PALEOECOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

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INTRODUCTION

The study of stromatoporoid paleoecology allows workers to investigate both the fundamental environmental controls on these hypercalcified sponges and their wider paleoenvironmental significance in Paleozoic sedimentary rocks. The two principal objectives are as follows.

1. To determine how stromatoporoids lived, what controlled them, and how they varied through geological time.
2. To apply stromatoporoids to address interpretations of paleoenvironments at a variety of spatial scales (from individual fossils to entire reef systems).

The second main objective is the principal focus here, with treatment of paleoenvironmental controls of stromatoporoid distribution, aspects of community-scale ecology, and the role of stromatoporoids in wider (global) applications, such as changing sea level. For further information on the shapes, growth habits, and individual paleoenvironmental controls of Paleozoic stromatoporoids, see sections on external morphology (p. 419–486) and functional morphology (p. 551–573). These sections contain data on substrate preferences and growth banding and refer to case studies that may be studied in conjunction with the information presented here.

KEY ASPECTS

Interpreted as sponges, stromatoporoids were filter feeders presumed to have been subject to processes influencing supply of detrital organic matter. Modern hypercalcified sponges have little tolerance of fine sedimentary material (WÖRHEIDE, 1998), so fossil stromatoporoids are presumed to be similar. However, Paleozoic stromatoporoids are found commonly in fine-grained, carbonate, sedimentary rock, which may include substantial amounts of siliciclastic, muddy material, though stromatoporoids are rare in clastic-only sedimentary rocks. Stromatoporoids are therefore presumed to have developed mechanisms to overcome the clogging effects of such sedimentary material. Evidence that this was achieved by growth above the substrate, thereby forming primary cavities, is clear in Devonian stromatoporoids, but equivocal in the majority of Ordovician and Silurian examples. That stromatoporoids were able to survive so well on muddy substrates may have played a significant part in their success in middle Paleozoic settings, up to the Frasnian–Famennian extinction event. Evidence from individual stromatoporoids shows they often appeared to recover well from both episodic sedimentation (by growth from unaffected portions of skeletons), and also from disturbance (by reoriented growth attitudes) (Fig. 367). Figure 368 shows the full range of results in stromatoporoids of processes that affected the sea floor when stromatoporoids were alive. Figure 369 shows the results of experimental work on the stability of major growth forms of stromatoporoids on different substrates and current regimes that may influence interpretations of their paleoecology.

Modern hypercalcified sponges grow at very slow rates (DUSTAN & SACCO, 1982; BENAVIDAS & DRUFFEL, 1986) and ecologically often occur as a cryptic fauna, subordinate to corals in reef facies. In contrast, stromatoporoids dominated Silurian and Devonian reef facies and built skeletons that were commonly tens of centimeters in diameter. The largest published stromatoporoid in the Devonian of Poland is 8.5 m in diameter (RACKI & SOBSTEL, 2004), but an even larger specimen of *Actinostroma*

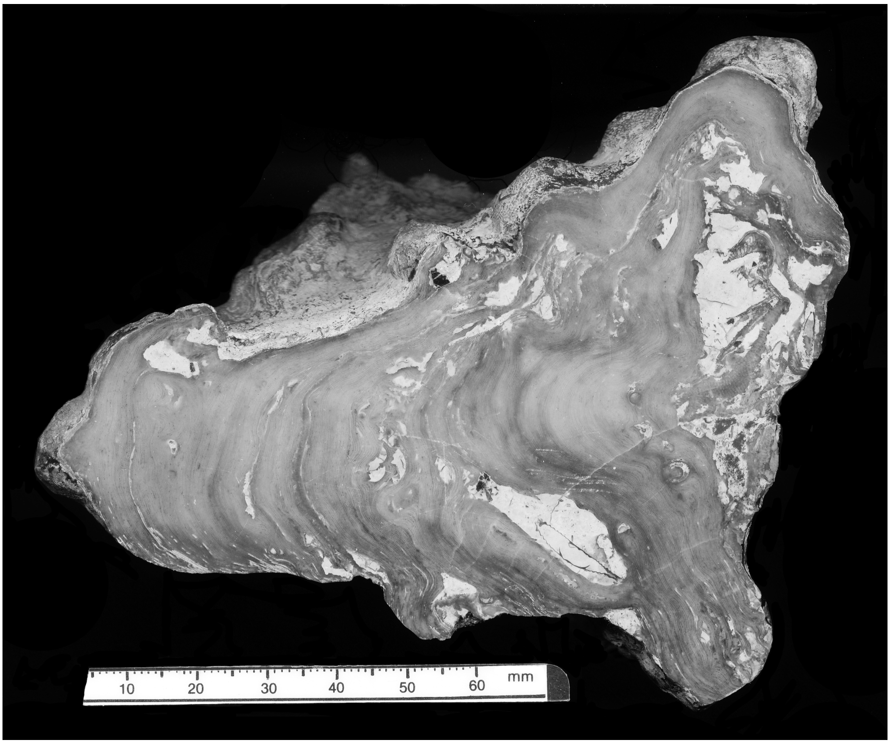


FIG. 367. Longitudinal section of a specimen of *Petridiostroma linnarssoni*, Visby Formation, lower Wenlock, Gotland, that was collected in the field occupying a sideways orientation on the bedding surface; specimen shows interdigitated sediment through the skeleton, which may be interpreted as indicating small-scale episodic sedimentation between the successive phases of upward growth of the organism while it occupied a muddy environment. Then a sudden reorientation occurred, with a rotation of 90° to the left, as a result of storm action, and in the following recovery, the skeleton can be seen to have resumed growth on upper slopes in its final orientation prior to final burial (Kershaw, 2012; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

expansum, 30 m wide and about 1.5 m thick, occurs in the Nora Member of the Shell Rock Formation (mid-Frasnian) near Rockford, Iowa (Carl Stock, personal communication, 2005). These large sizes imply that stromatoporoids grew at rates as least as fast as modern corals, yet there is no evidence that stromatoporoids contained symbiotic photosynthetic algae (notwithstanding the views of KAŹMIERCZAK, 1976; KAŹMIERCZAK & KRUMBEIN, 1983; and KAŹMIERCZAK & KEMPE, 1990, that stromatoporoids were cyanobacteria). Furthermore, modern sponges can grow well in nutrient-rich waters, in contrast to modern reefs (and, by analogy, fossil reefs), which are found in low-nutrient settings. Consequently, with respect to growth rate and nutrient requirements and the implications for their ecology, the modern hypercalcified sponges are only partially analogous to fossil stromatoporoids.

Stromatoporoids are most abundant in carbonate platform settings of various types, less abundant in siliciclastics, reefs, and related facies, and they probably responded favorably to low-nutrient conditions. They were apparently stenohaline (therefore normal marine) organisms.

