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PART E, REVISED, VOLUME 4, CHAPTER 12: BIOSTRATIGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

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INTRODUCTION

Although all life forms have a limited existence in time, some are more valuable than others for recognizing a particular time interval. Such species have short stratigraphic ranges and wide distribution, and are, therefore, potentially useful in distinguishing short intervals of time. Also, for groups to be potentially valuable for dating, they must have been studied and understood taxonomically. In addition, students of groups of fossils that are valuable in biostratigraphy must be able to agree on a consistent taxonomy. The stromatoporoids only partly meet these requirements. Only within the past three decades has the broadening of the species concept allowed the recognition of species from one region to another. Previous research was concentrated on distinguishing new taxa by refining the differences between specimens, and the species established in one continent or country were rarely identified in other parts of the world. For example, STEARN (1979) compared monographic descriptions of Frasnian faunas from the Ardennes (Belgium), Poland, and the Czech Republic, and showed that the taxonomic principles used by the investigators to distinguish species led to the conclusion that none of the 132 species of stromatoporoids were common to all three areas, even though they are separated presently by only a few hundred kilometers in Europe.

Faunas that do not have common species cannot be correlated. Not until a broader species concept, and an appreciation of the degree of variation inherent in stromatoporoid species are accepted, can the true biostratigraphic potential of the group be fully assessed. Yet, despite this realization, some stromatoporoid species and assemblages have been recognized as having wide distribution and short duration, and they therefore have considerable potential for zonation and correlation.

Stromatoporoids occur commonly in Ordovician, Silurian, and Devonian carbonate successions but have seldom been used primarily as biostratigraphic indicators. They occupied mainly warm, well-circulated, shallow, marine, carbonate shelves, especially the reef and shoal habitats of equatorially disposed continental platform and island-arc settings. In reef and shoal facies, stromatoporoids are often the only fossils available for biostratigraphic studies. Notwithstanding their prominence in many Paleozoic carbonate successions, they have remained comparatively poorly understood. Taxonomic approaches have long been founded on differentiating a species on the basis of a single, or a few specimens, rather than evaluating the variation that existed among many individuals of a particular species. In addition, some taxonomists have used traits (such as astrorhizae, e.g., BOGOYAVLENSKAYA, 1965, and subsequently) for essential specific characters and for guides to phylogeny and classification, which are regarded as trivial by other research workers, making their taxa difficult to recognize in other parts of the world.

The basic framework of a modern-type of stromatoporoid taxonomy was presented by NICHOLSON (1886, p. 2) some 120 years ago. He stressed the necessity for investigation of diagenetic alteration across a large number of specimens and assessment of the range of variability in populations of the

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species with use of adequate numbers of collected samples. However, NICHOLSON's approaches were not adopted by many stromatoporoid workers, at least not until the last few decades. Too many workers have been intent on multiplying the numbers of species based on differences between a few, often fragmentary specimens. A more rigorous approach is required for sampling and studying a stromatoporoid species. This entails using a larger number of specimens as the basis for fully describing the range of diagnostic morphological features: the variability of form and attributes of the species that arose from diagenetic alteration.

Three promising approaches to biostratigraphic correlation using Ordovician–Devonian stromatoporoids are the following.

1. Compilation of range charts (both at genus and species levels).
2. Establishment of sets of laterally adjacent successions of species-based zonal assemblages (NESTOR, 1982, 1990a, 1999a).
3. Development of a succession of species-based zonal assemblages tied to the zonation of conodonts (STEARN, 1997a, 2001).

Continuity of rigorous taxonomic work through the Ordovician to the Devonian stratigraphic record is needed to provide the basis for more precise biostratigraphic analyses, using one or more of the above-mentioned approaches, hopefully leading to recognition of many more diagnostic, zonally restricted, but widely distributed stromatoporoid species. Each of the three biostratigraphic approaches is further discussed below.

RANGE CHARTS

KÜHN (1939, p. 14–15) assembled one of the earliest broad-scale compilations of the stratigraphic distribution of important stromatoporoid genera. Another, more comprehensive, tabular representation of Paleozoic and Mesozoic stromatoporoid species was presented by YAVORSKY (1951). This was useful for generalized correlation across the former Soviet Union (mainly Russia), with many of the species listed by YAVORSKY exhibiting series-length (or epoch-duration) time ranges (that is, restricted either to the middle Silurian, Middle Devonian, or Upper Devonian). YAVORSKY (1929, 1955, 1957, 1961, 1962, 1963, 1965, 1967), RIABININ (1936, 1937, 1939, 1941, 1951, 1953), and GORSKY (1938) also demonstrated the value of stromatoporoids as generalized guide fossils for regional geological exploration work in the Ordovician, Silurian, and Devonian successions of the former Soviet Union.

LECOMPTE (1951, 1952), in a monographic treatment of the Devonian stromatoporoid species from the Ardennes of Belgium, also included a tabular presentation of species data—recognizing about half of the 115 species as being confined to 1 of the 5 main stratigraphic subdivisions (Couvinian 1 substage, Couvinian 2 substage, Givetian stage, Frasnian 1 substage or Frasnian 2 substage)—but they did not provide any further biostratigraphic details. Similar tables of the species distribution were presented by RIABININ (1951, 1953) for the local stages (horizons) of the Silurian in Estonia and Podolia (Ukraine).

The view that the stromatoporoids were biostratigraphically important fossils was first clearly proposed by GALLOWAY and ST. JEAN (1957, p. 31, 85) in their monographic treatment of Middle Devonian stromatoporoids from the central United States. They suggested that stromatoporoids were likely to prove to be zonal fossils, as useful in the Devonian as the trilobites were in the Cambrian, or the graptolites in the Ordovician! FLÜGEL (1959, table 25) emphasized the stratigraphic importance of stromatoporoid genera. His range chart, based mainly on GALLOWAY's (1957) taxonomy, showed that many of the genera were restricted to either the Ordovician or the Devonian. FLÜGEL stressed that a number of genera and species could be viewed as index fossils for the Devonian, especially the Middle Devonian. FLÜGEL (1962) also presented a general review of the biostratigraphic significance of stromatoporoid faunas in the Silurian and Devonian.

In the 1960s and 1970s, Silurian stromatoporoid faunas of different regions were described, and the stratigraphic distribution of species was recorded. This description and stratigraphic placement opened the possibility of using stromatoporoids in local stratigraphy and increased their value for correlating stratigraphic sequences. NESTOR (1964a, table 2, 5; 1966, table 2, 4) published range charts of genera and species distributed in regional stages of the Upper Ordovician and Silurian of Estonia and commented on the occurrences of some species from other areas. MORI (1968, table 1; 1970, table 1) published range charts of stromatoporoid species in the stratigraphic units of the Wenlock and Ludlow strata on Gotland (Sweden), and roughly correlated the stratigraphic successions of Gotland and Estonia using the assemblages of species in common. MORI (1978, table 1) also presented the stratigraphic distribution of Silurian stromatoporoids from the Oslo area, Norway, and compared them with the Gotland and Estonian stromatoporoid successions. BOL'SHAKOVA (1973, p. 19–20) recorded the stratigraphic distribution of stromatoporoid species in the Silurian sequence of Podolia. BOGOYAVLENSKAYA (1973) described the Silurian stromatoporoids from different districts of the Urals and used common species for correlation of stratigraphic units. In North America, Silurian stromatoporoids were described from eastern Quebec (STEARN & HUBERT, 1966), northwestern Baffin Island (PETRYK, 1967), and from Somerset Island of Arctic Canada (SAVELLE, 1979). All of these works also include range charts. NESTOR (1976) authored a monograph on Ordovician and Silurian stromatoporoids from the Siberian platform and additionally distinguished a succession of species assemblages.

