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Recovery of the stromatoporoid fauna after the Late Ordovician extinction

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Abstract. The Late Ordovician extinction of stromatoporoids was a gradual rather than an abrupt process of decrease in diversity through the Late Ordovician to Early Silurian transition. A transformation of a labechiid-dominated Ordovician stromatoporoid fauna into a clathrodictyid-dominated Early Silurian fauna embraced a wide time interval, from the beginning of the late Caradoc to the end of the middle Llandovery (Aeronian). It roughly coincided with a proposed global cooling, or "ice-house" period in Earth history. During this period the earliest labechiids with poorly calcified (probably aragonitic) skeletons were replaced by more advanced labechiids and clathrodictyids with well-calcified skeletons. The generic diversity of stromatoporoids reached its lowest value in the early Rhuddanian with representatives of only four genera, *Clathrodictyon, Ecclimadictyon, Pachystylostroma* and *Forolinia*. During the late Rhuddanian and early Aeronian the earliest representatives of the families Actinostromatidae (*Plectostroma*) and Atelodictyidae (*Intexodictyon*) were added, respectively. Generic diversity abruptly increased in the late Aeronian (reaching at least 12 genera) when the first representatives of the Gerronostromatidae (*Petridiostroma*), Pseudolabechiidae (*Pachystroma*), Stromatoporidae (*Lineastroma*) and Syringostromellidae (*Syringostromella*) appeared. During the Telychian the generic diversity of actinostromatids and stromatoporids increased further and the first densastromatids (*Densastroma*) appeared. A comparatively long duration of Late Ordovician extinction and Early Silurian recovery of the stromatoporoid fauna is probably best explained by general global cooling, including several glacial episodes in addition to the well-known end-Ordovician (*Hirnantian*) ice age, unfavourable for stromatoporoids as thermophilic organisms.

Key words: diversity, extinction, Late Ordovician, Llandovery, recovery, stromatoporoids

Introduction

The Ordovician stromatoporoid fauna was dominated by labechiids having a cystose (vesicular) structure. In addition, the first representatives of clathrodictyids (laminate stromatoporoids) appeared in the middle Caradoc. During the Silurian, representatives of all other orders of stromatoporoids were added, and in the Wenlock fauna a high diversity of stromatoporoids has been previously recorded. However, the transition from the comparatively low-diversity Ordovician to the high-diversity Middle Silurian fauna has been inadequately documented and therefore phylogenetic relationships of some groups of stromatoporoids (densastromatids, syringostromatids, etc.) are still obscure. This lack of information about the ties between Ordovician and Wenlockian faunas has inhibited elaboration of a sound classification of stromatoporoids.

Previously, only in Estonia (Nestor, 1964) and in Norway (Mori, 1978) has the succession of the Llandovery stromatoporoid faunas been studied in detail, and the data were summarized recently (Nestor, 1999a). However, due to ecological conditions (preserved facies in available sequences record overly deep water), the uppermost Llandovery (upper Telychian) in those places is almost barren of stromatoporoids. A subregional hiatus at the end of the Aeronian also limits completeness of the stromatoporoid succession. Recent dating of lower Silurian rocks in North America show that the upper Aeronian and Telychian faunas are well developed, and as a result, the Baltoscandian and North-American stromatoporoid successions complement each other well. Therefore the authors of the present paper initiated a project, supported by the U.S. National Research Council (NRC) and by the Petroleum Research Fund (PRF), to consider the recovery of the stromatoporoid fauna after the Late Ordovician extinction event, in order to describe more thoroughly the main diversification of the stromatoporoids during the Early Silurian (Llandovery).

