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PART E, REVISED, VOLUME 4, CHAPTER 14: PALEOBIOGEOGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

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[Specific authorships of Ordovician, Silurian, and Devonian biogeography are indicated within]

INTRODUCTION

Data points on the accompanying maps represent occurrences of stromatoporoids as best determined by the authors. We used simplified versions of the base maps of GOLONKA (2002) for plotting the data. One point may represent several localities in one larger area (e.g., Frasnian of Alberta) and may represent several different stratigraphic levels in one area (e.g., within Frasnian of Iowa). Most points represent faunas that have been described in the literature, but a few others are superficial reports of stromatoporoid occurrences or unpublished records known to one of the authors. The exact location of some data points has been easy to determine (e.g., Michigan), whereas others have proved problematic using the Golonka base maps (e.g., Ulachan–Sis Range; Donets Basin). We relied heavily on the work of STEARN and others (1999) to determine which genera are present at each data point, but where the responsible author had more detailed and/or up-to-date information, that information was employed. Great significance should not be paid to small latitudinal changes in geographic ranges between adjacent stages and ages, as they may result from different placement of symbols within the same geographic locality.

Stromatoporoids lived in shallow, tropical to subtropical seas; thus, the extent of their geographic distribution through time can be viewed in terms of distance from the equator. The obvious interpretation would be that the warmer the Earth, the larger the latitudinal range of stromatoporoids; however, some exceptions to this generalization have been observed.

On continental portions of tectonic plates, as eustatic sea level rose, epeiric seas formed in low-lying areas, providing new, more extended regions for stromatoporoid habitation. Increases in eustatic sea level result from the melting of glacial ice as a byproduct of global warming, and/or from an increase in the rate of seafloor spreading, which raises the level of the seafloor, causing seawater to spill onto low-lying parts of continents (e.g., LIEBERMAN, 2000, p. 86).

There is no uniform agreement among biogeographers where it comes to the delineation of synchronous areas containing different assemblages of taxa, known as biogeographic units (CECCA, 2002, p. 81). Among paleontologists, KAUFFMAN (1973), working with Cretaceous bivalves, determined that a realm is a biogeographic unit containing more than 75% endemic taxa (i.e., at least 75% of the genera present are found in no other realm), an approach accepted in theory by BOUCOT (1975) for Paleozoic brachiopods. OLIVER (1977) found percentages of endemism for rugose coral genera in the Early and Middle Devonian ranged from 33% in the Siegenian (Pragian) to 92% in the late Emsian. Similar data are presented here, because it is at the level of genus that the group is most clearly defined and characterized, thanks in part to the recent work of STEARN and others (1999) and in the *Treatise Online* (NESTOR, 2011; STEARN, 2011; WEBBY, 2012a; and see WEBBY & STOCK, *Treatise Online,* Part E, Revised, vol. 4, Chapters 16B and 16D, respectively).

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ORDOVICIAN

B. D. Webby

A number of reviews of global and regional aspects of Ordovician stromatoporoid biogeography have been presented by Webby (1980, 1992; in Webby & others, 2000) and by Lin and Webby (1989). Also Bogoyavlenskaya and Lobanov (1990), Bogoyavlenskaya (2001), and Bogoyavlenskaya and Yelkin (2006) have discussed various biogeographic relationships during the initial global spread of Ordovician stromatoporoids. In most cases, these studies have been hampered by the lack of a well-constrained, unified timescale to establish close ties for precisely correlating the stromatoporoid-bearing assemblages, especially on a global basis. Only now, with the more reliable and well-calibrated, internationally based, Ordovician stratigraphic framework and time scale (Sadler & Cooper, 2004; Webby & others, 2004), can more reliable age determinations of assemblages be made across different regions and paleolatitudes of the globe.

In the 1980 survey of the distribution of Ordovician stromatoporoids, Webby argued that: (1) the earliest known stromatoporoids (labechiids) appeared in the Chazy Group successions of eastern North America (Kapp & Stearn, 1975), and in near-age equivalents of Tasmania and Scotland (Webby, 1977, 1979b), with a comparatively low-diversity assemblage (up to five genera) during the upper Llanvirn–Llandeilo interval, now recognized as representing the middle to latter part of the Darriwilian age (=late Middle Ordovician); (2) the main diversification occurred a little later, during the early Caradoc or early part of Sandbian age (=early Late Ordovician), with a tripling of the generic diversity, and establishment of a separate northern China province marked by first appearances of four endemic genera (*Lophiostroma, Aulacera, Ludictyon, Sinodictyon*); (3) in the middle Caradoc to early Ashgill (=late Sandbian to middle Katian ages), the first clathrodictyid stromatoporoids (and the first cliefdenellid sphinctozoan sponges) appeared in Australian and Eurasian sequences, forming apparently a separate provincial element; and (4) during the middle–late Ashgill (middle Katian to Hirnantian, or latest Ordovician) the development of single, more cosmopolitan, mixed, American–Eurasian assemblage developed, as the labechiids declined, though the cylindrical *Aulacera* and the clathrodictyids remained important. This succession of events now needs revision in terms of the more precise stage-level correlations (see below).

The review of Ordovician stromatoporoid and coral assemblages presented by Webby (1992) revealed a markedly different global biogeographic pattern based on the 22 known stromatoporoid, 120 tabulate, and 67 rugose coral genera. The focus was mainly on the more diverse assemblages, through what is now regarded as most of Late Ordovician time (a period of about 15 myr), because there was a marked lack of precision in establishing stage-level correlations. If smaller time intervals had been used, it is probable that samples from some regions would not have been large enough to provide meaningful results. On the other hand, by taking a larger interval, some degree of masking of biogeographic relationships was inevitable, especially where lithospheric plates moved significant distances across paleolatitudes during the Late Ordovician, and/or where major global cooling and warming events were taking place, as within the interval of the end-Ordovician glaciation (Webby, 1984). Nevertheless, a broad, twofold, biogeographic subdivision of assemblages was recognized, with the stromatoporoids associated with compound rugose and tabulate corals of the North American–Siberian Realm having an essentially broad, bandlike, paleoequatorial spread. The other, more restricted, southern, intermediate paleolatitude association included corals (solitary rugosans and some halysitine and heliolitine tabulate corals), but no accompanying stromatoporoids. This latter association represents the cooler, more temperate Euroasiatic Realm. The North American–Siberian Realm has a wide, circumglobal spread, equatorally extending to about 30° N and S of the paleoequator, remaining within the influence of warm equatorial currents. In most places, the typical stromatoporoid-compound rugose coral and *Tetradium* coral biofacies of the North American–Siberian Realm were considered to be associated with warm tropical waters of normal salinity, but in a few places, evaporites may also occur in association with this biofacies. Additionally, the assemblages of stromatoporoids and corals contributed to the development of frame-building Mid–Late Ordovician reefs, and their distribution has been shown to exhibit a direct relationship to paleomagnetically determined low paleolatitudes, with stromatoporoid growth usually extending to about 30° N and S of the paleoequator (WEBBY, 1980, 1984, 2002).

Other studies have been more regionally focused. For example, BOL'SHAKOVA and ULITINA (1985) depicted the distribution and provincial relationships of Late Ordovician (Ashgill) stromatoporoids in three different tectonic belts of Outer Mongolia, and LIN and WEBBY (1989) compared the Australian and Chinese Ordovician stromatoporoid and coral distributions in terms of their biogeographic significance. The stromatoporoids were also employed as just one component in a comprehensive biogeographic analysis of the whole described Australasian Ordovician biota (as part of a survey by a team of experts involving 17 fossil groups), to assess relationships with provincially significant biotas of equatorial Gondwanan and other adjoining regions, set in the context of available palaeogeographic reconstructions, based on palaeomagnetic data and tectonic considerations, such as known data about plate margins and the differentiation of discrete terranes (WEBBY & others, 2000).

A comparative survey between the Australian and Chinese stromatoporoid faunas by LIN and WEBBY (1989) was also undertaken, showing that the earliest (Llanvirn to lower Caradoc, i.e., upper Darriwilian to Sandbian) Chinese assemblages differed markedly from counterparts in eastern Australia. However, this particular comparison has proven, with recent application of the more reliable, internationally based, stratigraphic framework, to be not entirely valid, because the respective successions were of different ages. Higher in the respective successions, the ages were correctly determined (mid-Caradoc–Ashgill, i.e., mainly Katian), and the Australian (especially the New South Wales island-arc occurrences) and Chinese stromatoporoid taxa exhibit remarkably similar biogeographic relationships, even down to species level. For example, *Rosenella woyuense, Labechiella regularis,* and *Pseudostylodictyon poshanense* are northern Chinese (and Kazakhstani) provincial elements that also occur in the lower Eastonian (=lower Katian) successions of New South Wales. In addition, northwestern Chinese (and southwestern Siberian–Altai–Shoria Mt. regions) have the distinctive species *Ecclimadictyon amzassensis* (now assigned to genus *Camptodictyon* NESTOR, COPPER, & STOCK, 2010, p. 84) and *Labechiella variabilis* that are also represented in the middle–upper Eastonian (=mid-Katian) sequences of New South Wales. On the other hand, the correlative Tasmania Shelf successions have members of the genera *Thamnobeatricea, Pachystylostroma,* and *Aulacera* that suggest closer biogeographic ties with North America (Laurentia).

Later, WEBBY (in WEBBY & others, 2000, p. 69–70), in outlining again the biogeographic affinities of Australian Ordovician stromatoporoids, concluded that the assemblages in the New South Wales island-arc complexes consistently had closest affinities with associations in southeastern Asia and China, excluding most of the South China Platform, whereas the Tasmanian Shelf faunas seemed to develop rather mixed provincial relationships, dominantly Asian, except for two separate intervals: first in the Gisbornian (early Sandbian) and second during the late Eastonian (mid-Katian), when distinctive invasions of Laurentian stocks occurred.

Bogoyavlenskaya and Lobanov (1990) supported the view that the earliest labechiid assemblages appeared in the Chayzan (late Darriwilian–early Sandbian) reefal complexes of eastern North America (Kapp & Stearn, 1975), and that the early dispersal of stocks from eastern North America (Laurentia) may have extended more widely than previously thought, not only across the Iapetus Ocean, but well beyond, to the basins of the Uralian and Mongolian fold belts across Asia (Bogoyavlenskaya & Lobanov, 1990, fig. 6). They reported occurrences of the Chazy-type labechiid, *Pseudostylodictyon kayi,* in the Garevska Formation of the western slopes of the Urals, and a similar form from north of the Betpak-Dala desert region of Kazakhstan, which greatly extends the range of this species into Asia. However, there were equally significant early diversification centers for labechiid stromatoporoids, such as northern China (and perhaps Siberia), and these may have been even more important in providing early stocks that were capable of migrating into other parts of Asia (see discussion in Webby, 2012b, p. 7–9).

Bogoyavlenskaya (2001) also provided a generalized outline of the global spread of Ordovician stromatoporoids within a broadly based framework of three biogeographic divisions: a North Atlantic belt for the faunas distributed across North America and Europe; the Ural-Mongolian belt across Middle Asia; and a Pacific belt, encompassing the faunal assemblages of China and Australia. In addition, Bogoyavlenskaya and Yelkin (2006, p. 190, fig. 4) proposed the southern part of the Siberian platform as a center of origin for the stromatoporoids and showed in a world map how they inferred the early (Mid-Ordovician) stocks may have dispersed globally from the Siberian so-called center to the main regions of: (1) North America and Western Europe; (2) Eastern Europe (Russian platform); (3) China-Kazakhstan; and (4) Australia. An attempt was also made to recognize new endemic and relict endemic elements of the faunas and to differentiate more cosmopolitan and more regional components of the faunas. However, these surveys employed poorly constrained stratigraphic frameworks and made little effort to take account of contemporary plate tectonic approaches or the different available paleogeographic reconstructions that combine paleomagnetic and faunal data.

In the present review of the distribution of Ordovician stromatoporoids, the occurrences are plotted on a simplified plate tectonic base map for the late Middle to Late Ordovician (between 464 and 443 myr) produced by Golonka (2002, see fig. 7), following the approach adopted by all authors of this biogeography section. However, it is important to note that a part of the Ordovician map reconstruction covering the area of the northern China Block (extending from Inner Mongolia to Korea) shows a questionable paleoposition. Webby (2002), in a global survey of Ordovician reefs, demonstrated that the Late Ordovician stromatoporoid and coral reefs on the platform margins of northern China (region of Ordos Basin in Shaanxi and Inner Mongolia), occupied an anomalously high paleolatitude (42° N), and this may have implications also for the positioning of East Gondwana (see discussion below). In commenting on the global spread of reefs during the late Mid–Late Ordovician, Kiessling (2002, p. 636) calculated the tropical spread as being between 34° S and 25° N, though he acknowledged that the paleopositions for northern China and (Outer) Mongolia (Amuria), where rich Ashgill coral and stromatoporoid associations and local reefs occur (Bol'shakova & Ulitina, 1985), were anomalous. Overall,

Table 1. Geographical distribution of stromatoporoid (labechiid only) assemblages in the Darriwilian stage (Middle Ordovician). The seven middle Darriwilian–upper Darriwilian sites are represented in Figure 1 by *black circles* (numbered as indicated here); †genera that were the only forms that apparently did not survive into the Late Ordovician (new).

Genera (Labechiida)	Vermont, New York 4	Slopes of W. Urals 14	Siberian Platform 16	Kazakhstan 19	Malaysia: Langkawi Is. 24	Korean Peninsula 25	N. China: Anhui-Liaoning 26
Rosenella					+		+
Cystostroma	+				+?		
Pseudostylodictyon	+	+		+			+
Priscastroma†			+				
Labechia	+				+?		+
Labechiella					+	+	+
Pachystylostroma	+						
Aulacera							+
Ludictyon							+
Sinodictyon†							+
Thamnobeatricea							+
Lophiostroma							+

the spread of Ordovician stromatoporoids has been found to be within limits of near 30° N and S of the paleoequator (Webby, 1980). Kiessling (2001) recognized the tropical reef zone as significantly narrower during the Ordovician than in the Silurian and Devonian. However, Kiessling's (2002, p. 636) data indicate rather conflictingly that the late Middle to Late Ordovician reefs spread across 59° of paleolatitude, whereas the spread during the Llandovery was 55° of paleolatitude, so the main expansion of tropical reefs was actually from the Wenlock onward, not starting immediately after the end of the Ordovician.

Whereas Golonka (2002) has shown northern China attached to the northeastern margins of East Gondwana during the Ordovician, and it probably remained more or less in contact with Gondwana until it rifted away in the latest Devonian, the Li and Powell (2001) and Cocks and Torsvik (2002) reconstructions represented northern China as a discrete offshore terrane during the Late Ordovician (not a part of East Gondwana). Li and Powell (2001) regarded northern China as being peri-Gondwanan, and between 20° and 30° N paleolatitude, whereas Cocks and Torsvik (2002) considered the terrane as being more isolated, near the paleoequator, becoming a part of the peri-Gondwanan collage of terranes during only the latest Ordovician. Both of these latter reconstructions seem better able to explain why the northern China terrane had such a varied Late Ordovician stromatoporoid fauna; at the time, the block was within 30° N of the paleoequator, maybe peri-Gondwanan, but not a part of East Gondwana.