The stratigraphic ranges of species have also been used to establish correlations of the Devonian rocks. MISTIAEN (in BRICE & others, 1977) presented a table of ranges for the Ferques section in the Boulonnais area of northern France and compared the occurrences with those in the Ardennes of Belgium and in other countries. In addition, MISTIAEN (1980) described the species from the Ferques section, recognized 13 levels characterized by distinctive stromatoporoid faunas, and compared the faunas with those in the stratigraphic sections through the Givetian interval of the Ardennes described by LECOMPTE. MISTIAEN (1982) also analyzed the distribution of faunas around the Givetian-Frasnian boundary in the Boulonnais, Ardennes, Poland, and the Czech Republic. In 1988, he recognized there were 3 stromatoporoid-based Givetian zones and 2 in the Frasnian part of the Boulonnais section.

MISTIAEN (1985) also showed the distribution of Devonian stromatoporoid species in the reefal complexes of the Central Mountains of Afghanistan. He presented tables showing distributions of stromatoporoid species in a number of stratigraphic sections, as well as the overall Devonian ranges of taxa, with ties to the main global conodont, graptolite, and other biozonations. The Middle Devonian fauna in particular is closely related to counterparts in the Ardennes (LECOMPTE, 1951, 1952) and the Boulonnais area (MISTIAEN in BRICE & others, 1977; MISTIAEN, 1980, 1982, 1988). The correspondence of European stratigraphic ranges with those of Afghan taxa confirmed that the stromatoporoids were both members of the same comparatively wide-ranging, provincial Old World Realm. Less close relationships exist with other so-called Old World faunas in other regions, such as the Czech Republic (ZUKALOVA, 1971; MAY, 2005), the Kutnetsk Basin (Siberia), southern China, and Australia. MISTIAEN (1985, fig. 17–18) was able to determine the age relationships of the discrete reefal complexes to within a Devonian stage, based on the overlapping stratigraphic ranges of the stromatoporoid faunas (36 species belonging to 19 genera), at least through the Emsian to early Frasnian interval.

The documentation of stromatoporoid faunas in China commenced mainly following the discoveries of abundant faunas during the nationwide geological surveys and stratigraphic work from 1949 onward (Yang & Dong, 1962). Through the 1970s and 1980s, numerous species were described from the Middle Ordovician to Upper Ordovician, lower Silurian, and especially from the rich assemblages through the Devonian of southern China (Dong & Yang, 1978; Yang & Dong, 1979; Dong, 1982; Dong & Wang, 1982; Dong & Wang, 1984; Wang, Dong, & Fu, 1986; Wang, 1988; Dong, 2001). Some of these assemblages were useful for correlation and/or for establishing age relationships of particular stromatoporoid-bearing successions. Several of the above-cited publications included tabular presentations of species ranges: for example, through the Middle Ordovician to Devonian successions of the Xinjiang Autonomous Region (northwestern China) by Dong and Wang (1984), and the Devonian sequences in southern China: parts of Guangxi province by Yang and Dong (1979) and Sichuan province by Wang (1988).

Nestor and Stock (2001) presented range charts of the distribution of genera in North America and Baltoscandia as part of a discussion of the extinction of stromatoporoid faunas leading up to the end-Ordovician glaciation, and then their recovery through the early Silurian (Llandovery), including their generalized spread into other regions, such as Ireland, Novaya Zemlya, the Siberian Platform, and the Yangtze Platform.

Where stromatoporoid generic ranges were well understood, for example, in the Devonian (as shown by Stearn, 1979, fig. 1), the data could be plotted in a range chart for broad-scale correlation work. In this chart, most of the Devonian is divided into stage-age subdivisions (the exception being the Lower Devonian series-epoch couplet). Many Devonian genera are long ranging, through more than one stage-age interval, but a few short-ranging (key) genera are also represented, such as *Araneosustroma,* encompassing the Lower Devonian series; *Pseudoactinostroma* in the Eifelian stage; *Columnostroma* in the Givetian; and *Bullulodictyon, Arctostroma, Styloporella,* and *Euryamphipora,* in the Frasnian. Other slightly longer-ranging genera also have correlation potential because their first and/or last appearances coincide with particular stage (or series) boundaries. Remarks on the patterns of development of the Lower Devonian faunal successions were also presented by Webby, Stearn, and Zhen (1993, fig. 4). In the figure, first and last appearances of key, short-lived genera characterize boundaries between the Lochkovian, Pragian, and lower Emsian. The scheme provides a broad basis for identifying diagnostic stromatoporoid assemblages to stage level.

We here present a set of range charts to show the stratigraphic distribution of genera worldwide (Fig. 1–3). Although the genus is, in taxonomic usage, a more artificial concept than species, it provides a reasonable means of attaining broadly based global correlations employing stratigraphic ranges.

The first stromatoporoids were the labechiids; they remained the dominant group through the Mid–Late Ordovician, but declined through the Silurian, with few persisting into the Early–Mid-Devonian, and then showed a resurgence during the Late Devonian. In general, the genera do not seem to have much biostratigraphic potential (Fig. 1), though within the Ordovician the assemblages exhibit some successional changes, from associations of morphologically simpler families Rosenellidae, Labechiidae, and Aulaceratidae taxa in the Darriwilian, to the more complex, skeletal meshworks of some genera of the families Stromatoceriidae, Platiferostromatidae, and Stylostromatidae, with mamelon columns and flanged pillars in the Late Ordovician and early to mid-Silurian. A number of labechiids in the Late Devonian (Famennian), such as the platiferostromatids (*Platiferostroma*, *Vietnamostroma*) and more specialized stylostromatids (*Pennastroma, Spinostroma*), show further differences that may have some correlation potential.

Two of the present authors (Stearn and Webby) have very different explanations for