Sources

We have studied new material collected by Stock from northern Michigan, Iowa, Oklahoma, Missouri, New York, Ohio and Alabama, as well as stromatoporoids from Anticosti Island collected by P. Copper. Description of these materials is still in progress therefore, identification to genus level only is used in this paper. Some new genera are being established, but they are here only designated in faunal lists and range charts by the closest valid generic name, and placed in quotation marks. Older documentation of stromatoporoids was taken into consideration only if it was possible to assign taxa to specific levels of the standard global stage framework (Rhuddanian, Aeronian, Telychian). Data included are that of Parks (1908, 1909) on Silurian stromatoporoids from the Ontario, Michigan and Hudson Bay areas Petryk (1967) from Baffin Island Mori (1978) from Norway Nestor (1964, 1976, 1983, 1999b) from Estonia, the Siberian Platform, Novaya Zemlya and Ireland, respectively Dong and Yang (1978), Yang and Dong (1980) from South China and Tesakov *et al*. (1985) from the Siberian Platform. Range charts of Ordovician stromatoporoid genera from North America were compiled based on the papers of Parks (1910), Raymond (1914, 1931), Galloway and St. Jean (1961), Kapp and Stearn (1975), and Bolton (1988). Classification follows that in the recent paper by Stearn *et al*. (1999).

Late Ordovician extinction

In order to establish the character of the Late Ordovician extinction and subsequent recovery of the stromatoporoid fauna, range charts of genera through the Ordovician/Silurian boundary were compiled in the most complete sequences of North America and Baltoscandia. The former (Figure 1) demonstrates that after an intense early Caradoc ("Chazyan"-early Chatfieldian) radiation among labechiids (11 genera appeared) a gradual retreat and still-stand followed until late Aeronian-Telychian time, when 17 genera appeared, among them the earliest representatives of the orders Actinostromatida and Stromatoporida.

In North America, some of the Ordovician labechiid genera (*Cryptophragmus, Thamnobeatricea, Stromatocerium* s.s.) disappeared by the end of the Caradoc, some others (*Pseudostylodictyon, Cystostroma, Cystistroma, Radiostroma, Aulacera, Dermatostroma*), followed during the Ashgill. Most of these genera (except *Aulacera*) disappeared from the North American stromatoporoid fauna by the end of Richmondian (Rawtheyan) time, which was when the sharpest decrease in diversity occurred during the Late Ordovician. The lowest generic diversity was in Gamachean time (three genera) and in the Rhuddanian-early Aeronian (four genera). Nothing remarkable happened at the Ordovician/Silurian boundary except the disappearance of *Aulacera*, a giant columnar stromatoporoid. In other words, there was no mass extinction of stromatoporoids at the very end of the Ordovician.

The picture is rather similar in the Baltic-Scandinavian area (Figure 2), except that the Ordovician record of stromatoporoids is much less complete. After the first appearance of stromatoporoids in the middle Caradoc (Oandu-Rakvere Regional Stages), there is a gap in the record of their distribution. From the lower-middle Ashgill (Vormsi-Pirgu Stages) only rare, scattered occurrences of *Clathrodictyon, Cystostroma, Cystistroma* and *Plumatalinia* are known. The uppermost Ordovician (Porkuni Stage) is characterized by abundant individuals of *Clathrodictyon* and *Ecclimadictyon* with rare *Pachystylostroma* and *Stelodictyon*, i.e. the generic content of the stromatoporoid fauna is very close to that of the lowermost Silurian. No sign of a mass extinction of stromatoporoids at the very end of the Ordovician has been identified in this region either.

The delay in the appearance of stromatoporoids in Baltoscandia has been explained by the progressive drift of the ancient Baltica continent from a moderate climate zone to the subtropics by middle Caradoc time (Webby, 1980). Their disappearance again soon afterwards may be explained by rotation of Baltica, or by the cessation of its northward move, although there may be another explanation. Recent investigations (Grahn and Caputo, 1992 Legrand, 1995 · Caputo, 1998) confirm that the well known Hirnantian glaciation at the end of the Ordovician was not a unique event but occurred as one of several glacial episodes within a longer "ice-house" period lasting from Late Ordovician to Early Silurian time (Frakes *et al*., 1992).

Patzkowsky and Holland (1993) observed a sharp faunal changeover from a warm-water, coral- and stromatoporoid-dominated benthic assemblage, to a cooler-water, bryozoan-dominated assemblage occurring in eastern North America approximately at the transition from the Turinian (Black River) to Chatfieldian (Trenton). Patzkowsky *et al*. (1997) also recognized a positive excursion of carbon isotope compositions in the lowermost Chatfieldian. An approximately synchronous carbon isotopic event has been recorded in Estonia in late Keila time (Ainsaar *et al*., 1999). It supports the global character of middle Caradoc cooling hypothesized by some investigators (Lavoie, 1995) as the probable onset of Late Ordovician glaciation.