The geographical distribution of the Ordovician stromatoporoid genera is compiled in three tables, representing the late Middle Ordovician (mid–late Darriwilian) associations (Table 1), the early Late Ordovician (Sandbian) assemblages (Table 2), and the latest Late Ordovician (Katian and Hirnantian) associations (Table 3). The distribution of the stromatoporoid localities is plotted on the simplified base map (Fig. 1).

MIDDLE DARRIWILIAN–LATE DARRIWILIAN

All available evidence points to the earliest stromatoporoids (the labechiids) appearing rather suddenly in association with a significant metazoan biodiversification event in

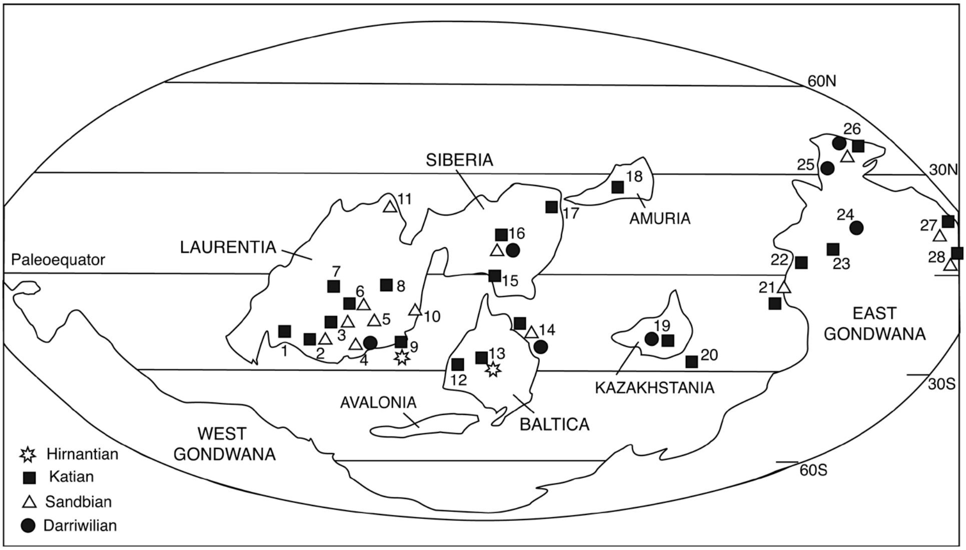

FIG. 1. Ordovician paleobiogeographic map based on GOLONKA's (2002) reconstruction showing the distribution of Middle Ordovician–Upper Ordovician stromatoporoid assemblages. Note the clustering of Ordovician sites in low paleolatitudes, mainly between 30° N and S. Key to symbols: mid–late Darriwilian, *black circles;* Sandbian, *open triangles;* Katian, *black squares;* Hirnantian, *open, seven-pointed stars;* localities: *1,* Texas and New Mexico; *2,* Alabama, Kentucky, and Tennessee; *3,* Ohio, Indiana, Iowa, and Michigan; *4,* Vermont, New York, and Pennyslvania; *5,* southern Quebec; *6,* southern Ontario; *7,* Manitoba; *8,* islands of northern Hudson Bay and Ungava Bay; *9,* Anticosti Island; *10,* Scotland; *11,* Chukchi Peninsula; *12,* southern Norway; *13,* Estonia; *14,* western slopes of Urals; *15,* Taimyr Peninsula; *16,* Siberian Platform; *17,* Altai-Sayan region; *18,* Tuva and Mongolia; *19,* Kazakhstan; *20,* Central Asia; *21,* Tarim (Xinjiang); *22,* Qinghai (northwestern China); *23,* Zhejiang and Jiangxi (southeastern China); *24,* Langkawi Island (Malaysia); *25,* Korean Peninsula; *26,* Anhui, Liaoning, Hebei, and Shaanxi (northern China); *27,* central New South Wales (Australia); *28,* Tasmania (new).

low paleolatitudes. This event produced many new community assemblages, best characterized by the Chazy-type reefs of eastern North America, on the Laurentian Platform (PITCHER, 1971; KAPP, 1974, 1975; WEBBY, 2002, p. 145, fig. 6). The labechiids are first recorded from seven main sites worldwide (numbered: 4, 14, 16, 19, 24, 25, and 26 [Table 1]), involving the differentiation of five of the seven known families of labechiids and containing more than half of the known genera (WEBBY, 2004, 2012b).

Stromatoporoids are most common in the Crown Point Formation of the Lake Champlain area of New York and Vermont, where four labechiid genera are known. They occur as large, isolated, meter-size, skeletal masses of variable growth form, like microatolls (KAPP, 1974) or may develop in prominent, frame-building roles of the Chazy-type reefs (PITCHER, 1964; KAPP, 1975). *Pseudostylodictyon* (*P. lamottense*) appeared in the Day Point Formation and is therefore the earliest stromatoporoid to be seen in North American successions (KAPP & STEAN, 1975). Its ancestors were thought by KAPP and STEARN to be derived from an encrusting sponge that began to precipitate a carbonate (aragonite) skeleton, probably earlier in the Middle Ordovician. Species of *Labechia* and *Pachystylostroma* in succeeding beds of the Crown Point Formation apparently evolved from this *Pseudostylodictyon* stock (KAPP & STEARN, 1975). *Pachystylostroma* was initially an endemic genus. The genus *Cystostroma* has also been recorded from the Crown Point succession (GALLOWAY & ST. JEAN, 1961), in the same area. All these stromatoporoid diversification and reef-building events occurred in on-shelf sites, in warm, shallow, subtidal seas of the Laurentian Platform (Webby, 2002).

The most diverse associations of early labechiids are recorded from a number of localities of the widely distributed, moderately thick (up to 270 m) sequence of massively bedded limestones (in places mottled and dolomitic) of the Machiakou Formation on the North China Platform (extending to parts of Anhui, Shandong, Shaanxi, Hebei, Liaoning, and Jilin provinces). None of the rich stromatoporoid collections from the Machiakou Formation have been precisely located in respective sequences, so it is not yet possible to establish a meaningful faunal succession or understanding of evolutionary relationships based on first appearances within the respective successions. However, it is likely that most of them come from the upper parts of the respective Machiakou sequences, correlating with middle Darriwilian–late Darriwilian. A total of nine labechiid genera have been recorded from the region, and they all appear to have evolved in on-shelf, warm, shallow, subtidal locations of the North China Platform. A few genera have localized distributions, such as *Pseudostylodictyon* and *Lophiostroma* from Shandong (Yabe & Sugiyama, 1930; Ozaki, 1938), *Sinodictyon* from Liaoning (Yabe & Sugiyama, 1930), and *Thamnobeatricea* from Anhui (Dong, 1982), whereas *Rosenella, Aulacera,* and *Ludictyon* occur in both Shandong and Anhui (Ozaki, 1938; Dong, 1982). The genera *Labechiella* and *Labechia* have the widest distribution across northeastern China (Liaoning, Shandong, Anhui, Shaanxi). All these genera, with the exception of *Pseudostylodictyon* and *Labechia,* were initially endemic to the northern China region. The previous recognition of this assemblage as a separate northern China province (Webby, 1980) is probably no longer justified, given that, with improved assessments of age, the marked northern Chinese diversification can be more confidently recognized as commencing, like the first appearances of the less diverse Laurentian Chazy assemblages, at the very beginning of the record of skeletonized labechiid faunas.

The Korean Peninsula is recognized in the Middle Ordovician as being a part of the North China Block, and it includes stromatoporoid-bearing sequences (Fig. 1, site no. 25). *Labechiella* has been recorded from both North and South Korea (Yabe & Sugiyama, 1930; Kano & others, 1994; Kano & Lee, 1997). The South Korean material comes from the Yeongheung Formation of the Yeongweol area and is of mid-Darriwilian age (Kano & others, 1994; Choi & Lee, 1998). These latter sequences probably accumulated in more open marine platform conditions than those with the more diverse faunas in northern China.

Labechiids from the Langkawi Islands of Malaysia (Webby, Wyatt, & Burrett, 1985) are associated with Unit J of the lower Setul Limestone, a succession now renamed the Kaki Bukit Limestone Formation (Cocks, Fortey, & Lee, 2005). The assemblage of four stromatoporoid genera (Fig. 1, site no. 24) were earlier suggested to have a pre-Chazyan Whiterockian age (Wongwanich & others, 1983; Stait & Burrett, 1984). However, more complete correlation of the Langkawi Ordovician sequence, as presented by Laurie and Burrett (1992), indicates that Unit J is more likely Darriwilian in age, though possibly not latest Darriwilian. Consequently, these stromatoporoid ranges coincide closely with the range of occurrences from northern China. From a biogeographic standpoint, the Langkawi assemblage is associated with the Sibumasu terrane, according to Cocks, Fortey, and Lee (2005, p. 715), either as a part of the peri-Gondwanan collage of small terranes, close to East Gondwana, or it was separated by a larger ocean from Gondwana. The similarities between the northern China and Sibumasu stromatoporoid assemblages suggest close late Mid-Ordovician biogeographic links, with occupation of

TABLE 2. Geological distribution of stromatoporoid (labechiid only) assemblages in the Sandbian stage (Upper Ordovician). The 13 Sandbian-age sites are represented by *open triangles* in Figure 1; *genera that made their first appearances in the Sandbian (new).

Genera (Labechiida)	Alabama, Kentucky, Tennessee, Pennsylvania 2	Ohio, Indiana, Iowa, Michigan 3	Vermont, New York, Pennsylvania 4	Southern Quebec 5	Southern Ontario 6	Girvan, Scotland 10
Rosenella			+	+		
Cystostroma	+			+?		
Pseudostylodictyon						
Labechia	+			+	+	+
Labechiella						
**Stratodictyon*			+			
**Stromatocerium*	+	+	+	+	+	
**Cystistroma*	+	+	+	+	+	
Pachystylostroma					+	
**Stylostroma*						
Aulacera			+	+		
**Cryptophragmus*	+	+	+	+	+	
Thamnobeatricea			+	+	+	
**Dermatostroma*					+	

rather similar low paleolatitudes in shallow, subtidal, warm-water seas.

Three other middle Darriwilian–late Darriwilian sites have been recorded in Eurasia (Table 1), each represented by one labechiid genus. The first is site no. 14, with the occurrence of *Pseudostylodictyon* from the Garevka Formation of the western slopes of the Urals (BOGOYAVLENSKAYA & LOBANOV, 1990; KHROMYKH, 1999b, table 1). It probably comes from a position on the margins of the Baltica (eastern European) paleocontinent (COCKS & FORTEY, 1998, fig. 1). A similar occurrence of *Pseudostylodictyon* is recorded from a second site (no. 19) by BOGOYAVLENSKAYA and LOBANOV (1990), from a similar stratigraphic level in the northern Betpak–Dala desert region of Kazakhstan. This site is another along the line of interconnected basins of the Uralian–Mongolian belt across Asia (BOGOYAVLENSKAYA & LOBANOV, 1990, p. 83, fig. 6). The third site (no. 16) is from the Moiero River basin section of the Siberian Platform and represents the first appearance of a labechiid, the genus *Priscastroma*, with basically very simple cystose elements (KHROMYKH, 1999a, 1999b). The age relationships of this occurrence are clearly established within the upper Kochakan Formation (Muktei horizon), which correlates with the middle–upper part of the Darriwilian stage (WEBBY & others, 2004; see also WEBBY, 2012b). According to FORTEY and COCKS (2003), the Siberian paleocontinent remained in a low-latitude, tropical position, lying astride the paleoequator during Mid-Ordovician time (COCKS & TORSVIK, 2002; FORTEY & COCKS, 2003).

The earliest stromatoporoids were exclusively labechiids and achieved a circumpaleoequatorial distribution during the mid–late Darriwilian. Within the present resolution of dating of the various successions, it is not possible to say that any one region evolved its skeletonized faunas earlier than another. The northern China faunas were the most diverse and endemic, but this region did not necessarily act as a center of origin for the rest. It seems more likely that a simple, noncalcifying, wide-ranging, root stock existed earlier in the warm, shallow, circumpaleoequatorial seas and provided the sources for the development of mineralized skeletons of a number of different morphologies in at least three main regions–northern China, Laurentia, and Siberia (see

TABLE 2 (*continued from facing page*).

Genera (Labechiida)	Russia: Chukchi Peninsula 11	Slopes of western Urals 14	Siberian Platform 16	Tarim: southern Xinjiang 21	Northern China: Hebei 26	Macquarie Arc: New South Wales 27	Tasmanian Shelf 28
Rosenella							
Cystostroma		+	+	+?			
Pseudostylodictyon	+						
Labechia	+			+	+	+	+
Labechiella				+	+	+	
**Stratodictyon*						+	+
**Stromatocerium*	+		+		+		+
**Cystistroma*							
Pachystylostroma				+			
**Stylostroma*				+			
Aulacera							
**Cryptophragmus*							
Thamnobeatricea							
**Dermatostroma*							

further discussion in WEBBY, 2012b). *Pseudostylodictyon* appears to represent the most basic skeletonized genus, both in Laurentia and northern China, and may be ancestral to a number of lines of descent in the two regions: for example, leading to *Pachystylostroma* and *Labechia* in Laurentia, and to *Rosenella*, the cylindrical forms (*Thamnobeatricea, Ludictyon, Sinodictyon,* and *Aulacera*), and perhaps even to *Labechiella* and *Lophiostroma* in northern China.

SANDBIAN

The stromatoporoid assemblages of the Sandbian stage (=lower–midddle Caradoc) were entirely labechiids, and they were associated with a second, less intense, diversification that spread more widely across low paleolatitudes (WEBBY, 2004). The global distribution of Sandbian genera is shown in Table 2. A number of regions show labechiid faunas for the first time, such as Scotland, Chukchi Peninsula (northeastern Russia), Xinjiang (northwestern China), and eastern Australia (New South Wales, Tasmania). A sixth labechiid family, the Stromatoceridae, appeared in addition to the continued representation of the five families that had evolved previously in the Darriwilian. A number of genera, the labechiid *Stratodictyon*, stromatocerids *Stromatocerium, Cystistroma*, stylostromatid *Stylostroma*, aulaceratid *Cryptophragmus,* and lophiostromatid *Dermatostroma* made their first appearances during this interval. No clearly recognizable provincialism existed during the interval. Some genera that previously existed as endemics in northern China made their first appearances in Laurentia. Overall, the most diverse assemblages are recorded from sites in Laurentia. Only a few genera are recognized as endemic during the Sandbian interval: *Cryptophragmus, Dermatostroma,* and *Cystistroma,* in eastern Laurentia; and *Stylostroma* in Tarim (northwestern China).