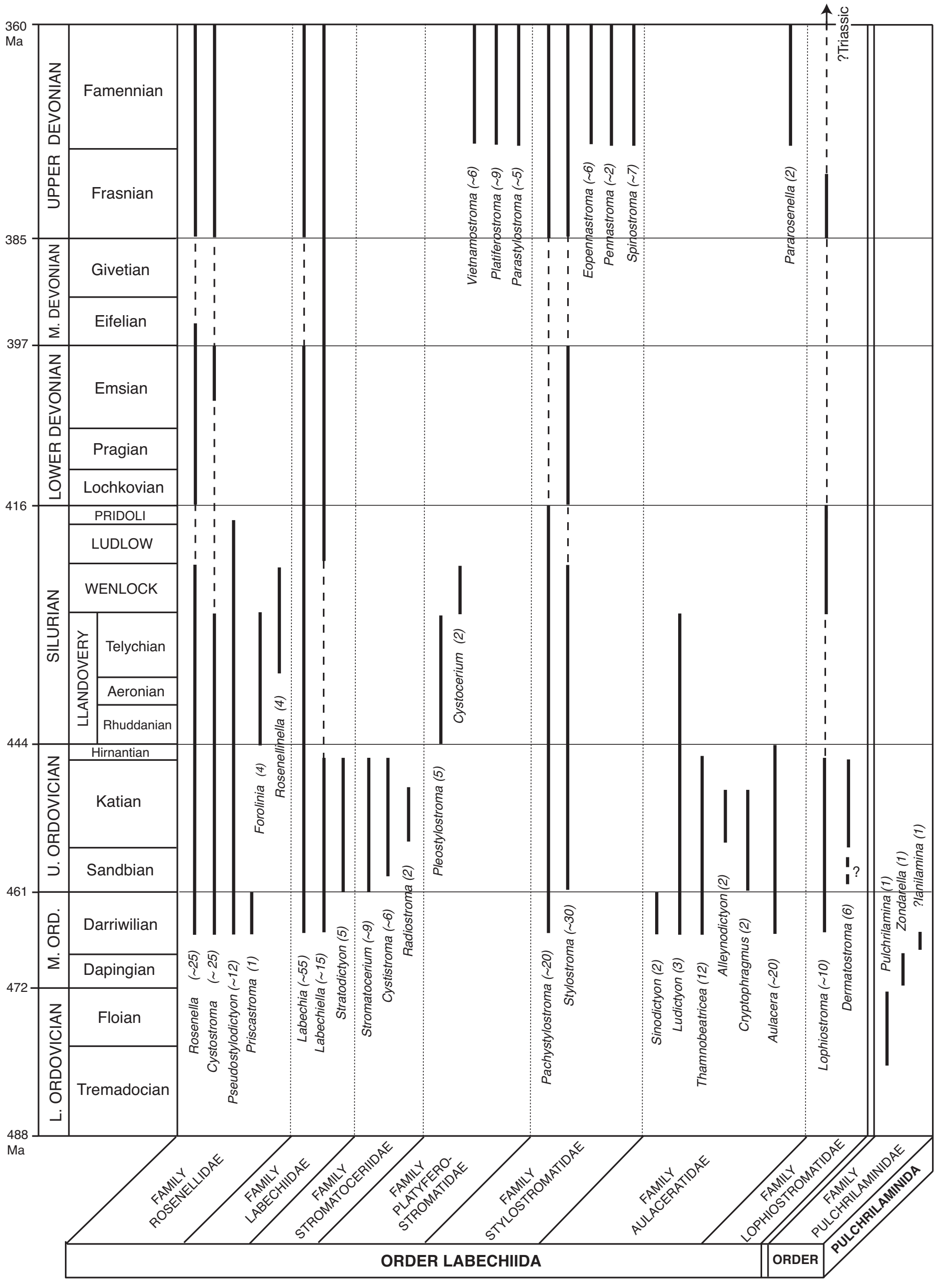

FIG. 1. Stratigraphic ranges of the labechiid genera of the class Stromatoporoidea and the pulchrilaminid genera of the class Uncertain (see WEBBY, 2012); *fine dashed lines* depict apparent gaps in the continuity of the record; *thick dashed line* with a question mark signifies a doubtful extension of a taxon range (e.g., range of *Dermatostroma);* note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Lophiostroma* is the only labechiid genus to have a possible post-Paleozoic record, here shown with an *upwardly directed arrow* and of ?Triassic age (see BOIKO, 1970). Note also that STEARN and STOCK (2010, p. 4) listed *Lophiostroma* as an excluded taxon for calcareous crusts in the upper Paleozoic of Japan (new).

the late Silurian to Mid-Devonian decline then Late Devonian resurgence of the labechiids. STEARN considers that some of the genera, for example, *Labechia, Stylostroma,* and *Pachystylostroma,* have such long and discontinuous ranges as to suggest that their Late Devonian representatives are not directly descended from their Ordovician precursors, but evolved anew from some persistent rootstock; in other words, they represent Elvis taxa (ERWIN & DROSER, 1993). The almost complete absence of labechiids from the Eifelian–Givetian interval, when other stromatoporoids reached their greatest diversity, supports this hypothesis. STEARN also suggests that the uncommon Mid-Devonian occurrences of labechiids may be misidentifications of simple cystose structures common in the space-filling strategies of other fossil organisms (rugosans, tabulates, hydrozoans, bryozoans, mollusks) (ST. JEAN, 1986, p. 1053, commenting on STEARN, 1983).

On the other hand, WEBBY prefers to regard the patterns of disappearances and reappearances of labechiid genera through the Silurian to Late Devonian as representing Lazarus taxa—that the gaps in the continuity of the labechiid records are artifacts of their relatively poor preservation and low diversity. A number of labechiids were found in well-exposed and dated reefal sequences of Lockhovian–Pragian and Emsian–Eifelian ages of the Broken River region of Queensland by WEBBY and ZHEN (1997); that is, from intervals that were previously represented by gaps in the continuity of the labechiid record. These Lochkovian–Pragian (species of *Cystostroma* and *Labechiella*) and late Emsian–early Eifelian labechiids (species of *Stylostroma* and *Rosenella*) form a sparse, poorly preserved component of associations that are dominated by richly diverse and well-preserved nonlabechiid stromatoporoids. In other words, the poorly preserved minor component of labechiids was only found at the various localities because of the high quality of the exposures available for study. It is considered likely that the labechiid component may be difficult to find in less well-preserved successions, leaving only the dominantly, less altered nonlabechiids for study. The Broken River example is instructive in demonstrating that labechiids were continuing to live in associations with Early to earliest Mid-Devonian nonlabechiids, and they may yet prove to form part of a more or less continuous line of labechiid descent from Ordovician precursors into the Late Devonian. More intensive collecting and study of sequences (especially Devonian carbonate) is expected to bridge the gaps in continuity of the labechiid record prior to the Late Devonian.

The clathrodictyids have their roots in the Late Ordovician (*Clathrodictyon, Ecclimadictyon*, ?*Plexodictyon*) (Fig. 2; and see NESTOR, 2011). They reached their peak of diversity in Silurian time were numerous also in the Early and Middle Devonian, but only a few persisted to the end of the Devonian. Many genera are relatively long ranging and almost cosmopolitan (*Clathrodictyon, Ecclimadictyon, Gerronostromaria, Petridiostroma*), but some rare and peculiar forms (*Bullulodictyon, Gerronodictyon, Belemnostroma*) also occur. The representatives of the families Clathrodictyidae and Gerronostromatidae are widespread in both Silurian and Devonian rocks, but most of the representatives of the family Actinodictyidae are restricted to the Silurian. On the other hand, the representatives of the families Atelodictyidae and Tienodictyidae mostly occur in Devonian rocks. They include such genera as *Anostylostroma, Atelodictyon, Pseudoactinodictyon,* and others that are valuable for correlation.

The generic diversity of the actinostromatids peaked in the middle of the Silurian, when a rapid evolutionary radiation took place in the families Pseudolabechiidae, Actinostromellidae, and Densastromatidae (Fig. 2). Only a few genera (*Actinostromella, Araneosustroma*) of these families range into the Lochkovian. Comparatively short-ranging