OVERVIEW OF FEATURES

The following sections identify features of stromatoporoid paleoecology and present the current state of knowledge. Figures

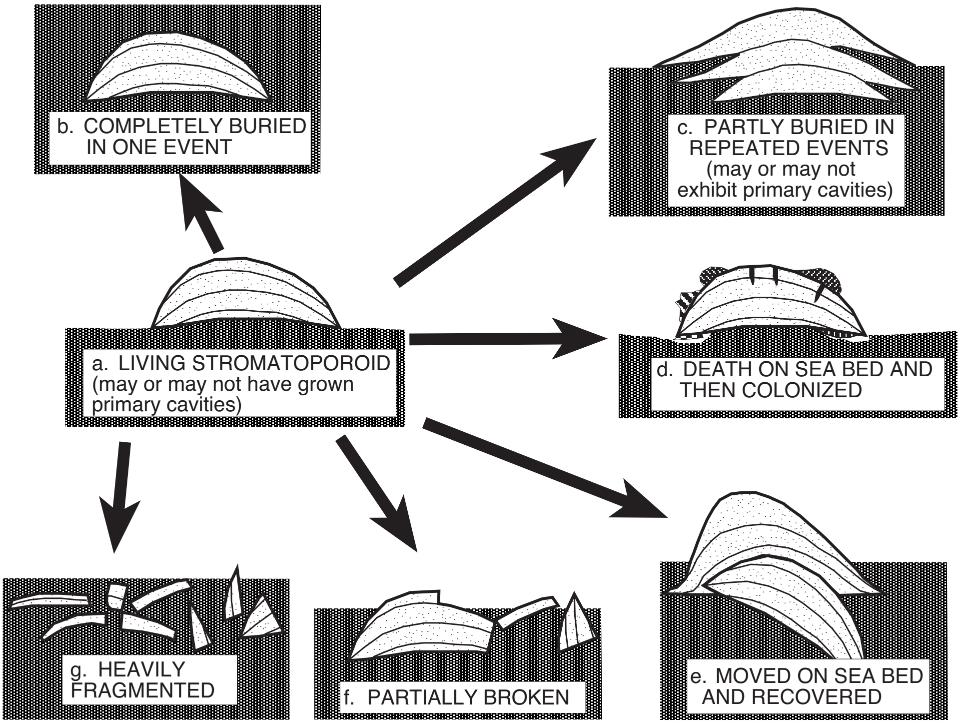


FIG. 368. Fossil stromatoporoid skeleton geometries demonstrating events affecting sea bed during life and in early postmortem, prior to final burial. *a,* Living stromatoporoid prior to burial; *b,* completely buried; *c,* partial burial with flank recovery, but the flanges of skeleton may have grown into the water to form original cavities (see p. 419–486); *d,* death without burial may be suspected for cases with epifauna but may instead have been buried then exhumed; *e,* dislocation during life is recorded in changes of growth attitude; *f–g,* variations of degree of damage to stromatoporoids on the sea floor, either during life or soon after death, and such taphonomic information may be valuable in paleoenvironment reconstruction (Kershaw, 2012).

368–372 give key information about the paleoenvironmental controls on stromatoporoids.

GROWTH FORM DEVELOPMENT

Stromatoporoid early growth often formed sheetlike skeletons across the substrate, and subsequent growth was concentrated in central areas, producing a smooth, nonenveloping profile (KERSHAW & RIDING, 1978); uncommonly, others are fully enveloping (see p. 425). The resulting basal surfaces of skeletons display concentric ridges where successive overlapping layers touch the substrate, enhanced into minor ragged edges, which may be due to a little sedimentary material collected on the edges as successive layers grew. Form usually changed as individuals grew: early growth of a stromatoporoid was commonly laminar, with later growth focused in central regions to form a domical shape. Some samples, which have a final bulbous form, are observed in longitudinal section to have gone through laminar and then domical forms in the process. Therefore, determination of growth form should take into account such changes in growth form history within individual specimens, where they are visible in cut sections; individuals of the same species within an assemblage may display different growth forms if they died before the final form could develop, and species-level taxonomy is crucial in such investigations. An example of the history of a single specimen in relation to

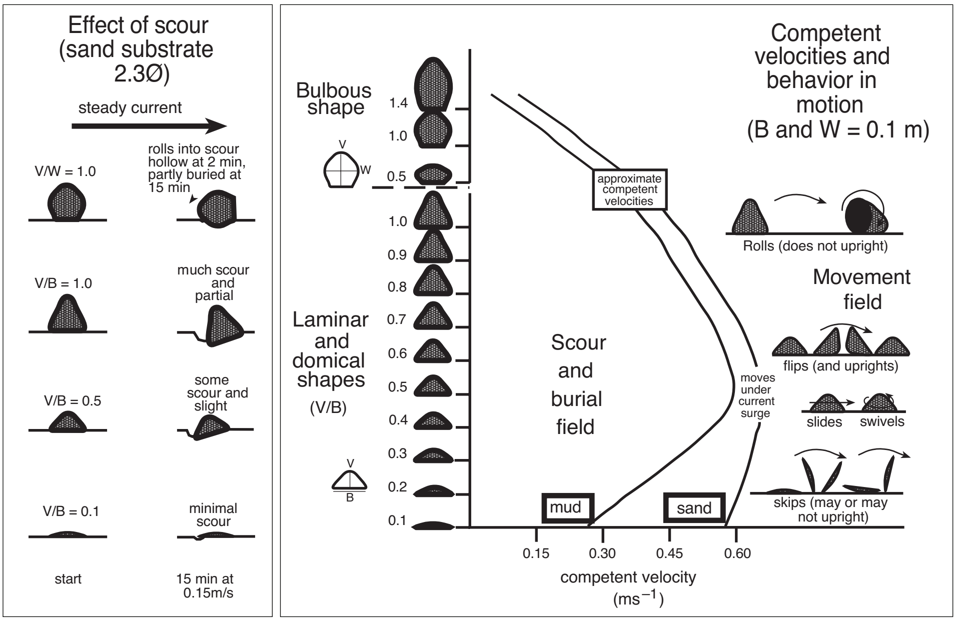


FIG. 369. Results of experimental work on model stromatoporoids illustrating the range of behavior of simple-shaped forms under steady and surge current influence on sand and mud substrates. Models were not fixed to the substrate, emulating fossil stromatoporoids. The data show that stromatoporoids are more stable on muddy substrates; this is circumstantial evidence that may partly account for their common occurrence on such substrates. Stability is inherent in the common low- to mid-domical shapes, and the slow currents used in these experiments serve to emphasize the important role of obstructions, which prevented movement of fossil stromatoporoids in reefs in many cases. Responses of more complex forms were not tested, and divergence from this simple pattern is expected; *V,* maximum vertical dimension; *B,* maximum basal dimension; *W,* maximum width in bulbous forms (therefore not the base); ø (phi), grain size of the sediment from international standards of grain size (Kershaw, 1998; reproduced with kind permission of the Palaeontological Association).

environmental influences is given in Figure 367.