In the north-central Appalachians (Pennsylvanian, New York, Vermont; site no. 4; Table 2 and Fig. 1), a localized, early Sandbian appearance of genus *Stratodictyon* (*S. valcourensis*) is recorded (KAPP & STEARN, 1975) from the uppermost part of the Chazy succession (Valcour Formation), and then, elsewhere in the region, other genera (*Rosenella, Stromatocerium, Cystistroma, Cryptophragmus, Thamnobeatricea,* and

Aulacera) appear in the succeeding Black River Group beds—part of the Turinian stage (lower Mohawkian series) of the North American Middle Ordovician; now recognized as equivalent to the lower part of the internationally ratified Upper Ordovician series (see WEBBY & others, 2004). The genera *Stromatocerium, Cystistroma,* and *Cryptophragmus* are the most widely distributed forms across the on-shelf regions of the eastern Laurentian platform (sites no. 2–6; see Table 2 and Fig. 1). The Girvan area of Scotland is likely also to have been a part of the Laurentian margin during Sandbian time (WOODCOCK in FORTEY & others, 2000), and includes an isolated occurrence of *Labechia* (WEBBY, 1977) from within the Stinchar Limestone Formation (site no. 10; see Fig. 1), from a stratigraphic level close to the base of the Sandbian (equivalent to uppermost Chazy in Vermont and New York). The Chukchi Peninsula of northeastern Russia also had links with Laurentia, remaining close to Alaska and the northwest of Canada throughout the Paleozoic (GOLONKA, 2002). The Sandbian stromatoporoid assemblage from this region (site no. 11) comes from the Isseten Formation of the Chegitun River Basin (ORADOVSKAYA, 1988), and includes *Stromatocerium*, *Labechia,* and *Pseudostylodictyon* (KHROMYKH, 1977, 1999b).

Other Russian localities, from the western slopes of the Urals (BOGOYAVLENSKAYA, 1973b) and in the Moiero River Basin section of the Siberian Platform (NESTOR, 1976), include rather sparse Sandbian faunas. BOGOYAVLENSKAYA (1973b) reported an occurrence of *Cystostroma* from the so-called Middle Ordovician, part of the Trypyl River section from the western slopes of the Urals (site no. 14), and she also claimed an occurrence of *Ecclimadictyon* from the Uls River section on the western slopes of the northern Urals as being of Middle Ordovician age. However, this stratigraphic determination is likely to be erroneous, as no clathrodictyid stromatoporoids appeared elsewhere in the global record before the middle of the Upper Ordovician (that is, early in the Katian Stage; see discussion in WEBBY, 2012b). In upward continuation of the Siberian Moiero River Basin section, which included the mid–late Darriwilian genus *Priscastroma* (site no. 16), NESTOR (1976) recorded two genera, *Cystostroma* from a horizon close to the Mid–Late Ordovician boundary (Krivoluk horizon; see KANYGIN, MOSKALENKO, & YADRENKINA, 1988) and *Stromatocerium* from the succeeding Mangazey horizon, also of Sandbian age.

DONG and WANG (1984) have described stromatoporoids of probable Sandbian age from two horizons within the Malieciken Group of the Altun Mountains in northwestern China, Xinjiang (site no. 21; see Fig. 1). The Altun Mountains are associated with the southeastern part of the Tarim terrane (LI, ZHANG, & POWELL, 1996; FORTEY & COCKS, 2003) or paleoplate (CHEN & others, 2001). Two stromatoporoid-bearing horizons comprise a lower, dominated by *Labechia* and *Stylostroma*, and an upper, having the same genera, and, in addition, *Labechiella, Pachystylostroma,* and *?Cystostroma*. The Kunlun Mountains in the southwestern part of the Tarim terrane also include a stromatoporoid-bearing horizon of the Malieciken Group, including *Labechia* and *Labechiella*. DONG and WANG (1984) commented on the uncertainties of the age determinations, suggesting that these Tarim assemblages were slightly younger than the mid–late Darriwilian (Majiagou Formation equivalent) assemblages of northern China. That implies a Sandbian age, though, given the early appearance of *Stylostroma* (not recorded elsewhere until later, i.e., early Katian), these assemblages may conceivably be younger. However, CHEN (in WANG & others, 1996, p. 70, 83) reported a contrary view, with what appears to represent the same two stromatoporoid-bearing horizons in a sequence given a different stratigraphic name but from the same Altun Mountains, that underlie a graptolite- and conodont-dated sequence of mid-Darriwilian–lower Sandbian age, suggesting the stromatoporoid-bearing horizons may be older. Clearly, in this remote region, much remains to be done to clarify the stratigraphic and tectonic relationships. Given the morphological development of the Altun labechiid faunas, it is unlikely that they represent assemblages as old, or older, than those of the Majiagou Formation in northern China; therefore, following DONG and WANG (1984), they are preferably regarded here as having a Sandbian age.

Another Chinese Sandbian association (site no. 26) with *Labechia* and *Labechiella* is recognized from the Fengfeng Formation at Fengfeng, near Handan city, southern Hebei province, North China Platform (AN in LAI & others, 1982; LIN & WEBBY, 1989, p. 209). The Fengfeng Formation occupies a position directly overlying the Majiagou Formation (ZHOU & FORTEY, 1986; CHEN & others, 1995; WANG & others, 1996).

In eastern Australia, the earliest known stromatoporoids are found in sequences that are close to the Mid–Upper Ordovician boundary. In two areas in central New South Wales (site no. 27), the Gunningbland area of the Junee-Narromine Volcanic Belt and the Wahringa area of the northern Molong Volcanic Belt, small assemblages of characteristic labechiids have been described (PICKETT & PERCIVAL, 2001; PERCIVAL, WEBBY, & PICKETT, 2001), representing occurrences that include the genera *Stratodictyon*, *Labechia, Labechiella* (some skeletons being preservationally gradational into *Stromatocerium*), and ?*Aulacera*. Both stromatoporoid-bearing successions accumulated in shallow-water limestones on the fringes of partially emergent offshore volcanic islands of the Macquarie Arc (formerly Macquarie Volcanic Belt; WEBBY, 1976). The Gunningland and Wahringa assemblages are established as having a Sandbian (=Australian Gisbornian) age.

The early stromatoporoid assemblages in Tasmania (site no. 28) occur in the carbonate successions of the lower Gordon Group of the Florentine Valley and Mole Creek areas on the Tasmanian Shelf (WEBBY, 1979b, 1991), from what may have been a remnant of the main East Gondwanan margin, or a microcontinent (WEBBY, 1987). The genera comprise *Rosenella*, *Labechia, Stratodictyon*, *Stromatocerium,* and *Thamnobeatricea*. The abundant Tasmanian species, *Stromatocerium bigsbyi,* bears a near identical *Labechiella regularis*–type morphology to skeletons in the Wahringa Limestone Member of central New South Wales, except for a much greater tendency for its solid pillars to be secondarily replaced, becoming calcite spar–filled "hollow" pillars. These lower Tasmanian stromatoporoid-bearing units are also regarded as having a Sandbian age.

KATIAN

The widest geographical spread of Ordovician stromatoporoids occurred during the Katian Stage (=middle Caradoc to middle Ashgill). This Late Ordovician interval has a duration of about 10 myr, that is, about twice the length of the preceding Sandbian Stage (GRADSTEIN & others, 2004). The global distribution is represented by the occurrences of genera from 22 sites, shown in Table 3 and Figure 1, and shows almost complete differentiation of labechiids, with appearances of 2 more short-ranging genera (*Radiostroma, Alleynodictyon*), as well as the initial diversification of clathrodictyid stromatoporoids during the early–mid-Katian. Four clathrodictyid genera, *Clathrodictyon, Ecclimadictyon, Stelodictyon,* and ?*Plexodictyon* make their appearances. Their differentiation into two families (Clathrodictyidae, Actinodictyidae) is difficult to sustain in Katian occurrences, because these early genera exhibit such a wide range of forms between those showing regular and crumpled types of laminae (see WEBBY, 2012b). A number of regions, such as Norway, Estonia, Taimyr Peninsula, Altai-Sayan Belt, Tuva, Mongolia, Qinghai (Qaidam Platform) and Zhejiang (southern China), exhibit stromatoporoid faunas for the first time. The wide distribution of stromatoporoids (both labechiids and clathrodictyids) seems to have coincided with the maximum circumequatorial spread of Ordovician reefs (WEBBY, 2002). The

TABLE 3. Geological distribution of stromatoporoid assemblages in the Katian and Hirnantian stages (Upper Ordovician). The 22 Katian-age sites are represented by most of the columns in the table and depicted in Figure 1 by *black squares.* Also, 2 Hirnantian-age sites are represented by 2 extra columns at the right extreme side of the table and are shown in Figure 1 by *open, seven-pointed stars;* *, genera that made their first appearances in the Katian (new).

Order Genus	Texas, New Mexico 1	Kentucky, Tennessee 2	Ohio, Indiana 3	Southern Ontario 6	Northern and southern Manitoba 7	Northern Hudson and Ungava Bays 8	Anticosti Island 9	Baltica: southern Norway 12	Baltica: Estonia 13	Slopes of western Urals 14	Taimyr Peninsula 15
Labechiida											
Rosenella											+
Cystostroma		+		+	+	+			+	+	+
Pseudostylodictyon	+						+				
Labechia	+	+	+	+		+		+			+
Labechiella											+
Stratodictyon											
Stromatocerium		+	+		+					+	+
Cystistroma		+				+?			+		
**Radiostroma*								+			
Pachystylostroma				+				+			
**Stylostroma*								+			
Aulacera		+	+		+	+	+				
**Alleynodictyon*											
Cryptophragmus											
Ludictyon											
Thamnobeatricea											
Lophiostroma											+
Dermatostroma		+	+								
Clathrodictyida											
**Clathrodictyon*					+		+	+	+	+	
**Stelodictyon*											+?
**Ecclimadictyon*				+	+			+		+	+?
Camptodictyon											
*?*Plexodictyon*											
Labyrinthodictyon											
Actinostromatida											
**Plumatalinia*									+		

appearance also of the genus *Plumatalinia* may mark the beginnings of the actinostromatid stromatoporoids; the genus first appeared in Estonia during the late Katian, and possibly is a kind of missing link between labechiids, much as *Pseudostylodictyon* and the Silurian actinostromatids, but some qualifications about this relationship need to be maintained (see discussion in WEBBY, 2012b).

Katian stromatoporoids are widely distributed across Laurentia and have been documented by a number of workers, such as GALLOWAY and ST. JEAN (1961) and BOLTON (1988), from the most westerly occurrences (site no. 1) in Texas and New Mexico to Anticosti Island (site no. 9). All seven Laurentian sites (no. 1–3, 6–9) exhibit labechiids, and a few of these, additionally, include records of the first clathrodictyid stromatoporoids (*Clathrodictyon, Ecclimadictyon*); e.g., from sites in southern Ontario, Manitoba, and Anticosti Island (BOLTON, 1988). For example, in the Central Appalachian areas of Tennessee and Kentucky, labechiid genera *Labechia, Cystostroma, Stromatocerium, Cystistroma, Aulacera,* and *Dermatostroma* have been reported (GALLOWAY & ST. JEAN, 1961).

TABLE 3 (*continued from facing page*).

Order Genus	Siberian Platform 16	Altai-Sayan Fold Belt 17	Tuva, Mongolia 18	Kazakh-stan 19	Central Asia 20	Tarim: northern Xinjiang 21	Chaidam: Qinghai 22	Southern China: Zhejiang 23	Northern China: Shaanxi 26	Macquarie Arc: New South Wales 27	Tasman-ian Shelf 28	Anti-costi Island 9	Baltica: Estonia 13
Labechiida													
Rosenella	+									+	+		
Cystostroma	+	+	+		+					+	+		
Pseudostylodictyon			+							+	+		
Labechia	+	+	+	+			+	+		+	+	+	
Labechiella	+	+	+	+	+		+		+	+	+		
Stratodictyon	+		+							+			
Stromatocerium	+		+			+	+						
Cystistroma	+									+			
**Radiostroma*													
Pachystylostroma		+	+								+		
**Stylostroma*											+		
Aulacera	+										+		+
**Alleynodictyon*									+	+			
Cryptophragmus	+												
Ludictyon			+										
Thamnobeatricea											+		
Lophiostroma	+		+			+							
Dermatostroma													
Clathrodictyida													
**Clathrodictyon*			+					+	+	+	+	+	+
**Stelodictyon*								+		+			+
**Ecclimadictyon*				+?	+?		+	+	+	+	+	+	+
Camptodictyon		+								+			
*?*Plexodictyon*										+			
Labyrinthodictyon												+	
Actinostromatida													
**Plumatalinia*													

Sequences in different parts of Manitoba have included records of the labechiids *Cystostroma, Stromatocerium,* and *Aulacera,* and clathrodictyids *Clathrodictyon* and *Ecclimadictyon*, and on Anticosti Island within the Vaureal Formation, there are numerous records of *Aulacera* (some giant sized) and rare *Clathrodictyon* [see BOLTON (1988), and *Pseudostylodictyon* (NESTOR, COPPER, & STOCK, 2010, fig. 4–5)]. *Dermatostroma* appears to be the only endemic genus in the Katian record of Laurentia.

Stromatoporoids play an important part as contributors to reefs in the Katian successions of the Oslo region, southern Norway; site no. 12 (HARLAND, 1981; WEBBY, 2002). In areas near Lake Mjøsa (SPJELDNAES, 1982), the lower Katian stromatoporoid assemblage includes *Labechia, Pachystylostroma,* and *Stylostroma,* and the possibly endemic genus *Radiostroma* (WEBBY, 1979a), though NESTOR and STOCK (2001, p. 334, fig. 1) have listed it as being present also in North America. Additionally, stromatoporoids have been recorded from the uppermost Katian; for example, from the informal Norwegian stage 5a interval, at Stavnestangen in the Ringerike area, with *Stylostroma,* *Pachystylostroma, Labechia*, *Clathrodictyon,* and *Ecclimadictyon* (Kaljo, Klaamann, & Nestor, 1963; Nestor, 1999b). In Estonia (site no. 13), two temporally distinct and approximately correlative, stromatoporoid associations also occur: the lower Katian (=Oandu regional stage) with occurrences of *Cystostroma* and *Cystistroma*, and the uppermost Katian (=Vormsi and Pirgu regional stages; see Hints & Meidla, 1997), with records of *Cystostroma, Cystistroma, Clathrodictyon,* and *Plumatalinia* (Nestor, 1999b). All these records developed in shallow shoal to open shelf conditions of the extensive epicontinental sea, which covered much of the western side of Baltica (Jaanusson, 1982; Cocks & Fortey, 1998).

The Katian stromatoporoids from the western slopes of the Urals include the records Bogoyavlenskaya (1973b) assigned to the Rassokha horizon (and equivalents); these comprise *Cystostroma, Stromatocerium,* and probably both *Clathrodictyon* and *Ecclimadictyon* (despite her probably mistaken recognition of *E. geniculatum* as having a Middle Ordovician age; see Bogoyavlenskaya, 1973b, p. 22–23), and given that elsewhere, Bogoyavlensakya (1984, p. 69) has listed *Ecclimadictyon*, like *Clathrodictyon,* as having an Upper Ordovician–Silurian range.