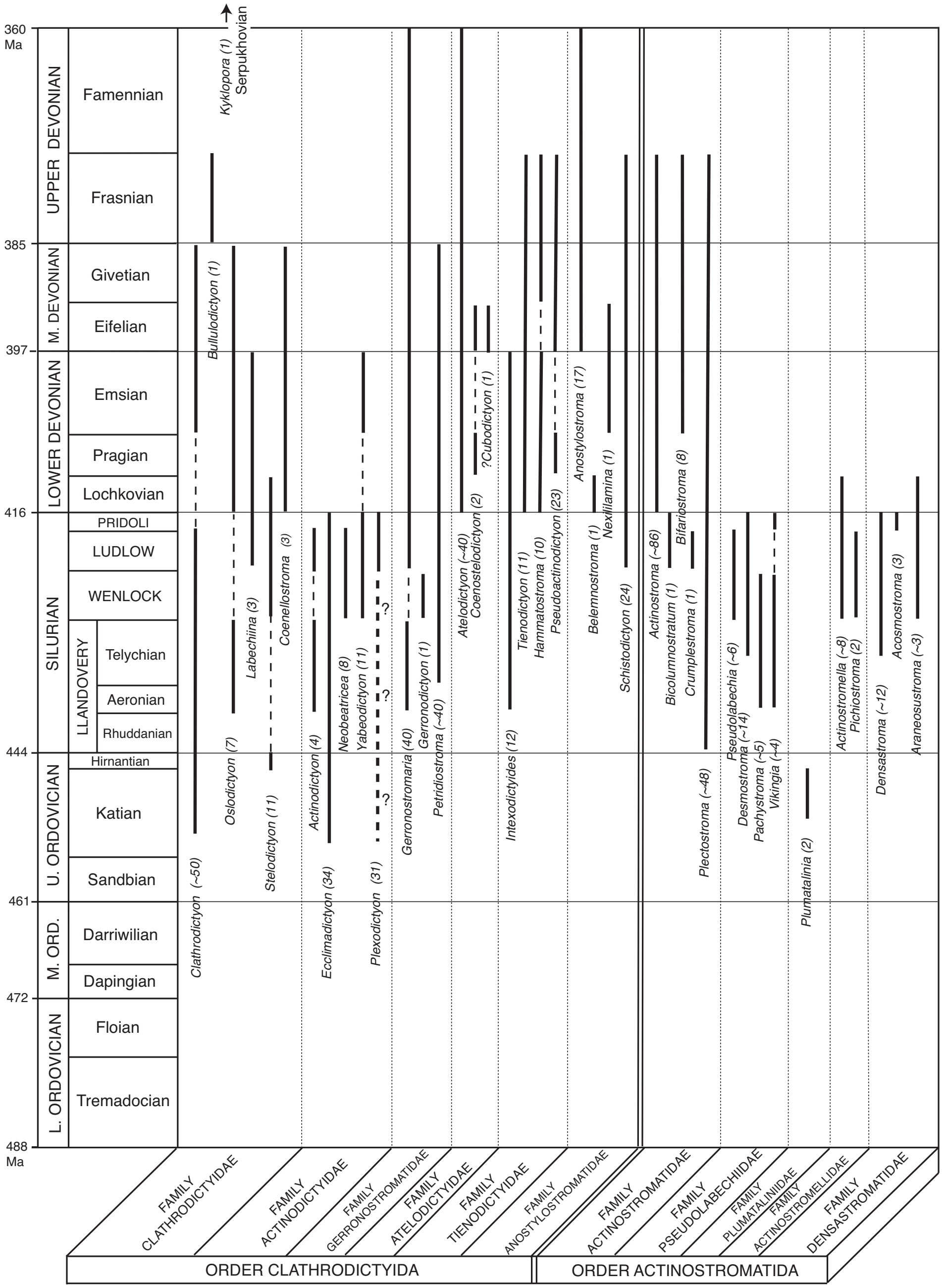

FIG. 2. Stratigraphic ranges of clathrodictyid and actinostromatid stromatoporoid genera of the class Stromatoporoidea; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Kyklopora* is the only genus that has a restricted post-Devonian record, with a limited occurrence in the Lower Carboniferous (Serpukhovian stage), according to NESTOR (2011, p. 1) (new).

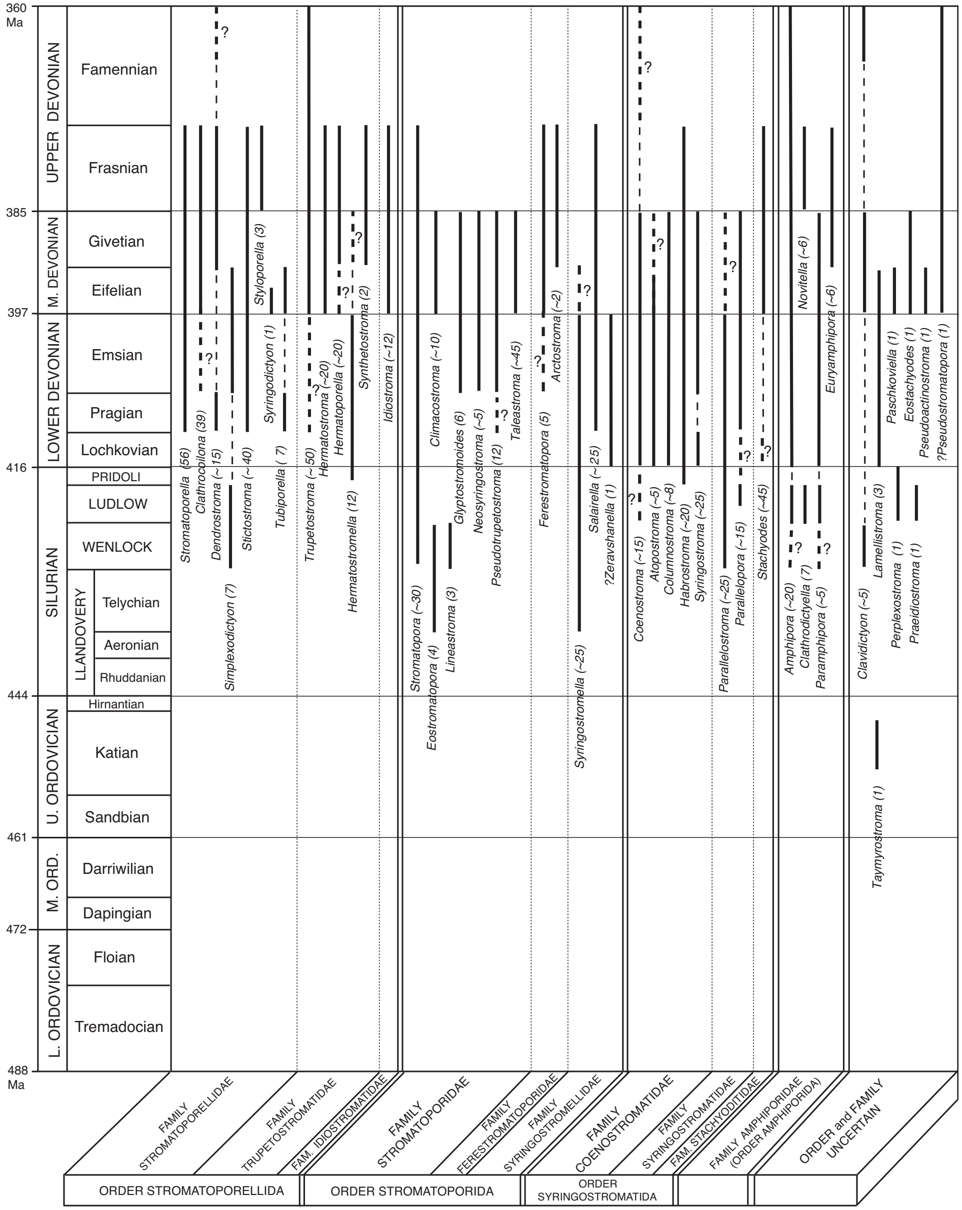

FIG. 3. Stratigraphic ranges of stromatoporellid, stromatoporid, and syringostromatid stromatoporoid genera, as well as representatives of order and family Uncertain of the class Stromatoporoidea; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history (new).

genera include stratigraphically valuable species, for example, index species of such Baltoscandian stromatoporoid communities as *Vikingia tenuis, Araneosustroma stelliparratum,* and *Actinostromella vaiverensis* (NESTOR, 1999a). Three of the most common genera of actinostromatids (*Actinostroma, Bifariostroma, Plectostroma*) belong to the family Actinostromatidae and are the main representatives of actinostromatids in the Devonian.

The orders Stromatoporellida, Stromatoporida, and Syringostromatida mainly include Devonian taxa with a few genera (*Simplexodictyon, Stromatopora*, *Syringostromella, Parallelostroma*) originating in the Silurian (Fig. 3; STEARN, 2011). Among the stromatoporellids, such genera as *Clathrocoilona, Stictostroma, Stromatoporella, Trupetostroma*, and *Hermatostroma* are the most characteristic of this almost cosmopolitan fauna. Most of the common stromatoporellid genera extend through the Eifelian–Frasnian acme of stromatoporoid diversity. Rather similar are the ranges of the stromatoporids. Such genera as *Climacostroma, Glyptostromoides, Neosyringostroma, Taleastroma*, and *Pseudotrupetostroma* appear to have biostratigraphic potential, but the genus *Stromatopora* itself has a very long range from the Ludlow to Famennian. Some earlier records of *Stromatopora* are now treated as representatives of *Lineastroma* and *Eostromatopora* (NESTOR, 1999b). The family Syringostromatidae was characteristic of the Early Devonian and Eifelian. The acme of the family Coenostromatidae was also in the Early Devonian, but *Parallelostroma* appeared earlier in the Wenlock and *Habrostroma* in the Pridoli. *Atopostroma* may prove to be an excellent indicator of Lower Devonian rocks, though the presence of the genus in a reefal deposit of Givetian age in Afghanistan (MISTIAEN, 1985) remains an anomaly. Difficulties in recognizing the genera of the Amphiporidae limit their usefulness for biostratigraphy.

It should also be noted that there are two "stromatoporoid" genera with post-Devonian records, one supposedly a labechiid referred to the genus *Lophiostroma,* implying it formed part of an extended range until the Triassic (see Fig. 1), and the other is the clathrodictyid genus *Kyklopora* (see NESTOR, 2011, p. 1) recorded only from the Carboniferous (Upper Mississippian, Serpukhovian Stage, see Fig. 2); no earlier record of this form is known. It remains uncertain whether these post-Devonian records represent convergences derived from different "stromatoporoid-type" stocks (e.g., WOOD, 2011) during the upper Paleozoic to Mesozoic (i.e., an Elvis taxon of ERWIN & DROSER, 1993), or, whether, at least in the case of *Lophiostroma*, it reappeared in the Triassic as a Lazarus taxon at the end of its range in a long-lived, more or less continuous line of descent from Middle Ordovician precursors.