PHOTOTROPISM AND DEPTH

Circumstantial evidence that stromatoporoids were photoresponsive employs size and growth rates in relation to modern coral-dominated reef systems (BAARLI, JOHNSON, & KEILEN, 1992; WOOD, ZHURAVLEV, & DEBRENNE, 1992), morphology (KLOVAN, 1964), and association with algae (e.g., BAARLI, JOHNSON, & KEILEN, 1992). In contrast, although modern sponge biomass (noncalcified types only) may be 50% bacteria (WILLENZ & HARTMAN, 1989), these are not photosensitive. In Devonian stromatoporoid morphotype data, laminar and tabular forms are more common in fore reefs than in other large domical-bulbous-irregular forms. Laminar forms grew better in the finer sediment, deeper water facies of the Canadian Leduc reefs (and also occur in back-reef facies), while massive and subspherical forms (domical, bulbous, and irregular) dominate reef facies and are less common in fore reefs (KLOVAN, 1964). Geopetally constrained, fore-reef, paleoslope data in the Canning Basin reef-rimmed shelves (PLAYFORD, 1980; PLAYFORD & COCKBAIN, 1989) imply depths comparable to modern reef systems. The earliest laminar stromatoporoids are Ordovician in age and may have occupied deeper water (approximately 30 m depth) habitats (BOURQUE & AMYOT, 1989, p. 255); such laminar shapes could have existed in deeper, poorly lit environs,

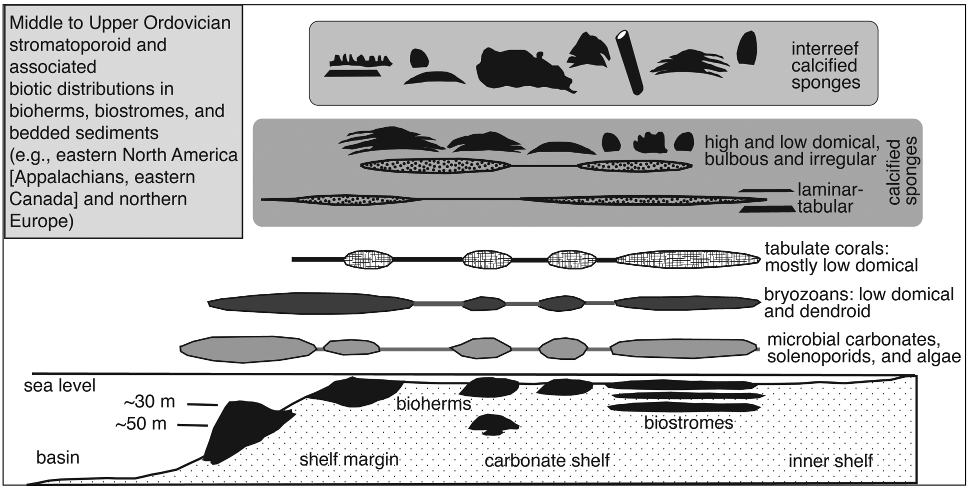


Fig. 370. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Ordovician carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Ordovician labechiid-dominated stromatoporoid morphotypes exhibit a wide range across carbonate banks. Stromatoporoids commonly occur with solenoporid-rich rudaceous carbonates. Level-bottom community dwellers (e.g., Mid-Ordovician [Chazyan] *Pseudostylodictyon* and Upper Ordovician *Aulacera*) are the largest stromatoporoids. Note: the stromatoporoids are commonly associated with facies rich in microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

as do some modern corals. Arguments favoring algal (=?microbial) symbiosis (e.g., Cowen, 1988) are circumstantial, and papers that record relatively deeper water, laminar forms (Klovan, 1964, at Redwater; Krebs, 1974, in Europe; Kobluk, 1975, at Miette—see Wilson, 1975, p. 144) do not contain sufficient species-morphotype information to demonstrate flattening at depth within a species. Also, low profile is common in stromatoporoids and may relate instead to sedimentation rate and substrate type, similarly poorly investigated.

PALEOENVIRONMENTAL DISTRIBUTION

Stromatoporoids with diameters up to tens of centimeters grew in deeper facies, lagoons, and small reefs, and up to several meters in larger reefs and mounds, and they occupy up to 90% of reef volume (Machel & Hunter, 1994, p. 162). Stromatoporoids were limited in deeper facies and in mud mounds, occurring uncommonly as small individuals (e.g., Bourque & Raymond, 1989). Siliceous sponges played a role in deeper water mounds (e.g., Brunton & Dixon, 1994) and have been postulated as major elements of stromatactoid-rich mud mounds by Bourque and Gignac (1983, 1986), but none of these are the calcified forms typified by the stromatoporoid skeleton. In contrast, stromatoporoids may be major elements of framestones, bafflestones, bindstones, and debris in both biostromes and bioherms (e.g., Watts, 1988a; Sønderholm & Harland, 1989; Riding & Watts, 1991; James & Bourque, 1992; de Freitas, Dixon, & Mayr, 1993; Kershaw, 1993; Machel & Hunter, 1994). Absence of a rigid frame is common in stromatoporoid reefs, and, except where bound by microbial growth (e.g., Devonian platform-margin reef limestones of the Canning Basin), presumably they could not withstand high-energy conditions (de Freitas, Dixon, & Mayr, 1993). They usually did not build up high

