltic nature of the Missouri Ashgillian fauna has

previously been recognized in formations of Latest Ordovician (Hirnantian) age by Amsden (1974, brachiopods) and by Elias (1982, corals). Elias labeled this region of Missouri, Illinois, and, tentatively, Northeastern Oklahoma, as the Edgewood Province, and suggested that the fauna migrated into this region from the south during the Late Hirnantian transgression, which resulted from deglaciation. However, the bryozoan fauna in this region is found in the Fernvale, Maquoketa, Orchard Creek and Girardeau Formations, which range from Mid Ashgill to Early Hirnantian in age. This indicates that the Baltic fauna migrated in at a much earlier time than has previously been recognized. Caradocian faunas in this region are similar to those recognized elsewhere in the Midcontinent; therefore the migration of Baltic bryozoan faunas into this region probably occurred in the Mid Ashgill.

The Missouri-Southern Illinois region is near the northern extent of the Mississippi Embayment, and is a seismically active zone, which was the site of the New Madrid Earthquake. Crustal instability in this region is related to the presence of a Late Precambrian rift zone, termed the Reelfoot Rift (Ervin and McGinnis, 1975). Precambrian rifting gave way to the development of the Reelfoot Basin in Cambrian-Ordovician time (Schwalb, 1969). The depositional center of the Reelfoot Basin was located in Western Tennessee in the Cambrian. By the Early Ordovician, the center of deposition had moved northward into Western Kentucky, and by Silurian time the center of the basin was located in Southern Illinois. Schwalb has dated the timing of

basin development through a series of isopach maps, and related the thick accumulation of Maquoketa sediments to a downwarping of the basin which occurred after deposition of the Caradoc age Kimmswick Limestone. Elevation of the adjacent Ozark and Nashville Domes was associated with basin subsidence through lateral displacement of mantle material from beneath the rift.

The development of the Reelfoot Basin may be related to the migration of the Baltic fauna into the Missouri-Southern Illinois region. First appearances of Baltic genera in this region occurred during Maquoketa time, which coincides with evidence for Maquoketa basin subsidence. Perhaps basin subsidence allowed free migration of Baltic continental margin faunas into the Reelfoot Basin. This biogeographic information may be regarded as an independent test for the timing of basin subsidence. A Baltic brachiopod fauna was described from the Hirnantian age Keel Formation in the Arbuckle Mountains of Oklahoma by Amsden (1974). The Arbuckle Mountain region is also the site of a Precambrian rift zone which developed into an Ordovician basin (Ross, 1976). Perhaps migration of Baltic brachiopods into this region was related to synchronous Late Ordovician basinal subsidence in Oklahoma.

The Reelfoot Basin evidently provided a source for some migration of Baltic genera into adjacent areas of the continental interior which led to the formation of the Maquoketa Biome. The Baltica genera Diplotrypa and Sceptropora newly appeared in the Missouri-Southern Illinois area during Maquoketa time, and simultaneously appeared in several of the areas which constitute

the Maquoketa Biome (Northwest Illinois, Northeast Illinois, Wisconsin and Central Tennessee). Anstey (1986) also noted the predominance of Baltoscandian genera in the Maquoketa Biome. Although most biomes can be related to differences in lithofacies, the presence of Baltic immigrants differentiates the Maquoketa Biome from the Red River-Stony Mountain Biome in Ashgillian carbonate terranes in North America. Witzke (1987) attributed Maquoketa phosphorite deposition in the midcontinent to a transgression in which poorly oxygenated water upwelling at the Ouachita continental margin deposited the phosphatic shales and limestones of the basal Maquoketa. The subsiding Reelfoot Basin may have provided a nearer source for the upwelling of poorly oxygenated water. The Maquoketa transgression may also have carried bryozoan larvae from the basin to nearby areas on the craton, providing immigrants to the Maquoketa Biome.

SUMMARY

Bryozoan biogeography reflects many of the same patterns observed in earlier studies of brachiopods and trilobites. Provinciality is high in the Middle Ordovician, with four provinces recognizable in the Llandeilo and Caradoc (North American, Baltic, Siberian and Mediterranean). In the Ashgill, a cosmopolitan fauna emerged as two provinces are recognizable: A North American-Siberian Province and a Baltic-Mediterranean

Province.

The merging of the North American-Siberian and Baltic Provinces took place in the Silurian with continued closing of the Iapetus Ocean. This merging was a gradual process however, as Western Newfoundland and Southeast New York had Baltic affinities as early as Caradoc time. In the Mid Ashgill, the midcontinent Missouri-Southern Illinois area took on a Baltic aspect, and in the Llandovery, the Anticosti Island fauna had Baltic affinities. However, North American localities in the midcontinent areas of Cincinnati, Ohio, Tennessee, New York and Ontario remained provincial even in the Llandovery, although several Baltic genera migrated to North America at this time. It was not until the Wenlock when North America, Siberia and Baltica coalesced into a single province. This complete merging of Baltic and North American bryozoan faunas postdated the merging of brachiopod and trilobite faunas, perhaps due to a lower migratory capacity for the bryozoa, or possibly due to more powerful quantitative techniques of discrimination used in this study.

Climatic zonation appears to have been important in the development of provinciality in the Silurian, as a north-temperate Mongolian Province developed on the northern portion of the Siberian plate and extended to the northern portion of the South China plate in the Llandovery and Wenlock. The Silurian closes with a cosmopolitan fauna showing no provinciality in the Ludlow and Pridoli.

CHAPTER TWO

TIMING AND BIOGEOGRAPHY OF THE EARLY RADIATION OF THE BRYOZOA

INTRODUCTION

Bryozoans first appeared in the Lower Ordovician, and like many other groups in Sepkoski's (1981) Paleozoic Fauna, greatly diversified in the Middle Ordovician. Diverse faunas have been described from three major continental plates: North America, Baltica and Siberia, and smaller faunas have been described from Southern Europe, North Africa, Australia, China, and the British Isles. Within continental plates, faunas often differ from geosynclinal shelf localities to localities on the continental platform. A major extinction took place in the Late Ordovician, and global diversity dropped significantly. The major orders of Bryozoa show differences in the timing of their radiations, with the trepostomes being most abundant in the Ordovician and declining in the Silurian relative to the other groups. In the following review, the early radiation of the Bryozoa is examined through an analysis of the first appearances of 2156 species of bryozoans recorded from the Ordovician and Silurian strata of the world. These data are then used to test hypotheses on the environmental and geographic factors involved in evolutionary innovations.

TIMING OF THE RADIATION

The earliest recorded bryozoan was described from the Late Tremadoc Kindblade Formation of Oklahoma (Ross, 1966a). Bryozoan diversity gradually expanded in the Arenig, Llanvirn and Llandeilo before reaching its maximum in the Caradoc. Early Ordovician originations were greatest in Baltica; however the major radiation during the Middle Ordovican was most prominent on the North American plate. In North America, 464 new species and 31 new genera have been described from Caradocian sediments, although only two new families appeared (Figures 26, 27 and 28).

The Caradoc radiations coincide with a major eustatic transgression, which began in the Llandeilo and inundated the cratonic interior of North America. This Caradocian transgression has also been reported from the British Isles and Poland (McKerrow, 1979 and Leggett et al, 1981). The role of transgressions in inducing radiations was predicted by Fortey (1984), who associated the flooding of cratonic interiors and formation of epeiric seas with rapid increases in rates of speciation in epicontinental areas, due to spatial heterogeneity and the "species area effect". Cooper (1977) also related marine transgressions to biotic diversification and increased rates of evolution. However the subsequent Llandoverian transgression was not associated with a major radiation.

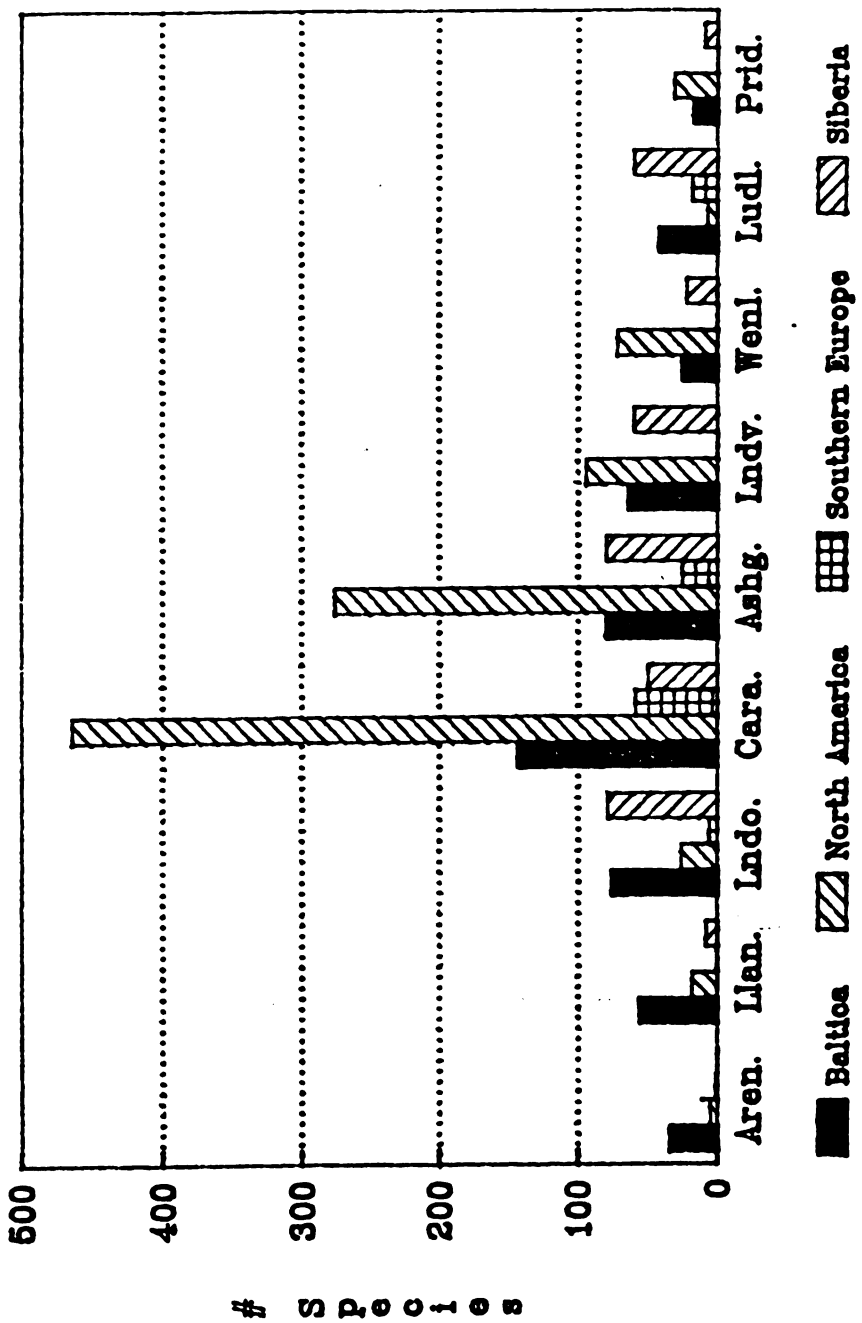

Figure 26. Originations of bryozoan species per continental plate during the Ordovician and Silurian. Aren.=Arenig, Llan. =Llanvirn, Lndo.=Llandeilo, Cara.=Caradoc, Ashg.= Ashgill, Lndv.=Llandovery, Wenl.=Wenlock, Ludl.=Ludlow, Prid.=Pridoli.

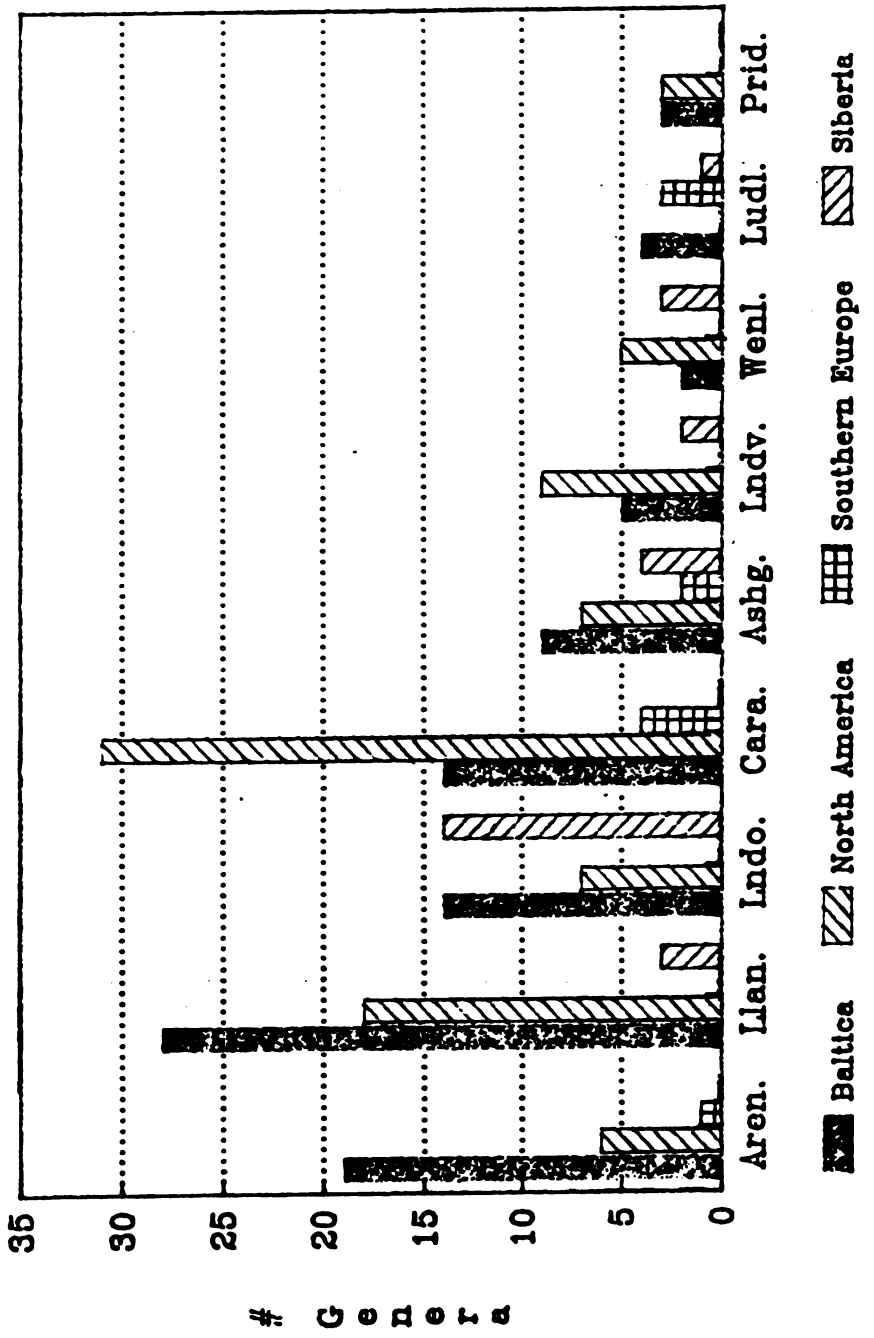

Figure 27. Originations of bryozoan genera per continental plate during the Ordovician and Silurian.