BIOSTRATIGRAPHIC STANDARDS BASED ON CONCURRENT COMMUNITY SUCCESSIONS

NESTOR (1982, 1984, 1990a) adopted a novel approach to establishing a biostratigraphic standard for Late Ordovician to Silurian stromatoporoid faunas in the Baltic-Scandinavian region, based on the spread of assemblages across a full range of onshore to offshore environments, from lagoonal, to shoal and reef, to open shelf, and into some slope habitats (Fig. 4). Later, NESTOR (1999a) linked the associations (communities) of stromatoporoids with the standard benthic assemblages (BA1–BA5) of BOUCOT (1975). The complete spectrum of laterally equivalent associations was particularly well developed in the Silurian rocks.

Associations of taxa in the open shelf, reef, and shoal facies, representing BOUCOT's BA2–4 assemblages, were more diverse, temporally shorter-ranging, and spatially more widely distributed. The more cosmopolitan, open shelf taxa were considered by NESTOR (1999a) to have the greater potential for use in the stromatoporoid biostratigraphy, because they had geographically wider ranges. Examples in the Llandovery include the *Clathrodictyon boreale–Ecclimadictyon microvesiculosum* community, which is moderately diverse, spans two regional stages, and spreads laterally into both open shelf and shoal lithofacies. Its two name-bearing species have been recorded from the same interval in many parts of the world, including Anticosti Island (Canada; Nestor, Copper, & Stock, 2010, p. 22). The succeeding *Clathrodictyon variolare* community is also diverse, characteristic of the open shelf, and has a short time range (only part of one regional stage); and typical elements of the community (*C. variolare, Ecclimadictyon fastigiatum, Stelodictyon conodigitatum*) are widely recognized elsewhere (e.g., Norway, Novaya Zemlya, Anticosti Island, Iowa, Alabama). The stromatoporoid assemblages at opposite ends of the environment spectrum—in the lagoon (BA 1) and the deeper marginal shelf to slope (BA 4/5)—were the least diverse and had the longest ranges in time.

A community-based approach was also applied by Nestor (1999a) to establish the Late Ordovician stromatoporoid faunal succession in Baltoscandia, but no lateral equivalents were recognized, as in the Silurian succession. The six temporally distinct Late Ordovician examples comprise: (1) the reef (shoal)-type assemblages with labechiids in the Oandu stage of Estonia and Mjøsa Formation of Norway (early Katian); (2) the first clathrodictyids with some labechiids in the above-storm-base, open-shelf assemblages of the Vormsi to early Pirgu (i.e., from mid- to late Katian) in Estonia; and (3) some clathrodictyids and labechiids again in the reef (shoal)-type assemblages of the late Pirgu to Porkuni (late Katian to Hirnantian) interval of Estonia and Norway.

The development of Nestor's (1999a) laterally equivalent, community-based correlation scheme was based primarily on the more complete Silurian successional record of stromatoporoid faunas across the Baltic-Scandinavian region. This record was derived largely from the major documentation of the Silurian stromatoporoid faunas by Nestor (1964a, 1964b, 1966) in Estonia, and by Mori (1968, 1970, 1978) from the Island of Gotland (Sweden) and the Oslo region of Norway. In Estonia, Nestor (1964a, 1964b, 1966) recognized 65 valid Silurian stromatoporoid species belonging to 20 genera, he revised Riabinin's (1951) earlier work on the faunas and outlined a broadly based, fivefold, stromatoporoid species-based, assemblage zonation that more or less paralleled the existing tabulate coral zonation. The Llandovery (Juuru, Raikküla, and Adavere regional stages) was divided into three stromatoporoid zones. Broadly based zonal indices for the Wenlock (Jaani to Jaagarahu stages) and Ludlow (Paadla and Kuressare stages) intervals were characterized by a species name bearer and other diagnostic index fossils. The units including reefs, such as those included in the Llandovery (upper Juuru), Wenlock (Jaagarahu), and Ludlow (Paadla) stages, were particularly rich in species. However, the lack of detailed studies of Silurian stromatoporoids in other areas prior to the late 1960s prevented these broadly based stromatoporoid zonal indices being used for wider-ranging correlation, except for one example establishing a tie, based on stromatoporoids between the lower Ludlow Paadla stage of Estonia and the Malinovetsky Horizon of Podolia, southwestern Ukraine (Nestor, 1966, p. 73).

The Silurian stromatoporoids that occur abundantly through the Gotland reefal and nonreefal successions in Sweden were studied by Mori (1968, 1970). Sixty-eight species belonging to 24 genera were described. The ranges of the species were relatively short, confined to one or two stratigraphic units within the Wenlock or Ludlow (see Mori, 1968, table 1; 1970, table 1), possibly due to facies constraints. Nevertheless, approximately one-third of these species are known to occur also in Estonia and provide a useful means of biostratigraphic correlation, at a number of different levels, through respec-

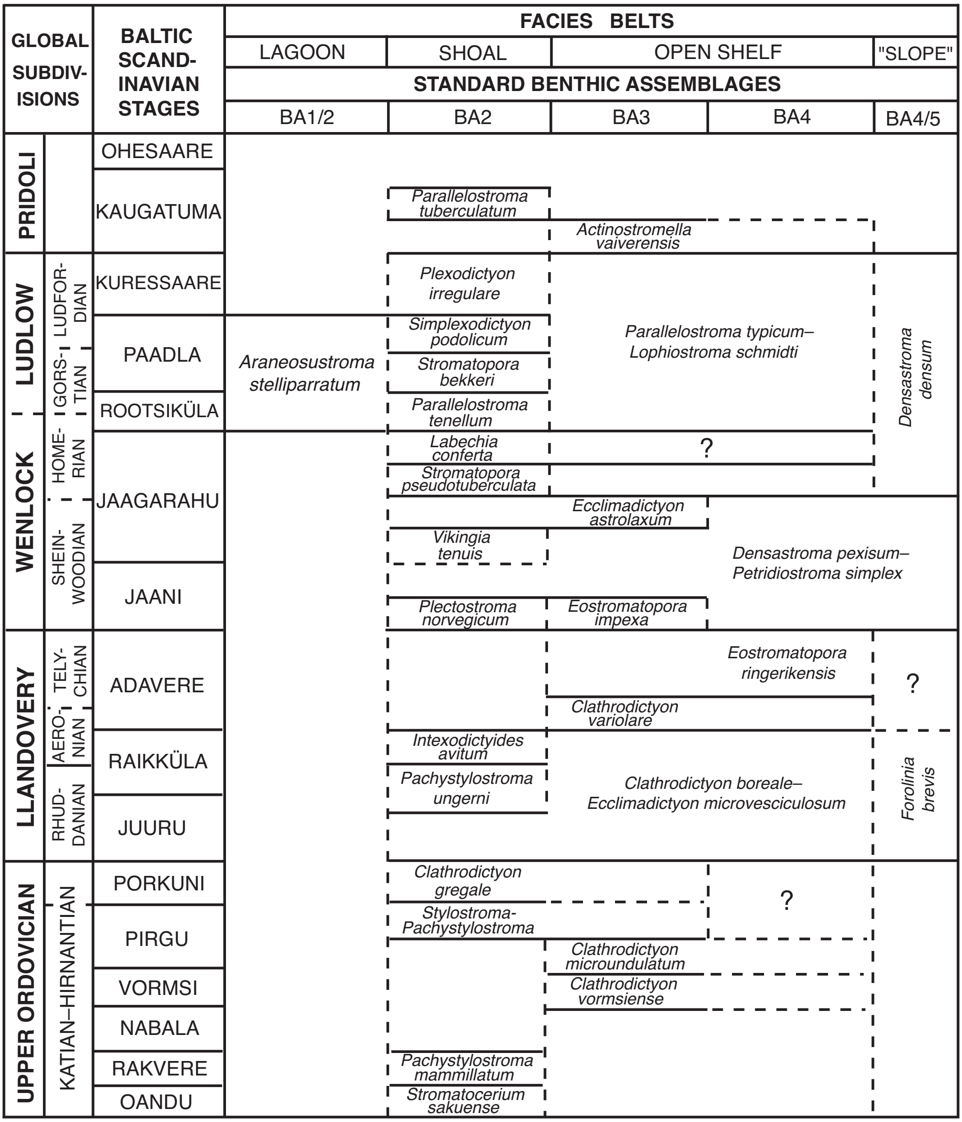

Fig. 4. Diagrammatic representation of biostratigraphically useful, laterally equivalent, stromatoporoid assemblages of Upper Ordovician–Silurian sequences of Baltoscandia across the main facies belts of Nestor's (1990a) Paleobaltic basin, and Boucot's (1975) Standard Benthic Assemblages (BA) (adapted from Nestor, 1999a).

tive Wenlock and Ludlow successions (see Mori, 1968, table 2; 1970, table 4).