In view of the above, it seems reasonable to explain the comparatively low diversity and scarcity of the stromatoporoid fauna during the late Caradoc to the middle Aeronian as caused by the unfavourable and changeable environmental conditions during the global "ice-house" period, which severely affected stromatoporoids treated as thermophilic organisms (Webby, 1980 Nestor, 1984).

The earliest Ordovician labechiids were characterized by comparatively poorly calcified skeletons, heavily subjected to alteration processes, dissolution and recrystallization (Parks, 1910 Galloway and St. Jean, 1961 Kapp and Stearn, 1975 Webby, 1979). Kapp and Stearn (1975) suggested that heavy recrystallization and relict fibrous microstructure indicate the primarily aragonitic content of their skeleton. In the middle Caradoc time the first clathrodictyids (*Clathrodictyon, Ecclimadictyon*) appeared, supplied with much better preserved, well-calcified skeletons characteristic of the more advanced groups of stromatoporoids. Transition from an aragonitic to a calcitic skeleton probably took place

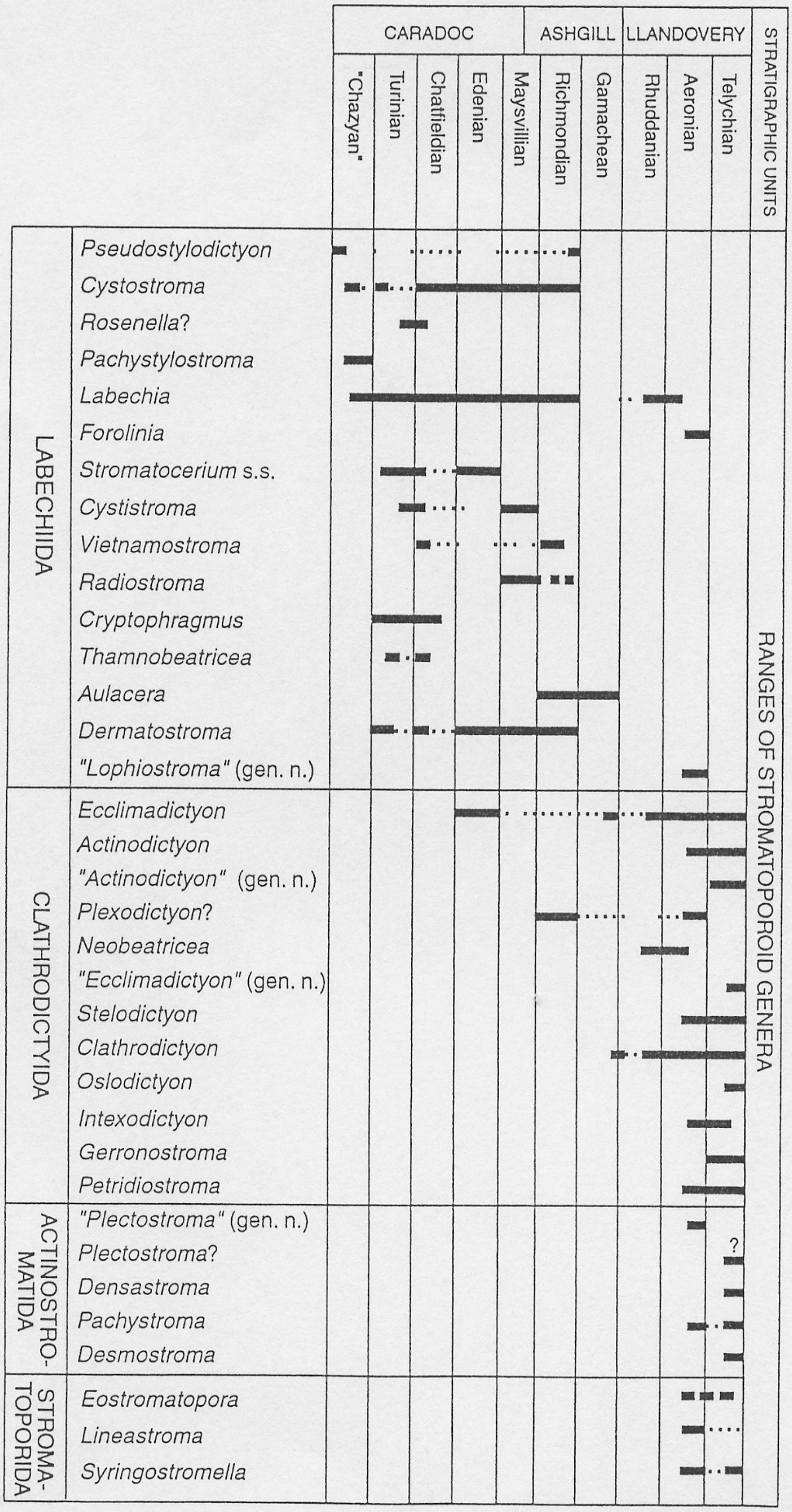

Figure 1. Range chart of the Ordovician and Llandovery stromatoporoid genera in North America.