A number of Upper Ordovician (Katian) stromatoporoids have been recorded by Khromykh (2001) from sections along the Paranaya and the lower Taimyr rivers within the southern (carbonate) facies belt of the Taimyr Peninsula (site no. 15). They include the labechiid genera *Cystostroma, Rosenella, Labechia, Labechiella, Stromatocerium*, and *Lophiostroma*, and, apparently, the clathrodictyids *Ecclimadictyon* and *Clathrodictyon* (these forms are mentioned, but not described), and genus *Taymyrostroma*, with uncertain relationships within the class Stromatoporoidea (see Order and Family Uncertain in Stearn, 2011, p. 56). This southern belt is considered to be a part of the Siberian plate, probably marginal to it during the Late Ordovician (Fortey & Cocks, 2003, p. 270). Katian assemblages from the main cratonic areas of the Siberian Platform (site no. 16), from main localities along major waterways such as the Moiero and Podkammennaya Tunguska rivers, as well as other areas (e.g., the Verkhoyansk-Kolyma Fold Belt of northeastern Siberia), include *Rosenella, Cystostroma, Labechiella, Stromatocerium, Cystistroma, Aulacera, Cryptophragmus,* and *Lophiostroma* (Yavorsky, 1955, 1961; Nestor, 1976; Bogoyavlenskaya, 1977). The Verkhoyansk-Kolyma Fold Belt incorporates a number of terranes that apparently remained close to the margins of the Siberian plate through the Cambrian and Ordovician, but rifted away during Middle Paleozoic time, according to Golonka (2002). Because faunal connections remained closely linked to Siberia through the Late Ordovician, the stromatoporoid data for the Siberian craton and the northeastern fold belt region has been combined in site no. 16 (Fig. 1), though at least one record, that of *Stratodictyon* (Bogoyavlenskaya, 1973b), is restricted to the northeastern fold-belt region (Sette Daban Range).

In the Altai-Sayan Fold Belt of southwestern Siberia, specifically the Gornaya Shoriya and the Gorny Altai regions (site no. 17), stromatoporoids were first recognized by Khalfina (1960), including *Rosenella, Labechiella,* and a distinctive clathrodictyid, later determined to be *Ecclimadictyon amzassensis,* but recently reassigned to the genus *Camptodictyon* Nestor, Copper, & Stock, 2010. The biogeographically important species, now determined to be *C. amzassensis,* is found in three areas of the fold belt in Gornaya Shoria, the central part of Gorny Altai, and in the intervening Uymen'-Lebed Zone (Sennikov & others, 1988). Sampled localities lie along an arcuate, paleogeographically defined, carbonate platform that developed within the fold belt during Katian time (Yolkin, & others, 2001, p. 16). A markedly close species-level biogeographic tie exists between the occurrences of *C.*

amzassensis in the Altai-Sayan region (those considered to be the same species from localities in the Chinese Altai Mountains of far northwestern Xinjiang, only 600 km to the south [Dong & Wang, 1984; Lin & Webby, 1988, p. 233]) and records of *C. amzassensis* from the peri-Gondwanan, Macquarie Arc terrane of central New South Wales (Webby, 1969, 1976). Other species-level links also exist between the Altai-Sayan and New South Wales regions among labechiids with common occurrences, such as *Rosenella* (*R. woyuensis*) and *Labechiella* (*L. regularis*), adding weight to the closeness of the biogeographic connection. This accords with the views of Fortey and Cocks (2003, fig. 15), that the Altai-Sayan region had developed as an isolated terrane and had moved to a peri-Gondwanan, low paleolatitude, position by Late Ordovician (Katian) time.

The Tuva Mountains of southern Russia and Mongolia have been linked in a separate Tuva-Mongol Arc during the Early Paleozoic (Şengör & Natal'in, 1996), though, as Fortey and Cocks (2003) have indicated, because the faunas of both regions maintained such close Siberian affinities, debate continues as to whether the arc terrane was part of Siberia or independent of it. The integration may have occurred in the Ordovician, or the arc remained a separate entity, but close to Siberia, during Ordovician time. Alternatively, the Tuva-Mongolia region has been regarded by Golonka (2002, p. 25), following Zonenshain, Kuzmin, and Natapov (1990), as being represented by the Amuria terrane that formed off Siberia by "collision between microcontinents" during the latest Cambrian to Early Ordovician. The Katian stromatoporoids of Tuva and Mongolia are combined in site no. 18, though in Tuva only three genera are recorded (Bogoyavlenskaya, 1971), whereas a more diverse fauna occurs in Mongolia (Bol'shakova & Ulitina, 1985), including *Cystostroma, Pseudostylodictyon, Rosenella, Labechia, Labechiella,* ?*Stratodictyon, Ludictyon, Lophiostroma,* and *Clathrodictyon*. Bol'shakova and Ulitina (1985) have recognized that across Mongolia there were three regional collections, each exhibiting a different mix of faunal components, but overall suggesting closer zoogeographic links to Siberia and Central Asia than to North America and Europe, as might be expected.

Stromatoporoids have rarely been reported from Kazakhstan (site no. 19) or Central Asia (Tadjikistan, Uzbekistan, Kyrgyzstan; site no. 20). *Labechiella* is known from the Dulankarian horizon (mid-Katian) of southern Kazakhstan (Khalfina, 1958) and the Zeravshan Range of Tadjikistan (Karimova & Lessovaya, 2007), and *Cystostroma* is reported from Kyrgyzstan (Yavorsky, 1961). Previously, Webby concluded (1992) that such Central Asian Late Ordovician sequences contained predominantly solitary rugose and tabulate coral faunas (rarely stromatoporoids), representing cooler water assemblages of the southern mid-paleolatitude Euroasiatic Realm, but it is possible that a short-lived phase of global warming may have been responsible for some rare appearances in mid-paleolatitudes; for example, as a consequence of the Boda event in the late Katian (Fortey & Cocks, 2005).

The Katian stromatoporoid distributions within China are differentiated, based on available paleogeographic reconstructions, into four sets of assemblages, represented by sites no. 21 (Tarim), no. 22 (Qaidam), no. 23 (southern China), and no. 26 (northern China), respectively. The first is an assemblage of *Labechia, Stromatocerium,* and *Lophiostroma* (Lin & Webby, 1989) from the Houcheng area of northwesterm Xinjiang (site no. 21) and recorded from a sequence considered by Chen and others (1992, p. 171) to be part of the cratonic Yining Basin; this latter occupied a position near the outer (northern) margin of the Tarim plate (Chen & Rong, 1992).

Two other stratigraphically distinct assemblages (Lin & Webby, 1988) occur in a section south of Golmud City, Qinghai province (site no. 22). The lower unit contains *Labechiella* and *Stromatocerium*, and the upper includes *Labechia* and *Ecclimadictyon*. The genus *Stelodictyon* was not recorded from the upper assemblage (cf. NESTOR, 1999b, p. 128). Paleogeographically, these occurrences occupy a position toward the southern margin of the Chaidam (or Qaidam) Platform, which probably represented another small and discrete, peri-Gondwanan terrane (CHEN & RONG, 1992; METCALFE, 1996).

The southeastern part of the southern China plate became an uplifted extension of the Cathaysian land during the Late Ordovician, separating the broad, stable, Yangtze Platform from the transitional Jiangnan belt, with its basinal and slope facies, and more localized platform areas marginal to the Cathaysian land; the marginal areas include a variety of shallow carbonate reefs and slope deposits that are mainly exposed across parts of the Zhejiang and Jiangxi provinces (CHEN & RONG, 1992; WEBBY, 2002). These deposits (site no. 23) contain late Katian stromatoporoids, the labechiid *Pachystylostroma*, and the clathrodictyids *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* (LIN & WEBBY, 1988; BIAN, FANG, & HUANG, 1996).

A number of Katian stromatoporoid assemblages occur in successions along the southern and western margins of the uplifted Ordos Platform (northern China plate; site no. 26); some come from shelf-edge reefs (YE & others, 1995; ZHOU & YE, 1996). In Shaanxi province, the stromatoporoids occur in two stratigraphically distinct horizons, the lower (Taoqupo Formation) with *Clathrodictyon* and *Ecclimadictyon* (some forms appear to have been mistakenly identified as *Forolinia* by YE & others, 1995, pl. 8,*3*), and the upper (Beigoushan Formation) with *Labechia*, *Labechiella, Clathrodictyon,* and *Ecclimadictyon* (LIN & WEBBY, 1988, 1989; YE & others, 1995). *Clathrodictyon* is also recorded from Inner Mongolia (LIN & WEBBY, 1988).

Varied assemblages of stromatoporoids occur in the early to mid-Katian (=Eastonian) successions of the central New South Wales Macquarie Arc (site no. 27) and the Tasmanian Shelf (site no. 28) in eastern Australia. Three stratigraphically distinct assemblages are recognized in the central New South Wales carbonate successions (WEBBY, 1969; WEBBY & MORRIS, 1976), across Macquarie Arc remnants (Molong and Junee-Narromine volcanic belts), as follows: (1) exclusively labechiid associations from the lower Cliefden Caves Limestone Group and equivalents with *Pseudostylodictyon, Stratodictyon, Rosenella, Labechiella, Cystistroma,* and *Alleynodictyon*; (2) labechiids (*Pseudostylodictyon, Labechia, Cystostroma*, *Alleynodictyon*) and first clathrodictyids (*Ecclimadictyon, Clathrodictyon, Camptodictyon,* ?*Stelodictyon,* and ?*Plexodictyon*) from the upper Cliefden Caves Limestone Group and equivalents; and (3) labechiid *Pseudostylodictyon*, along with clathrodictyids *Ecclimadictyon, Camptodictyon,* and ?*Plexodictyon,* from the upper Ballingoole Limestone (upper Bowan Group) and equivalents.

The Katian assemblages in the Gordon Group limestones of the Tasmanian Shelf (WEBBY & BANKS, 1976; WEBBY, 1991) are counterparts to the New South Wales assemblages 1 and 2 noted above; they comprise: (1) the labechiid associations of *Pseudostylodictyon, Rosenella, Labechia, Labechiella, Stylostroma, Thamnobeatricea*, and *Alleynodictyon* from the Dogs Head to Overflow Creek formations (middle–upper Chudleigh Subgroup) of the Mole Creek section and correlatives; and (2) labechiids (*Cystostroma, Labechia, Labechiella*, ?*Stromatocerium, Stylostroma, Pachystylostroma, Aulacera*) and the first clathrodictyids (*Clathrodictyon, Ecclimadictyon*) from the Den Formation (uppermost Chudleigh Subgroup) of the Mole Creek section and equivalents. In terms of biogeographic relationships, it should be noted that *Stylostroma, Pachystylostroma*, *Thamnobeatricea,* and *Aulacera* are found in Tasmania but have not been recorded from the New South Wales arc faunas. Also, at the species level, there are important differences, because none of the Tasmanian species of *Clathrodictyon* or *Ecclimadictyon* is conspecific with counterparts in New South Wales. On the other hand, the distinctive *C. amzassensis*, which is recorded in the Altai-Sayan, Chinese Altai, and New South Wales regions, has not been recognized in Tasmania. *Alleynodictyon* is apparently the only endemic genus to occur across eastern Australia.

In terms of the early clathrodictyid stromatoporoids (Webby in Webby & others, 2000, p. 70), it seems that the main stocks involved in the initial dispersal were the genera *Clathrodictyon* and *Ecclimadictyon*. These genera show a marked range of variability between their more characteristic regular, or more crumpled, types of laminae (see further discussion in Webby, 2012b). Both genera achieved a comparatively rapid circumequatorial distribution during the early Katian (=late Caradoc). In contrast, *Camptodictyon* was restricted to arc-related settings in the Russian and Chinese Altai and New South Wales; *Stelodictyon* and ?*Plexodictyon* maintained a limited spread between the peri-Gondwanan New South Wales arc, southern China, and Baltica; and ?*Plexodictyon* possibly also spread to Laurentia (see Nestor & Stock, 2001, fig. 1). These latter genera achieved more cosmopolitan distributions in the Silurian.

HIRNANTIAN

Only a few sites worldwide exhibit Hirnantian stromatoporoids. The Hirnantian was a relatively short interval of time (about 1.5 myr), dominated by glacioeustatic sea-level changes, glaciation during the early to middle part, and global warming in the last part (Brenchley, 2004; Finnegan & others, 2011). The documented records of Hirnantian stromatoporoids (two right-hand columns, Table 3) are limited to localities on Anticosti Island, eastern Canada (site no. 9), and the Porkuni horizon of Estonia (site no. 13). On Anticosti Island, the stromatoporoid genera occur in the Ellis Bay Formation and are dominantly the cylindrical labechiid *Aulacera* and the clathrodictyids *Clathrodictyon* and *Ecclimadictyon* (Bolton, 1988; Cameron & Copper, 1994), as well as *Labyrinthodictyon* Nestor, Copper, & Stock (2010, p. 74). In the Arina Formation (Porkuni stage) of Estonia, the stromatoporoids include the labechiid *Pachystylostroma* (rare) and clathrodictyid genera *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* (Nestor, 1964, 1999b). There are also records of *Aulacera* from the Stonewall Formation of southern Manitoba (Bolton, 1988) and abundant *Pachystylostroma* in a carbonate bank from the informal Norwegian stage 5b interval at Ullerntangen in the Ringerike area, Norway (Hanken & Owen, 1982, p. 128) that represent additional, confirmed Hirnantian localities.

SILURIAN

Heldur Nestor

The present review of the biogeography of the Silurian stromatoporoids is mainly based on publications containing systematic descriptions and photos of species that enabled, in case of need, reinterpretation of generic identifications according to the taxonomic nomenclature used in the present paper. In some cases, trustworthy species lists and range charts from biostratigraphic publications were taken into account. Insufficiently precise stratigraphic datings prevented the use of older publications, e.g., most of Riabinin's and Yavorsky's data, though contributions by Riabinin (1951, 1953) have been retained (see listings in next paragraph, p. 18).

The Silurian stromatoporoids treated herein have been studied from the following districts: Ontario, Hudson Bay, and other, scattered localities of North America (Parks, 1907, 1908, 1909); eastern Quebec (Parks,

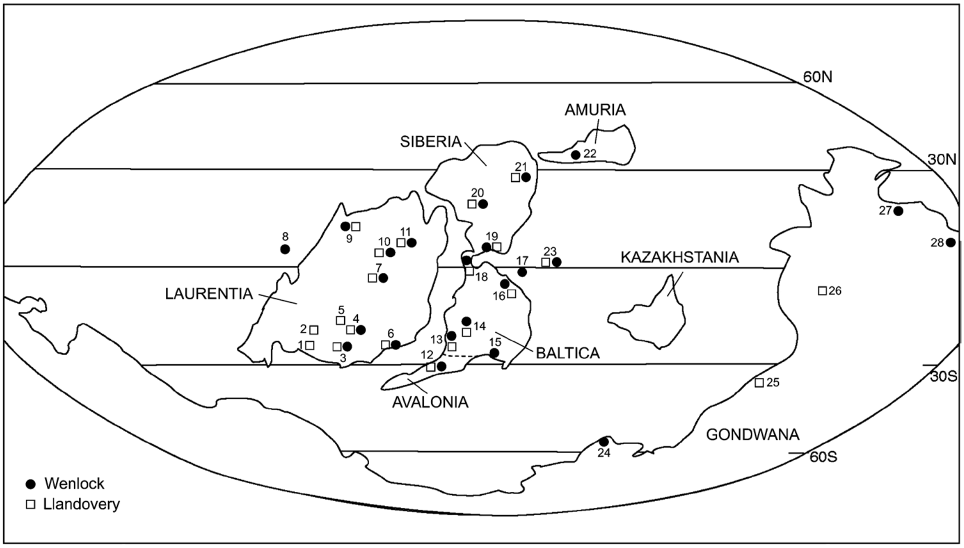

Fig. 2. Geographical distribution of stromatoporoids in the lower Silurian (Llandovery, Wenlock). The names of the localities are shown in Tables 4 and 5; *dashed line* separates cratons of Avalonia and Baltica (new).