In addition, Mori (1978) undertook a comparative survey of Silurian stromatoporoid assemblages from the Oslo region (Norway) in order to reveal their relationships to contemporaneous occurrences in Estonia and Gotland. Of the 15 species, 10 are from the Llandovery, 3 are from the Wenlock, and the remaining 2 are probably from the Ludlow. Two-thirds of the species are found in other areas of the Baltic (Estonia, Gotland). However, Mori's (1978, table 1) stratigraphic distribution chart shows that not all these common occurrences are strictly coeval.

Through the past three decades, Nestor (1982, 1984, 1990a, 1999a) has refined the biostratigraphy of the Baltic Silurian on the basis of community associations. He noted that parallel shallower and deeper-water communities could be differentiated within the respective stromatoporoid zonal successions and suggested that the succession of shallower associations may prove suitable as a zonal standard for use in Balto-Scandinavia and further afield. In 1982, Nestor defined five superposed, shorter-ranging, shallow-water associations (*Eostromatopora impexa, Vikingia tenuis, Ecclimadictyon astrolaxum, Labechia conferta,* and *Parallelostroma tenullum* communities), and two laterally equivalent, longer-ranging, deeper-water associations (*Densastroma pexisum* and *D. densum* communities) in the Wenlock and Ludlow (Fig. 4). Additionally, he identified a restricted nearshore association dominated by *Araneosustroma stelliparratum* in the late Wenlock of Estonia that represents a lateral equivalent of the normal shallow-water association of the *P. tenullum* community on Gotland. A detailed log of the stromatoporoid species, through the 29-m-thick, lower Wenlock biostratigraphic reference section of Vattenfallet, close to Visby (Gotland), identifying representatives of the *Eostromatopora impexa* community in the upper Visby Marl, and members of the *Vikingia tenuis* community in overlying beds of the Högklint Limestone (Fig. 4), was also contributed (Nestor, 1979).

A more complete listing of the distribution of stromatoporoid taxa in the Silurian of Estonia was presented in Nestor (1990a), together with a more comprehensive subdivision of the community-based zonation of stromatoporoids across lower energy lagoonal, high-energy shoal (or reefal), lower energy, open shelf, and slope facies belts (Nestor, 1984, 1990a). In the latter work, the complete list of the Upper Ordovician and Silurian stromatoporoid species from Estonia and Sweden was published, including 104 species belonging to 25 genera. The genera, except for *Clathrodictyon* and *Ecclimadictyon*, exhibit only moderate levels of species diversification. Species of *Clathrodictyon* and *Ecclimadictyon,* especially those from the Llandovery interval, have records of 13 and 10 species, respectively; that is, they were relatively much more diverse than the rest. This suggests that the taxa have been oversplit, and that it would be useful, at least for biostratigraphic purposes, to have them reevaluated using a broader species concept.

An updated version of the community-based biostratigraphic standard of the Baltic-Scandinavian Silurian stromatoporoids was presented by Nestor (1999a), with the addition of supplementary data from Norway. As a result, 22 different successive and concurrent Silurian stromatoporoid communities were defined (see Fig. 4). The succession is most completely developed in the onshore, high-energy shoal (or reef) facies that occupies the position of Boucot's (1975) Benthic Assemblage BA2, with the species represented by the most diverse, short-ranging forms. Nestor (1999a) further noted that some 99 species have now been recorded through the Baltic-Scandinavian Late Ordovician to Silurian succession in the shoal reef (BA2 position), as compared with 49 species in the inner open shelf (BA3 position). The combined, relatively diverse, short-ranging shoal and inner open shelf assemblages provide the best composite basis for establishing the biostratigraphic standard, with potential use for correlating sequences well beyond the Baltic-Scandinavian region.

Nestor's (1999a) Silurian reef and shoal assemblages were the most diverse, and though the taxa exhibited the shortest time ranges, they unfortunately had mainly narrower spatial distributions. Therefore, these shorter-range, more specialized, reef and shoal species were not as useful for establishing interregional correlations, but they were still important for determining the spatial and temporal relationships of reefs and shoals in the Baltic-Scandinavian region and, less commonly, based on a few species, farther afield. Nestor (1990b) also demonstrated in a global biogeographic survey of Silurian stromatoporoid genera that very limited evidence of provincialism exists. Consequently, the impact of provincialism on species-based correlations is probably minimal.

Nestor's (1999a) approach to establishing a laterally equivalent, community-based, biostratigraphic standard, using the Silurian stromatoporoid succession in the Baltic-Scandinavian, is a good model for application to other continental platform regions of the world, for example, in North America and China. In these regions, as in Balto-Scandinavia, there is a wide range of well-exposed Paleozoic stromatoporoid-bearing carbonate successions available for study across a range of onshore to offshore environments and the potential to closely tie such regional, community-based stromatoporoid zonal indices to well-established and highly resolved zonal schemes based on other fossil groups such as conodonts and graptolites (see below).

LINKAGES WITH OTHER ZONATIONS

The comparison of zonal successions based on different fossil organisms is an essential part of the work of the biostratigrapher. An unrivaled succession of 28 named conodont zones has been established for worldwide correlation of Devonian rocks (Ziegler & Klapper, 1985), but zonal schemes based on stromatoporoid taxa remain at a much more rudimentary stage of development. Stearn's (1997a, 2001) biostratigraphic work on the stromatoporoid assemblages of the Devonian reef-bearing carbonate succession in Western and Arctic Canada has already demonstrated the group's value for correlation across North America and their potential for wider-ranging, perhaps global, correlation of the reef facies. Because diagnostic conodonts rarely occur in reefs, precise stratigraphic relationships must be established between the stromatoporoid assemblages and the diagnostic conodont zones of the laterally equivalent strata. Conodont work in Western and Arctic Canada by Uyeno (1974, 1990, 1991), Uyeno and Klapper (1980), and others permits the age relationships of the stromatoporoid-bearing reefs to be assigned to a particular part of the conodont zonal succession (Fig. 5).

Stearn (1997a, 2001) regarded all ten stromatoporoid assemblages spanning the Devonian as having value for correlation in North America, and more than half the assemblages (those extending through the Lower Devonian, lowermost and uppermost Givetian, and Famennian intervals) as having wider, intercontinental, correlation potential. Stearn (2001) included a range chart showing the ranges of diagnostic species for each assemblage. This work involved adopting a broader species concept than previously and placing a large number of previously described species (about 50%) in synonomy. His approach recognized that the complex skeletons of stromatoporoids exhibit a far wider variability than was thought previously. The assemblages define some time units that range through entire stage divisions and others that are of substage duration. Most of the listed species (Stearn, 2001, fig. 1) have comparatively short time ranges.

Prosh and Stearn (1996) presented in greater detail the Emsian–early Eifelian records of stromatoporoid ranges (a fauna comprising 25 species in 22 genera) from Arctic Canada, with ties to the well-established, standardized, conodont zonation. Nearly half the Arctic species are common to other regions (eastern North America, Asiatic Russia, southeastern Australia, and China). More than half the species span more than one conodont zone (within the Emsian–earliest Eifelian interval), but one third of the species exhibit very short stratigraphic ranges, of approximately one conodont zone.