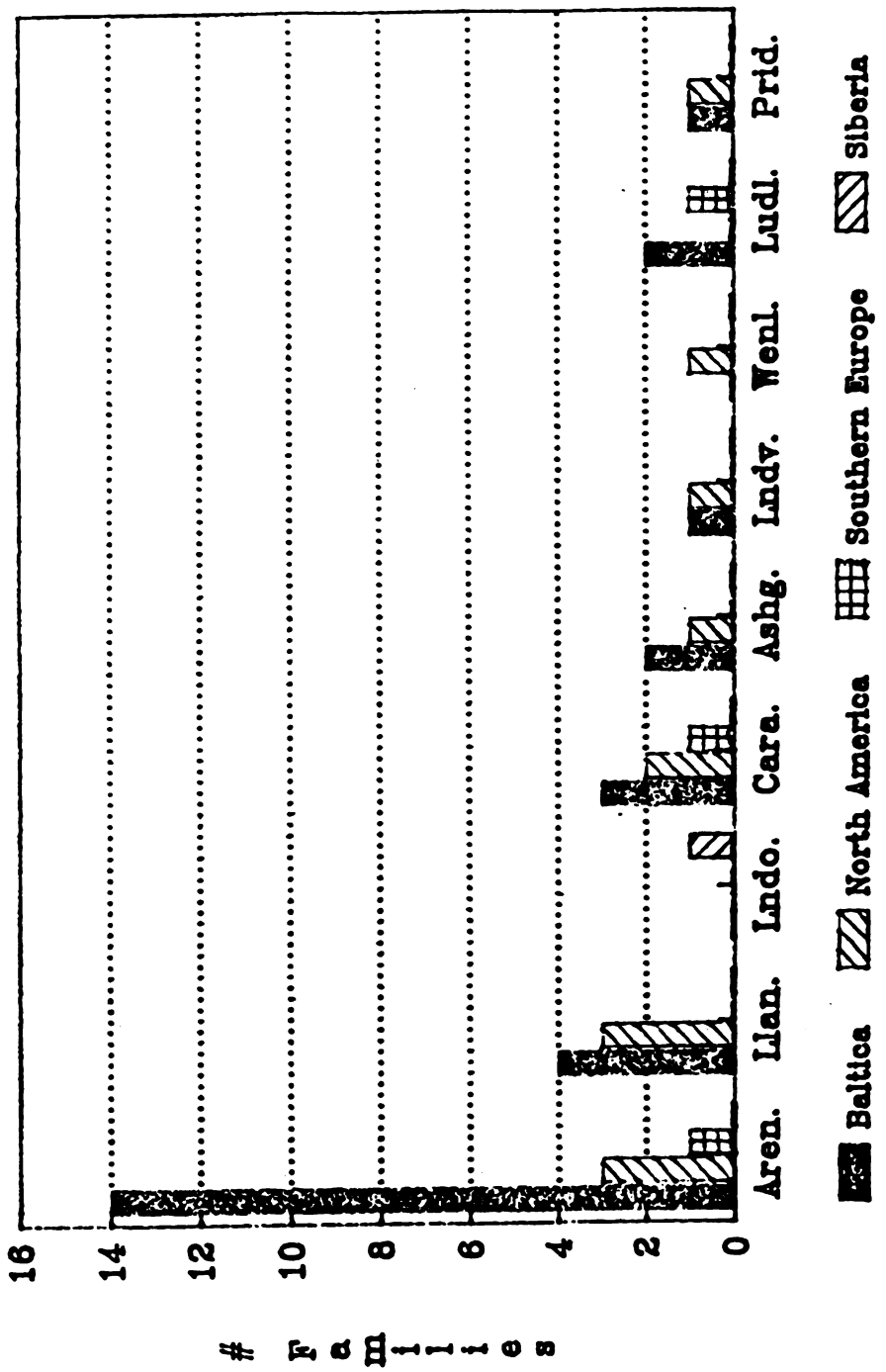

Figure 28. Originations of bryozoan families per continental plate during the Ordovician and Silurian.

Diversification at the species level continued in the Ashgill of North America, as 276 new species have been described; however only seven new genera were reported from North America during the Ashgill. The rate of speciation was actually highest during the Llandeilo, in the early stages of the transgression, as approximately 47 new species per million years appeared (Figures 29, 30 and 31). Due to the short duration of the Llandeilo (approximately 4 Ma), the absolute number of new species originating is much less than the Caradoc. Following the Llandeilo, the Caradoc and Ashgill have remarkably similar rates of evolution of new species (approximately 32 new species/Ma) Rates of evolution of new genera were highest in the Llandeilo and Llanvirn.

Following the Ashgill, evolutionary rates dropped considerably in the Silurian, again remaining remarkably constant through the Llandovery, Wenlock and Ludlow at 23 new species/Ma. Although total diversity dropped considerably following the Late Ashgill extinctions (Figures 32 and 33), no major rediversification of the Bryozoa is seen in the Llandovery. This depression of the speciation rate may be related to the high incidence of generic extinction observed in the Wenlock through Pridoli (Figure 34), as existing genera may have gradually dwindled by not producing enough new species to replace extinctions. The low evolutionary rates observed in the Silurian may also be related to the decreasing Silurian provinciality brought about by continental convergence.

Bryozoan suborders may be divided into two evolutionary

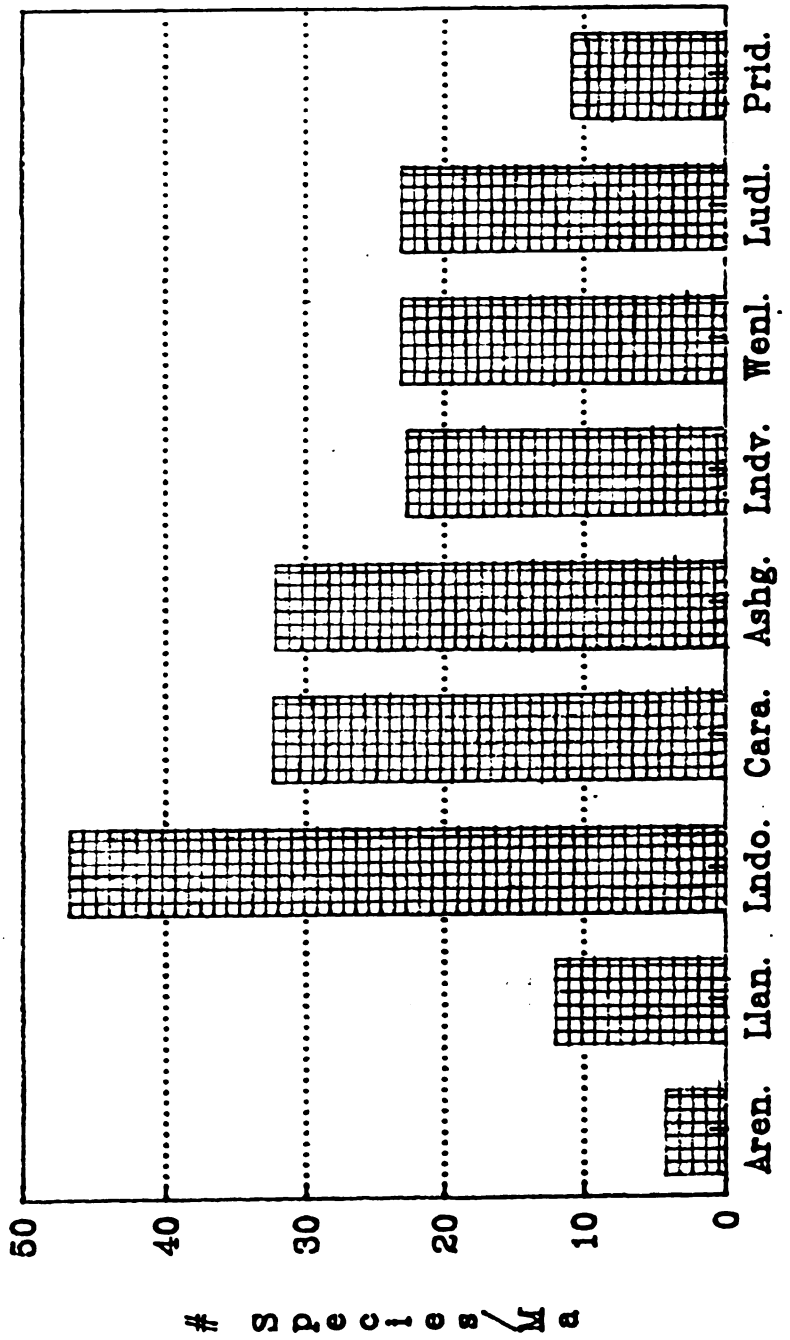

Figure 29. Worldwide bryozoan speciation rates for the Ordovician and Silurian, expressed as number of new species per million years.

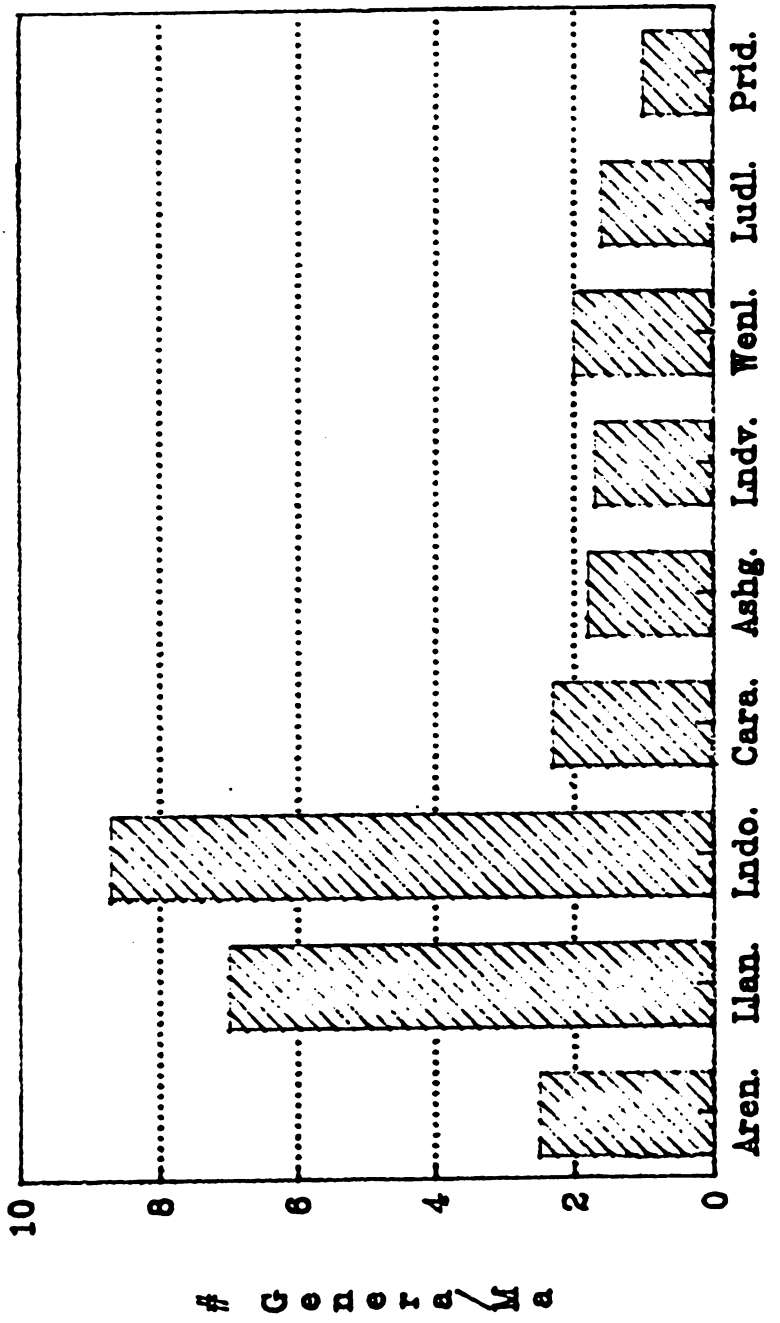

Figure 30. Worldwide bryozoan evolutionary rates for the Ordovician and Silurian, expressed as number of new genera per million years.

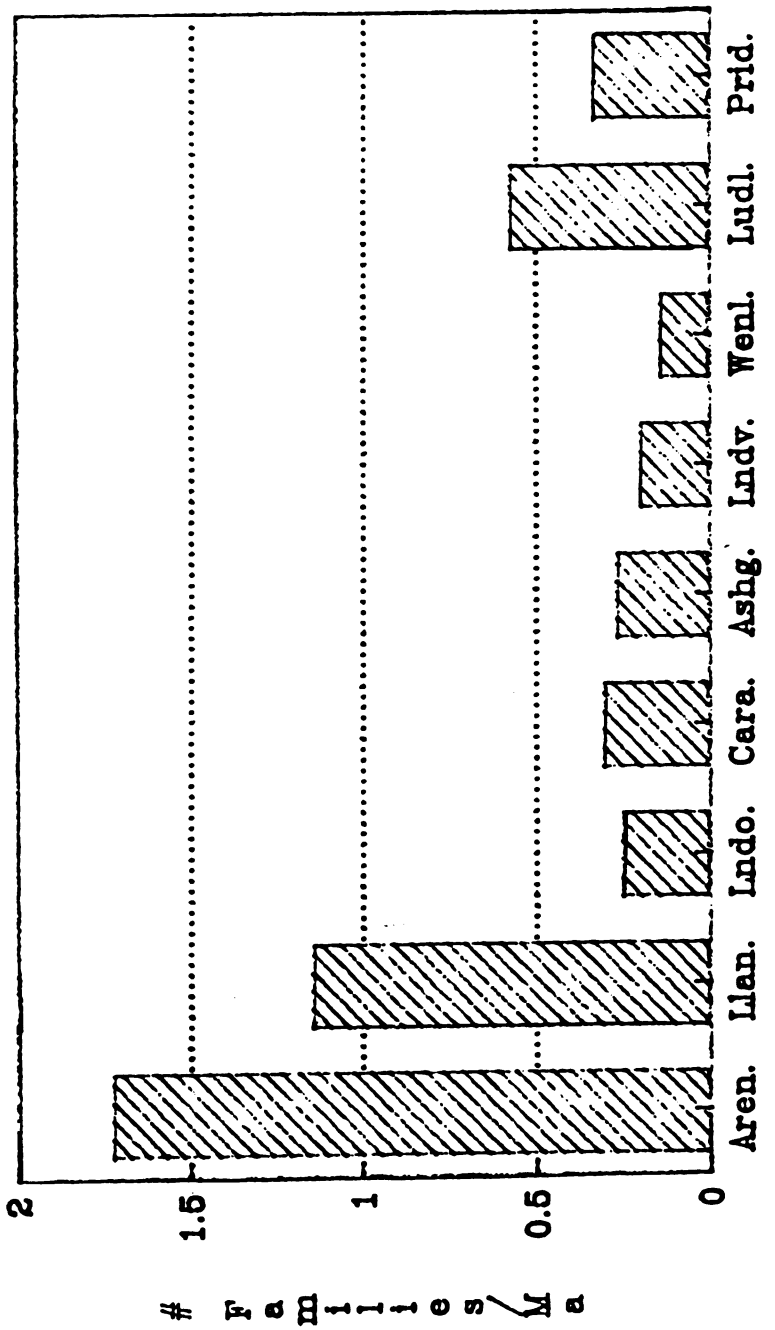

Figure 31. Worldwide bryozoan evolutionary rates for the Ordovician and Silurian, expressed as number of new families per million years.

Figure 32. Total diversity of bryozoan species for the Ordovician and Silurian, expressed as number of species recorded in each stage.

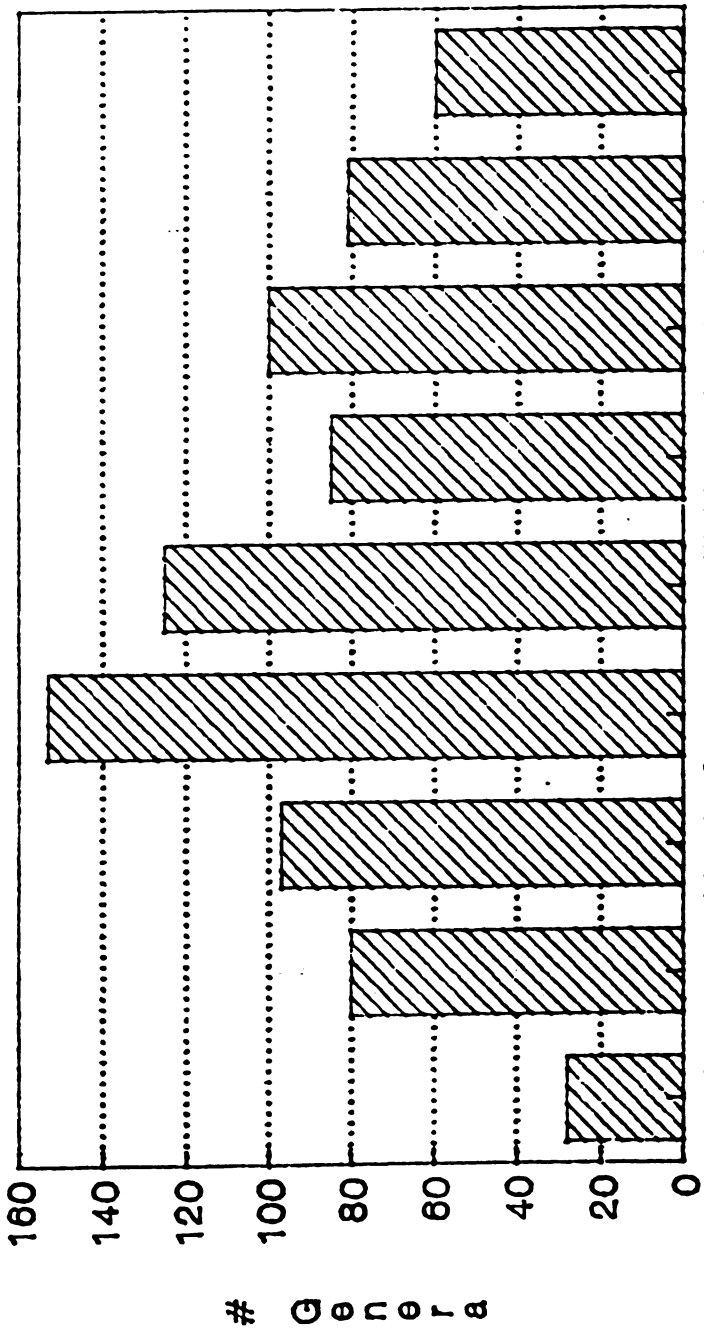

Figure 33. Total diversity of bryozoan genera for the Ordovician and Silurian, expressed as number of genera recorded in each stage.