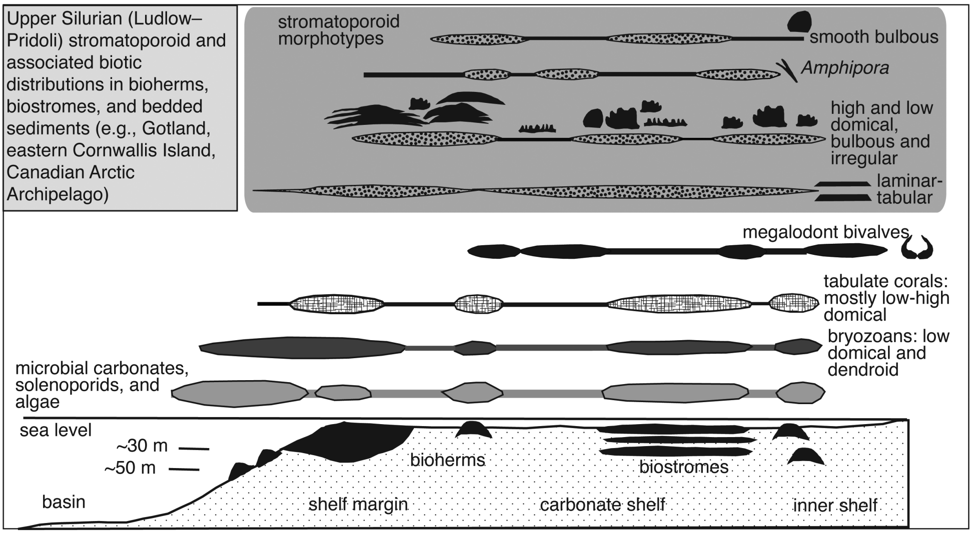


FIG. 371. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Silurian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Late Silurian, predominantly nonlabechiid morphotypes occur in a wider range of niches than Ordovician stromatoporoids and have a greater range of skeletal architecture and taphofacies variation. A wider variety of forms are evident in Silurian than in Ordovician bioherms; in Silurian biostromes, there are predominantly smooth, bulbous-to-high domical forms. Note: Silurian and Devonian reef-dwelling stromatoporoids both have a spatial and temporal association with photosymbiotic megalodontid bivalves and microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

reef profiles. Unbound stromatoporoid buildups are discrete objects (RIDING, 1981) made of closely juxtaposed fossils, called cluster reefs by RIDING (1990).

Nevertheless, stromatoporoids apparently grew best in the shallower, more turbulent waters of Paleozoic reefs, outcompeting corals and other organisms, and forming low diversity stands in the climax stages of reef development (e.g., WILSON, 1975), which is true in many biohermal reefs (e.g., the Silurian Högklint reefs of Gotland, Sweden: RIDING & WATTS, 1991; Devonian reefs in South Devon, United Kingdom: SCRUTTON, 1977a, 1977b); but some exceptionally stromatoporoid-rich assemblages formed as biostromes in lower-energy, shelf-ramp settings conditions in Silurian and Devonian platforms. Furthermore, MONTY, BERNET-ROLLANDE, and MAURIN (1982) drew attention to the fact that although stromatoporoids are major reef-builders in the Devonian, they are not abundant in all cases. Presumption of shallow water may not always be justified. Summaries of the distribution of stromatoporoids in Ordovician, Silurian, and Devonian facies are provided in Figures 370–372 respectively.

STROMATOPOROID TAPHONOMY

Impact damage to stromatoporoids can be observed both in Paleozoic-age events and in the presently occurring erosion of modern outcrops; recently eroded stromatoporoid clasts found in quarries and cliffs are similar in nature to their Silurian counterparts. Breakage is governed by form, degree of fixation to the Paleozoic seabed, the degree to which latilaminae are developed, and the amount of diagenetic alteration of skeletons, especially along latilaminae. Skeletal breakage, as well as attitude in outcrop, may influence form recognition. Furthermore, the common effect of pressure

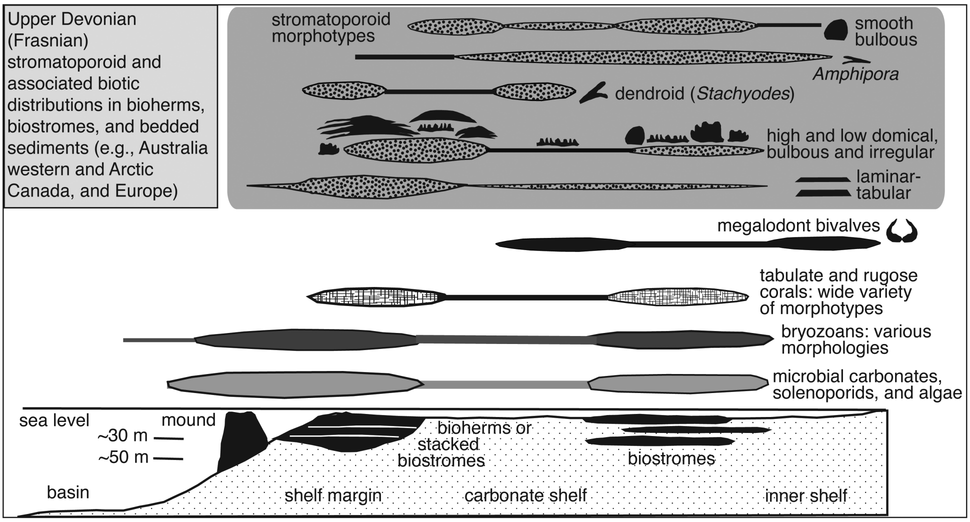


FIG. 372. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Devonian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Upper Devonian, predominantly nonlabechiid morphotypes have the widest range of morphotype distribution, skeletal architecture, and taphofacies. Late Devonian stromatoporoid morphotypes tend to have a wider variety of irregular forms and a greater tendency for encrusting than Silurian forms. Note: Silurian and Devonian reef-dwelling stromatoporoids both have a spatial and temporal association with photosymbiotic megalodontid bivalves and microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

solution degrades the margins of stromatoporoids, so that marginal damage may not be preserved. Stromatoporoid taphonomy is, of course, crucial in paleoenvironmental analyses and underlies much of the analogy drawn between modern coral reefs and Devonian stromatoporoid reefs. Examples of the importance of taphonomic aspects are: (1) a delicate branching species of the genus *Amphipora* occurs as fragmented branches across Devonian reef complexes, and its preferred growth site is poorly understood; it is not known whether it was restricted to quieter waters of back-reef settings, or if it grew over a reef complex; (2) the very thin laminar genus *Lophiostroma,* in Ludlow biostromes on Gotland, is commonly found as fragments, because it is less robust than other stromatoporoids in the assemblage, affecting its preservation potential relative to other stromatoporoids. Most studies have been qualitative, but quantitative work (e.g., KOBLUK, 1974; KOBLUK, BOTTJER, & RISK, 1977; KERSHAW, 1990), especially where fragments are identified and size-classed, has much potential (KERSHAW & BRUNTON, 1999); if, for example, the fragments show differences in taxonomic distribution from the in-place stromatoporoids, inferences can be made about fragmentation and transport in a stromatoporoid-bearing deposit.

STRATIGRAPHIC GROWTH FORM TRENDS

Ordovician and Silurian stromatoporoid growth forms are conservative, but expand to a modern-looking form distribution in the Devonian (ANDRICHUK, 1958; FISCHBUCH, 1962). However, stromatoporoids lack the branching habit of the modern dominant reef coral *Acropora*. Ordovician and Silurian reefs are similar in structure and function, and differ mainly in taxonomic composition (COPPER, 1988, p.

137). Many upper Silurian reefs resemble Devonian platform margin systems and include important elements of microbial binding (e.g., BOURQUE & AMYOT, 1989). Devonian reefs (e.g., GISCHLER, 1995) may contain substantial submarine cement; the presence of cement in Devonian reefs appears to have enhanced the preservation of primary cavities in stromatoporoids, in contrast to the Silurian (as discussed in p. 425).