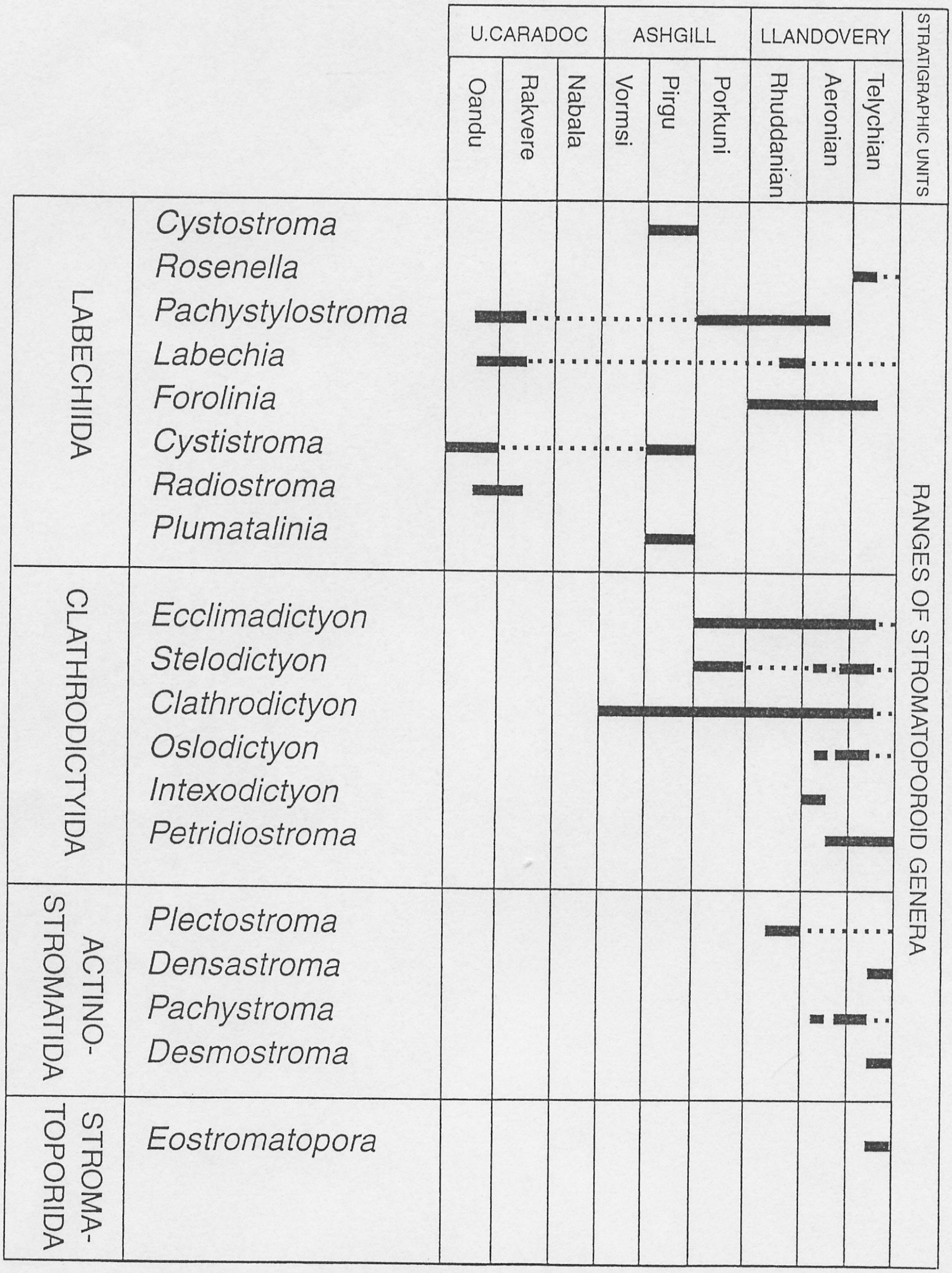

Figure 2. Range chart of the Ordovician and Llandovery stromatoporoid genera in Baltoscandia.

among labechiids also. For example, the ancient *Labechia prima* group (Webby, 1979) was gradually replaced by the species *Labechia huronensis, L. macrostyla, L. regularis* etc., with more perfectly preserved skeletal elements, particularly pillars, that are characteristic of Silurian representatives of this genus. The replacement of the aragonitic skeletal substance with calcite commenced roughly at the supposed time of transition from a warm climate mode to a cool mode,

Order	TAXA	Earlier	RHUDDANIAN EARLY	RHUDDANIAN LATE	AERONIAN EARLY	AERONIAN LATE	TELYCHIAN EARLY	TELYCHIAN LATE	Later
LABECHIIDA	ROSENELLIDAE								
	Pachystylostroma	+	E	E	E			I	+
	Forolinia		E	NE	ENz	MQN(Y)	E(Y)		
	Rosenella	+				(Y)	E(Y)		+
	LABECHIIDAE								
	Labechia	+		E		(Y)	S(Y)	S	+
	STYLOSTROMATIDAE								
	Stylostroma	+				(Y)	(Y)	S	+
	AULACERATIDAE								
	Ludictyon	+				(Y)	(Y)		
	LOPHIOSTROMATIDAE								
	"*Lophiostroma*" (gen. n.)					Q			
CLATHRODICTYIDA	CLATHRODICTYIDAE								
	Clathrodictyon	+	QE	MQNE	MQENzS	MQBNS(Y)	MQB NENzSY	MQBHS	+