1933; Stearn & Hubert, 1966); Anticosti Island (Bolton, 1981; Nestor, Copper, & Stock, 2010); New York and Virginia (Stock, 1979; Stock & Holmes, 1986); Baffin Island (Petryk, 1967); Somerset Island (Savelle, 1979); northern Greenland (Poulsen, 1941); England (Nicholson, 1886, 1889, 1891, 1892); Ireland (Nestor, 1999a); Norway (Mori, 1978); Gotland Island (Mori, 1968, 1970); Estonia (Riabinin, 1951; Nestor, 1964, 1966, 1990b); Podolia (Riabinin, 1953; Bol'shakova, 1973; Bogoyavlenskaya, 1969; Bogoyavlenskaya in Tsegelnjuk & others, 1983); Bohemia (May, 2005); Urals (Bogoyavlenskaya, 1973a, 1976); Novaya Zemlya (Nestor, 1981, 1983); Siberian Platform (Nestor, 1976; Khromykh in Tesakov & others, 1980, 1985); Altai and Salair (Khalfina, 1961); Tuva (Bogoyavlenskaya, 1971, 1976); Mongolia (Bol'shakova & Ulitina, 1985; Bol'shakova & others, 2003), northern China (Dong, 1984; Dong & Wang, 1984); southern China (Dong & Yang, 1978; Yang & Dong, 1980; Wang in Jin & others, 1982); Central Asia (Tian Shan) (Lessovaya, 1962, 1971, 1972, 1978; Lessovaya & Zakharova, 1970); Turkey (Weissermel, 1939); Iran (Flügel, 1969); Japan (Sugiyama, 1939, 1940); northern Queensland (Webby & Zhen, 1997); New South Wales (Birkhead, 1976, 1978).

Biogeography of the Silurian stromatoporoids was considered earlier in papers by Kaljo, Klaamann, and Nestor (1970) and Nestor (1990a). Nestor and Stock (2001) summarized data on the distribution of the stromatoporoid genera in the Llandovery. Bogoyavlenskaya (1981) considered distribution of the Pridoli stromatoporoids in the former U.S.S.R. Unpublished data of Nestor (1983)on stromatoporoids from Severnaya Zemlya, and those of Stock and Nestor (1998–1999) from Alabama, Ohio, Oklahoma, Iowa, and northern Michigan, are also used in the present review.

The main districts of stromatoporoid occurrences are plotted on the simplified base maps of Golonka (2002) (Fig. 2–3). Geographical distribution of the Silurian stromatoporoid genera is represented in Tables 4–7.

LLANDOVERY

During the Llandovery, stromatoporoids were widespread in epicontinental seas and continental shelves of the Laurentia, Baltica, and Siberia cratons, which were situated close together in low paleolatitudes, within subtropical to tropical climatic zones (Fig. 2) and associated with carbonate sedimentation. Only a few occurrences of Llandovery stromatoporoids have been recorded from the marginal areas of eastern Gondwana (southern China, Iran), which also are placed in low paleolatitudes. The occurrences of Llandovery stromatoporoids ranged from ~30° N (Tuva) to ~35° S (Iran).

After a gradual extinction of the Ordovician labechiid-dominated stromatoporoid fauna, only a few genera survived, and the early Silurian fauna became clathrodictyid dominated (NESTOR & STOCK, 2001). In most regions, the early Llandovery (Rhuddanian) is represented by a hiatus in the stromatoporoid succession. Abundant, but low-diversity, stromatoporoid fauna has been recorded from Estonia and Anticosti, where only four genera, *Clathrodictyon, Ecclimadictyon, Pachystylostroma,* and *Forolinia,* are present. The first two, belonging to the order Clathrodictyida, became the most common cosmopolitan elements of the Llandovery stromatoporoid fauna. Labechiids maintained an accessory role and were more common in the Siberian and Chinese faunas. During the Llandovery, a marked generic diversification and areal extension of stromatoporoid faunas took place. The earliest representative of the family Actinostromatidae, genus *Plectostroma,* appeared in Estonia in the late Rhuddanian. In the Aeronian (middle Llandovery), among Clathrodictyida, representatives of Tienodictyidae (*Intexodictyides*) were added in the sections of Estonia, Anticosti, Michigan, Baffin Island, as well as gerronostromatids (*Gerronostromaria, Petridiostroma*) in the sections of Baffin Island, Anticosti, and Norway. At the same time, first representatives of the order Stromatoporida appeared: *Eostromatopora* (Stromatoporidae) in Baffin Island and *Syringostromella* (Syringostromellidae) in northern Michigan. In the late Llandovery (Telychian), the first densastromatids (*Densastroma*) and pseudolabechiids (*Desmostroma, Pachystroma*) were added in Michigan, Iowa, Baffin Island, Anticosti, Estonia, and Gotland.

Thus, during the second half of the Llandovery, a gradual diversification and expansion of stromatoporoid faunas took place. The center of origination of the new taxa shifted from the margins of the Iapetus Ocean (Anticosti, Norway, Estonia) to the Michigan Basin and the Canadian Arctic, where the earliest representatives of Gerronostromatidae (*Gerronostromaria, Petridiostroma*), Stromatoporidae (*Eostromatopora*), and Syringostromellidae (*Syringostromella*) continued to be represented in the Aeronian and extended their area of occupation in the Telychian to other districts of Laurentia and Baltica. The most conservative Llandovery stromatoporoid faunas were in Siberia and southern China, where labechiids (*Labechia, Pachystylostroma, Forolinia, Rosenella, Stylostroma, Ludictyon, Pleostylostroma*) maintained an important role, along with *Clathrodictyon* and *Ecclimadictyon.* Actinostromatids and stromatoporids were quite rare, with the exception of *Plectostroma* (Siberian Platform, Altai, Tian Shan) and *Lineastroma* (Siberian Platform), belonging to the families Actinostromatidae and Stromatoporidae, respectively. It is worth mentioning that the first probable syringostromatid—?*Parallelopora* (originally described as *Gerronostromaria dragunovi* YAVORSKY, 1961)—is also recorded from the Llandovery of the Siberian Platform (KHROMYKH in TESAKOV & others, 1985).

In summary, at the generic level, the provincialism of the Llandovery stromatoporoids is rather weakly expressed. Paleobiogeographic peculiarities of stromatoporoid faunas in different regions depend on the presence of temporary endemics, i.e., genera making their first appearance in one region and spreading afterward into other areas.

TABLE 4. Distribution of stromatoporoid genera in the Llandovery (+, general occurrences of Llandovery genera; *x,* records of more restricted upper Llandovery occurrences; *?,* uncertain or doubtful generic entries) (new).

Order Genus	Alabama	Oklahoma	Ohio	Michigan, Ontario	Iowa	Eastern Quebec	Hudson Bay	Northwestern Canada	Baffin Island	Northern Greenland
	1	2	3	4	5	6	7	9	10	11
Labechiida										
Forolinia	+					+				
Labechia										
Ludictyon										
Pachystylostroma				+		+				+
Pleostylostroma										
Rosenella										
Stylostroma										
Clathrodictyida										
Actinodictyon							x		x	
Clathrodictyon	x	+	+	+	+	+			+	+
“Clavidictyon”				+	+	+				
Ecclimadictyon		+	+	+	x	+			+	+
Gerronostromaria				?	x		?		x	
Intexodictyides				+	+	+			+	
Neobeatricea							x			
Oslodictyon				x	x	x		x		
Petridiostroma				x	x	+				
?*Plexodictyon*			+				x			
Stelodictyon	?			+	x					
Actinostromatida										
Densastroma				x	x					
Desmostroma					x	x				
Pachystroma				x	x	x				
Plectostroma							x		x	
Stromatoporida										
Eostromatopora									x	
Lineastroma										
Stromatopora							?			
Syringostromella				+	x		x			
Syringostromatida										
?*Parallelopora*										

WENLOCK

In the beginning of the Wenlock, the Silurian marine transgression reached its maximum extent. Vast areas of Siberia and eastern Gondwana were covered with warm, tropical epicontinental seas. Wide inland seas (Michigan, Illinois, Hudson, and Williston basins) were located in the interior of Laurentia. Extensive platform margin seas (Baltic and Petchora basins) were situated at the opposite margins of the Baltica craton, as well as in the present-day Canadian Arctic. Therefore, the Wenlock stromatoporoid faunas were the most widespread during the entire Silurian. Extensive stromatoporoid-dominated reef tracts and complexes have been recorded from the margins of the Michigan and Hudson basins, Gaspé region, Baltic area, Podolia, western and northern Urals, Arctic islands, Siberian Platform, Central Asia (Tian Shan) and the Verkhoyan-Kolyma region (COPPER, 2002). The Wenlock stromatoporoid occurrences range from ~35° N (Mongolia) to 50–55° S (Bohemia), according to the base maps of GOLONKA (2002), used herein. The paleomaps of SCOTESE and MCKERROW (1990), however, showing Bohemia in a somewhat more northward position (40–45°S), in the African sector of Gond-

TABLE 4 (*continued from facing page*).

Order Genus	Ireland 12	Norway 13	Estonia, Gotland 14	Western Urals 16	Novaya Zemlya 18	Severnaya Zemlya 19	Siberian Platform 20	Altai, Salair, Tuva 21	Tian Shan 23	Iran 25	Southern China 26
Labechiida											
Forolinia		+	+		x				+		+
Labechia			+	+		+	+	+	+		+
Ludictyon											+
Pachystylostroma	x		+				x				+
Pleostylostroma											+
Rosenella			x				x				+
Stylostroma							x				+
Clathrodictyida											
Actinodictyon											
Clathrodictyon		+	+		+	+	+	+	+		+
"Clavidictyon"							+				+
Ecclimadictyon		+	+			+		+	+	+	?
Gerronostromaria	x										
Intexodictyides			+					?			+
Neobeatricea							x				
Oslodictyon		x	x						x		
Petridiostroma	x	+	x					x			
?*Plexodictyon*											+
Stelodictyon				+							
Actinostromatida											
Densastroma			x								
Desmostroma			x								
Pachystroma			x								
Plectostroma			+	+			+	x	x		
Stromatoporida											
Eostromatopora	x	x									
Lineastroma							x				
Stromatopora											
Syringostromella											
Syringostromatida											
?*Parallelopora*							x				

wana, seem to represent more convincing Wenlock reconstructions.

During the Wenlock, diversification of stromatoporoid faunas continued. The most remarkable event was the appearance of the genus *Simplexodictyon,* the earliest representative of the order Stromatoporellida, recorded from Kentucky, Estonia, Gotland, Altai, Tian Shan, northern Queensland; i.e., from all of the main paleocontinents (Table 5). Except for doubtful records of ?*Parallelopora* from the Llandovery of the Siberian Platform (KHROMYKH in TESAKOV & others, 1985), the first confirmed representative of the order Syringostromatida, genus *Parallelostroma*, was distributed in the Wenlock in many regions: Baffin Island, Gotland, Podolia, Novaya Zemlya, Severnaya Zemlya, Siberian Platform, and New South Wales. Wide geographical distribution of new phylogenetic stocks demonstrates good intercommunication of the Wenlock stromatoporoid faunas of different paleocontinents and lack of biogeographic provincialism.

In the Wenlock stromatoporoid fauna, clathrodictyids maintained their leading position. *Petridiostroma* and *Stelodictyon* gained a cosmopolitan status beside *Clathrodictyon* and *Ecclimadictyon,* already widespread in the Llandovery. A very unusual taxon, *Gerronodictyon*, was specific for the eastern Urals and may be treated as a real

TABLE 5. Distribution of stromatoporoid genera in the Wenlock (new).

Order Genus	Kentucky, Indiana	Michigan, Ontario	Eastern Quebec	Hudson Bay	Alaska	Baffin Island	England	Norway	Gotland, Estonia	Podolia
	3	4	6	7	8	10	12	13	14	15
Labechiida										
Cystocerium										
Labechia	+						+		+	+
Lophiostroma	+	+	+							
Pachystylostroma									+	
Rosenella		+							+	
Rosenellinella										
Clathrodictyida										
Actinodictyon									+	
Clathrodictyon	+	+	+	+			+		+	+
"Clavidictyon"										
Ecclimadictyon		+	+				+	+	+	+
Gerronodictyon										
Gerronostromaria										
Neobeatricea										
Petridiostroma	+						+		+	+
Stelodictyon		+		+			+	+	+	+
Yabeodictyon			+						+	
Actinostromatida										
Actinostromella									+	
Araneosustroma									+	?
Densastroma	+		+				?		+	+
Desmostroma	+								+	+
Pachystroma		+	+						+	
Pichiostroma	?									
Plectostroma							+		+	
Plumatalinia									?	
Pseudolabechia										+
Vikingia					+				+	+
Stromatoporellida										
Simplexodictyon	+								+	
Stromatoporida										
Eostromatopora	+								+	
Lineastroma						+				+
Stromatopora							+	+	+	+
Syringostromella								+	+	+
Syringostromatida										
Columnostroma										
?*Parallelopora*									+	
Parallelostroma						+			+	

TABLE 5 (*continued from facing page*).