PALEOENVIRONMENTAL ANALYSIS

GENERAL RELATIONSHIPS

Growth form was controlled by environmental (extrinsic) and genetic (intrinsic) factors (NICHOLSON, 1886a, p. 27–29; GALLOWAY, 1957, p. 374; KISSLING & LINEBACK, 1967; FISCHBUCH, 1968, fig. 23; LEAVITT, 1968, p. 323; MORI, 1968, 1970; KAPP, 1974, 1975; CORNET, 1975; HOGGAN, 1975; KOBLUK, 1975; KERSHAW, 1981, 1984, 1990; COCKBAIN, 1984; KANO, 1989, 1990). Most species are limited to a narrow morphospace that varies depending on interaction between paleoenvironment and morphospecies. Short-lived events are also recorded, particularly sedimentation and movement effects during life (Fig. 368). However, since these effects do not influence the basic shape (a domical stromatoporoid that reoriented several times in life so that its shape is rounded is still intrinsically domical), then underlying controls on form, if they can be identified, may provide important data on the overall character of the paleonvironment.

Several studies illustrate the selective advantage of dominantly lateral growth in stromatoporoids (MEYER, 1981; BJERSTEDT & FELDMANN, 1985; HARRINGTON, 1987; KANO, 1990; KERSHAW, 1990). STEARN's (1982b) comparison of stromatoporoids with modern coral growth forms, which may provide analogues, revealed no parallel patterns; and the forms of modern reef animals are not even useful guides to modern reef environments, thereby emphasizing the care needed for interpretation of stromatoporoids. NESTOR (1984) discussed the range of controls on stromatoporoids. A general summary, derived from many sources, is presented in Figure 373, which summarizes a diverse range of aspects of stromatoporoid paleoecology (see also p. 423–485).

Large stromatoporoids reflect long periods of growth (YOUNG & KERSHAW, 2005) and highlight their ability to survive events affecting the seabed. Depending on the nature of the assemblage, stromatoporoids have potential to reveal regional and even global processes. Examples of Paleozoic stromatoporoid assemblages demonstrate the range of process-response relationships in order to emphasize their value in paleoenvironmental analysis at these different scales; these are demonstrated in the Ordovician, Silurian, and Devonian systems, and summarized in Figures 370–372.

COMMUNITY-SCALE ECOLOGY—OUTCROP SCALE

Here, selected examples from the literature and outcrops illustrate characters and problems of interpretation of stromatoporoid assemblages at relatively small scale in outcrop studies. The small-scale approach is most commonly adopted by field geologists investigating the factors that may have been responsible for controlling growth (further examples are presented on p. 423–485).

Middle Ordovician Stromatoporoids, Chazy Group, Vermont, USA

Large stromatoporoids appear in Middle Ordovician level bottom and mound environments at the start of Paleozoic stromatoporoid dominance in many shallow marine facies (WEBBY, 1986, 1994; FLÜGEL & FLÜGEL-KAHLER, 1992, p. 178), although stromatoporoid abundance varies within the Ordovician buildups (DESROCHERS & JAMES, 1989). KAPP (1974, 1975) and KAPP and STEARN (1975) noted that laminar to high domical forms are abundant in the

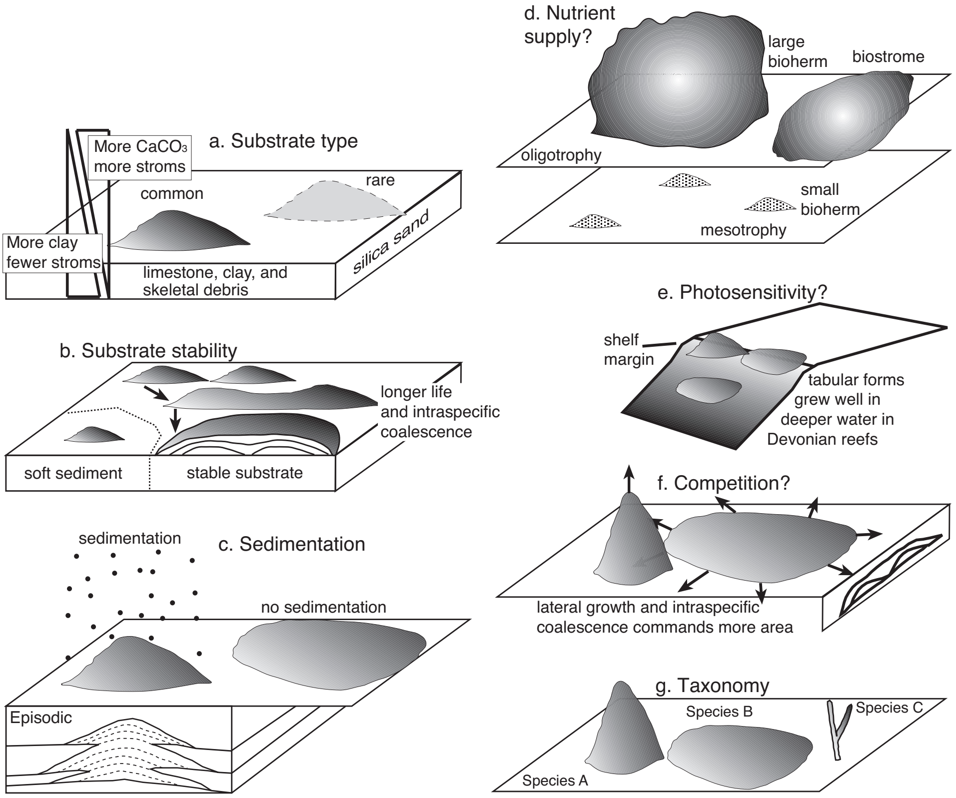


FIG. 373. Diagram summarizing stromatoporoid growth controls, which encompass the range of environmental boundaries that may be expected to have operated on Paleozoic stromatoporoids. *a,* Stromatoporoids are found mostly associated with calcareous sediments low in clay and are rare in coarser siliciclastic sediments; *b,* stromatoporoids grew most successfully on stabilized sediments of skeletal debris and were smaller on clay-rich limestones; coalescence of neighboring individuals of the same species is a likely means of increasing size; *c,* sedimentation is suspected to be a major control on stromatoporoid growth; stromatoporoids that grew in conditions of little sediment deposition grew larger; *d,* stromatoporoid-dominated reefs may have grown in low-nutrient conditions, by analogy with modern reefs that are best developed in such oligotrophic environments; *e,* stromatoporoids in deeper water environments commonly developed a laminar or tabular form, which may be due to photoresponsive tissue; however, there is no unequivocal evidence that stromatoporoids possessed a photoresponsive capability; *f,* whether or not stromatoporoids developed a competitive ability is unclear; no proof of competitive interactions has been published (Fagerstrom & others, 2000); *g,* stromatoporoid growth form was influenced by taxonomy in at least some species, with a predominance of lower profile forms (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

Middle Ordovician Crown Point Formation, Lake Champlain area, Vermont, and have a component of taxonomic control on form; *Pseudostylodictyon lamottense* (SEELY) grew into high domical shapes (see Fig. 287), whereas species of *Pachystylostroma* and *Labechia* were laminar (KAPP, 1974, p. 1235). *Pachystylostroma* and *Labechia* are present only in mounds, whereas *Pseudostylodictyon* occurs mainly in level bottom sediments. Stromatoporoids occupy the greatest biovolume of mound faunas, but are low in diversity within individual mounds dominated by single stromatoporoid species, or different species may dominate in different mounds (KAPP, 1975, p. 201).