	Stelodictyon	+				MQ(Y)	MQNEY	MS	+
	Clavidictyon?					(Y)	(Y)	S	+
	Oslodictyon	+				(N)	NE	M	+
	ACTINODICTYIDAE								
	Ecclimadictyon		E	QNE	QENz	MQBN	MQBNEY	MBQ	+
	Neobeatricea			Q	M				+
	Plexodictyon?	?				M(Y)	(Y)	H	+
	"*Actinodictyon*" (gen. n.)						M	M	
	Actinodictyon						Q	BH	+
	"*Ecclimadictyon*" (gen. n.)							M	
	ATELODICTYIDAE								
	Intexodictyon				E	MQB(Y)	Y		+
	GERRONOSTROMATIDAE								
	Petridiostroma					MN	QNE	MIN	+
	Gerronostroma						(M)B	(M)HI	+
ACTINOSTROMATIDA	ACTINOSTROMATIDAE								
	Plectostroma			E				H	+
	"*Plectostroma*" (gen. n.)					M			+
	PSEUDOLABECHIIDAE								
	Pachystroma					M	E	MBQ	+
	Desmostroma							MQGS	+
	DENSASTROMATIDAE								
	Densastroma							MG	
STROMATOPORIDA	STROMATOPORIDAE								
	Eostromatopora						B	BIN	+
	Lineastroma					M			+
	SYRINGOSTROMELLIDAE								
	Syringostromella					M		H	+
	Number of genera		4	7	6	12(18)	14(18)	20	

Figure 3. Stratigraphic and geographic distribution of Llandovery stromatoporoid genera. Abbreviations B-Baffin Island, E-Estonia, G-Gotland, H-Hudson Bay, I-Ireland, M-N. America Midcontinent, N-Norway, Nz-Novaya Zemlya, Q-Quebec (Anticosti+Gaspe), S-Siberian Platform, Y-Yangtze Platform (South China).