Order Genus	Western Urals 16	Eastern Urals 17	Novaya Zemlya 18	Severnaya Zemlya 19	Siberian Platform 20	Altai, Salair, Tuva 21	Mongolia 22	Tian Shan 23	Bohemia 24	Northern Queens-land 27	New South Wales 28
Labechiida											
Cystocerium				+	+						
Labechia			+		+	+					+
Lophiostroma				+							+
Pachystylostroma		+			+						
Rosenella			?			+					
Rosenellinella											
Clathrodictyida											
Actinodictyon		+	+	+	+	+					
Clathrodictyon					+	+	+	+			+
"Clavidictyon"				+	+		+				+
Ecclimadictyon	+	+	+	+	+		+	+		+	+
Gerronodictyon		+									
Gerronostromaria											?
Neobeatricea			+		+						
Petridiostroma	+	+	+		+	+	+	+			
Stelodictyon			+	+	+		+		+		+
Yabeodictyon				+	+						
Actinostromatida											
Actinostromella											
Araneosustroma			+	+							
Densastroma					+		?				+
Desmostroma							+	+			
Pachystroma				+							
Pichiostroma											
Plectostroma				+	+	+		+			
Plumatalinia					?						
Pseudolabechia		+									
Vikingia			+	+	+						
Stromatoporellida											
Simplexodictyon				?	+	+	?	+		+	
Stromatoporida											
Eostromatopora					?						
Lineastroma				+	+						+
Stromatopora					+			?			
Syringostromella			+	+	+	+		+	+		?
Syringostromatida											
Columnostroma						+					
?*Parallelopora*					+						
Parallelostroma			+	+	+						+

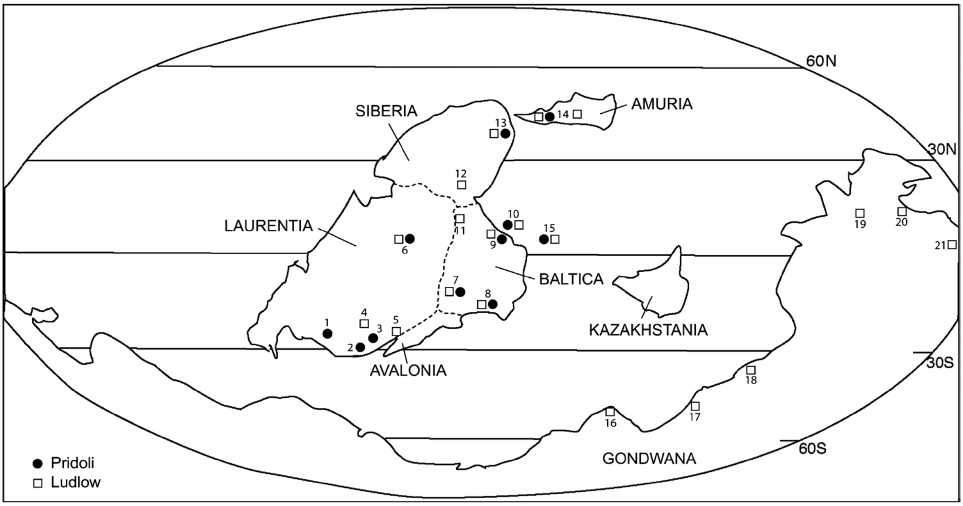

FIG. 3. Geographical distribution of stromatoporoids in the upper Silurian. The names of the localities are shown in Tables 6 and 7; *dashed lines* separate named cratons that during the late Silurian were merged to form the Laurussia paleocontinent (new).

endemic genus. A rapid diversification took place in the order Actinostromatida. Actually, it had started already in the latest Llandovery. First, actinostromellid genera *Actinostromella* and *Pichiostroma* appeared in the Gotland sections and Kentucky section respectively. *Araneosustroma,* of the family Densastromatidae, was also added, as well as *Pseudolabechia* and *Vikingia* of the family Pseudolabechiidae. *Densastroma* and *Plectostroma* became the most widespread genera among the order Actinostromatida.

Representatives of Stromatoporida (*Eostromatopora, Lineastroma, Stromatopora, Syringostromella*), which had already appeared in the late Llandovery, but had a restricted distribution, expanded their area of distribution considerably during the Wenlock.

In summary, the present, rather uneven, data from different regions do not provide evidence of the existence of faunal provinces in the Wenlock stromatoporoids. However, the species lists from the western and eastern slopes of the Urals (BOGOYAVLENSKAYA, 1973a, 1976) contain only a few common species, suggesting that the eastern Urals represented a Silurian island-arc setting, and that it was situated further away from the Baltica paleocontinent.

LUDLOW

The Ludlow epoch was characterized by the final closure of the Iapetus Ocean, which evoked progressive upheaval of the Laurentia, Baltica, and Siberia paleocontinents, sea-level lowstands, and regressions. The epi- and intracontinental basins of North American and Siberian platforms became largely restricted marine, evaporitic, and unfavorable for inhabitation of stromatoporoids. It was a time of decline in prominence of shallow shelf coral-stromatoporoid reefs, but expansion of microbial-sponge reefs in off-shelf and slope settings (COPPER, 2002). The main stromatoporoid localities of Ludlow age are situated on the platform margins (Fig. 3): Gaspé Peninsula (North America); Baltic area, Podolia, and Ural-Novaya Zemlya district (eastern European Platform); Kureika River (Siberian Platform). Some new stromatoporoid localities were added in the Ludlow: Turkey, Inner Mongolia, and Japan (Kitakami Mountainland). The occurrences of the Ludlow stromatoporoids range from ~45°

N (Mongolia, Inner Mongolia) to ~50° S (Bohemia, Turkey), using the base maps of Golonka (2002), but the latitudinal range decreases to about 40° N and S, which seems more realistic if the paleomaps of Scotese and McKerrow (1990) are employed (see Nestor, 1990a).

The Ludlow stromatoporoid fauna was almost as diverse as that of the Wenlock. It was still dominated by clathrodictyids and actinostromatids, but representatives of the Labechiida became very rare. In the order Clathrodictyida, genus ?*Plexodictyon s.s.* became almost as widespread and cosmopolitan as *Clathrodictyon, Ecclimadictyon,* and *Petridiostroma*, but more remarkable is the addition of *Schistodictyon* in the stratigraphic sections of northern China, Tian Shan, Bohemia, and New South Wales, whereas this genus does not appear from the Laurussian cratons (Laurentia, Baltica, Siberia).

Compared with the Wenlock, there were no remarkable changes in the generic content or distribution of actinostromatids, stromatoporids, and syringostromatids. In the order Stromatoporellida, *Hermatostromella* (originally *Amnestostroma*) was added to the widespread *Simplexodictyon* in the region of the eastern Urals. The presence of the fine-columnar to dendroid stromatoporoids *Amphipora s.l.* and *Clathrodictyella* deserve special mention as the earliest representatives of the very specific order Amphiporida, which became widespread in the Devonian. *Clavidictyon s.s.* and *Praeidiostroma* may belong to the same order, but their systematic position remains in dispute.

The generally cosmopolitan nature of the stromatoporoid fauna remained during the Ludlow, though a restricted distribution of some specific taxa points to a certain tendency to endemism or provincialism. First, the eastern Urals were characterized by the presence of *Gerronodictyon, Praeidiostroma, Hermatostromella* (syn. *Amnestostroma*) and specific species of *Stelodictyon, Gerronostromaria, Clathrodictyella,* and *Amphipora* (syn. *Stellopora*). Second, *Schistodictyon*, which is common to northern China, Tian Shan, New South Wales, and Bohemia, is not recorded from North America, Siberian, and eastern European platforms. Third, the genus *Lophiostroma* (order Labechiida, family Lophiostromatidae) appears in the Ludlow of Gotland, Estonia, Podolia, and Bosporus district of Turkey, although this genus had only been present previously in the Ordovician.

PRIDOLI

In the Pridoli, the regressive trend of development continued in many parts of the world, and occurrences of stromatoporoids became less common (Fig. 3). Stromatoporoids have not been described from the Pridoli of the Gondwana supercontinent or the Siberian craton, except Salair. In North America, the findings are restricted to the foreland basin of the Appalachians (Alabama, Virginia, New York), and to arctic Canada (Somerset Island). The richest stromatoporoid localities are situated around the Baltica paleocontinent (Estonia, Podolia, Urals), and in Tian Shan, which were located within the tropical climatic zone. The latitudinal range of stromatoporoids stayed the same as in Ludlow time.

There is almost no change in the taxonomic content of the Pridoli stromatoporoid fauna in comparison with the Ludlow fauna. Labechiids are represented by single findings of the most common genera: *Labechia*, *Lophiostroma, Pachystylostroma*, and *Rosenella*. In the order Clathrodictyida, the role of the family Clathrodictyidae decreased drastically, and the most common genera, *Clathrodictyon* and *Stelodictyon,* are practically lacking. ?*Plexodictyon* (family Actinodictyidae) became the most numerous and widespread genus of clathrodictyids. *Parallelostroma* (order Syringostromatida) also gained a prevalent position and practically cosmopolitan distribution. Amphiporids (*Amphipora s.l.* and *Clathrodictyella*) occur abundantly in the sections of Podolia, Urals, and Tian Shan, forming specific biogenic interbeds, but recorded data are

TABLE 6. Distribution of stromatoporoid genera in the Ludlow (new).

Order Genus	Michigan, Ontario	Eastern Quebec	Somerset Island	Gotland, Estonia	Podolia	Western Urals	Eastern Urals	Novaya Zemlya
	4	5	6	7	8	9	10	11
Labechiida								
Labechiella								
Lophiostroma				+	+			
Rosenella	?							
Clathrodictyida								
Clathrodictyon	+	+		+	+	+		+
Ecclimadictyon	+	+		+	+	+	+	+
Gerronodictyon							+	
Gerronostromaria		?				+	+	
Intexodictyides								
Neobeatricea		+						
Oslodictyon				+				
Petridiostroma				+	+	+	+	
?*Plexodictyon*			+	+		+	+	+
Schistodictyon								
Stelodictyon	+				+		+	
Yabeodictyon			+	+		+		+
Actinostromatida								
Actinostromella		+		+	+			
Araneosustroma				+			+	
Bicolumnostratum					+			
Crumplestroma								
Densastroma		+		+	+	+		+
Desmostroma					+			
Pichiostroma								
Plectostroma	+	+	+	+	+			+
Pseudolabechia				+				+
Stromatoporellida								
Hermatostromella							+	
Simplexodictyon			+	+	+		+	+
Stromatoporida								
Stromatopora		+		+	+			
Syringostromella	+			+	+		+	
Syringostromatida								
?*Parallelopora*				+				
Parellelostroma		+		+	+	+		+
Amphiporida								
Amphipora s.l.			+	+			+	
Clathrodictyella					+		+	+
Uncertain affinities								
Clavidictyon s.s.								
Praeidiostroma							+	

TABLE 6 (*continued from facing page*).

Order Genus	Siberian Platform 12	Altai, Salair, Tuva 13	Mongolia, northern China 14	Tian Shan 15	Bohemia 16	Turkey 17	Iran 18	Japan 19	Northern Queensland 20	New South Wales 21
Labechiida										
Labechiella								+		
Lophiostroma						+				
Rosenella										+
Clathrodictyida										
Clathrodictyon	+		+				+			+
Ecclimadictyon	+		+	?					+	+
Gerronodictyon										
Gerronostromaria										
Intexodictyides				+						+
Neobeatricea										
Oslodictyon										+
Petridiostroma		+	+	+				+		
?*Plexodictyon*		+	+							+
Schistodictyon			+	+	+					+
Stelodictyon		+								
Yabeodictyon				+						
Actinostromatida										
Actinostromella										+
Araneosustroma										
Bicolumnostratum										
Crumplestroma		+								
Densastroma	+		+					?		+
Desmostroma			+							?
Pichiostroma		+	?							
Plectostroma			+	+						
Pseudolabechia										
Stromatoporellida										
Hermatostromella	?									
Simplexodictyon		+	+	+					+	+
Stromatoporida										
Stromatopora	+		+	+				+		
Syringostromella		+	+	+						
Syringostromatida										
?*Parallelopora*										
Parellelostroma	+		+	+						+
Amphiporida										
Amphipora s.l.				+				+		+
Clathrodictyella				+						
Uncertain affinities										
Clavidictyon s.s.								+		
Praeidiostroma										

TABLE 7. Distribution of stromatoporoid genera in the Pridoli (new).

Order Genus	Alabama 1	Virginia 2	New York 3	Somerset Island 6	Estonia 7	Podolia 8	Western Urals 9	Eastern Urals 10	Salair 13	Mongolia 14	Tian Shan 15
Labechiida											
Labechia									+		
Lophiostroma						+					
Pachystylostroma					+						
Rosenella						+					
Clathrodictyida											
Ecclimadictyon								+			+
Intexodictyides											?
Labechiina									+		
Petridiostroma	+		?								
?*Plexodictyon*		+		+		+	+	+		+	+
Schistodictyon											+
Yabeodictyon				+							
Actinostromatida											
Acosmostroma		+	+								
Actinostromella	+				+						
Bicolumnostratum			+			+					
Densastroma					+	+		+			+
Desmostroma						+					?
Plectostroma					+	+				+	
Vikingia						+					
Stromatoporellida											
Simplexodictyon						+					
Stromatoporida											
Stromatopora			+			+				+	
Syringostromella	?					+		+		+	?
Syringostromatida											
Parallelostroma	+	+	+		+	+	+	+	+	+	+
Amphiporida											
Amphipora s.l.						+	+	+			+
Clathrodictyella						+	+	+			+
Uncertain affinities											
Perplexostroma						+					
Praeidiostroma								+			

insufficient to allow patterns of endemism for provincialism of the Pridoli stromatoporoid faunas to be ascertained.

Investigators of different groups of fossils have stressed the extremely low degree of provincialism of the Silurian faunas in comparison with the Ordovician and Devonian. BOUCOT and JOHNSON (1973) distinguished two faunal provinces for the brachiopods: (1) Silurian Cosmopolitan Province, embracing continents of the present Northern Hemisphere and Australia; and (2) Malvinokaffric Province, including southern parts of South America and Africa. In the Silurian, the Malvinokaffric Province was situated in the cold, high southern latitudes, uninhabited by stromatoporoids. In the second half of the Silurian, from the late Wenlock onward, the provincialism of brachiopods increased slightly. Therefore, BOUCOT and JOHNSON (1973) divided the Cosmopolitan Province into the Circum-Atlantic and Uralian-Cordilleran subprovinces. The analysis of the distribution of stromatoporoids confirms the almost cosmopolitan character of the early Silurian fauna of stromatoporoids and its slightly increasing provincialism in the late Silurian (particularly in the Ludlow), but too unequal information from different regions prevents recognition of clearly defined provinces or subprovinces for the stromatoporoids.

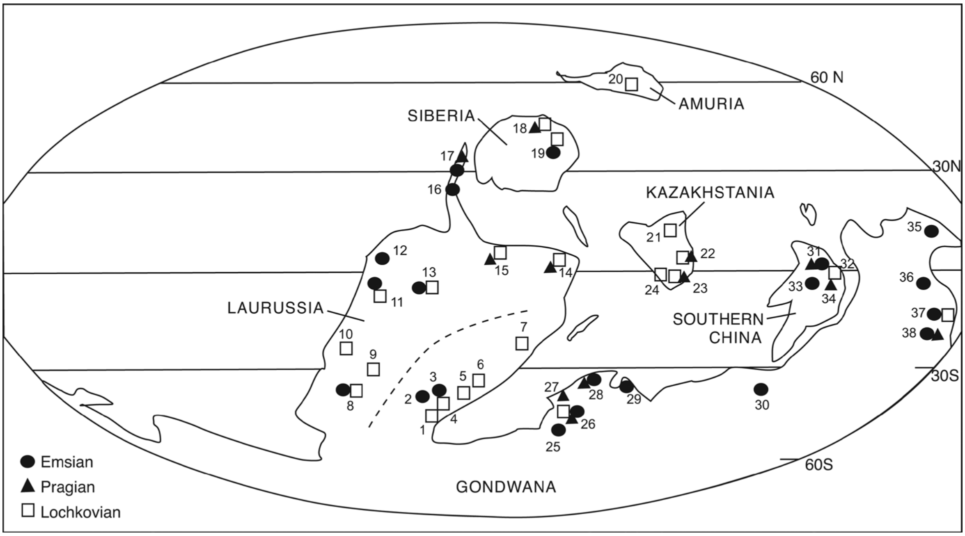

FIG. 4. Geographic distribution of Lower Devonian stromatoporoids; *dashed line* separates the two realms; localities 1–7 are in the Eastern Americas Realm, and localities 8–38 are in the Old World Realm. Key to localities: *1,* Virginia; *2,* Michigan; *3,* southern Ontario; *4,* New York; *5,* Maine; *6,* Gaspé, Quebec; *7,* Podolia, Ukraine; *8,* Nevada; *9,* Idaho; *10,* southern British Columbia; *11,* Yukon Territory and Northwest Territories; *12,* eastern Alaska; *13,* Arctic Canada; *14,* southern and eastern Urals; *15,* northern and western Urals; *16,* Kolyma Basin; *17,* Ulachan-Sis Range; *18,* Altai-Sayan and Salair; *19,* Kuznetsk Basin; *20,* Mongolia; *21,* Tian Shan; *22,* Central Asia; *23,* Turkestan and Zeravshan Range; *24,* Uzbekistan; *25,* southern Spain; *26,* northern Spain; *27,* northwestern France; *28,* Czech Republic; *29,* Carnic Alps, Austria; *30,* Afghanistan; *31,* Vietnam; *32,* Yunnan; *33,* Guangxi; *34,* Sichuan; *35,* Inner Mongolia; *36,* northern Queensland; *37,* New South Wales; *38,* Victoria (new).