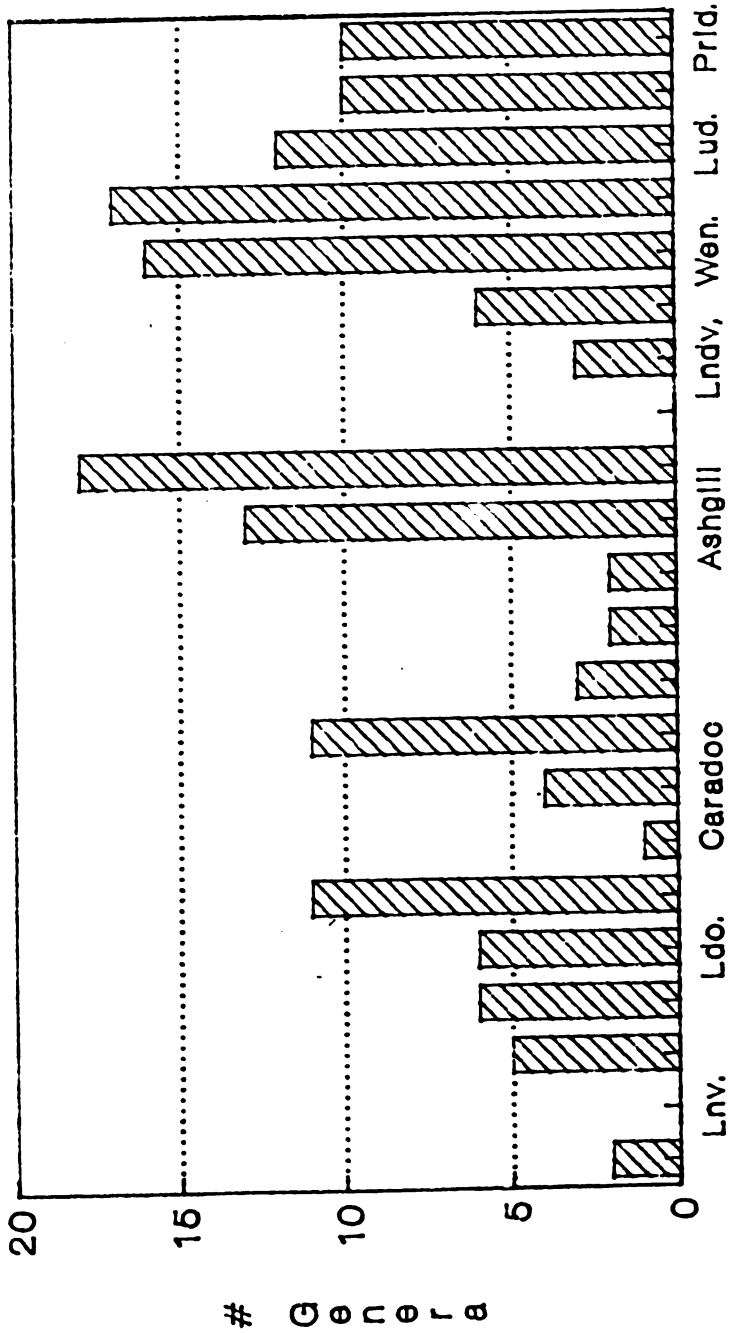

Figure 34. Extinctions of bryozoan genera for the Ordovician and Silurian. Extinctions are calculated at intervals of 4 million years based on last appearances of genera. Estimated ages of formations are taken from a relative time scale in Ross et al. (1982).

faunas: fauna one-suborders which radiated during the Ordovician; and fauna two-suborders which radiated following the Late Ordovician extinctions (Anstey, personal communication). Suborders in fauna one experienced a major rise in speciation rate during the Llandeilo and had their highest absolute numbers of originations during the Caradoc (Figures 35 and 36). Suborders in fauna two had higher speciation rates in the Silurian, with the exception of the Amplexoporina, which diversified greatly in the Caradoc (Figures 37 and 38). The Late Ashgill extinctions seemed to have a pronounced effect on evolutionary rates of the trepostomes, as post extinction speciation rates were approximately halved in the suborders Halloporina and Amplexoporina, and remained at low levels for the remainder of the Silurian. The cryptostome suborders Rhabdomesina, Fenestellina, and Ptilodictyina and the cystoporate suborder Fistuliporina, however, experienced increases in speciation rates from the Ashgill to the Llandovery. Trepostome suborders show very low species survivorship into the Silurian (Figure 39), and it is possible that the great reduction in trepostome diversity caused by the Late Ashgill extinctions is related to the reduced speciation rates observed in the Silurian. Gould and Calloway (1980) observed a similar major effect in the Permian mass extinction on brachiopods in the Mesozoic and Cenozoic. It appears that the Late Ashgill mass extinction was an event from which the trepostomes never recovered. The cryptostomes experienced the highest percentage survivorship into the Llandovery; however, their speciation rates began to decline

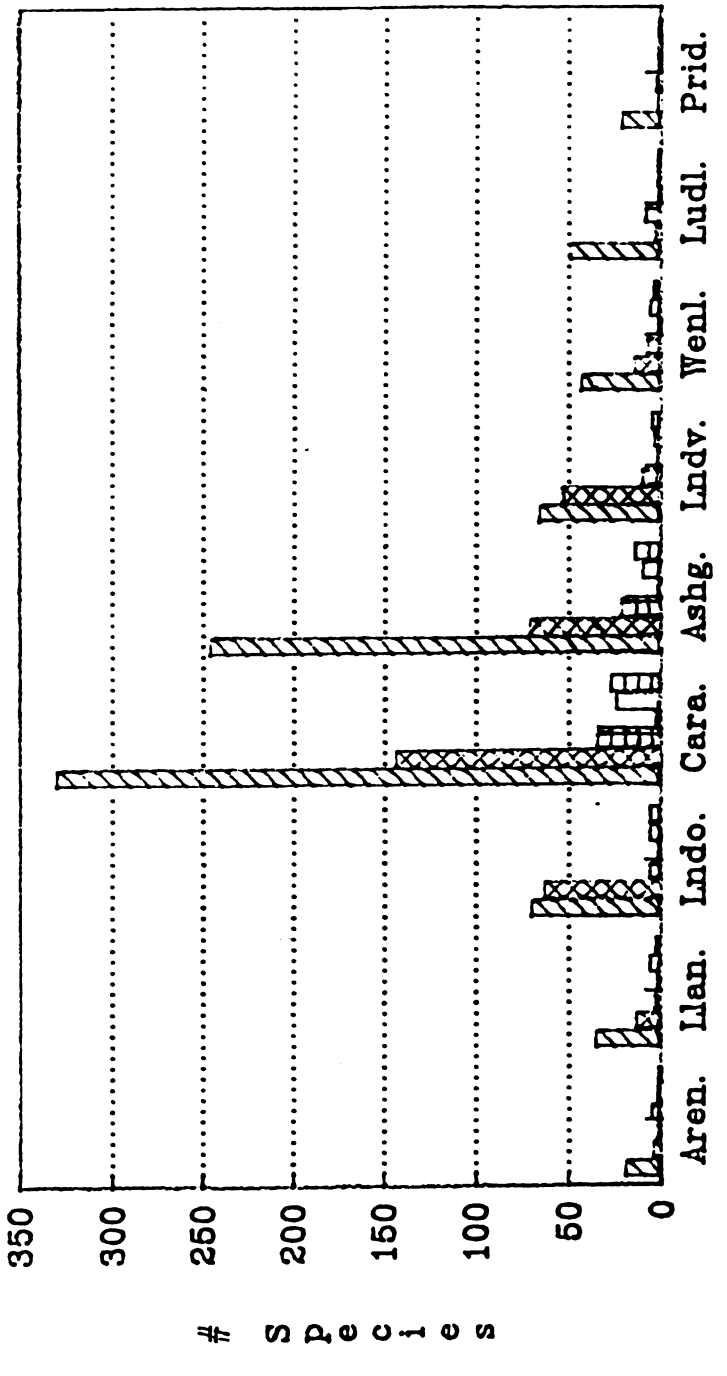

Figure 35. Number of new bryozoan species originations per suborder for the Ordovician and Silurian for evolutionary fauna one (suborders which radiated in the Ordovician).

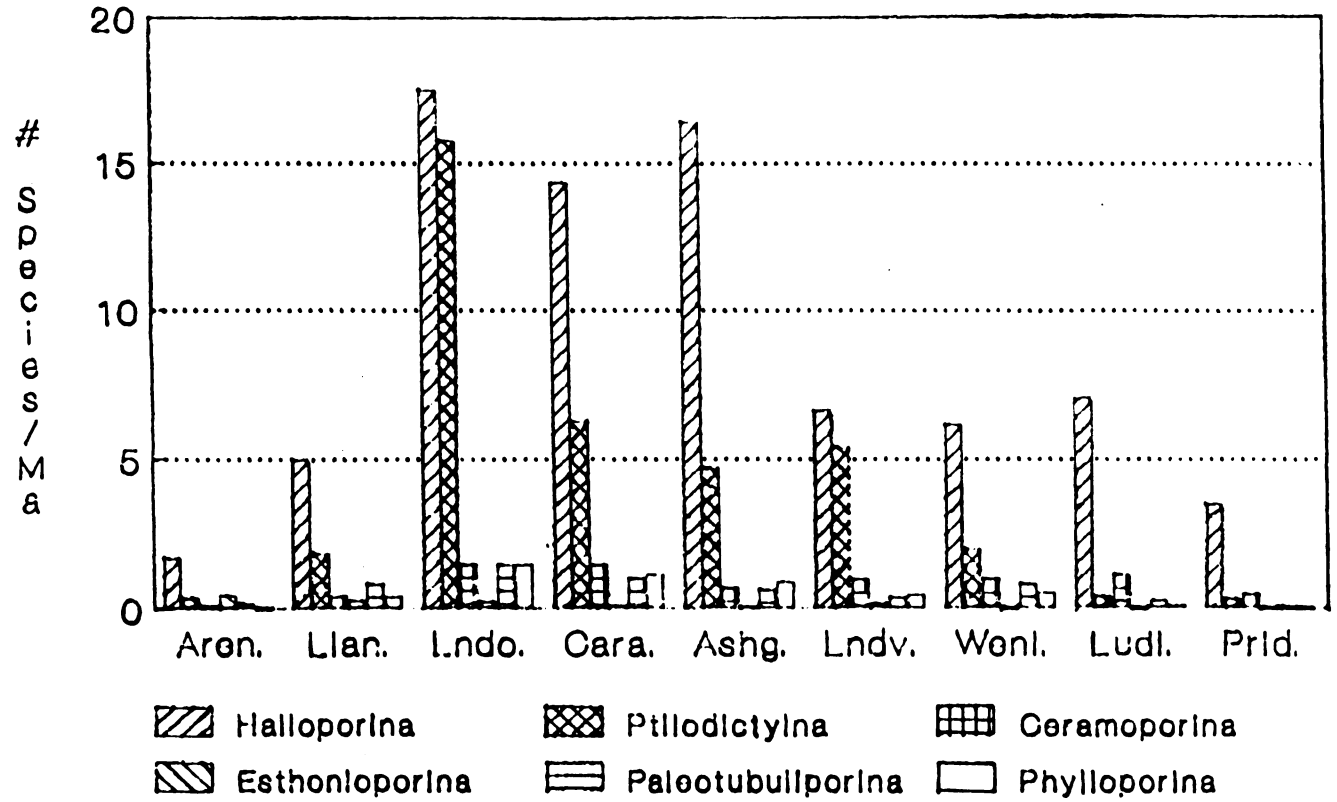

Figure 36. Speciation rates per suborder for evolutionary fauna one for the Ordovician and Silurian, expressed as number of new species per million years.

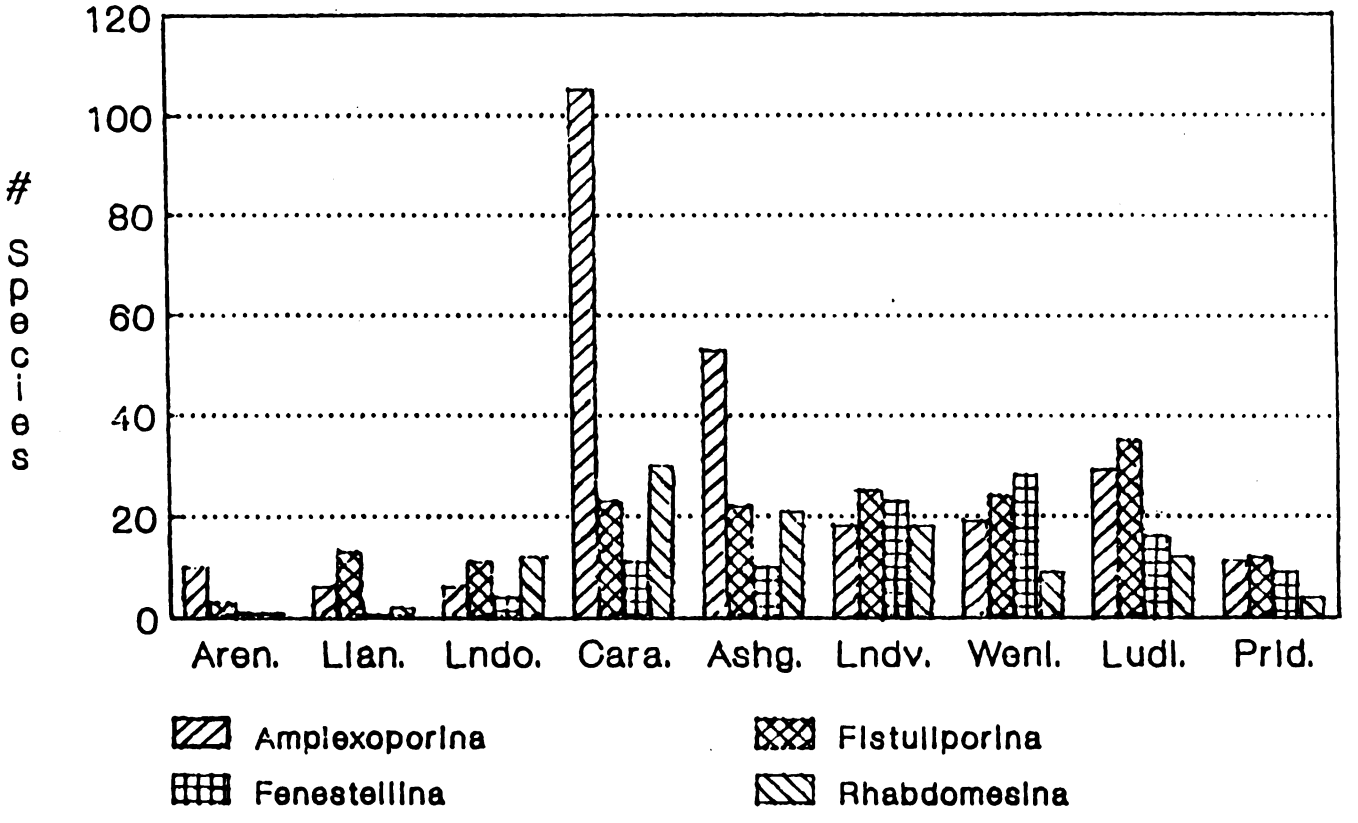

Figure 37. Number of new bryozoan species originations per suborder for the Ordovician and Silurian for evolutionary fauna two (suborders which radiated after the Ordovician).