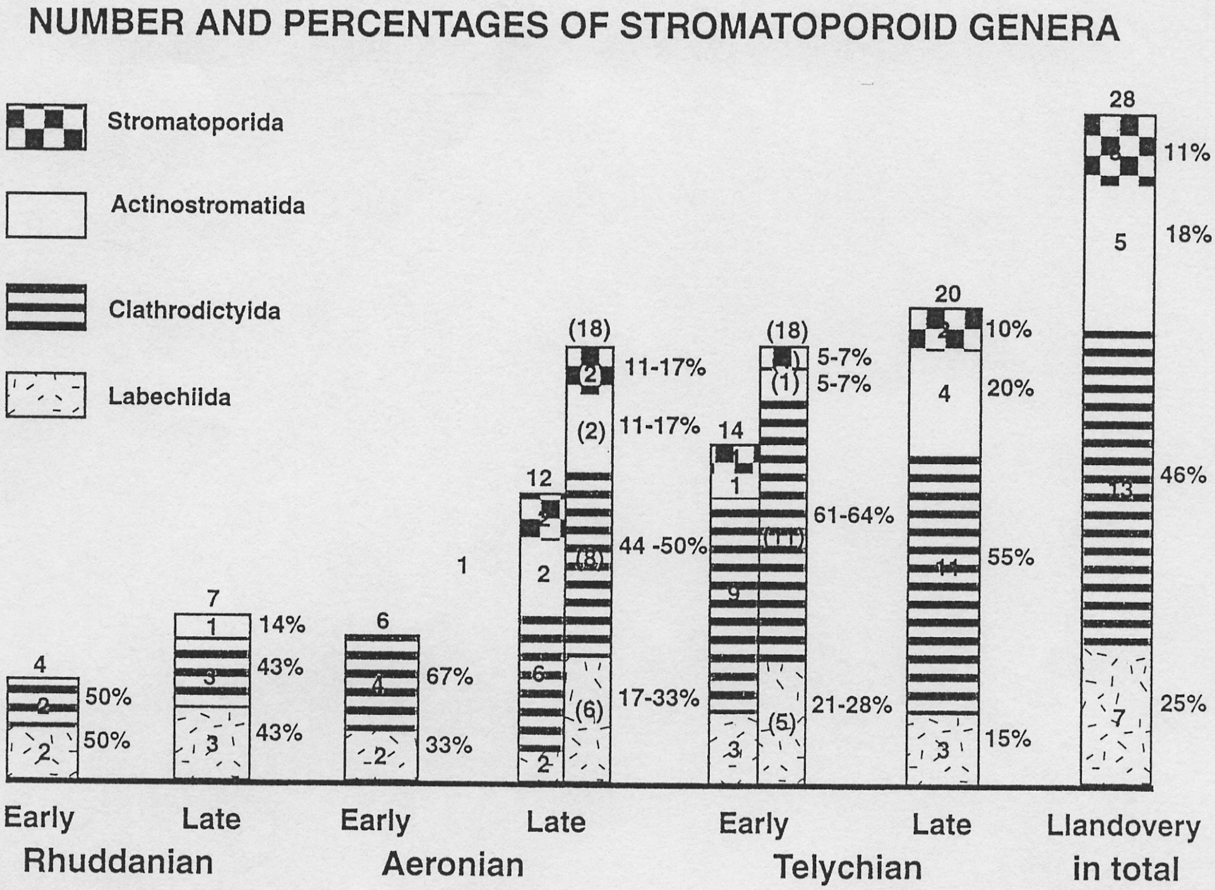

Figure 4. Number and percentage of stromatoporoid genera in subdivisions of the Llandovery. See explanations in text.

and might have been induced by the global lowering of water temperature.

To sum up, the Late Ordovician extinction and subsequent recovery of the stromatoporoid fauna at the beginning of Silurian time were longer-lasting processes than generally supposed. This was probably caused by the sensibility of thermophilic stromatoporoids to global cooling of the climate during the Late Ordovician-Early Silurian "ice-house" period. Other more tolerant groups of organisms suffered mainly from the very severe, but comparatively short Hirnantian glaciation, leading to their abrupt mass extinction.