Only *P. lamottense* formed large stromatoporoids (KAPP, 1974) as stacked, ragged domes due to episodic sedimentation (see Fig. 286–287) and may have grown quickly, because it is also the only species in the level bottom facies able to grow high enough to survive episodic sedimentation. Kapp (1974, p. 1236) noted that individuals began on small substrate irregularities, and although not stated in her papers, the indications are that they could grow directly on the sediment surface, a feature noted also by Kano and others (1994) in Middle Ordovician stromatoporoids of Korea. In Vermont, individuals are isolated and grew on several bedding planes (Fig. 374; and see Fig. 286.1); early growth showed lateral expansion with some enveloping latilaminae, then upward growth was apparently stimulated by episodic sedimentation to generate ragged forms (see Fig. 282.2–286.3; Fig. 287).

Specimens may be closely spaced, less than one meter apart (Kapp, 1974), and commonly asymmetrical (Fig. 374; and see Fig. 286.2), with growth axes of neighboring stromatoporoids commonly pointing in different directions, interpreted by Kapp as a result of variable local current vectors. Asymmetry is maintained through the vertical thickness, so for currents to be the cause, they would have to be peculiar to each stromatoporoid throughout its life, and the many intervening episodes of sediment deposition; asymmetry may be better explained by chance development of the growth form of individual stromatoporoids. Overall, the Vermont examples give considerable information about stromatoporoid paleobiology and autecology but also raise questions about the controls of form.

Silurian Level Bottom Stromatoporoids, Gotland, Sweden

Figure 375 summarizes features of an assemblage of small stromatoporoids from Gotland, but the principles apply to most level bottom stromatoporoid assemblages. *Densastroma pexisum* grew taller and apparently survived episodic sedimentation better than other species in the assemblage, leading to its higher abundance and lower degrees of raggedness (Kershaw, 1984). Note, however, the reappraisal of the nature of ragged margins in stromatoporoids (Kershaw, Wood, & Guo, 2006), reinterpreting at least some of them as flanges extending outward into the water column and not necessarily directly linked to episodic sedimentation (see p. 424), which, therefore, reduces the certainty of application of ragged margins as sedimentation rate indicators. Some tabulate coral species are likewise better adapted to episodic sedimentation (e.g., Gibson & Broadhead, 1989). An environmental energy index, using proportion of overturned stromatoporoids, could be used only broadly, because experimental work shows that domical stromatoporoids were usually restored to an upright position following disturbance (Fig. 369); nearly all stromatoporoids are upright in the muddy limestones, less so in coarser beds, interpreted as storm events (Kershaw, 1984).

Middle Devonian Level Bottom Stromatoporoids, Hope's Nose, Devon, UK

Low profile (laminar and low domical) stromatoporoids colonized coarse crinoidal grainstones and presumably helped to stabilize the substrate. The lack of ragged forms suggests periods of no sedimentation while they grew in well-aerated water, followed by sudden episodic deposition that overwhelmed them (Fig. 376).

Upper Devonian Bioherm, Lion Quarry, Southern Belgium

Figure 377 illustrates laminar and domical stromatoporoids in a Frasnian bioherm, in which large laminar and domical stromatoporoids occur together at particular levels, separated by layers containing small laminar stromatoporoids and layers with coarse debris. The larger stromatoporoids presumably grew in episodes of reduced deposition and relative substrate stability, interspersed with energetic events. These features are consistent with the interpretation of Monty, Bernet-Rollande, and Maurin (1982), that this bioherm lacks a frame and possibly formed in deeper water.

COMMUNITY-SCALE ECOLOGY— ANALYSIS OF ASSEMBLAGES

Stromatoporoid Diversity Indices as Paleoenvironmental Tools—Silurian and Devonian Examples

Quantification of modern organic diversity is achieved using diversity indices (e.g., PIELOU, 1966) but is problematic in fossils because of difficulties in precision of species definitions, time-averaging of communities, and taphonomy. FAGERSTROM (1983) applied diversity concepts qualitatively to Emsian and Eifelian stromatoporoid assemblages, where diversity in reefs is greater than in level bottom communities, and Eifelian reef organisms are strongly endemic; also reef environments are likely to have greater origination and extinction rates and consequently could play an important role in evolution of reef builders. COCKBAIN (1989) similarly noted higher species numbers in reef (25 taxa) compared to shelf (6 taxa) environments in Middle to Upper Devonian successions of Western Australia. In contrast, Devonian reefs in Nevada have lower diversity, with *Hammatostroma* abundant as tabular and bulbous shapes, although such reefs are considered as biostromes (HOGGAN, 1975). BRUNTON and COPPER (1994) categorized early Silurian reef biotas into groups, depending on numbers of species, and revealed a low diversity in reef cores, with up to 70% of volume being composed of only four species. COPPER (1988) drew attention to the lower diversity of modern reef communities in areas under great stress, whereas the rest of a reef complex usually exhibits a higher diversity.