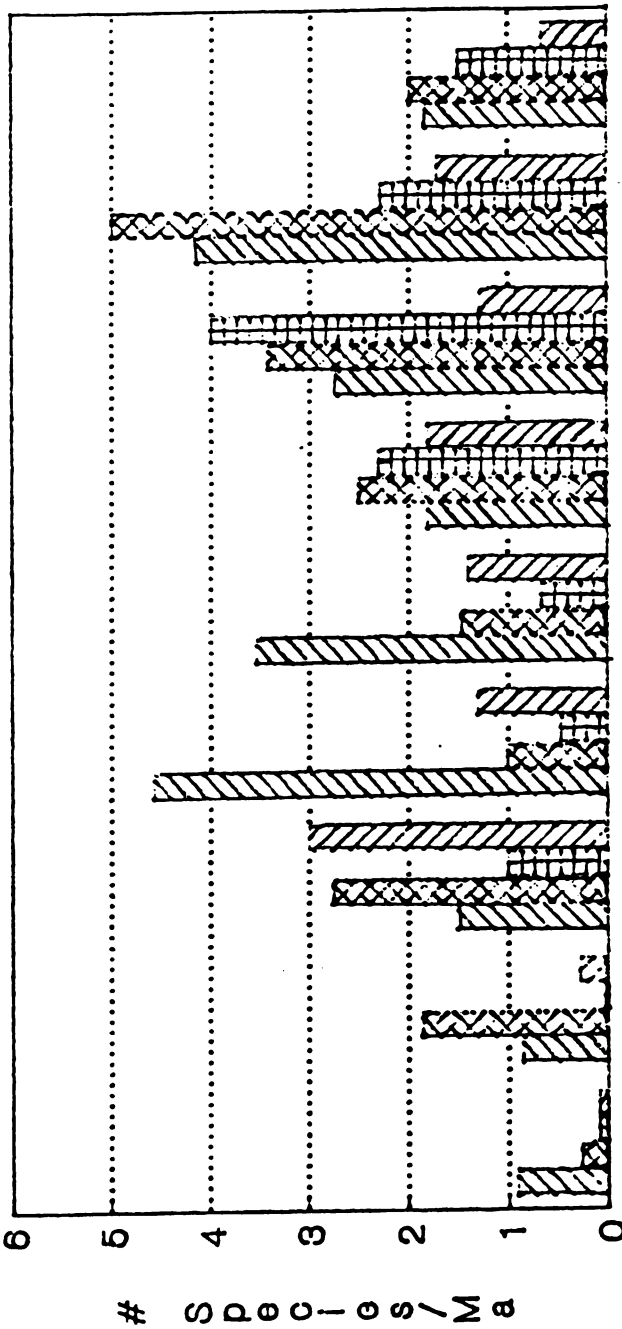

Figure 38. Speciation rates per suborder for evolutionary fauna two for the Ordovician and Silurian, expressed as number of new species per million years.

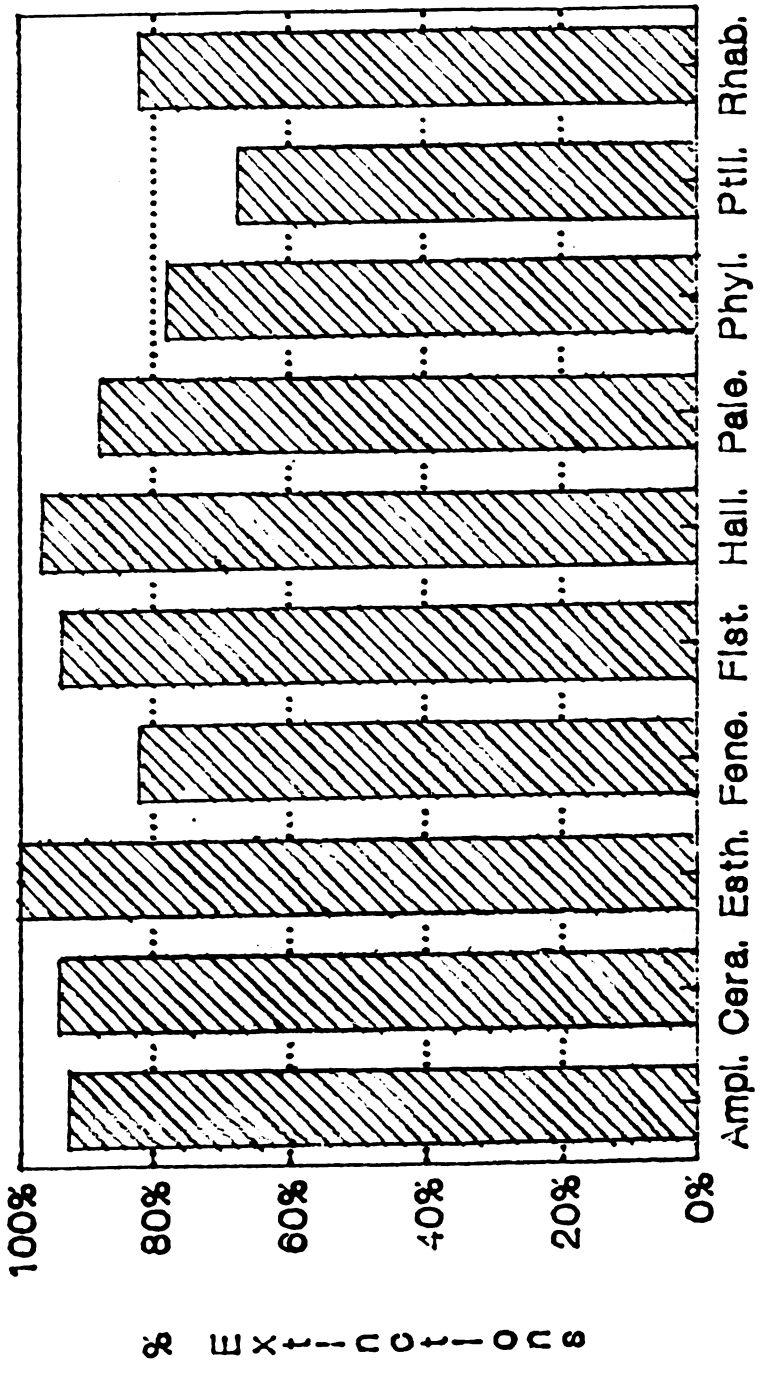

Figure 39. Percent extinctions of Late Ashgill bryozoan species per suborder, Ampl.=Amplexoporina, Cera.= Ceramoporina, Esth.=Esthonioporina, Fene.= Fenestellina, Fist.=Fistuliporina, Hall.=Halloporina, Pale.=Paleotubuliporina, Phyl.=Phylloporinina, Ptil.=Ptilodictyina, Rhab.=Rhabdomesina.

throughout the remainder of the Silurian. Both cystoporate suborders (Fistuliporina and Ceramoporina) were greatly affected by the mass extinction; however the fistuuliporines did not suffer a depression of speciation rates in the Llandovery and began diversifying at higher rates in the Wenlock and Ludlow, until a Pridoli decline.

LATITUDE AND CENTERS OF ORIGIN

Darlington (1957) first proposed that the tropics serve as a center for the evolution of new taxa. Since that time much research has been done to test this hypothesis for marine invertebrates. Stehli and Wells (1971) and Durazzi and Stehli (1972) found that the average ages of recent coral and benthonic foraminifera genera decreased towards the tropics, while diversity increased. They concluded that a strong relationship exists between diversity, temperature and evolutionary rates, and proposed a model in which the highest generic diversities correspond with regions of highest temperature in the tropics. New genera evolve in regions of high diversity and extend their ranges through time into regions of lower diversity and higher stress. Hecht and Agan (1972) also found a relationship between age and diversity of recent and Miocene bivalve genera, with the tropics again having higher diversities and younger generic ages. Recent Bryozoa, however, have highest species diversities at temperate latitudes between 30 and 60 degrees north of the

equator (Schopf, 1970).

Zinsmeister and Feldman (1984) proposed high latitude, shallow water, high stress environments to be centers of origin for new taxa, from studies of first appearances of Late Cenozoic molluscs, echinoderms and arthropods from Antarctica. Hickey et al. (1983) proposed Arctic origins for numerous Late Cretaceous and Early Tertiary land plants and vertebrates. Both studies stated that polar climatic conditions in the Cretaceous and Early Tertiary were mild in comparison with modern conditions. However Zinsmeister and Feldman emphasized that the climate was subject to extreme seasonality. They suggested that the seasonality and isolation of the Antarctic region were the primary cause of evolution of new taxa.

An opportunity to test these opposing hypotheses on latitudinal effects on evolutionary innovation is provided by documenting the early evolutionary history of the Bryozoa. The early evolution and radiation of the Bryozoa took place on latitudinally separated continents in the Early to Early-Middle Ordovician. Continental reconstructions from Scotese (1986) reveal that from the Late Cambrian to the Llanvirn, the continents of North America and Siberia were situated in equatorial realms, North Africa and Southern Europe were situated near the South Pole, and Baltica was situated in intermediate latitudes, between 30 and 60 degrees south of the equator. By Ashgill time, however, Baltica had moved into equatorial latitudes.

Although a few Early Ordovician species have been recorded

from China, the predominant record of early bryozoan evolution is preserved in the Early Ordovician sediments of Baltica, North America and Siberia. Diversities in the polar continents of North Africa and Southern Europe are low. Climatically, North America has been characterized by Spjeldnaes (1981) as having an equatorial, low latitude climate, while Baltica had a boreal or intermediate climate. Jaanusson (1972) also concluded that Baltica occupied a temperate climatic zone, despite the presence of widespread carbonate deposition. Lindstrom (1972) reported ice-marked sand grains from the Lower Ordovician of Scandinavia, indicating that the region did experience some cold climatic conditions. From the Arenig through the Llanvirn, when Baltica was situated in the south temperate zone, a total of 18 families, 47 genera and 90 species made their first appearances on Baltica. During this same time period only 6 families, 24 genera and 23 species appeared on the equatorially located North America, while 0 families, 3 genera and 8 species appeared in Siberia. Only 1 family, 1 genus and 1 species are recorded as appearing in the polar South Europe-North Africa region (Figures 26, 27 and 28).

The fact that the relatively high latitude, temperate, continent of Baltica served as the major evolutionary center for the Bryozoa lends support to the generality of the patterns observed by Zinsmeister and Feldman and Hickey et al. This indicates that high latitude, temperate, environments subject to extreme seasonality may be important centers of origin for new taxa. In the bryozoa, this effect seems to be particularly

pronounced at the family level. Webby (1984b) also suggested a probable Baltic temperate latitude origin for the Bryozoa.

THE OFFSHORE-ONSHORE HYPOTHESIS

Sepkoski (1981), in a factor analysis of the number of families within classes of Phanerozoic metazoans, defined three evolutionary faunas: (1) a Cambrian fauna dominated by trilobites and inarticulate brachiopods; (2) a Paleozoic fauna dominated by articulate brachiopods, crinoids, ostracodes, anthozoans, cephalopods and stenolaemate bryozoans; and (3) a modern fauna dominated by molluscs, echinoids, gymnolaemate bryozoans, bony fish, sharks, demosponges and malacostracean crustaceans. Sepkoski and Sheehan (1983), Sepkoski and Miller (1985) and Jablonski et al. (1983) found that the Paleozoic and modern faunas appear to have had their origins in nearshore environments and then expanded offshore with time. They suggested that nearshore environments may be conducive to diversification, possibly because of the frequent disturbances and stressful conditions found there, despite higher speciation rates offshore.

An effort was made to test their hypothesis by tabulating the geographic locations of first appearances of bryozoan taxa in Ordovician and Silurian formations of North America. Estimated ages of North American formations were taken from the stratigraphic correlation charts of Ross et al. (1982), Barnes et al. (1981) and Berry and Boucot (1970). Global first

appearances of bryozoan families and genera are strongly concentrated around the ancient continental margins of North America (Figures 40 and 41; taxa which appeared at an earlier time on other continents were not included). Locations which have high concentrations of originations include: Lake Champlain (12 genera and 2 families), the Arbuckle Mountains in Oklahoma (9 genera and 2 families), West-Central Utah (6 genera and 3 families), Southwest Virginia (11 genera and 1 family) and East Tennessee (6 genera). Also, six generic originations were recorded from the midcontinental region of Southern Indiana, most of which were found in the Osgood Formation (Silurian).

PALEOENVIRONMENTS OF EVOLUTIONARY CENTERS IN NORTH AMERICA

The Champlain Basin in New York and Vermont was the major apparent evolutionary center for North American Ordovician bryozoan genera. Faunas appear to have originated in the Day Point and Crown Point Formations of Llanvirn and Llandeilo age, and are associated with abundant carbonate reefs. Pitcher (1964) described these reefs as being formed in shallow water. Shallow water indicators include: quartz silt in the matrix of reefs, carbonate grainstones, oolites, oncolites, crossbedding and quartz sand bars in equivalent beds. Walker and Ferrigno (1973) classified these reefs as being located onshelf, analogous to modern shelf patch reefs.

Figure 40. Geographic locations of first appearances of bryozoan families in North America for the Ordovician and Silurian. The 2-family contour line parallels the ancient continental margin. Scale: one inch = approximately 650 kilometers.

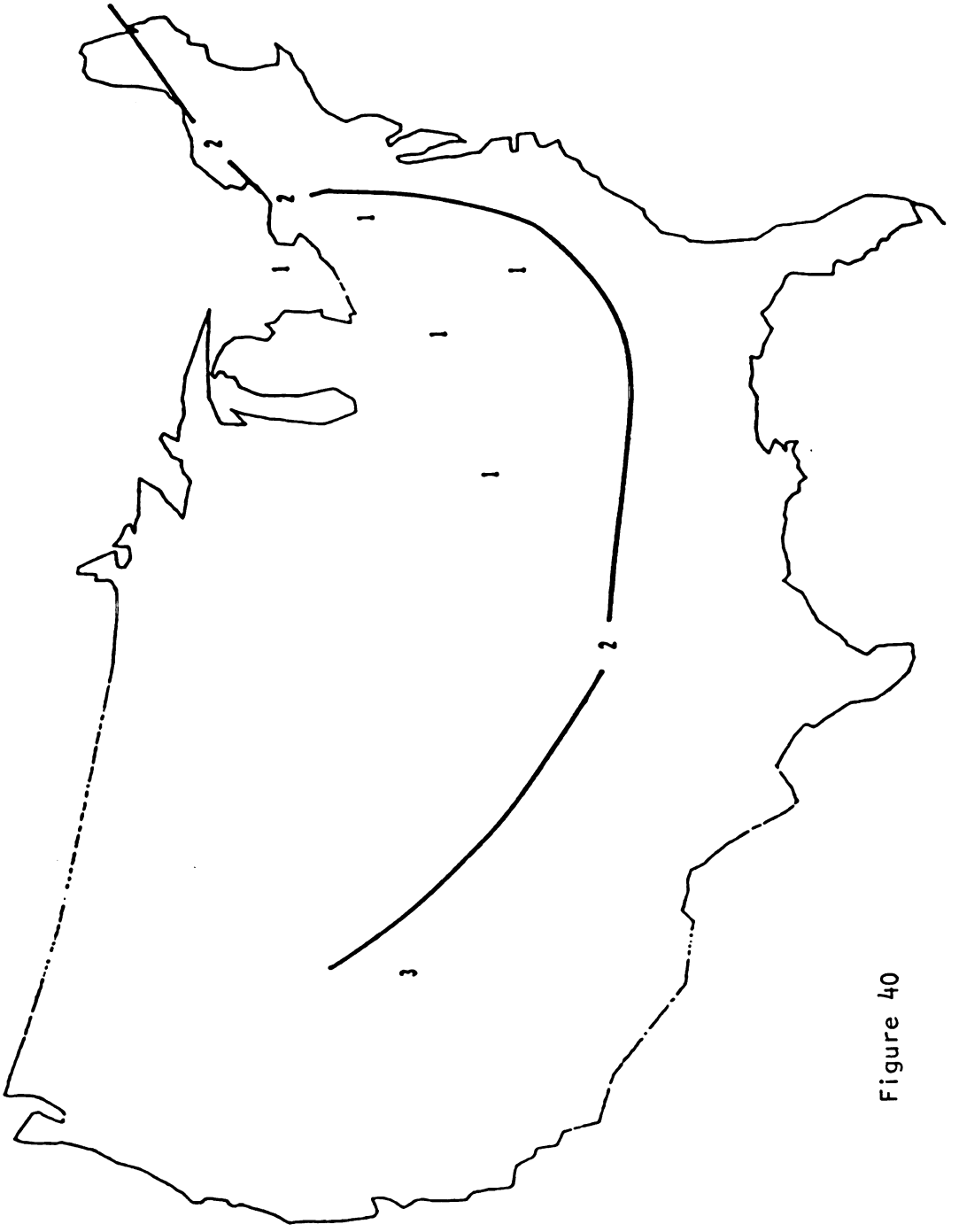

Figure 40

Figure 41. Geographic locations of first appearances of bryozoan genera in North America for the Ordovician and Silurian. The 6-genera contour line parallels the ancient continental margin. Scale: one inch = approximately 650 kilometers.