DEVONIAN

CARL W. STOCK

The Devonian Period is divided into three epochs: Early, Middle, and Late. In ascending order, the Early Devonian contains three stages/ages: Lochkovian, Pragian, Emsian; the Middle Devonian contains two: Eifelian and Givetian; and the Late Devonian two: Frasnian and Famennian. Stromatoporoids reached their peak abundance during the Givetian and Frasnian (STOCK, 1990), suffered a near-extinction at the close of the Frasnian, and were extinct by the end of the Devonian. One exception is *Kyklopora,* from the the Upper Mississippian of the Donets Basin, Ukraine, which may be a clathrodictyid descendant (NESTOR, 2010) or may derive from a different line of descent from post-Devonian stromatoporoid-type hypercalcified sponges (WOOD, 2011). Generic diversity peaked in the Eifelian but was high from the Emsian through Frasnian (Table 8).

In Devonian paleogeography, a new tectonic plate develops. The Ordovician–Silurian Laurentia, Baltica, and Avalonia plates merged to form the Laurussia plate (see GOLONKA, 2002), known to some as the Euramerica plate (e.g., JOHNSON, KLAPPER, & SANDBERG, 1985).

DISTRIBUTION OF DEVONIAN DATA

The Lower Devonian map is based on the latest Silurian–Early Devonian map of GOLONKA (2002, fig. 11), and the Middle and Upper Devonian maps are founded on the Middle–Late Devonian map of GOLONKA (2002, fig. 13). The total latitudinal range and the northernmost and southernmost occurrences of Devonian stromatoporoids by stage are given in Table 8.

The southernmost occurrence of Lochkovian stromatoporoids is in Virginia (Fig. 4, no. 2), and the northernmost is in Mongolia (Fig. 4, no. 17), for a range of 105°. The Pragian

TABLE 8. Devonian stromatoporoid genera in time and space ; *?,* hiatus with no specimens of the genus confirmed within the time interval (and consequently not included in generic totals); *Prev.,* genera originating prior to the Devonian; *O,* Old World Realm; *E,* Eastern Americas Realm. Use of *O* and/or *E* for the Frasnian and Famennian represent areas formerly in both of those realms (new).

Order Genus	Prev.	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Labechiida								
Rosenella	x	O	?	O	O	?	O	O
Cystostroma	x	?	?	O	?	?	O	O
Labechia	x	O	?	O	?	?	O	O
Labechiella	x	?	O	O	O	O	O	O
Stromatocerium	x	?	?	O				
Platiferostroma								O
Parastylostroma							O	O
Stylostroma	x	O	?	O	?	?	O	O
Pachystylostroma	x	?	?	?	?	?	?	O
Pennastroma								O
Spinostroma								O
Pararosenella								O
Lophiostroma	x	?	?	?	?	?	O	
Vietnamostroma								O
Clathrodicyida								
Clathrodictyon	x	?	?	O	OE	OE		
Bullulodictyon							O	
?*Coenellostroma*				O	O			
Oslodictyon	x	O						
Stelodictyon	x	E						
Yabeodictyon	x	?	?	O				
Gerronostromaria	x	?	O	O	OE	OE	O	O
Petridiostroma	x	OE	?	?	OE	OE		
Atelodictyon		O	O	O	OE	OE	OE	O
Coenostelodictyon		O						
?*Cubodictyon*					O			
Intexodictyides	x	E	O	O				
Tienodictyon				O	O			
Anostylostroma					OE	OE	O	O
Belemnostroma		O						
Hammatostroma						O	OE	
Nexililamina				O	O			
Pseudoactinodictyon				OE	OE	OE	O	
Schistodictyon	x	?	O	O	OE	OE	O	
Actinostromatida								
Actinostroma		O	O	O	O	OE	OE	
Bifariostroma				O	O	O	O	
Plectostroma	x	O	O	O	O	O	O	
Actinostromella	x	O						
Araneosustroma	x	O						
Stromatoporellida								
Stromatoporella			O	OE	OE	OE		
Clathrocoilona				O	O	OE	OE	
Dendrostroma						OE	O	
Simplexodictyon	x	?	?	O	O			
Trupetostroma					OE	OE	OE	
Stictostroma				OE	OE	OE	OE	
Syringodictyon					E			
Styloporella							O	
Tubuliporella			O	?	O			
Hermatostroma					O	OE	OE	
Hermatoporella						O	OE	
Hermatostromella	x	O	O	O				

TABLE 8 (*continued from facing page*).

Order Genus	Prev.	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Synthetostroma						O	O	
Idiostroma					O	OE	O	
Stromatoporida								
Stromatopora	x	O	O	O	O	OE	O	O
Climacostroma					O	O		
Glyptostromoides				O	O	O		
Neosyringostroma				O	O	OE		
Pseudotrupetostroma				O	O	O		
Taleastroma					OE			
Ferestromatopora						OE	O	
Arctostroma						O	OE	
Syringostromella	x	OE	O	O				
Salairella			O	O	O	O	O	
Syringostromatida								
Syringostroma		O	?	OE	OE	E		
Atopostroma		OE	?	O				
Columnostroma		E	O	?	E	O		
Coenostroma	x	E	?	O	OE	OE		
Parallelopora				OE	OE	O		
Habrostroma	x	OE	O	OE	OE	OE		
Parallelostroma	x	OE	O					
Stachyodes					O	OE	OE	
Amphiporida								
Amphipora	x	O	O	O	OE	OE	OE	O
Euryamphipora							O	
Novitella							O	
Vacuustroma				O	?	O	O	
Total genera	27	24	17	37	39	37	35	17

range is 90°, with extremes in northern Spain (Fig. 4, no. 23) and Altai-Sayan and Salair (Fig. 4, no. 15). The range remained at 90° in the Emsian, but shifted slightly southward, with southern Spain being southernmost (Fig. 4, no. 22) and the Ulachan-Sis Range and the Kuznetsk Basin being equally northernmost (Fig. 4, no. 14, 16).

Eifelian stromatoporoids range from Morocco (Fig. 5, no. 40) to the Ulachan-Sis and Sette-Daban Ranges (Fig. 5, no. 23–24) for a total of 82°. The Givetian range is slightly smaller (80°), with the same northern extreme as in the Eifelian and the southern extreme in Kentucky (Fig. 5, no. 7).

The total range for the Frasnian (78°) is down slightly from the Givetian, but the extremes have shifted slightly, with the northernmost occurrence being in the Ulachan-Sis Range (Fig. 6, no. 16) and the southernmost occurrence being in both Nevada and Afghanistan (Fig. 6, no. 2, 43). The southern extent of Famennian stromatoporoids was limited to Germany (Fig. 6, no. 34), but the northernmost occurrence of stromatoporoids remained in the Ulachan-Sis Range, resulting in a total paleolatitudinal spread of 70°.

Examination of Table 9 reveals that in five of the seven stages, the northern limit of the total range extends further from the paleoequator than does southern limit. In only the Emsian is the paleolatitudinal limit to the south greater than the northern limit—the limits are equal in the Pragian. This sort of asymmetry was noted on older plate reconstructions of SCOTESE (1986), by STOCK (1990) for the Devonian stromatoporoids, and PEDDER and OLIVER (1990) for Emsian rugose corals. STOCK (1990) concluded that the absence of a large land mass in the northern hemisphere, relative to the large land mass in the southern hemisphere, may have led to warmer sea temperatures in the north, allowing an asymmetry of the tropical and subtropical climates in which the stromatoporoids dwelled. He also suggested

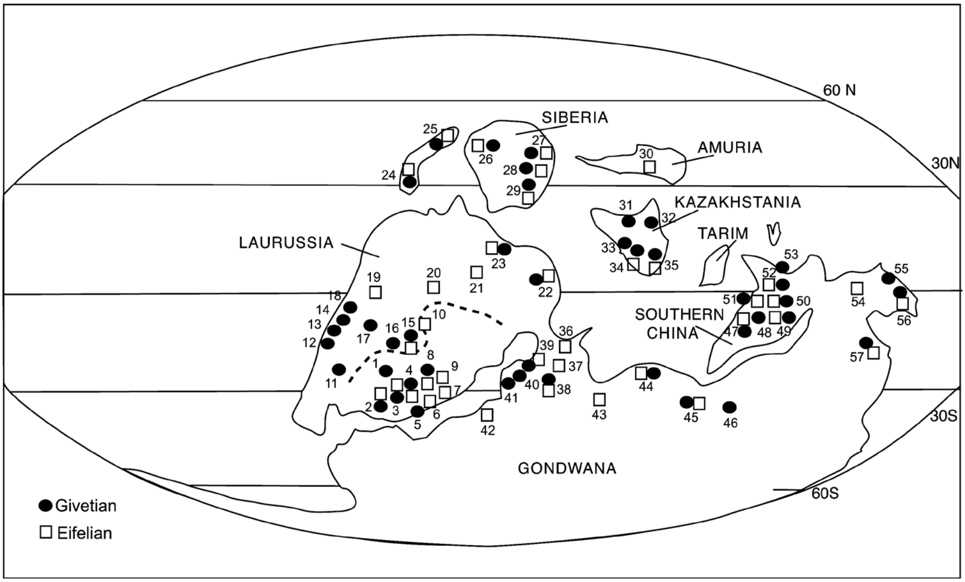

FIG. 5. Geographic distribution of Middle Devonian stromatoporoids. The *dashed line* separates the two realms; localities 1–10 are in the Eastern Americas Realm, and all the known localities (11–57) worldwide are in the Old World Realm. Key to localities: *1,* Iowa; *2,* Missouri; *3,* Illinois; *4,* Indiana; *5,* Kentucky; *6,* Ohio; *7,* New York; *8,* Michigan; *9,* southern Ontario; *10,* northern Ontario; *11,* Nevada; *12,* northern California; *13,* Oregon; *14,* Washington; *15,* Manitoba; *16,* Saskatchewan; *17,* Alberta; *18,* northern British Columbia; *19,* Yukon and Northwest Territories; *20,* Arctic Canada; *21,* Russian Platform; *22,* southern Urals; *23,* northern Urals; *24,* Omolon; *25,* Ulachan-Sis; *26,* Sette-Daban Range and Far East; *27,* Altai-Sayan and Salair; *28,* Kuznetsk Basin; *29,* western Siberian Platform; *30,* Mongolia; *31,* Karaganda; *32,* Tian Shan; *33,* southern Kazakhstan; *34,* Uzbekistan; *35,* Zeravshan Range, Isfar, and Kashkadar; *36,* Poland; *37,* Czech Republic; *38,* Germany; *39,* Belgium; *40,* France; *41,* northern Spain; *42,* Morocco; *43,* Turkey; *44,* Caucasus; *45,* Afghanistan; *46,* Xizang (Tibet); *47,* Hunan; *48,* Guizhou; *49,* Sichuan; *50,* Yunnan; *51,* Guangxi; *52,* Vietnam; *53,* Northeast China; *54,* Qinghai; *55,* Xinjiang; *56,* northeastern Thailand; *57,* northern Queensland (new).

that the Siberian plate might have been plotted too far north, as that is where the northernmost data points were located. In the GOLONKA (2002) plate reconstructions, Siberia remains fairly far north—up to 55° N—but not as far north as with SCOTESE (1986)—60–80° N. The northernmost landmass on GOLONKA's (2002) reconstructions is in the Lower Devonian, where the Amuria plate extends to 65° N.

Another aspect revealed by the data in Table 9 is that the total latitudinal range of stromatoporoids decreased through the Devonian. A first hypothesis might be that the Earth cooled throughout the Devonian, resulting in shrinking of the tropical and subtropical climates toward the equator. Generally speaking, global cooling accompanies a fall in eustatic sea level, and global warming accompanies a rise in eustatic sea level (e.g., FRAKES, FRANCIS, & SYKTUS, 1992); however, JOHNSON and SANDBERG (1988) indicated that, following relatively low eustatic sea level during the Early Devonian, sea level rose throughout the Eifelian and Givetian, peaking near the end of the Frasnian, with a precipitous fall in association with the Frasnian–Famennian boundary. According to JOACHIMSKI and others (2002), global temperature rose irregularly through the Middle Devonian, with an abrupt fall near the end of the Givetian, followed by a general rise during the Frasnian, followed by another abrupt fall near the end of the Frasnian. During the Famennian, Earth cooled, and eustatic sea level fell, due at least in part to the onset of glaciation (e.g., CROWELL, 1999). Thus, the latitudinal

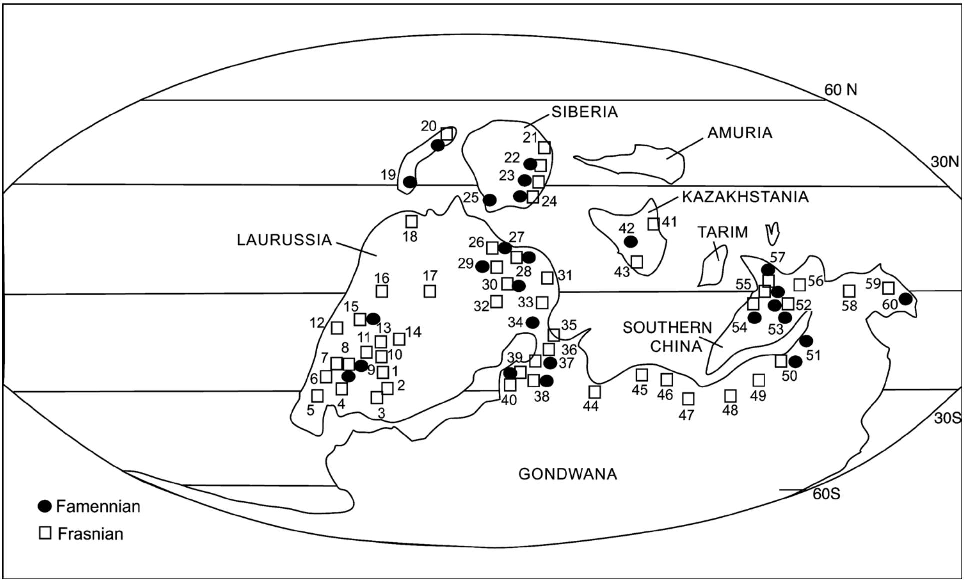

FIG. 6. Geographic distribution of Upper Devonian stromatoporoids. Key to localities: *1,* Nebraska; *2,* Iowa; *3,* Missouri; *4,* New Mexico; *5,* Sonora; *6,* Arizona; *7,* Nevada; *8,* Utah; *9,* Wyoming; *10,* North Dakota; *11,* Montana; *12,* Washington; *13,* Saskatchewan; *14,* Manitoba; *15,* Alberta; *16,* Northwest Territories; *17,* Arctic Canada; *18,* northern Alaska; *19,* Omolon; *20,* Ulachan-Sis; *21,* Altai-Sayan; *22,* Kuznetsk Basin; *23,* western Siberian Platform; *24,* Yogorsk Peninsula; *25,* Novaya Zemlya; *26,* Bolshaya Zelenets and Dolgi Islands; *27,* Voivo-Vozh; *28,* northern Urals; *29,* Pechora Basin and Timan; *30,* Russian Platform; *31,* southern Urals; *32,* St. Petersburg region; *33,* Lower Volga and Volgograd; *34,* Donets Basin; *35,* Poland; *36,* Czech Republic; *37,* Belgium; *38,* Germany; *39,* France; *40,* northern Spain; *41,* Tian Shan; *42,* Kazakhstan; *43,* Uzbekistan; *44,* Turkey; *45,* Caucasus; *46,* Iran; *47,* Afghanistan; *48,* Xizang; *49,* Carnarvon Basin; *50,* Canning Basin; *51,* Bonaparte Basin; *52,* Sichuan; *53,* Guizhou; *54,* Hunan; *55,* Guangxi; *56,* Yunnan; *57,* Vietnam; *58,* northeastern China; *59,* Qinghai; *60,* Xinjiang (new).

contraction toward the paleoequator of the geographic range of stromatoporoids through the Devonian appears to contradict what would be expected of global warming and rise of eustatic sea level for at least the Eifelian through the Frasnian. A factor that could explain at least some of the apparent contradiction in the range of stromatoporoids, and the increase in temperature and sea level, is the loss of appropriate habitat.