Additionally, Prosh and Stearn (1993, 1996) asserted that a number of the species from Arctic Canada allowed precise correlation with faunas described by Galloway and

St. Jean (1957) and Fagerstrom (1982) from the midcontinental United States. In particular, occurrences of four stromatoporoid species [*Stromatoporella perannulata* Galloway and St. Jean; *Stictostroma gorriense* Stearn; *Habrostroma proximlaminatum* (Fagerstrom); and *Parallelopora campbelli* Galloway & St. Jean] in the Blue Fiord succession of the Arctic, which is well dated by conodonts, and in the Detroit River Group of the Michigan Basin, have led to the proposal that the Detroit River Group is entirely Emsian, rather than Eifelian, in age, and the conodont dating for this group has been misinterpreted (Prosh & Stearn, 1993, 1996). However, Klapper and Oliver (1995) disputed this correlation on the basis that the conodonts of the Detroit River Group and correlatives in eastern North America are of Middle Devonian age, and two of the four stromatoporoid species have ranges extending up into the Eifelian. They claimed the stromatoporoid species had diachronous relationships—that they needed a long time to migrate from the Arctic to the eastern regions of America because of biogeographic barriers (but see Prosh, 1995, for counterarguments).

In summary, Stearn (1997a, 2001) has suggested that the Devonian succession of Arctic and Western Canada could be divided into ten biozones on the basis of distinctive stromatoporoid faunas (Fig. 5). He proposed that the stromatoporoids of these ten assemblages could form the basis of correlation between reef successions on the continental and perhaps intercontinental scale. The restriction of certain species to narrow time intervals and their wide geographic extent gave hope, in his view, that stromatoporoid biostratigraphy would be as effective in the reef facies as the graptolites have proven to be in the black shale facies. At present, this goal has not been attained and will not be until the data on stratigraphic distribution are brought together with a consistent taxonomy and within the context of a much more complete knowledge of global patterns of provincial change through Devonian time.

OTHER BIOSTRATIGRAPHIC RECORDS

ORDOVICIAN AND SILURIAN

Webby (1969) introduced three informal subdivisions based on diagnostic coral and stromatoporoid assemblages for correlation of the Upper Ordovician island-arc carbonate successions of the Molong Volcanic Belt, central New South Wales (NSW), Australia. Fauna I included a number of distinctive labechiids, and Faunas II and III were characterized by the first appearances of clathrodictyids and continued presence of other labechiids. Pickett (1985) recognized an older, pre-Fauna I assemblage (with earlier labechiids) in the adjacent Junee-Narromine Volcanic Belt, and Pickett and Percival (2001) later replaced Webby's numbered stromatoporoid assemblages with four, formalized, composite coral/sponge assemblage zones, in ascending order: *Foerstephyllum-Billingsaria-*Stratodictyon; Hillophyllum-Tetradium-*Rosenella; Propora-*Ecclimadictyon-Cliefdenel la*; and *Favistina-Halysites-Plasmoporella* (asterisks denote the stromatoporoids). These assemblage zones have not been applied outside central NSW, though generalized correlations between the informally numbered NSW faunal assemblages and the Tasmanian associations (see below) have been previously made (see Webby, 1979; Webby in Webby & others, 1981, p. 9–10; Webby, 1991; Webby in Young & Laurie, 1996, p. 83–84). The two lower coral-sponge assemblage zones span Australasian regional stages from Gisbornian (=global Sandbian Stage) to lowermost Eastonian, and the two upper zones range between the middle and upper Eastonian. These latter three Eastonian zones equate with lower-middle parts of the global Katian Stage (Webby & others, 2004; Bergström & others, 2006).

Stromatoporoids are important constituents of the Ordovician carbonate succession (Gordon Group) on the Tasmanian Shelf (Webby, 1979, 1991). The two lower faunal assemblages exhibit abundant and varied labechiids, and similarly span the Gisbornian and lower part of the Eastonian, and the two

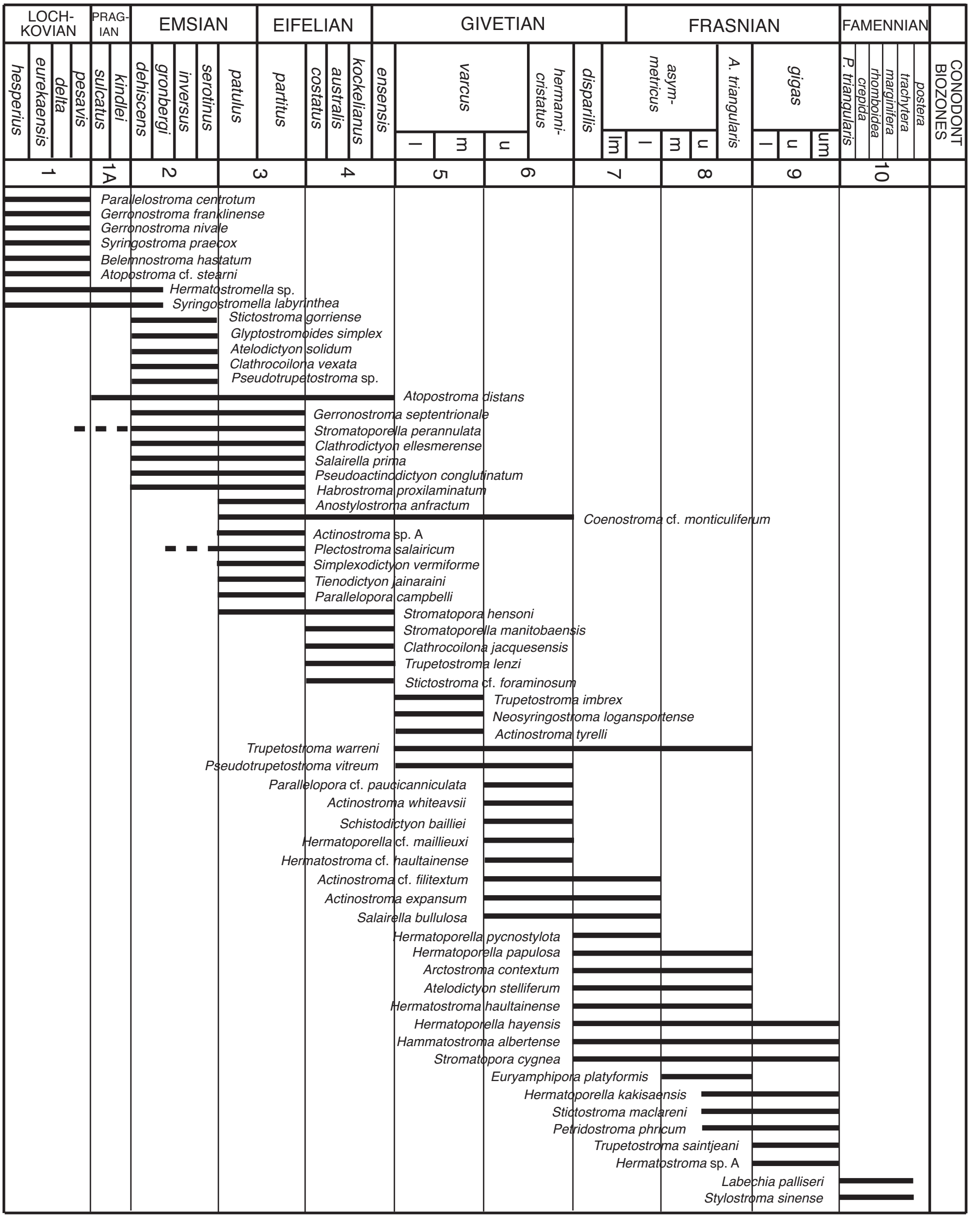

FIG. 5. Diagram depicting stratigraphic ranges of diagnostic stromatoporoid species that form the basis for establishment of ten stromatoporoid assemblage zones through Devonian successions of Arctic and Western Canada by Stearn (2001), and ties to the standardized conodont zonation of Klapper and Ziegler (1979), Klapper and Johnson (1980), Orchard (1989), and Uyeno (1990, 1991).

upper assemblages, composed of labechiids and abundant clathrodictyids, have a mid-late Eastonian age. A general similarity exists in the stromatoporoid successional patterns of the Tasmanian Shelf and offshore NSW island arc, but few species are common to the stromatoporoid assemblages of the two regions (WEBBY in WEBBY & others, 2000).