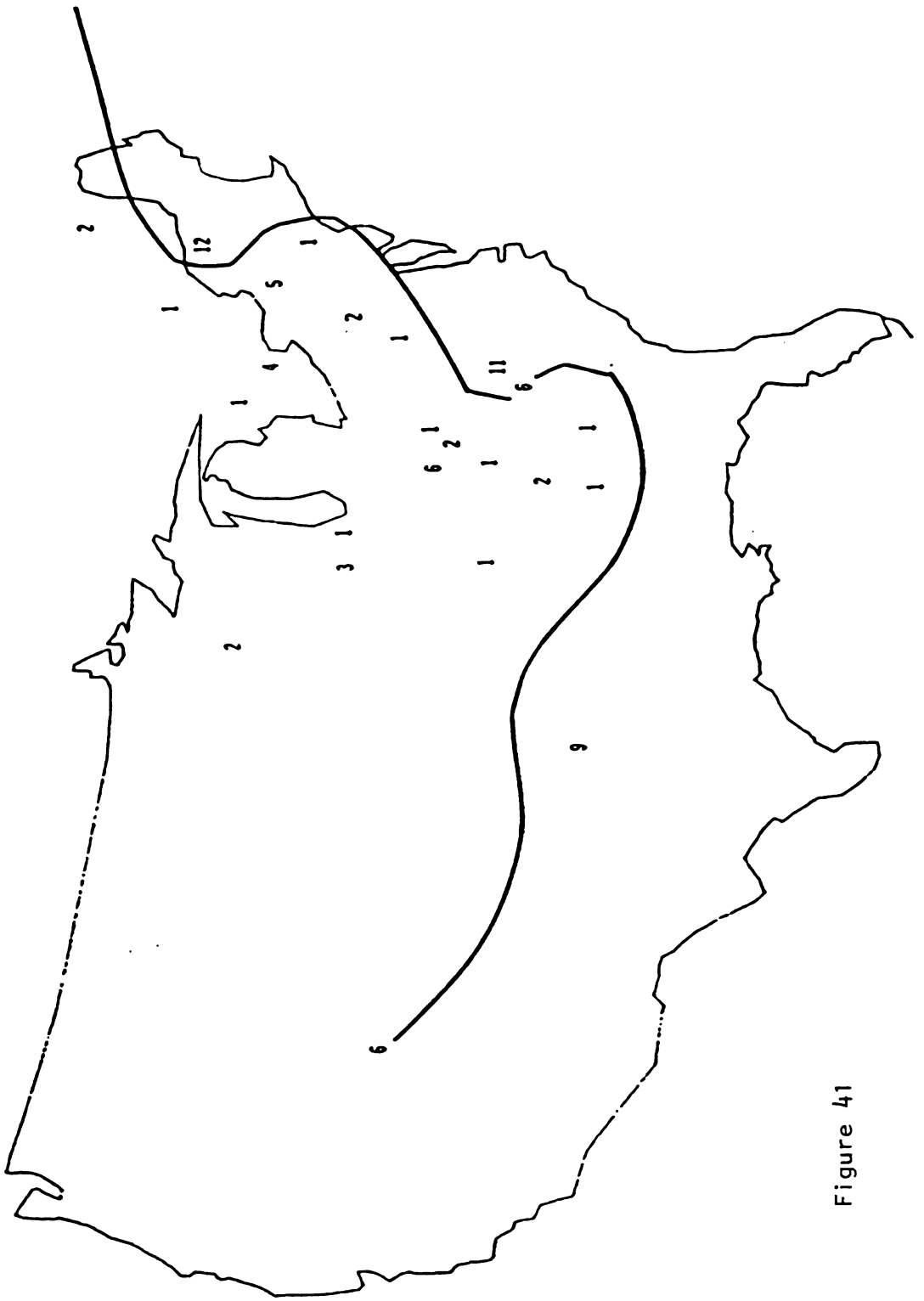

Figure 41

In Virginia, bryozoans originate mainly in the Llanvirn through Caradoc New Market, Lenoir and Edinburg Formations. Fichter and Diecchio (1986) and Read (1980) have classified the New Market as representing shallow intertidal to subtidal deposits, the Lenoir as representing a shallow, subtidal carbonate ramp facies, and the Edinburg as a shelf edge facies containing carbonate turbidites. The Edinburg contains six of the 11 generic first appearances; however, Fichter and Diecchi state that most of the Edinburg fauna has been transported from the shallow shelf as turbidites. Thus it is likely that the Virginia fauna represents shallow water conditions, although it is questionable whether the fauna is derived from the innermost shelf.

Six genera and three families appear in the Arenig-Llanvirn Kanosh and Lehman Formations of the Pogonip Group in West-Central Utah. Hintze (1951) described the Pogonip Group as containing large amounts of fine quartz arenaceous material and shallow water indicators such as intraformational conglomerates, ripple marks, cross laminations and beds of worn and sorted trilobite fragments. Hintze concluded that the area lay near the eastern shore of an epeiric sea.

In Oklahoma, the majority of new taxa are found in the Llanvirn through Caradoc Simpson Group of the Arbuckle Mountains. The bryozoan bearing formations of the Simpson Group are the McLish, Oil Creek, Tulip Creek and Bromide Formations. Ham (1969) described the Simpson Group as a sequence of formations, each of which contains a basal sandstone, overlain by skeletal

calcarenites, carbonate mudstones and shales. Bryozoans are found in the upper shale and limestone units of each formation. The Simpson is regarded as being a transitional group of intermediate depth, which can be differentiated from the underlying shallow water Arbuckle Group by the absence of hemispherical stromatolites and from the overlying deep water Viola Limestone, by the absence of graptolites. However, the McLish has been noted to contain Girvanella oncolites in great concentrations. The oldest bryozoan known was described by Ross (1966a) from the Late Tremadoc Kindblade Formation of Oklahoma. The species Ceramopora unapensis was found in a carbonate mound unit containing abundant lithistid sponges, quasisponges, orthid brachiopods and the blue green alga Girvanella.

The fauna from East Tennessee is found in a large reef from the Lower Caradoc Holston formation. Six genera make their first appearances in the fauna. The reef fauna was described by Walker and Ferrigno (1973), who interpreted the paleoenvironment to be offshore, on the eastern edge of a carbonate shelf.

In summary, first appearances of bryozoan genera and families are highly concentrated around the ancient continental margin of North America. The most diverse localities can be classified into three paleoenvironmental units:

1. Reefs or carbonate mounds are present in the Chazy Group of Lake Champlain, the Holston Formation of East Tennessee and the Kindblade Formation of Oklahoma.
2. Indicators of shallow water or inner shelf conditions are found in the Chazy Group of Lake Champlain, the Pogonip Group

of Utah, the New Market Formation of Virginia and the McLish Formation of Oklahoma.

3. Intermediate mid-shelf envirnoments have been inferred for the Simpson Group of Oklahoma and the Lenoir Formation of Virginia. The fauna of the Edinburg Formation was most likely transported as turbidites into deeper waters, from shallower, on-shelf localities.

This evidence from first appearances of bryozoan species and genera does lend some support to the hypothesis that nearshore environments serve as localities for the origination of higher taxa. However, some mid-shelf localities also seem to be evolutionary centers. Reef environments seem to be particularly important centers for the evolution of new taxa. Previous research on the onshore-offshore problem only focused on level-bottom communities and did not include reef communities, because of an implicit assumption that reef communities had a different evolutionary history than level-bottom communities. Sheehan (1985), however, stated that reefs follow the general evolutionary patterns of level-bottom communities. Reefs and level-bottom communities do show an interchange of fauna as, taxa originating in reefs radiated into level-bottom communities. It would not be surprising if other elements of the Paleozoic fauna, particularly corals, have similar first appearances of higher taxa in reefs.

EVOLUTION AT THE SPECIES LEVEL

Bryozoan speciation patterns in North America differ greatly from patterns of origination of genera and families (Figure 42). Coastal localities, which were evolutionary centers for genera and families, have relatively low numbers of species originations. The highest number of species originations is concentrated in the Cincinnati region, where bryozoans appear in abundance in the Late Ordovician Kope and Dillsboro Formations of Southern Indiana, Southern Ohio and Northern Kentucky. Anstey, Rabbio and Tuckey (1987a) suggested this intracratonic region lay in an area of relatively deeper water, centered between the Taconic clastic wedge to the east and the carbonate platform to the west. Other regions of high species originations include mid-craton areas such as the Middle Ordovician formations of the Central Tennessee Basin, the Middle Ordovician formations of Minnesota, and Middle Ordovician and Silurian strata in Central and Western New York. These results clearly imply that species-level evolution is not preferentially concentrated in nearshore environments. Similar results have been reported by Jablonski (1980) and Jackson (1974), who found that offshore bivalve taxa have higher speciation rates than onshore taxa.

Figure 42. Geographic locations of first appearances of bryozoan species in North America for the Ordovician and Silurian. The 60-species contour line outlines cratonic localities in Minnesota, Central Tennessee, Southern Indiana, Northern Kentucky and Central and Western New York. Scale: one inch = approximately 650 kilometers.

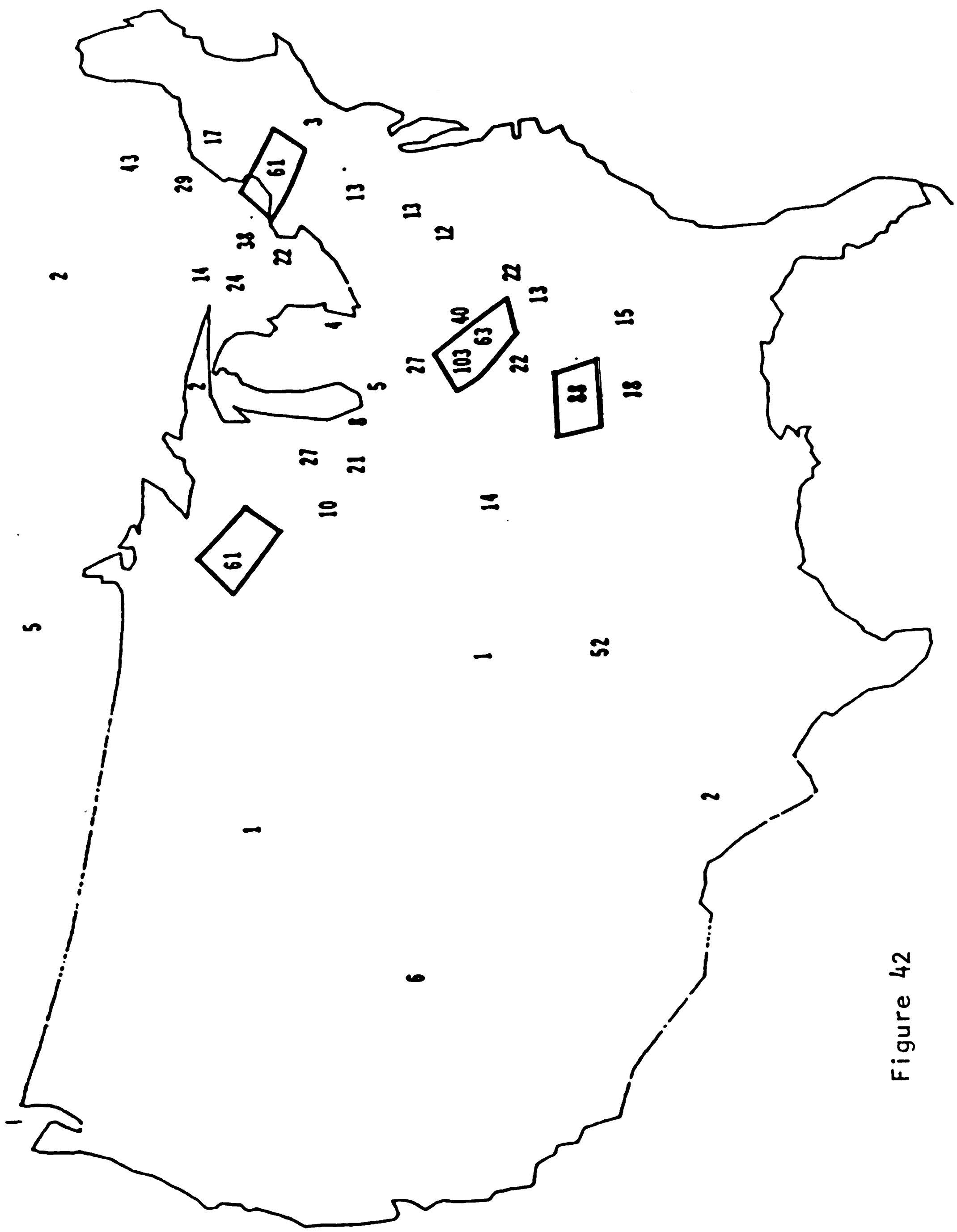

Figure 42

OCEANIC ISLANDS AS EVOLUTIONARY CENTERS

Data from exotic terranes have indicated that oceanic islands were important centers of origin for higher taxa of Bryozoa. Because of the highly deformed nature of rocks from these sites, fossil bryozoans are often unidentifiable, or identifiable only at higher taxonomic levels. Despite this, island faunas have yielded a number of first appearances of bryozoan genera and higher taxonomic groups. Among them are:

1. The Treiorwerth Formation, of the Anglesey region of Southeast Ireland, contains a Late Arenig bryozoan fauna consisting of generalized trepostomes and the oldest phylloporinid (Neuman, 1984; Neuman and Bates, 1978).
2. A Late Arenig fauna from New World Island, Newfoundland contains a number of unidentified trepostomes and the oldest bifoliate cryptostome (Neuman, 1984; 1976).
3. The oldest fenestrate bryozoan, Alwynopora orodamnus, was described from the Late Arenig Tourmakeady Limestone of West Ireland (Taylor and Curry, 1985).
4. A Late Ashgill fauna from the Portrane Limestone of Southwest Ireland contains a fauna with the first recorded appearances of the genera Discosparsa, Hederella, and Icthyorachis (Ross, 1966b). Icthyorachis had previously been known from Devonian age rocks, while Discosparsa had been known from the

Cretaceous.

5. The oldest described trepostome, Orbipora sp., was reported from the Lower Arenig Ogof Hen Formation of South Wales (Taylor and Cope, 1987).

The first four of these localities were described by Neuman (1984) as exotic terranes representing oceanic islands in the Iapetus Ocean. Neuman found that oceanic island faunas contain high percentages of endemic brachiopods, and cited the isolation, topographic irregularities and lack of competition encountered by pioneer species in these habitats as factors promoting endemism. Webby (1984b) noted that clathrodictyid stromatoporoids, coenosteoid heliolitid corals and several groups of rugose corals made their first appearances in island arc settings off the coast of Australia.

DISCUSSION

One possible interpretation of these results is that there may be a fundamental difference between speciation and the evolution of higher taxa such as genera and families. Jablonski and Bottjer (1983) suggested differences in speciation rates between onshore and offshore species may be related to wider geographic ranges and an increased frequency of planktotrophic larval development among nearshore taxa. They further state that because of their planktotrophic larval development, onshore taxa

are speciation and extinction resistant, but are more susceptible to speciation events involving genetic transiliencies, which may be sources of evolutionary novelty.

The mode of larval development for Ordovician Bryozoa is not known. However, an attempt was made to compare geographic ranges of nearshore vs. offshore genera, which might be correlated with larval type. Geographic ranges of high speciation, offshore localities (Southern Indiana, Southern Ohio, Northern Kentucky, Central Tennessee, and Minnesota) and nearshore and reef centers of evolution of higher taxa (Virginia, Oklahoma, Utah, Lake Champlain and East Tennessee) are compared in Table 4. Geographic range is estimated by the mean number of continents occupied per genus from the Arenig through Caradoc, when continents were still widely separated, and by per cent of endemic genera (confined to one continent) in each fauna.

Except for Utah, the mean number of continents occupied per genus is relatively constant for nearshore vs. offshore localities. Genera from Utah are more widespread, with each genus occupying an average of 4 continents, and no genera from Utah are endemic. However, Utah has a diversity of only 6 genera which is much lower than the generic diversities of other sites, which range from 26-59. Thus the data from Utah may not be as reliable, given the low sample size. Other nearshore and reef localities have a high percentage of endemic genera. This reflects the fact that many genera appeared at these sites and never migrated to other continents or invaded the continental interior. Many rare genera such as Amalgamoporous, Champlainopora, Chazydictya,

Table 4. Endemicity of bryozoan genera.