The Laurussia plate developed in two stages (see Fig. 2–4) with actual collision (an accretion event) of the Siberian Baltica, Avalonian, and Laurentian cratons by the Ludlow, and then in the Early Devonian, the Siberian craton rifted from the rest of Laurussia to again become an isolated craton, while the remains of Laurussia continued to approach Gondwana (in association with a partial closure of the Rheic Ocean). Stromatoporoids in southern Laurussia—including the area of present-day eastern United States (see spread of localities 1–9 on Fig. 5)—represent some of their southernmost occurrences. During the Middle and Late Devonian, the Acadian Orogeny took place in southeastern Laurussia, resulting in a northwestwardly prograding wedge of siliciclastic sediments. The introduction of siliciclastics caused increases in turbidity and substrate instability, both prohibitive for stromatoporoid habitation, and stromatoporoids withdrew from the eastern United States (STOCK, 1997). In addition, on the Gondwanan margin of Morocco, stromatoporoids invaded the region for a comparatively short time in the Middle Devonian (Eifelian) (see Fig. 5). A noticeable

TABLE 9. Latitudinal ranges of Devonian stromatoporoids by stage (new).

Age	Northernmost	Southernmost	Total
Famennian	45°	25°	70°
Frasnian	45°	33°	78°
Givetian	45°	35°	80°
Eifelian	45°	37°	82°
Emsian	40°	50°	90°
Pragian	45°	45°	90°
Lochkovian	60°	45°	105°

post-Lochkovian latitudinal contraction can be seen in the distribution of stromatoporoids from the higher southern paleolatitudes between Early Devonian (Lochkovian) to Late Devonian (Famennian) time (see map series, Fig. 4–6).

PALEOBIOGEOGRAPHIC UNITS

Most workers have divided the marine biota of the Devonian into three realms (e.g., BLODGETT, ROHR, & BOUCOT, 1990): (1) Malvinokaffric Realm—southern high latitude areas; (2) Eastern Americas Realm (EAR)—southeastern North America and northwestern South America; and (3) Old World Realm (OWR)—all separate marine habitats. These realms became established primarily on the basis of distributions of brachiopods (e.g., JOHNSON & BOUCOT, 1973) and rugose corals (e.g., OLIVER, 1977). Apparently, it was too cold for stromatoporoids in the Malvinokaffric Realm and the South American part of the Eastern Americas Realm. The barrier separating the OWR from the EAR was located in Laurussia (Fig. 4–5) and consisted of the Transcontinental Arch, which extended from Arizona and New Mexico to Minnesota and Wisconsin, and to the Canadian Shield, including most of central Canada, and probably extended into Greenland and the Baltic Shield, as a kind of so-called Laurussian inter-realm barrier (e.g., WITZKE, 1990).

The existence of two tropical to subtropical realms was in place at the beginning of the Devonian until late in the Middle Devonian. An exception to this is the total absence of stromatoporoids from the Pragian of the EWR, and North American parts of the OWR, first noted by STOCK (1990). There are two possible explanations for this absence. The Pragian to early Emsian is a time that coincides with extreme sea-level fall, at the end of SLOSS's (1963) Tippecanoe cratonic sequence, when much of North America was exposed to the erosion of its most recently deposited sediments (see also Devonian sea-level curve of JOHNSON, KLAPPER, and SANDBERG, 1985, fig. 12). Additional erosion in the Mesozoic and Cenozoic, especially by glacial ice during the Quaternary, also could have contributed to the removal of Pragian sedimentary rocks. The erosional hypothesis is given credence by two recent descriptions of Jurassic kimberlites on the Canadian Shield that contain Devonian normal marine carbonate xenoliths (COOKENBOO, ORCHARD, & DAOUD, 1998; MCCRACKEN, ARMSTRONG, & BOLTON, 2000).

Most researchers agree that the discrimination between the OWR and EAR ended during an episode of sea-level rise in the middle–late Givetian, known as the Taghanic Onlap, cycle IIa of JOHNSON and SANDBERG (1988). At this time, it is believed that the Laurussian inter-realm barrier was breached, allowing the mixing of OWR and EAR faunas. Seven genera, known from only the OWR during the Eifelian, invaded the EAR during the Givetian, but only one genus migrated from the EAR to the OWR at the same time (Table 8). OLIVER and PEDDER (1989) stated that the mixing of OWR and EAR rugose coral faunas during the Taghanic Onlap resulted in the extinction of all former EAR families and genera. BOUCOT (1990) saw a similar pattern for brachiopods at the same time. Eight stromatoporoid genera found in both the OWR and EAR during the Givetian became extinct in the areas of the former EAR during the Frasnian, but eight OWR-EAR Givetian genera remained in both areas in the Frasnian (Table 8).

The Frasnian–Famennian extinction profoundly affected the stromatoporoids; a total of 24 Frasnian genera became extinct before the Famennian (Table 8). During the Famennian, stromatoporoids were absent from the area of the former EAR; Stock (1997) concluded that the influx of siliciclastic sediments produced during the Acadian Orogeny and global cooling contributed to this absence.

During the Famennian, stromatoporoids retreated from many areas of Laurussia and Gondwana (Fig. 6). Stearn (1987) delineated three stromatoporoid faunas in the Famennian: (1) dominantly labechiids; (2) labechiids and clathrodictyids; and (3) mainly clathrodictyids, without labechiids, a more Frasnian-like assembly of genera. He suggested that labechiids might have been better adapted to cooler water than were the typically Devonian nonlabechiids. Bogoyavlenskaya (1982) described two Famennian stromatoporoid communities: (1) western slopes of the Urals, Novaya Zemlya, Donets Basin, several other parts of Russia, and southeastern China (e.g., Guangxi, Guizhou, Hunan); and (2) eastern slopes of the Urals, central Kazakhstan, and western Europe (France, Belgium, Germany, Czech Republic). At the time of publication, several of Bogoyavlenskaya's localities were thought to contain strata of earliest Carboniferous (Tournaisian) age; her so-called Etroeungtian (or Strunian) fauna, is presently equated with the late Famennian interval—a subdivision that remains to be defined at a level toward the base, or higher, within the *expansa* Zone of the Upper Devonian–Lower Carboniferous conodont succession (see Stearn, 2010, p. 2, table 1; adapted from Sandberg, Morrow, & Ziegler, 2002). They since have been placed in the Famennian. Faunas 1 and 2 of Stearn (1987) coincide with Bogoyavlenskaya's (1982) community 1, and his fauna 3 coincides with her community 2. Hamilton (1970) stated that, in Russia, the Famennian strata of the western slopes of the Urals, Novaya Zemlya, the Yogorsk Peninsula, Bolshaya Zelenets Island, and Dolgi Island were deposited in relatively shallow, miogeosynclinal environments, whereas strata on the eastern slopes of the Urals were deposited in deeper, eugeosynclinal environments. Stock (1990) noted that areas of shallower water contained dominantly labechiid and mixed stromatoporoid faunas (Stearn's [1987] faunas 1 and 2) and areas of deeper water contained dominantly nonlabechiids (Stearn's [1987] fauna 3). Stock (2005) suggested that global cooling associated with Famennian glaciations (e.g., Crowell, 1999), which probably made a significant contribution to nonlabechiid stromatoporoid extinctions at the end of the Frasnian, continued to adversely affect those genera most typical of the Lochkovian–Frasnian.

Table 10. Degrees of endemism of stromatoporoid genera through the Devonian (new). *OWR,* Old World Realm; *EAR,* Eastern Americas Realm; *NA,* not applicable, as stromatoporoids absent from area of EAR.

Age	OWR Endemic	EAR Endemic	Cosmopolitan
Famennian	17 (NA)	0 (NA)	0
Frasnian	24 (69%)	0 (0%)	11
Givetian	14 (54%)	1 (4%)	22
Eifelian	21 (57%	2 (11%)	16
Emsian	31 (84%)	0 (0%)	6
Pragian	17 (NA)	0 (NA)	0
Lochkovian	15 (75%)	4 (20%)	5

Table 10 summarizes the level of endemism of the Devonian stromatoporoid genera in the OWR and EAR by age. For the OWR, endemism ranged from 54% in the Givetian to 84% in the Emsian. In only the Lochkovian (75%) and Emsian (84%) was the 75% endemism criterion of Kauffman (1973) attained; however, in all ages, the minimum criterion of 33% of Oliver (1977) was exceeded.

Whereas the OWR contains an endemic stromatoporoid fauna, this is not the case for the EAR, where endemism ranged from 0% in the Emsian to 20% in the Lochkovian (Table 10). Clearly, the stromatoporoids do not support the EAR as a separate realm. Perhaps, the EAR existed as a province within one tropical to semitropical realm during the Devonian. The OWR covered a much greater area than did the EAR, and no doubt contained several provinces that have the same level of genus endemism as the EAR. This having been said, it is interesting to note that stromatoporoids in order Labechiida were absent from the EAR throughout the Devonian (Table 8).

CONCLUSIONS

In their paper on Devonian world paleogeography, Heckel and Witzke (1979, p. 116) stated, "Stromatoporoids are the most widely reported benthonic group confined to Devonian warm water between 35° N. and 40° S." Although the exact paleolatitudinal ranges plotted here do not always match those of Heckel and Witzke (1979), we still find a paleoequatorially centered, paleogeographic distribution of stromatoporoids in the Devonian, as well as in the Ordovician and Silurian. Examination of the full time range of stromatoporoids indicates several trends in terms of geographic range and endemism.

PALEOLATITUDINAL RANGE

Latitudinal ranges given here are understood to be approximations, limited by geographic uncertainties in the determination of collecting localities and time averaging used in constructing the base maps. The paleolatitudinal range of stromatoporoids in the mid–late Darriwilian and Sandbian was 55° and 75° in the Katian. In the Hirnantian, the range contracted to 10°, but it increased through most of the Silurian, with 65° in the Llandovery, 75–80° in the Wenlock, and 95° in the Ludlow. After a contraction of 75° in the Pridoli, a maximum range of 105° was attained in the Lochkovian. This maximum is heavily dependent on the far northern location of Amuria, as plotted by Golonka (2002); were that locality omitted, the Lochkovian range would have been 90°, the same as that determined for the Pragian and Emsian. The remainder of the Devonian shows a gradual decrease in paleolatitudinal range, with 82° in the Eifelian, 80° in the Givetian, 78° in the Frasnian, and 70° in the Famennian.

For 9 of the 15 time intervals documented here, there is an asymmetry to the paleolatitudinal range of stromatoporoids; the northern limit of their extent is at least 10° further from the paleoequator than it is south of the paleoequator. This is true for the mid–late Darriwilian through the Katian, the Pridoli through the Lochkovian—the latter dependent on the position of Amuria—and the Eifelian through the Famennian. A steeper climatic gradient may have existed in the Devonian of the southern hemisphere, relative to the northern hemisphere, due to the presence of the large landmass of Gondwana in the south and the presence of mostly ocean in the north (herein, p. 29). More than not, this paleolatitudinal asymmetry is associated with times of abundance for stromatoporoids (e.g., Katian, Eifelian–Frasnian), but it is not for the Wenlock and Ludlow. Symmetry to near symmetry of paleolatitudinal ranges in the Llandovery and Pragian–Emsian are associated with times of relatively low genus diversity, as well as low sea level associated with latest Ordovician–early Silurian glaciation (Grahn & Caputo, 1992; Finnegan & others, 2011) and the end of Sloss's (1963) Tippecanoe sequence in the Early Devonian.

PALEOGEOGRAPHIC ANOMALIES

There were three times when the paleogeographic ranges of stromatoporoids displayed anomalous patterns. The first of these was in the Hirnantian, when stromatoporoids were restricted to just two areas—southern Laurentia (20° S; Anticosti Island); and western Baltica (30° S; Estonia) (Fig. 1). Their limited distribution may be explained by the shortness of duration of the stage, the cooling effects of ocean waters, and extinction associated with the end-Ordovician glaciation (Webby, 2004).

The second is the complete absence of stromatoporoids from Gondwana during the Pridoli (Fig. 3), and the third is the complete disappearance of stromatoporoids from the Eastern Americas Realm during the Pragian (Fig. 4). With the exception of the Hirnantian, there are no obvious reasons to explain these anomalies. They could in part be artifacts of collecting—either given that not all potential stromatoporoid faunas of these ages have been sampled—or stromatoporoid-bearing strata of these ages may have been eroded, as postulated for the Pragian (herein, p. 33).

ENDEMISM

Provincialism is often characterized in a region by the appearance of significant endemicity of genus-level categories. In stromatoporoids, it developed to only a very limited degree through Middle–Late Ordovician and Early–Middle Devonian time. In the Ordovician, stromatoporoids were mainly confined paleoequatorially (Fig. 1) within the North American–Siberian Realm, but they did not show any marked regional (or provincial) differentiation through successive Middle–Upper Ordovician stage intervals.

There is no genus-level endemism among the Silurian stromatoporoids (herein, p. 28), a pattern that accords with the conclusions of BOUCOT and JOHNSON (1973) for the brachiopods of the warmer paleolatitudes. The Lochkovian–Givetian paleoequatorial Old World and Eastern Americas Realms are recognized, based on other taxa (e.g., brachiopods, corals), but no differentiation of the paleobiogeography can be recognized using the stromatoporoids alone (herein, p. 34).

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