Kapp and Stearn (1976) recognized three assemblage zones through the Day Point and Crown Point formations of the Chazy Group of Vermont (eastern North America) that effectively outline the rapid initial evolutionary expansion of the oldest indubitable reef-forming labechiid stromatoporoids during late Mid-Ordovician (late Darriwilian) time. Zone I of the upper Day Point to basal part of the Crown Point Formation contains only *Pseudostylodictyon lamottense*. The base of Zone II is characterized by appearances of the genera *Labechia* and *Pachystylostroma* (a total of five species) within the lower Crown Point. A further stage of diversification of *Pachystylostroma*, and the appearance of *Stratodictyon,* marked the succeeding Zone III, which spanned from the middle Crown Point through the Valcour Formation. Webby (1979, p. 240) noted that, although the main expansion of the Labechiida in North America and Tasmania appeared to be "strikingly rapid," the earliest part of the initial diversification in the Day Point and lower Crown Point formations of the Chazy Group apparently preceded the appearance of the earliest Tasmanian assemblage, in the Cashion Creek Limestone of Gisbornian age (Webby, 1991).

Bolton (1988) recorded the stratigraphic distribution of Ordovician stromatoporoid species across central and eastern Canada. His discoveries of new records of *Ecclimadictyon* established that the clathrodictyid stromatoporoids made their first appearances in North America during the Edenian; in global terms, early Katian (=Australasian mid-Eastonian, or British late Caradoc), as the group first appeared in Australia, northern China (Lin & Webby, 1988), and in Baltoscandia.

Stearn (1997b) outlined the main Silurian faunal assemblages represented in Canadian rocks at the generic level. He distinguished five assemblages and listed their distinguishing genera: (1) early Llandovery; (2) late Llandovery (Telychian); (3) Wenlock; (4) Ludlow; and (5) Pridoli. These faunas were cross referenced to a large correlation chart for the whole country.

DEVONIAN

Although stratigraphic position of Devonian stromatoporoids was indicated for species described in the first half of the twentieth century, no synthesis of stratigraphic ranges into a biostratigraphic scheme was attempted. Lecompte (1951) did not attempt any zonation or correlation of the Devonian species data from the Ardennes, but he found that about half of the species he distinguished were confined to one of the five intervals of stage (Givetian) or half-stage durations (Couvinian 1 & 2, Frasnian 1 & 2). The first paper written specifically on the biostratigraphy of stromatoporoids is that of Flügel (1962). He considered that the group had a potential for use in stratigraphy after reviewing the distribution of the major faunas that had been described until that time. In a subsequent review of the whole group (Flügel, 1975), he did not include a section on biostratigraphy but emphasized paleobiogeography and paleoecology.

Starting in the 1950s, Zukalova documented the stratigraphic distribution of stromatoporoids in the Givetian and Frasnian from the Moravian Karst, Czech Republic (1958, 1974). In 1971, she described the taxonomy of all the stromatoporoid species and recorded the ranges of all the 66 species of stromatoporoids (Zukalova, 1971, table 7). Later, the Givetian to Famennian stromatoporoid succession was divided into 7 biozones (Galle & others, 1988), and the ranges of the stromatoporoids in Moravia were plotted and keyed to conodont zones, but no attempt was made to apply this zonation to correlation problems beyond the Czech Republic.

Stearn (1975) attempted to divide a local section on Mount Haultain in the Rocky Mountains of Alberta into vertically successive assemblages on the basis of the overlapping ranges of stromatoporoid species. He interpreted these assemblages largely in terms of changing conditions on the reef front, but he also suggested that two zones, those of *Stromatopora parksi* and *Stictostroma mclareni,* could be useful for regional correlation.

For a 1979 review, STEARN compiled the stratigraphic position of Devonian species and used these to plot the ranges of Devonian genera. He distinguished three major faunal intervals. The Gedinnian to Emsian faunal interval was characterized by forms transitional from the Silurian, the Eifelian to Frasnian interval by the maximum stromatoporoid diversity, and the Famennian to Strunian interval by the return of the labechiids, and particularly *Stylostroma.* The Strunian, since ICS-IUGS ratification of the Devonian-Carboniferous boundary in 1990, has been adopted as the uppermost part of the Famennian (OLIVER & CHLUPAC, 1991; OGG, 2004).

LESSOVAYA (in KIM & others, 1978; LESSOVAYA, 1984) delineated in detail the ranges of Lower and Middle Devonian stromatoporoids in Uzbekistan and adjacent areas. She plotted the ranges of species across the boundary between these series. Also, LESSOVAYA (1982) distinguished the characteristic stromatoporoid assemblages of the Lochkovian, Pragian, and Kitabian stages in the southern Tian Shan.

MISTIAEN (1999), MISTIAEN and GHOLAMALIAN (2000), and MISTIAEN (in BRICE, MISTIAEN, and ROHART, 1999) have demonstrated that the Devonian stromatoporoid species from the Kerman and Chahriseh regions of central Iran are closely similar to Frasnian assemblages in Afghanistan (five out of the eight species in common), as well as to assemblages in Old World regions of Europe; for example, with ties based on three species in common to the *Syringostromella* ? *cooperi* Zone of the Boulonnais area of northern France (MISTIAEN, 1988; MISTIAEN in BRICE, MISTIAEN, & ROHART, 1999).

In the Devonian of the Michigan Basin, FAGERSTROM (1982, p. 64) identified three local stromatoporoid assemblage zones, named after relatively common species; in ascending order, *Anostylostroma columnare, Syringostroma sherzeri,* and *Amphipora nattresi,* but they were considered to be of little value for regional correlations.

COCKBAIN (1984) outlined a threefold assemblage zonal scheme for the Middle to Upper Devonian Canning Basin reef complexes of Western Australia, which comprise the *Anostylostroma ponderosum–Stromatopora cooperi* and the *Stachyodes costulata–Clathrocoilona spissa* zones. They are characteristic of the Sadler and Pillara limestones respectively (spanning from near the Givetian-Frasnian boundary into the Frasnian), and the overlying *Clathrocoilona saginata–Stromatopora lennardensis* Zone of the Windjana Limestone (Famennian). The *Stachyodes costulata–Clathrocoilona spissa* Zone has also been identified in the Gneudna Formation of the Carnarvon Basin (COCKBAIN, 1985) some 1200 km away, suggesting that this zonal scheme may have some potential for wider, intracontinental correlation. Note that *Syringostromella* ? *cooperi* (LECOMPTE, 1952), recognized in northern France (see two previous paragraphs, above), and *Stromatopora cooperi* LECOMPTE, 1952, in the Canning Basin, represent the same species and zonal index. It is remarkable therefore that this same species, either singly or coupled with another zonal indicator species, is available within a part of the Frasnian for use in even wider-range, intercontinental correlation, such as between northern Europe and Western Australia.

KREBEDÜNKEL (1995) has published detailed logs of outcrop sections in the Gladbach-Paffrath basin of western Germany, which include the listing of stromatoporoid species found in each bed. A chart (1995, fig. 12) showed the ranges of the species he identified in the Givetian and Frasnian strata. Plotted on another chart (1995, fig. 20) were the occurrences of species common to Europe, Russia, North America, Asia (China), and Australia.

Bogoyavlenskaya (2001) summarized the occurrence of stromatoporoids on the Russian Platform in terms of the Devonian conodont zonation. She also illustrated the changes in diversity of these faunas throughout the Devonian; by far, the most diverse faunas are of Frasnian age. No attempt was made to establish stromatoporoid-based zones or to use stromatoporoid ranges for correlation.

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