Locality	Mean number of continents occupied per genus	% Endemic genera per locality
1. Nearshore and reef:		
Lake Champlain	2.9	22
Oklahoma	3.2	18
Utah	4.0	0
Virginia	2.8	26
East Tennessee	3.0	21
Mean	3.2	17.4
2. Offshore, intracratonic:		
Central Tennessee	3.1	4
Northern Kentucky	2.9	13
Southern Indiana	3.0	12
Southern Ohio	3.0	10
Minnesota	2.9	12
Mean	3.0	10.2

Cricodictyum, Cystostictoporous, Heminematopora, Oeciophylloporina, Trepostomina, Hemiulrichostylus, Ottoseetaxis, Osburnostylus, Jordanopora, and Lammotopora are confined to reef or continental margin localities. Despite the high percentage of endemics at these sites, the total faunal assemblages have the same average generic ranges as the inner cratonic sites. This indicates that the continental shelf and reef localities have a mixed fauna, of cosmopolitan (planktotrophic?) and endemic (nonplanktotrophic?) genera.

Nearshore environments are typically characterized as unpredictable, high-stress, environments, with the implication that environmental stress may somehow be related to evolutionary innovation. In contrast, reefs are characterized as occupying predictable, low-stress environments. Given the large contribution of reefs and oceanic islands to evolutionary innovation in the Bryozoa, perhaps the relationship of environmental stress to evolutionary innovation has been overestimated. Reefs and islands are spatially heterogeneous, isolated environments. They offer the opportunity for species assemblages of small population size to form, often isolated from other reefs and islands by large distances. The occurrence of these isolated units of small population size may be related to the evolution of novel groups through the founder effect, the spatially heterogenous nature of the environment and the lack of selection pressure on pioneer species. Reefs often are found associated with island arcs and may have provided early colonization sites for newly evolved species.

Schopf (1977) viewed the evolution of new taxa as a process of increasing specialization, whereby specialized forms arise from generalized ancestors. Generalized taxa have life history strategies most suited for unstable, nearshore environments. Perhaps the reason higher taxa often appear in nearshore environments is because only generalized forms have the developmental plasticity necessary to allow evolutionary innovation. Thus, the fact that this process occurs nearshore is not because of any special evolutionary property of the nearshore environment, but because the generalized, ancestral forms are adapted to nearshore habitats.

Reef habitats are most suited for biotically competent, specialized forms. Reefs were abundant in North America from the Arenig through the Early Caradoc, but were rare from the Middle Caradoc through the Middle Ashgill, possibly because of an increase in terrigenous sedimentation from the Taconic Orogen and because rising sea levels deposited widespread black shales over the eastern midcontinent. They reappeared in the Late Ashgill in the Williston Basin, Mellville Peninsula and Anticosti Island areas of Canada; however, few novel groups appeared in reefs after the Early Caradoc.

Gould (1977) outlined how two forms of paedomorphosis (progenesis and neoteny) can act to preserve morphologic generality in stable and unstable environments. Progenesis (the acceleration of reproductive maturation) is a successful adaptive strategy in unstable environments. Gould states that when selection is focused on timing of reproductive maturity,

rather than on morphology, experimental morphologies can develop because morphology is suddenly released from the pressures of selection. Specialized adaptive strategies favor delays in timing of reproductive maturity. In these circumstances, juvenile features may be preserved in adult states (neoteny), lending the organisms a certain evolutionary plasticity. Anstey (1987) has documented several cases of paedomorphic traits in nearshore Paleozoic bryozoans.

SUMMARY

1. The early radiation of the Bryozoa was largely concentrated on the continent of Baltica, which was located in a temperate climatic zone in the Southern Hemisphere.
2. Worldwide diversities and evolutionary rates greatly increased in the Middle Ordovician, corresponding with a major eustatic transgression.
3. Following the Late Ordovician mass extinction, Silurian diversities and evolutionary rates were consistently lower than in the Ordovician.
4. First appearances of bryozoan genera and families in North America were largely concentrated in reefs and nearshore and mid-shelf environments around the ancient continental margin.
5. Oceanic islands also were centers of origin for genera and higher taxonomic groups of bryozoans and other marine invertebrates.
6. First appearances of bryozoan species were largely

concentrated offshore, in the stable craton.

7. Differences in the onshore vs. offshore evolution of taxa may be related to the presence of taxa with generalized (and often paedomorphic) morphologies in nearshore areas, and the spatial heterogeneity provided by the presence of reefs on the continental shelf.

CHAPTER THREE

GRADIENT ANALYSIS AND BIOSTRATIGRAPHIC CORRELATION

INTRODUCTION

Gradient analysis has been used to quantify spatial gradients in the distribution of taxa by ecologists and paleoecologists. Cisne and Rabe (1978) used reciprocal averaging to quantify spatial gradients in the distribution of fossils along an onshore-offshore transect in the Ordovician of New York. Anstey, Rabbio and Tuckey (1987a) used reciprocal averaging and polar ordination to quantify spatial gradients in the distribution of Late Ordovician bryozoan genera in North America and to quantify stratigraphic gradients in the distribution of bryozoan genera in a stratigraphic section in the Late Ordovician of southern Indiana. These stratigraphic gradients were inferred to represent bathymetric changes in the Late Ordovician epeiric sea. Cisne, Gildner and Rabe (1984) also constructed bathymetric curves for stratigraphic sections in New York and the upper Mississippi Valley, using detrended correspondence analysis. These sections were then correlated on the basis of synchronous changes in sea level. The application of gradient analysis to quantifying temporal gradients in the distribution of fossil species and genera makes it a potentially useful tool in biostratigraphy. Other multivariate techniques, such as cluster analysis and nonmetric multidimensional scaling, have also been used for quantitative stratigraphic correlations and construction of assemblage zones. Descriptions of these techniques may be

found in Brower (1985), Hazel (1977) and Cubitt and Reyment (1982).

Previous applications of gradient analysis have been high resolution studies of the presence-absence or abundances of taxa in measured stratigraphic sections. Changes in abundances of taxa reflect paleoenvironmental changes associated with transgressions and regressions. This approach differs from previous studies in that the presence-absence of species in formations spanning a long time interval (the Ordovican) is analyzed. The limited stratigraphic range of species enables gradient analysis to quantify an "age gradient" unrelated to short term environmental changes.

To test the biostratigraphic utility of gradient analysis, an analysis was done of the distribution of bryozoan species in the Ordovician of Estonia. Estonia was chosen for this analysis because it has a diverse bryozoan fauna and a complete sequence of Ordovician formations ranging from Arenig through Ashgill in age (Figure 43) exposed within a relatively small geographic area, thus minimizing the potential for spatial variation. The Balto-Scandian Ordovician formations lie in three major facies zones. Each zone maintains its individuality and geographic location throughout most of the Ordovician, and major faunal changes between formations are usually not associated with a change in lithology or facies (Jaanusson, 1976).

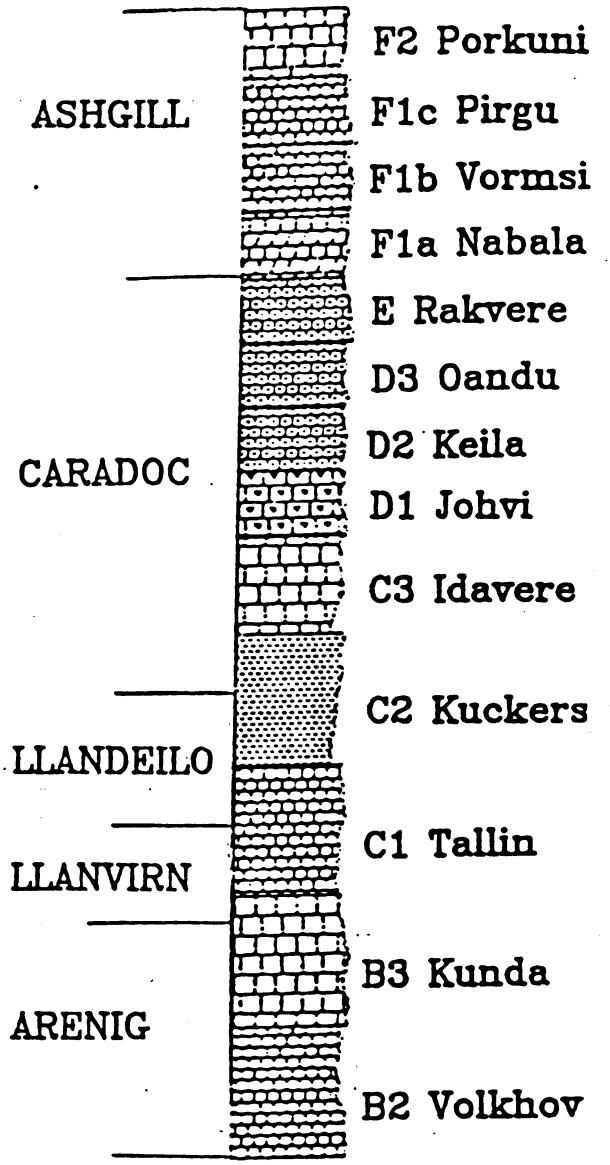

Figure 43. The Ordovician stratigraphic sequence of Estonia, from Alikhova (1976) and Mannil (1966).

METHODS

Data on the distribution of bryozoans in the Ordovician of Estonia were compiled from the publications of Bassler (1911), Mannil (1959) and Modzalevskaya (1953). A data matrix was compiled, listing the presence or absence of each species of the bryozoan fauna in each formation of the Estonian Ordovician sequence. This data matrix was used as input data for the gradient analytic technique of detrended correspondence analysis, (hereafter called DCA). DCA and reciprocal averaging are similar to factor analysis in that they reduce the dimensionality of the data matrix into a few major axes of variation. Sample scores are ordinated with respect to their distance between the two poles, or end points, of each axis. DCA and reciprocal averaging give identical results on the first axis, but differ on subsequent axes, as DCA axes are orthogonal, whereas subsequent axes of reciprocal averaging are often correlated with the first axis. A discussion of these gradient analytic techniques is provided in Gauch (1982).

RESULTS

Ordination scores for the Ordovician formations of Estonia are given in Table 5. DCA correctly ordinated the Estonian formations with respect to age on the first axis, with the exception of the B2 and B3 horizons which were juxtaposed, with the B3 being classified as older than the B2. The juxtaposition was probably due to the effect of two species, Diplotrypa petropolitana and Parvohallopora bicornis, which were listed as being present in the B2 horizon and abundant in the younger C and D horizons, but were not recorded from the B3. This had the effect of making the B2 appear more similar to formations of younger age. These ordination results clearly indicate that the first DCA axis serves as an "age" axis for Estonia.

A DATING OF THE ORDOVICIAN ERRATIC BOULDER FAUNA FROM POLAND

A bryozoan fauna from Ordovician erratic boulders from Poland was described by Kiepura (1962). The fauna is known to be Ordovician in age, however the precise age of the fauna has never been determined. A dating of this fauna was attempted by including the fauna from each boulder in the data matrix with the Ordovician fauna of Estonia. Boulders containing fewer than 5

Table 5. First axis DCA ordination scores for the Ordovician formations of Estonia

Eigenvalue = 0.819

Horizon	DCA Score	# of Genera	# of Species
F2	683	20	28
F1c	532	18	21
F1b	521	27	34
F1a	502	17	19
E	279	25	32
D3	195	47	73
D2	178	45	67
D1	139	39	66
C3	130	34	56
C2	101	48	88
C1	52	31	49
B2	15	8	10
B3	0	19	32

species were not included in the analysis. DCA ordination scores for this analysis are listed in Table 6. The Estonian Ordovician sequence is again ordinated with respect to age on the first axis, with the exception of the B2 and B3 horizons and the C2 and C3 horizons which are juxtaposed, although their ordination scores are almost identical. Erratic boulders 0.204 from Mochty (province of Warsaw) and 0.17 from Wielki Kack (province of Gdansk) are classified as being between the F1c (Pirgu) and F2 (Porkini) horizons in age. Ordination scores for the two boulders however, are closest to the F2 horizon, which is Hirnantian (Latest Ashgill) in age. This evidence indicates that these two erratic boulders from Poland are Hirnantian in age, and are thus equivalent in age to the erratic boulders from the Hirnantian of Ojlemyr, Gotland, whose fauna was described by Spjeldnaes (1984). Schallreuter and Hillmer (1987) also noted the similarity between the Ojlemyr fauna and the Polish boulder fauna.

A DATING OF THE NAUNGKANGYI FORMATION OF BURMA

The fauna of the Naungkangyi formation of the North and South Shan States of Burma was described in a series of papers by Reed (1906, 1915, 1936). In the North Shan States, the Naungkangyi is divisible into an upper member of predominantly shales and a lower member of sandy marls, while in the South

Table 6. First axis DCA ordination scores for the Ordovician formations of Estonia and erratic boulders 0.17 and 0.204 from Poland.

Eigenvalue = 0.821

Horizon	DCA Score	# of Genera	# of Species
F2	659	20	28
Boulder 0.17	628	10	14
Boulder 0.204	626	16	20
F1c	523	18	21
F1b	512	27	34
F1a	494	17	19
E	307	25	32
D3	210	47	73
D2	205	45	67
D1	150	39	66
C2	143	48	88
C3	140	34	56
C1	83	31	49
B2	20	8	10
B3	0	19	32

Shan the Naungkangyi exists as a series of shales and limestone lenses and is not divisible into upper and lower units (Pascoe, 1959). The age of the Naungkangyi members has been estimated by Pascoe to range from Llanvirn to Early Caradoc; however, Williams (1973) included the Naungkangyi fauna in the Upper Caradoc, in his cluster analysis of brachiopod faunas.

The Baltic affinities of the Naungkangyi fauna have been recognized by Pascoe (1959), and in Chapter one of this thesis. Because of the Baltic nature of the Naungkanyi fauna an attempt was made to estimate the temporal position of the fauna by including it in a DCA analysis with the Ordovician sequence of Estonia. Since some of the Naungkangyi bryozoan fauna are described only to the level of genus, the input data matrix consisted of the presence or absence of bryozoan species and genera in the Naungkanyi members and the Estonian formations.

First axis scores again show the Estonian sequence ordinated by age (Table 7). The Upper and Lower Naungkangyi formations from the North Shan and the Naungkangyi formation from the South Shan all cluster in age between the E (Rakvere) and F1a (Nabala) horizons of Estonia. Ordination scores for the South Shan Naungkangyi and the North Shan Lower Naungkangyi are closest to the ordination score for the E horizon of Estonia, while the Upper Naungkangyi Formation clusters closest to the F1a horizon. Alikhova (1976) placed the E horizon in the Upper Caradoc and the F1a horizon in the Lower Ashgill. Thus, this analysis indicates the Naungkangyi members to be of Late Caradoc to Early Ashgill

Table 7. First axis DCA ordination Ssores for the Ordovician formations of Estonia and the Lower Naungkangyi (L-Naung) and Upper Naungkangyi (U-Naung) Formations of the North Shan States and the Naungkangyi (S-Naung) Formation of the South Shan States of Burma.

Eigenvalue = 0.779

Horizon	DCA Score	# Genera	# Species
F2	624	20	28
F1c	491	18	21
F1b	487	27	34
F1a	466	17	19
U-Naung	420	5	5
S-Naung	285	9	11
L-Naung	285	7	10
E	284	25	32
D3	213	47	73
D2	199	45	67
D1	140	39	66
C3	132	34	56
C2	112	48	88
C1	67	31	49
B2	58	8	10
B3	0	19	32

age.

SUMMARY

Ordination analysis succesfully classified Estonian formations of known age along an "age" gradient on the first DCA axis, with one exception. When faunas of unknown age, from the same biogeographic province, were included in the analysis, the "age" gradient on the first axis remained intact and the undated faunas were time correlated with Estonian formations by their positions on the first axis. These results indicate that gradient analysis is a useful biostratigraphic tool because of its effectiveness in ordinating temporal gradients, as well as an effective ecologic tool as ecologists and paleoecologists have recognized.

This analysis also suggests that bryozoans are useful tools in biostratigraphy. Despite the fact that paleontologists such as E.O. Ulrich and R.S. Bassler recognized their stratigraphic value, bryozoans have rarely been used in recent biostratigraphic studies. Although species distributions are often facies-controlled, the relatively short stratigraphic ranges of many species make them useful for correlation within biogeographic provinces or subprovinces.