Llandovery diversification

Figure 3 shows distribution of stromatoporoid genera within subdivisions of the Llandovery of some best-studied regions. In most cases it has been possible to divide the standard stages (ages), Rhuddanian, Aeronian, Telychian, into lower (early) and upper (late) parts based mainly on the mass occurrences of pentamerids. In some cases the exact stratigraphic position of the records is uncertain in which case the abbreviation of the region name is shown in parentheses. Pre- and post-Llandovery records of the genera are shown by a plus sign (+) in the columns "Earlier" and "Later" respectively. The number of genera and percentage of representatives of different orders are shown in the histogram (Figure 4). The late Aeronian and early Telychian columns have been divided into two parts, the left side only taking into account certain data, with the right side also including less certain information, shown in Figure 3 in parentheses.

The histogram shows the very low generic diversity of stromatoporoids in Rhuddanian and early Aeronian time (four to seven genera), and its abrupt increase (12 to 20) beginning in the late Aeronian. During the Rhuddanian, labechiid and clathrodictyid genera were almost equally represented in the stromatoporoid fauna, but species diversity and general abundance of clathrodictyids were much higher. In the late Aeronian and Telychian clathrodictyids maintained their dominant position (44-64%), while labechiids lost their relative importance (17-33%), and actinostromatids (5-20%), as well as stromatoporids (5-15%) became significant components of the stromatoporoid fauna.

Qualitative changes

All labechiid genera, except *Forolinia* and "*Lophiostroma*" (gen. n.), extend upward into the Llandovery from the Ordovician (Figure 3). During the Llandovery a marked generic radiation took place among the clathrodictyids, in the fam-

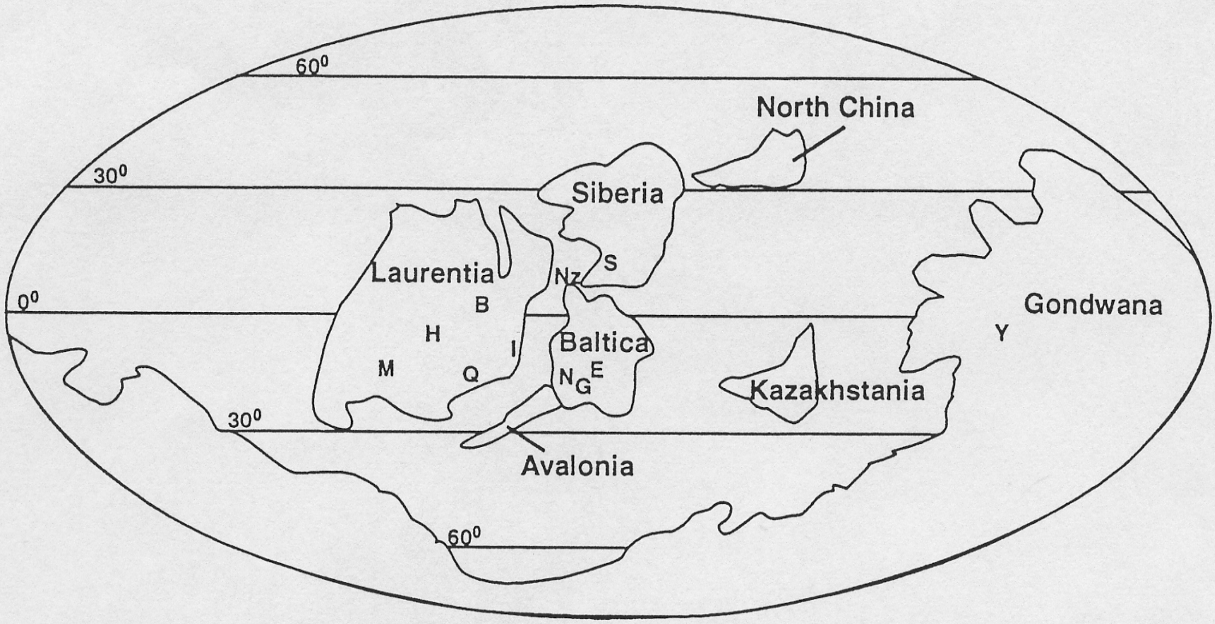

Figure 5. Distribution of analysed records of stromatoporoids, plotted on the Llandovery global map reconstruction, modified after Scotese and McKerrow (1990). Abbreviations of the region names as in Figure 3.

ilies Clathrodictyidae (increasing from two to four genera) and especially the Actinodictyidae (from two to six genera). The first representatives of true laminate stromatoporoids, the families Atelodictyidae (*Intexodictyon*) and Gerronostromatidae (*Petridiostroma, Gerronostroma*), appeared in the early Aeronian of Estonia and late Aeronian of Norway and North America respectively. The representatives of these families have distinct planar laminae and rod-shaped (Gerronostromatidae) or complicated, branching pillars (Atelodictyidae), which differ from the poorly differentiated, amalgamated laminae and pillars of the Actinodictyidae and Clathrodictyidae.