Although such general observations are valuable, numerical diversity indices, such as Shannon's Information Function (H) applied by STEARN (1975b) to the Devonian Ancient Wall stromatoporoid assemblages, provide a better comparative tool for paleoecological and paleoenvironmental work. Species diversity indices are calculated from relative abundance of individuals of each species, not just numbers of species, and greatest diversity lies in assemblages with equal numbers of each species. Approaches to diversity analysis were discussed by KREBS (1972), who noted that different methods have different advantages. Shannon's Information Function (H) is particularly applicable to assemblages of organisms in cases where there is no assumption of the shape of the distribution; furthermore H should be applied to random samples. STEARN (1975b) argued that stromatoporoids, being fossils that cannot be identified in the field, provide a good approximation to randomness in collection, since the collector is not influenced by selection of specimens with particular skeletal structures, especially in cemented limestones where internal structure is difficult to see. Nevertheless, truly random samples need to be collected using a grid system and random number tables, as applied by KERSHAW (1990). KREBS (1972, p. 455) pointed out in a footnote that the Shannon Function is correctly called the Shannon-Wiener Function, and sometimes incorrectly referred to as the

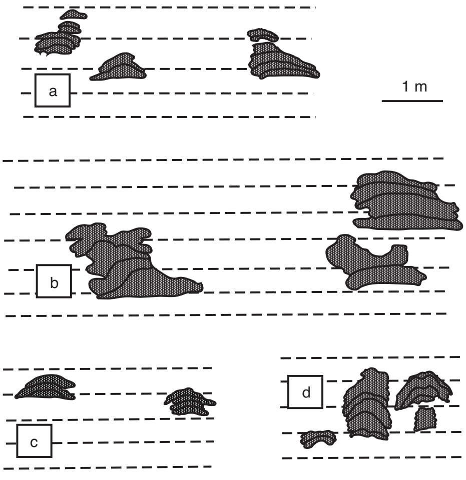
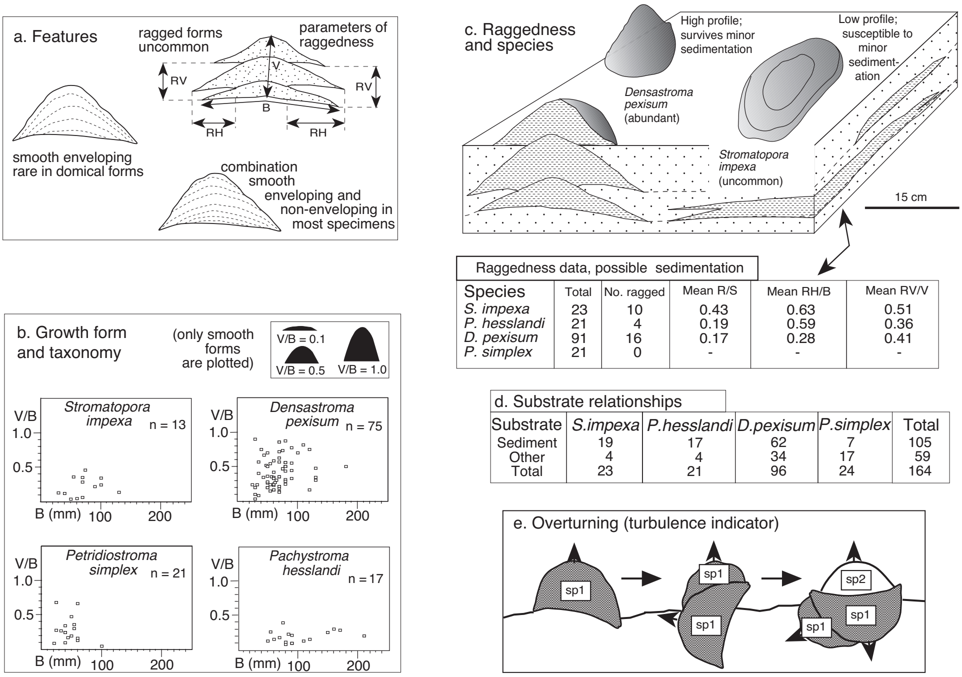


FIG. 374. Sketches of stromatoporoid vertical sections. Growth was apparently principally on soft sediment; individuals began growth at different levels and have ragged margins, suggesting that episodic sedimentation controlled growth initiation and development. Growth is biased in left or right directions. *a–c,* Fisk Quarry; *d,* Goodsell Quarry (drawn from photographs in Kapp, 1975).



Raggedness data, possible sedimentation

Species	Total	No. ragged	Mean R/S	Mean RH/B	Mean RV/V
S. impexa	23	10	0.43	0.63	0.51
P. hesslandi	21	4	0.19	0.59	0.36
D. pexisum	91	16	0.17	0.28	0.41
P. simplex	21	0	-	-	-

d. Substrate relationships

Substrate	*S.impexa*	*P.hesslandi*	*D.pexisum*	*P.simplex*	Total
Sediment	19	17	62	7	105
Other	4	4	34	17	59
Total	23	21	96	24	164

FIG. 375. Comparative stromatoporoid autecology in the Visby Formation, lower Wenlock, Gotland, Sweden, based on data from KERSHAW (1984). *a,* Features of stromatoporoids in this assemblage; *b,* morphological variation between species; *c,* selective advantage of a high profile form in this environment; *d,* species selection of substrate type; *e,* broad indication of frequency of dislocating currents shown by episodic overturning and recovery by species 1, and use of the upturned base of the first growth of species by species 2 (the horizontal arrows show the successive stages of growth development of the sample from left to right). Note that the raggedness data in view *c* may reflect sedimentation and/or growth to form primary cavities. *V,* maximum vertical dimension; *B,* maximum basal dimension; *V/B,* ratio of V to B, as an approximate measure of shape; *R/S,* ratio of number of ragged-margined to number of smooth-margined specimens; *RV,* vertical extent of raggedness; *RH,* horizontal extent of raggedness; *RH/B,* ratio of RH to B as an measure of horizontal extent of raggedness; *RV/V,* ratio of RV to V as a measure of vertical raggedness (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

Shannon-Weaver Function. As an attempt to demonstrate its utility, Figure 378 provides diversity indices calculated using the Shannon-Wiener Function (H) for a range of published species distributions of stromatoporoids from well-documented Silurian and Devonian examples, assembled by KERSHAW (1990). H was chosen by KERSHAW (1990), following its application by STEARN (1975b), in order to attempt to compare diversities of different stromatoporoid assemblages, using the same index. However, in the examples of Figure 378, comparisons are probably fully valid only *within* and not *between* datasets, because of uncertainty about whether the data collection methods were all random; therefore, these data give only a general guide to stromatoporoid diversity.

According to STEARN (1975b), the Shannon-Wiener Function (H) is calculated according to the formula:

$$H = -\sum_{i=1}^{S} p_i \log_e p_i$$

where S = number of species in the sample, and p_i is the proportion of the ith species of the sample (Table 32).