CHAPTER FOUR

THE LATE ORDOVICIAN MASS EXTINCTION

INTRODUCTION

The Late Ordovician has been recognized as one of four periods of Phanerozoic mass extinction, that significantly exceed background extinction levels (Raup and Sepkoski, 1982). Extinctions in this epoch affected a variety of marine invertebrates including trilobites, echinoderms, graptolites, conodonts and corals (Brenchly, 1984). The cause of the extinctions has been attributed to climatic cooling associated with the Late Ordovician glaciation, centered in North Africa (Stanley, 1984), and to the marine regression associated with the glaciation (Brenchly, 1984; Jaanusson, 1979). An analysis of the terminal stratigraphic occurrences of Late Ordovician bryozoan species and genera, drawn from a worldwide bryozoan data base, indicates that the Late Ordovician extinction of bryozoans is a composite of three discrete extinction events that significantly exceed background extinction levels: a Late Caradoc event (Onnian Stage) and two Late Ashgill events (Rawtheyian and Hirnantian Stages, respectively). This paper seeks to demonstrate differences in the fauna affected by each of these separate events, and to propose extinction mechanisms consistent with these differences.

ONNIAN EXTINCTIONS

A Poisson distribution test (Sepkoski and Raup, 1986) which compares extinction maxima with local minima was applied to test the significance of extinction peaks for bryozoan species and genera during the Ordovician and Silurian (Figures 44 and 45). In addition to a Middle Ordovician (Black River) event, these extinction peaks rise above the 95% confidence limits: a Late Caradoc peak, two Late Ashgill peaks and a Mid-Silurian peak.

The Late Caradoc extinction of bryozoan species totaled over 50% of all Late Caradoc species recorded from the continents of Baltica, Siberia and Southern Europe; however, only about 25% of North American species were affected (Figure 46). Endemic species and genera were significantly more prone to extinction than cosmpolitan taxa, as taxa confined to one continent suffered more than taxa on two or more continents (Figure 47). Extinctions were concentrated among stenotopic species and genera, as taxa confined to one lithotope suffered higher rates of extinction than taxa occupying mixed lithologies (Figure 48). Brenchly (1984) and Brenchly and Newell (1984) discussed Late Caradoc extinction events for trilobites and brachiopods and attributed them to a reduction in provinciality brought about by plate movements reducing the width of the Iapetus Ocean. This idea is supported by data on migrations of bryozoan genera, as Baltica and Siberia, where extinctions were high, received larger

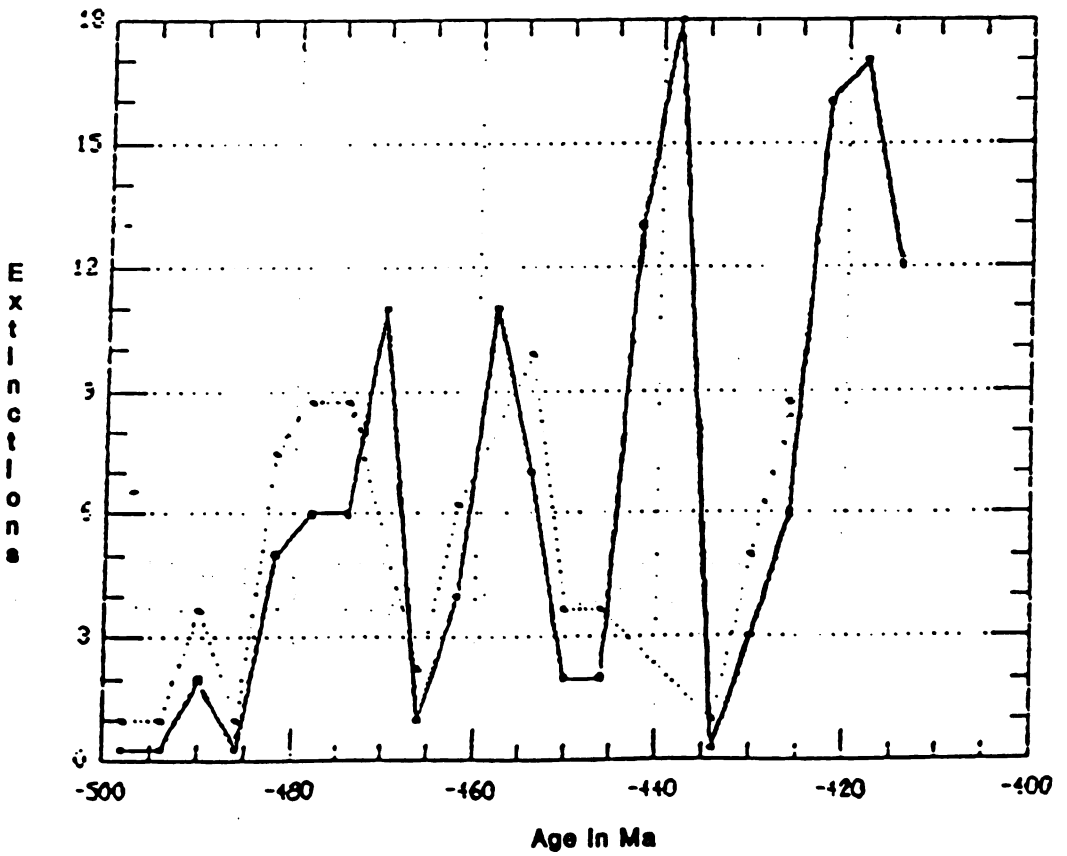

Figure 44. Ordovician and Silurian extinctions of bryozoan genera recorded in intervals of 4 million years. The dotted line represents the 95% confidence intervals of a Poisson distribution test which compares extinction maxima with local minima. Time scale is taken from stratigraphic charts of Ross et al. (1982).

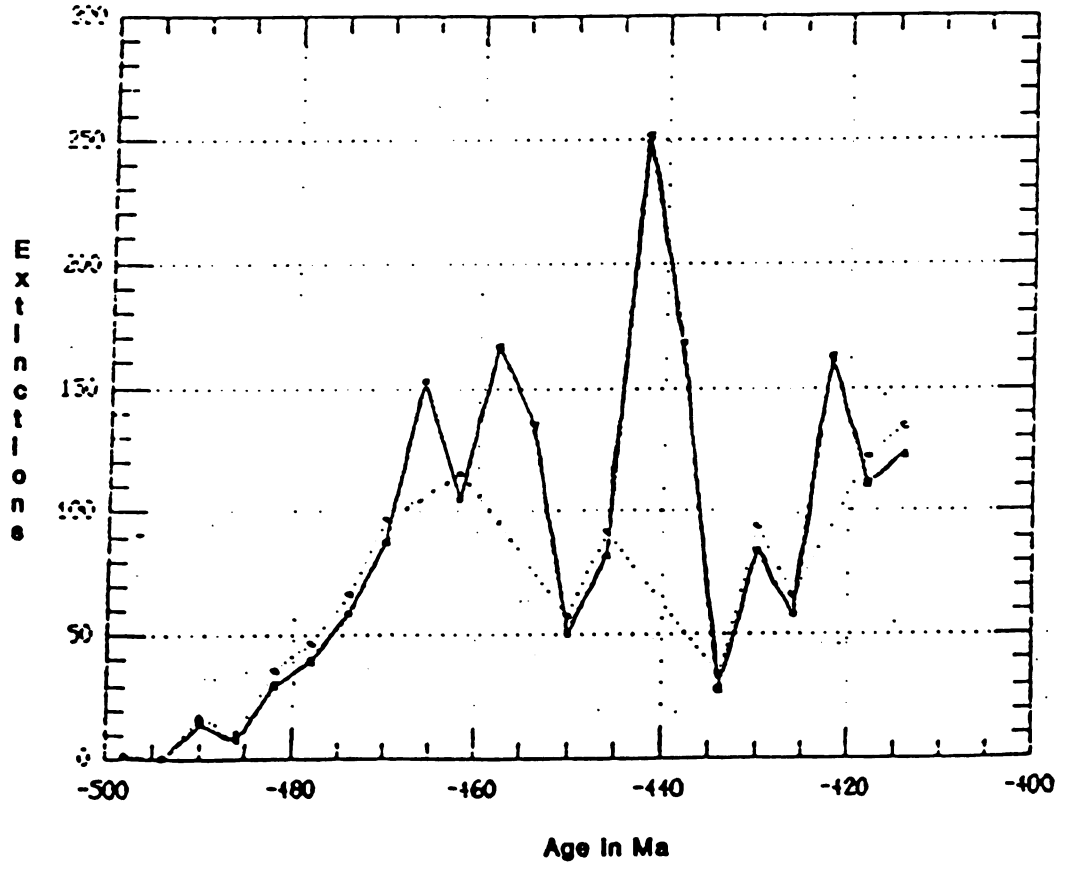

Figure 45. Ordovician and Silurian extinctions of bryozoan species, recorded in intervals of 4 million years. The dotted line represents the 95% confidence intervals of a Poisson distribution test, which compares extinction maxima with local minima. Time scale is taken from stratigraphic charts of Ross et al. (1982).

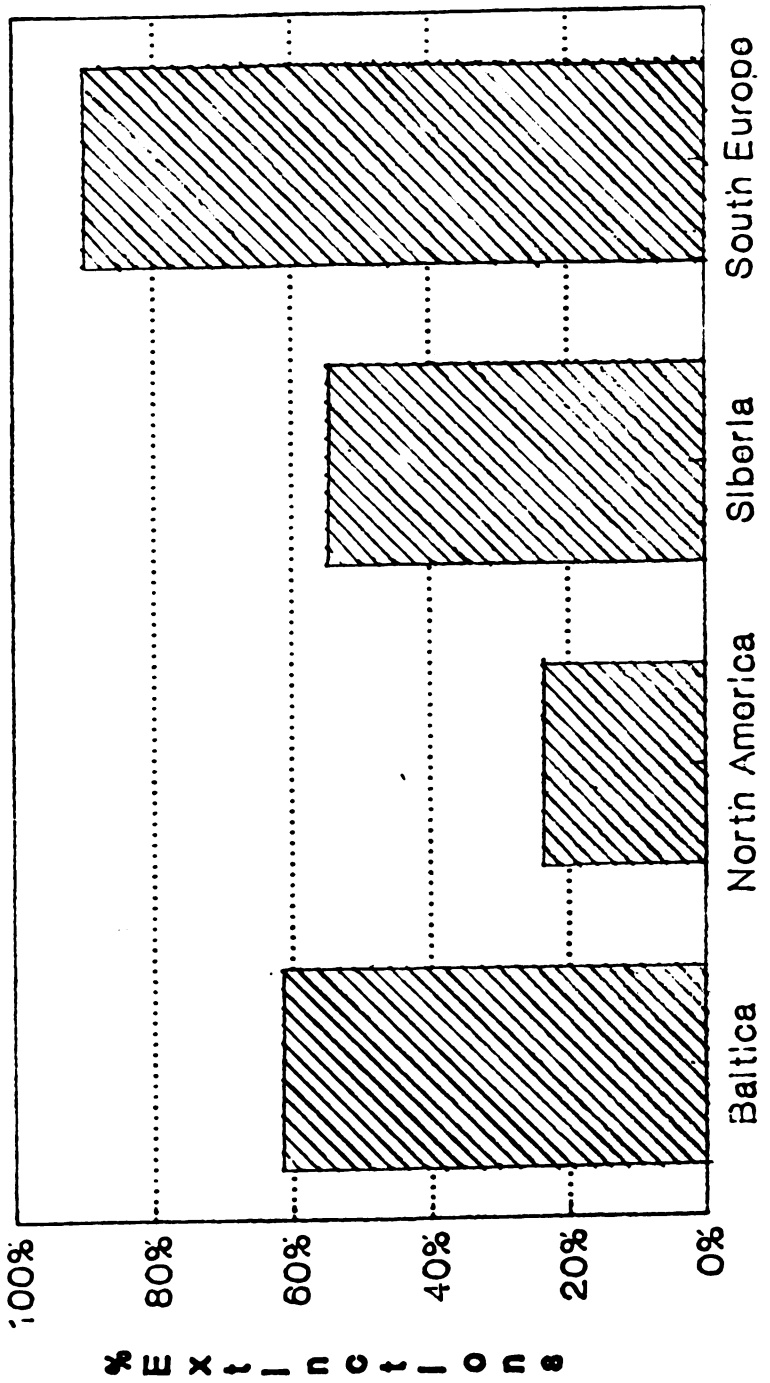

Figure 46. Extinctions of Late Caradoc bryozoan species listed as % of fauna extinct per continent.

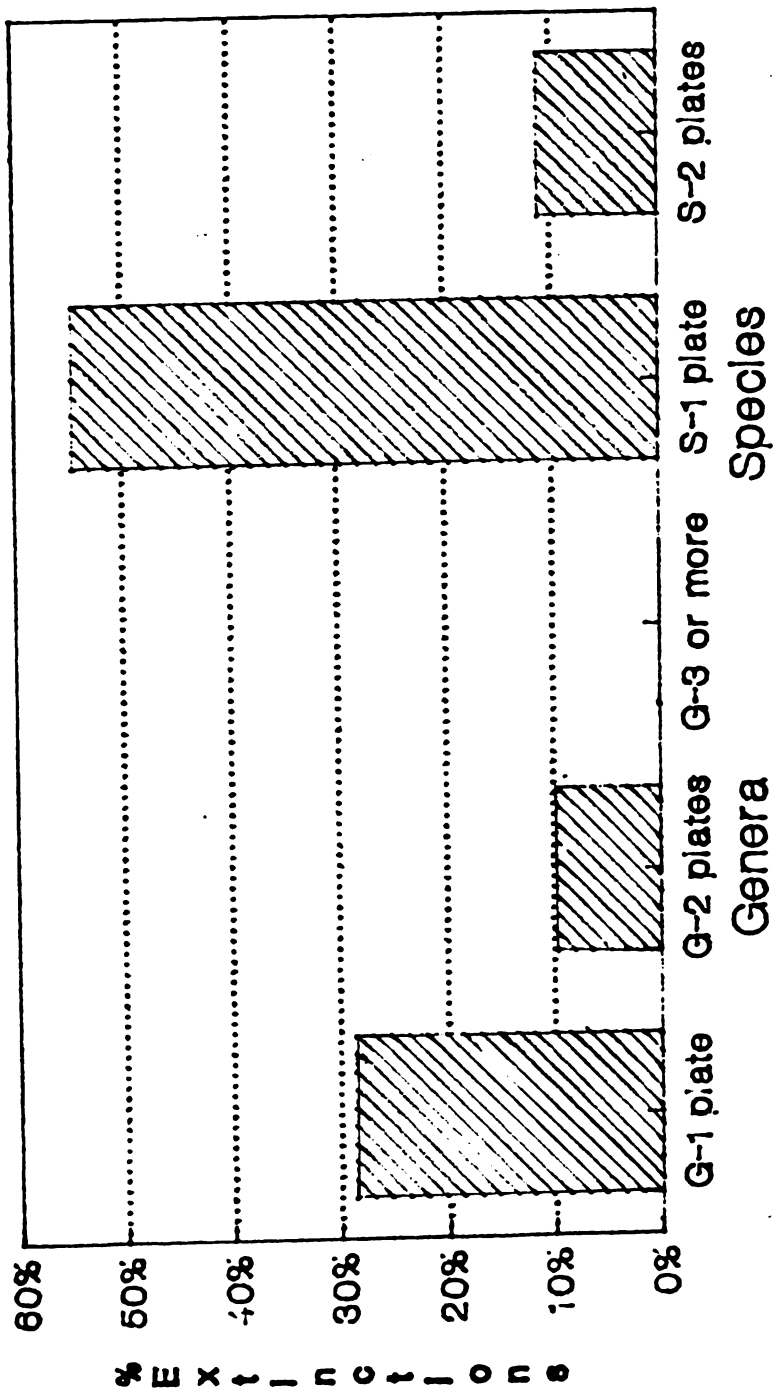

Figure 47. Extinctions of Late Caradoc bryozoan species and genera listed as % of fauna extinct per number of continental plates occupied.