The earliest actinostromatid from the Family Actinostromatidae with reticulate (latticed) structure, the genus *Plectostroma* has been described from the late Rhuddanian of Estonia. A peculiar new genus ("*Plectostroma*"), which combines characteristics of the Labechiida (cyst plates) and Actinostromatida (colliculi), has been found by the authors in upper Aeronian strata (Hendricks Formation) of northern Michigan. At the same time and in the same area there appeared the first stromatoporoids with clinoreticulate or clinofibrous subcolumns (*Pachystroma*). Conventionally, these are attributed to the Pseudolabechiidae (Stearn *et al*., 1999), but actually they are even more closely related to the Order Syringostromatida through the presence of clinoreticulate subcolumns. A third branch of actinostromatids, the Family Densastromatidae, characterized by the presence of an orthoreticulate microstructure, appeared in the latest Telychian (Iowa, Gotland). This means that by the end of the Llandovery all families of the Actinostromatida were represented in the stromatoporoid fauna except the Actinostromellidae.

Also, during the second half of Llandovery time the earliest representatives of the Order Stromatoporida emerged. We have discovered *Lineastroma* (Stromatoporidae) and *Syringostromella* (Syringostromellidae) in the late Aeronian of northern Michigan. *Eostromatopora* (Stromatoporidae) has been reported from Telychian strata of Baffin Island, Norway and Ireland (Nestor, 1999b). This indicates that the main branches of the Stromatoporida, except for the Ferestromatoporidae, also arose by the end of the Llandovery.

Biogeographic peculiarities

Occurrences of stromatoporoids analysed are shown on the Llandovery global map reconstruction, modified after Scotese and McKerrow (1990) (Figure 5). In the Rhuddanian and early Aeronian the origination center of the new taxa was Estonia where *Forolinia, Plectostroma* (Actinostromatidae) and *Intexodictyon* (Atelodictyidae) successively arose. In the late Aeronian, the center of origin shifted to the Michigan Basin (northern Michigan), where the earliest representatives of the genera *Petridiostroma* (Gerronostromatidae), *Pachystroma* (Pseudolabechiidae or Syringostromatidae), *Lineastroma* (Stromatoporidae) and *Syringostromella* (Syringostromellidae) first appeared. Anticosti Island with first records of *Neobeatricea* (late Rhuddanian) and *Actinodictyon* (early Telychian), as well as Baffin Island, with *Gerronostroma* and *Eostromatopora* (early Telychian) were less remarkable radiation centers.

The most conservative stromatoporoid faunas are those found in South China and Siberia where labechiids (*Labechia, Forolinia, Rosenella, Stylostroma, Ludictyon*) maintained an important role during the late Aeronian-Telychian, but actinostromatids and stromatoporids are apparently absent.

Conclusions

The Late Ordovician extinction and earliest Silurian recovery of stromatoporoid faunas were more prolonged events than commonly supposed, lasting from the late Caradoc to late Aeronian. They roughly correspond to the Late Ordovician-Early Silurian period of "ice-house" climate and were probably induced by the general cooling of the global climate.

During the Llandovery the generic diversity of stromatoporoids increased five times, from four to 20 genera. The sharpest increase occurred in the late Aeronian, with the doubling of generic diversity.

During the Llandovery first representatives of the families Gerronostromatidae, Atelodictyidae (Order Clathrodictyida), Actinostromatidae, Pseudolabechiidae, Densastromatidae (Order Actinostromatida) and Stromatoporidae, Syringostromellidae (Order Stromatoporida) appeared. It is almost a third of all known families of the Palaeozoic stromatoporoids, and demonstrates that the second half of the Llandovery was an important diversification phase in the stromatoporoid evolution.

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