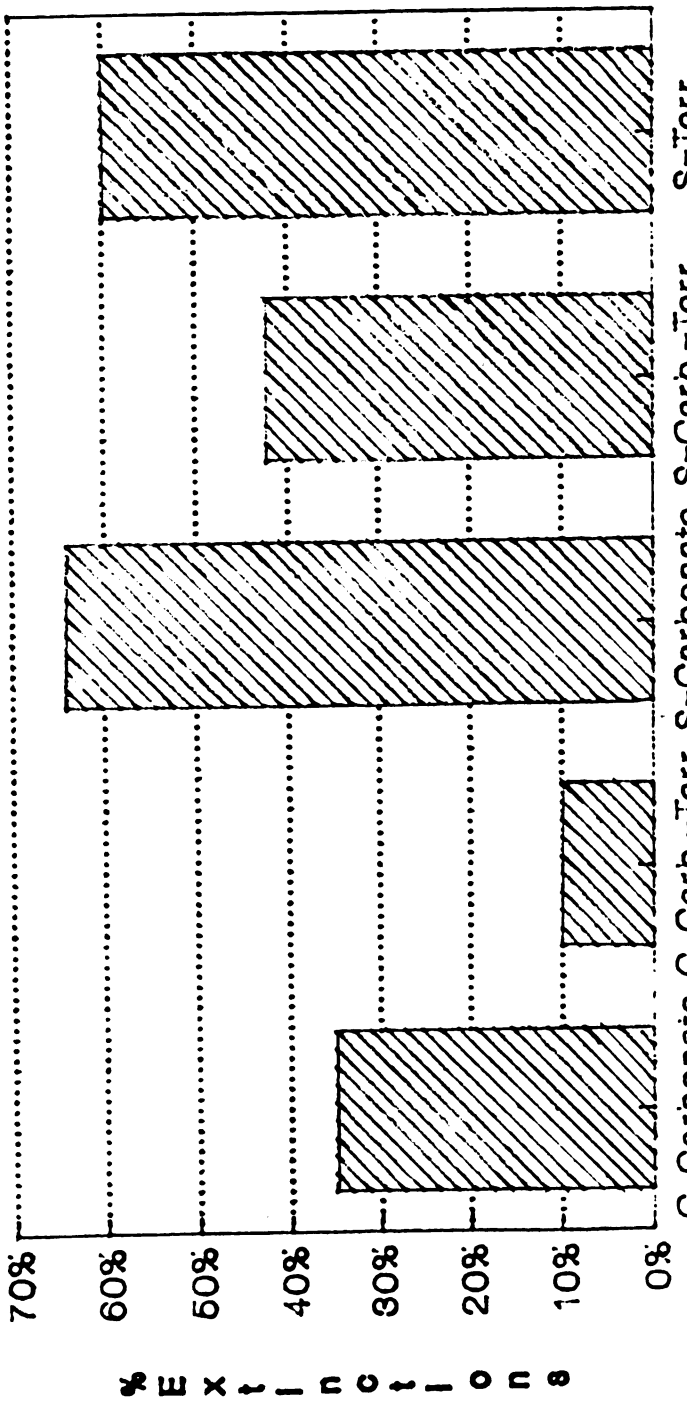

Figure 48. Extinctions of Late Caradoc bryozoan species and genera listed as % of fauna extinct per lithotope occupied.

numbers of migrants during the Late Caradoc, than North America, where extinctions were low (Figures 8, 9 and 10). Spjeldnaes (1981) described these migrations as the "Vaselemma" (Estonian E Horizon) wave and characterized them as being marked by an invasion of American trilobites, brachiopods and bryozoans into Europe. Perhaps extinctions in Baltica and Siberia were related to competition between migrants and stenotopic species which were unable to expand their range to other lithotopes.

RAWTHEYAN EXTINCTIONS

Although the Late Ashgill extinction appears as a single peak in Figures 44 and 45, it is a composite of two separate extinctions, one during the Rawtheyan stage and one during the Hirnantian (the final stage of the Ashgill). The stratigraphic divisions of the Ashgill are shown in Figure 49. Rawtheyan extinctions of bryozoa were concentrated in North America, where approximately 90% of Late Ashgill species went extinct. Baltica however, lost only about 5% of its species during the Rawtheyan (Figure 50). Because stratigraphic data on bryozoan distributions from Siberia, China and Southern Europe are imprecise, the effect of the Rawtheyan and Hirnantian extinctions on these continents cannot be determined. Rawtheyan extinctions were concentrated in terrigenous and mixed terrigenous/carbonate lithotopes, as opposed to those of pure carbonates (Figure 51). Extinctions

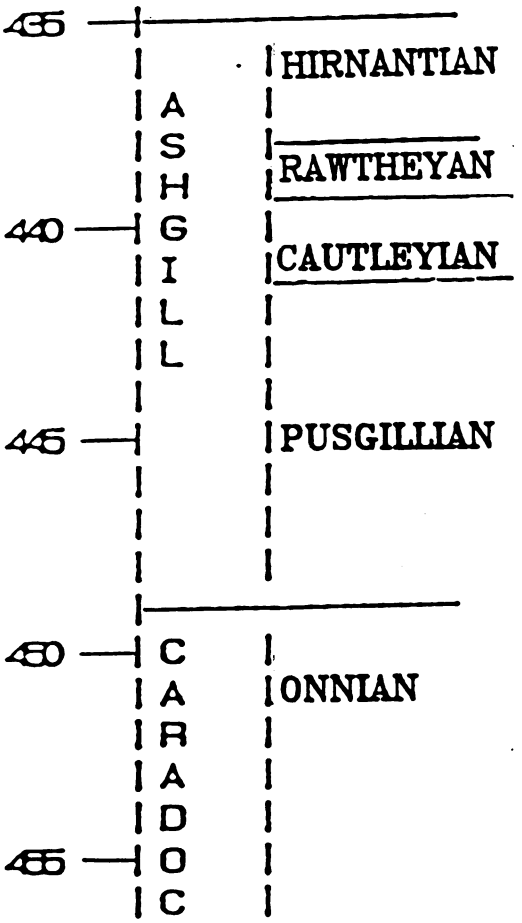

Figure 49. The stratigraphic stages of the Ashgill, from Ross et al. (1982).

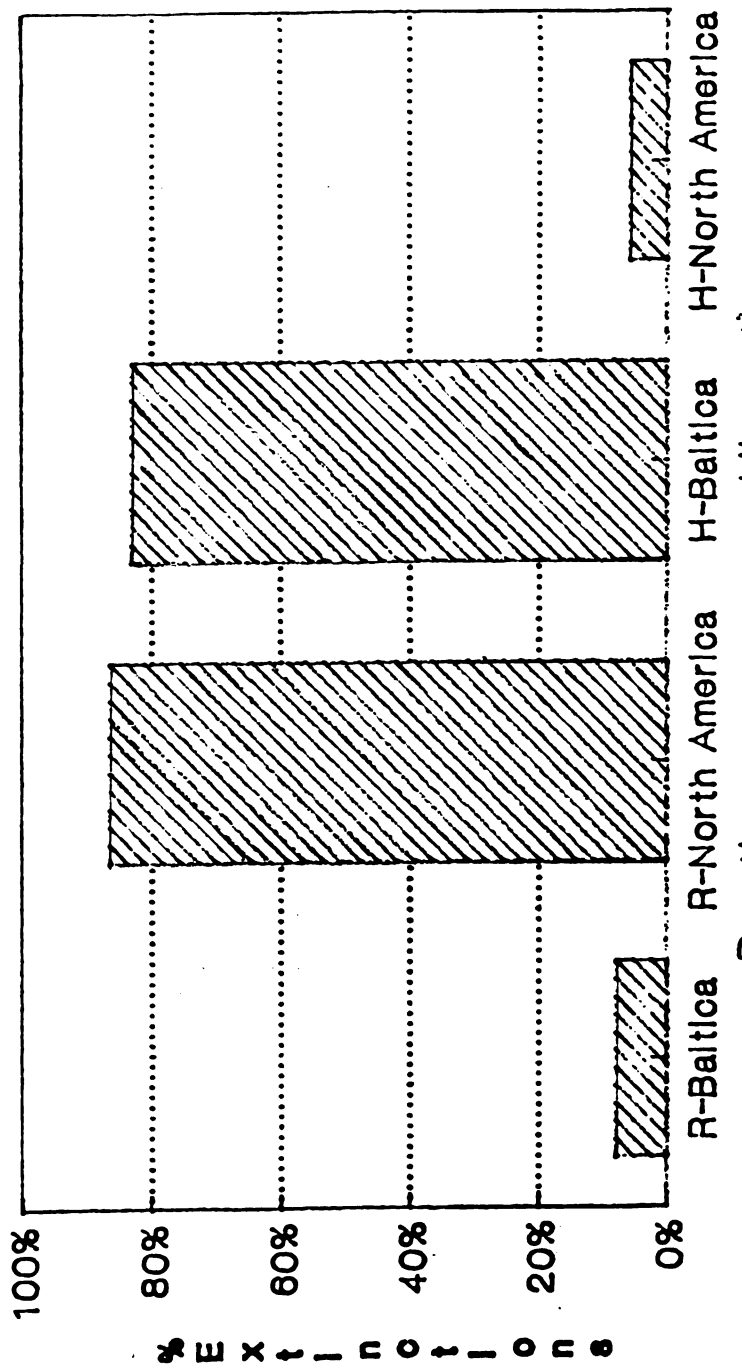

Figure 50. Rawtheyan and Hirnantian extinctions of bryozoan species in Baltica and North America listed as % of species extinct per continent.

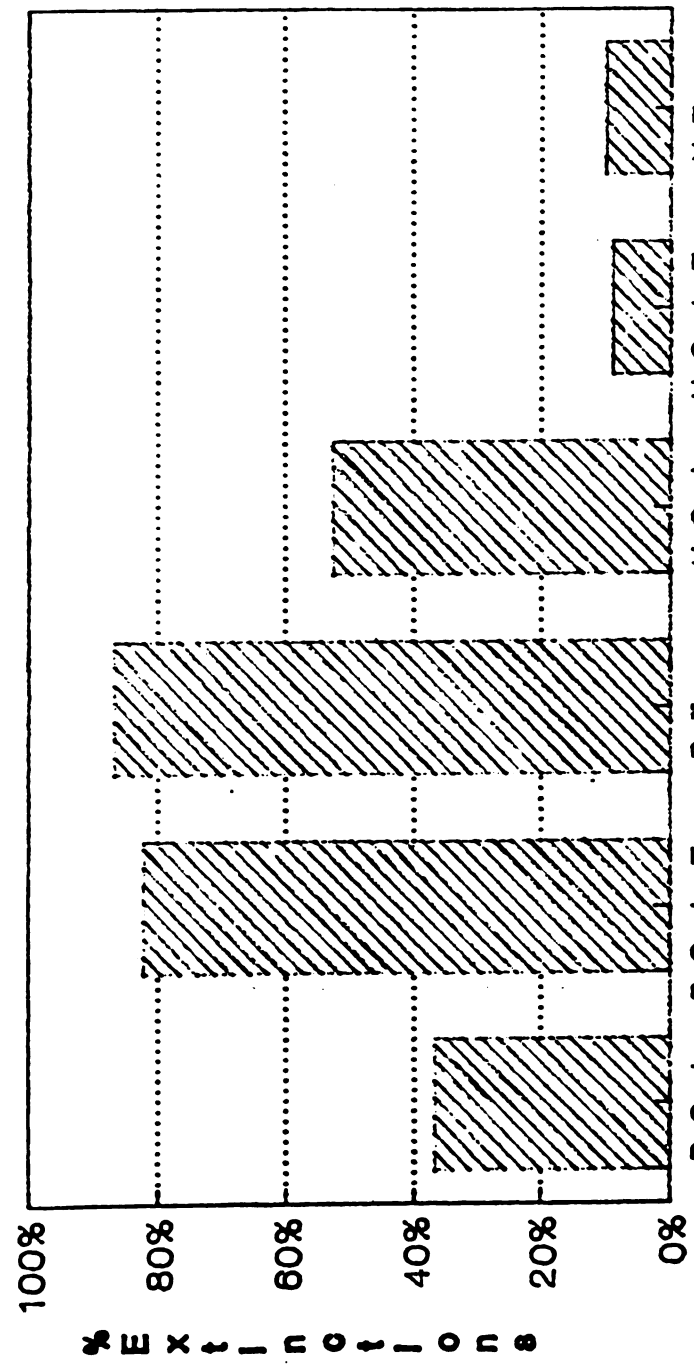

Figure 51. Rawtheyan and Hirnantian extinctions of bryozoan species listed as % of species extinct per lithotope occupied.

rates in terrigenous and mixed lithotopes exceeded 80% compared to about 35% for carbonate lithotopes. Extinctions were highly concentrated among species in the orders Trepostomata and Tubuliporata.

HIRNANTIAN EXTINCTIONS

A second wave of Late Ashgill extinctions occurred during the Hirnantian and the effects were quite different than those of the Rawtheyan. Hirnantian extinctions were concentrated in Baltica, which lost over 80% of its species, as opposed to North America, which lost approximately 20% (Figure 50). Hirnantian extinctions were concentrated in carbonate lithotopes as opposed to terrigenous and mixed lithotopes, with rates exceeding 50% for carbonates as opposed to approximately 10% for terrigenous and mixed (Figure 51). Hirnantian extinctions were high among species belonging to the orders Cryptostomata and Cystoporata.
The magnitude of the Hirnantian extinction was considerably smaller than the Rawtheyan at the species level. The Hirnantian extinctions also coincided with a large migratory wave of North American genera into Baltica (Figure 9). Spjeldnaes (1981) previously recognized this immigration as the 'Porkuni' (Estonian F2 Horizon) wave.

DISCUSSION

Two major causes have been proposed for the Late Ordovician mass extinction: global cooling (Stanley, 1984), and marine regression (Brenchly 1984, and others). Stanley's global cooling hypothesis does not explain the differing effects of the extinction on faunas from different lithotopes. Brenchly attributed the first phase of the Late Ashgill extinctions to the marine regression which decimated the shelf benthos via the species-area effect. Jablonski (1985) questioned the role of the species-area effect in extinctions by demonstrating the importance of oceanic islands as refuges during marine regressions. The shelf area around oceanic islands increases during regressions. This analysis suggests that marine regressions may cause extinctions by wiping out specific types of habitats rather than through the species-area effect.

The Rawtheyan extinctions of bryozoan species were concentrated in areas of terrigenous lithologies in North America, while areas of carbonate lithologies were relatively unaffected. Anstey (1986) found that over 50% of the genera in the terrigenous Reedsville-Lorraine Biome and the mixed terrigenous-clastic Cincinnati Biome did not survive into the Silurian. This may be due to the fact that species from carbonate environments were able to find similar habitats on the carbonate

shelves of oceanic islands, while species from terrigenous environments had their habitat destroyed during the marine regression. An oceanic island bryozoan fauna was described by Ross (1966b) from the Portrane Limestone of Ireland. This fauna, of Rawtheyan age, comes from an exotic terrane which was formerly an island in the Iapetus Ocean (Neuman 1984) and has affinities with North American and Baltic carbonate faunas. The disproportionate effect of the Rawtheyan marine regression on North American faunas is also evident in the brachiopods (Sheehan 1975), as Baltica was apparently less affected by the regression.

The presence of oceanic islands probably facilitated faunal migrations, as the largely carbonate shelves of Baltica received large numbers of immigrants during the Hirnantian. Hirnantian extinctions may be related to a reduction in provinciality associated with this migratory wave. Brenchly (1984), however, attributed the Hirnantian extinctions to a rapid rise in sea level at the end of the Hirnantian, which is evidenced by deposits of Early Silurian black shale at many Baltic localities. Sheehan (1987) associated this rapid rise in sea level with the spread of anaerobic conditions in deep water which led to the extinction of the Foliomena brachiopod community. Raymond et al. (1987) also associated rising sea level caused by glacial melting with increased equatorial seasonality and high equatorial extinctions in Carboniferous brachiopods. The Hirnantian migrations may, in turn, have been related to rising sea level, as Hallam (1977) found that cosmopolitanism among

Jurassic bivalves increased during transgressions.

CONCLUSION

1. The Late Ordovician extinctions of bryozoa occurred in 3 discrete phases: A. An Onnian phase, B. a Rawtheyan phase, and C. a Hirnantian phase.
2. Late Caradoc extinctions were concentrated on the continents of Baltica, Siberia and Southern Europe and affected primarily stenotopic and endemic species and genera. The Late Caradoc was also a time of immigration of new genera onto Baltica and Siberia.
3. Rawtheyan extinctions were concentrated among species occupying terrigenous and mixed terrigenous/carbonate lithotopes on North America.
4. Hirnantian extinctions were concentrated among species occupying carbonate lithotopes on Baltica, and were correlated with a wave of North American immigrants which appear in Baltica at that time.
5. These data appear to be consistent with a hypothesis which explains the Rawtheyan extinction through a destruction of terrigenous habitats in North America by a marine regression and the Hirnatian extinction through a reduction in provinciality and low oxygen conditions associated with the ensuing transgression.

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APPENDIX A

APPENDIX A

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