KREBS (1972, p. 455) used Log_2, although as long as a uniform approach is applied, comparisons of H values between samples collected by the same method will be valid. H is most easily calculated

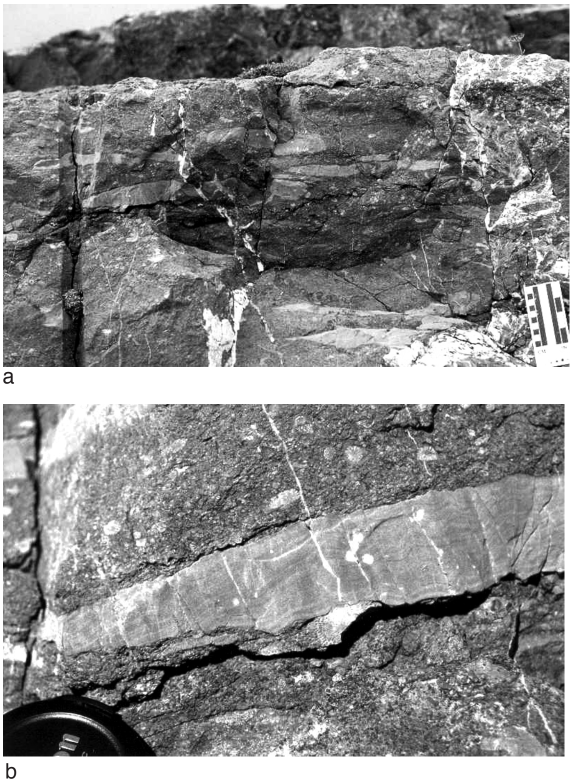


FIG. 376. Laminar stromatoporoids at Hope's Nose, Givetian, South Devon, United Kingdom. *a–b,* Growth of low profile stromatoporoids on mobile substrates made of crinoidal debris suggests a stabilizing effect provided by the stromatoporoids. The stromatoporoids probably grew in low-moderate energy conditions, because laminar forms are readily overturned by current flow (see Fig. 369); view *b* shows that themargin of stromatoporoid is modified by pressure solution, visible part of lens cap is 4 cm wide (Kershaw, 2012; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

using a spreadsheet, and an example is given below, for the marginward Peechee Member stromatoporoid assemblage collected by KOBLUK (1975), plotted on Figure 378, upper right (when viewed in a horizontal orientation).

Although H is calculated as a negative number, its sign is simply changed to positive for ease of expression. In Figure 378, the point plotted in relation to Table 32 is accompanied by text (2/76; 68%) that summarizes the data relating to that point, explained also in the key (Fig. 378, lower right when viewed in a horizontal orientation). The remainder of Figure 378 was constructed using spreadsheets, as above. Data plotted from STEARN (1975b, p. 1644) were taken from his summary. Diversity index data depend on sampling procedure, but also on quality of taxonomy; in the Högklint Formation of Gotland,

TABLE 32. Example of method of calculation of species diversity H index, used in Figure 378. The example comes from the reef marginward Peechee Member stromatoporoid sample collected by Kobluk (1975).

Species	No. of specimens	P_i	$\text{Log}_e\, p_i$	$P_i\, \text{Log}_e\, p_i$
1	52	0.684	–0.380	–0.2598
2	26	0.342	–1.073	–0.3669
total	76	1	–H	–0.6267
			H (rounded)	0.627

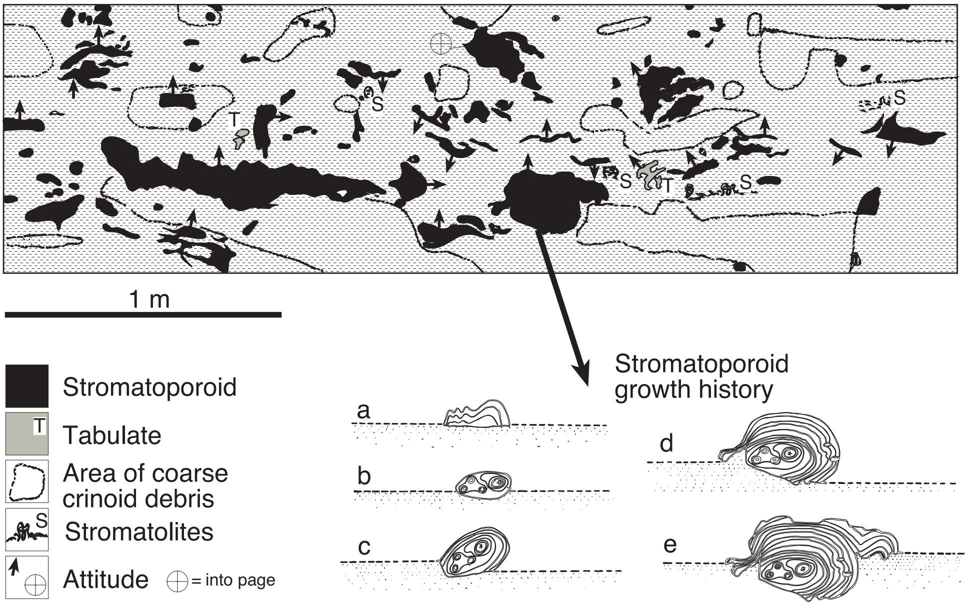


FIG. 377. Small area of vertical surface of reef, Lion Quarry, Frasnes, southern Belgium. A mixture of whole and fragmented stromatoporoids appear to occur in rhythms separated by coarser debris; stromatoporoids demonstrate growth on a probable loose substrate, with a prominent lateral growth aspect. The complex form of one specimen is interpreted as episodically reoriented in sequence *a–e.* Temporal energy reduction is indicated by occurrence of thin laminar stromatoporoids associated with microbial heads and mats. This diagram illustrates the problems of growth form classification, with some forms being more readily classifiable than others (see p. 431–461). In the *Attitude* box of legend, *into page* means that the specimen is lying on its side with its apex pointing away from the reader (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

for example, many stromatoporoids are so strongly recrystallized that they are unidentifiable (MORI, 1968), reducing the utility of the diversity index for that formation in comparison with others.

In Figure 378, only data for stromatoporoids are given, and total biotic diversity must differ from the indices, except in assemblages composed almost entirely of stromatoporoids. Such assemblages have many stromatoporoid species and thus a high diversity of stromatoporoids, but other components of such assemblages may be represented only by a few species each of tabulate and rugose corals, brachiopods, crinoids, and rarely other fossils. STEARN (1975b, p. 1637–1639) attributed progressive stromatoporoid diversity reduction at the Ancient Wall to increasing severity of the reef crest environment, as relief increased on the reef front, and the same conclusion may be drawn for data given by KOBLUK (1975) for both lagoon and reef margin communities of the Miette Complex (Fig. 378). Similarly, H, calculated for Devonian stromatoporoids of southern Belgium (CORNET, 1975), shows that large bioherm complexes sited in open water have a slightly lower stromatoporoid diversity than shelf biostromes and back-reef settings, and these biostromes are much richer in

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FIG. 378. *(Continued from facing page).*
UC(U), Lower and Upper Cairn Formation respectively; *MP* and *UP,* Middle and Upper Peechee Member, respectively; *b,* H is calculated from stromatoporoid data from named sites by Cornet (1975); *c,* MORI's (1968, 1970) data are from the range of stratigraphic units on Gotland; data from Kano (1989) and Kershaw (1990) focus on specific sites and stratigraphic units within the Gotland sequence. [1]Note that for the Gotland data set, the Högklint stromatoporoids are mostly poorly preserved and probably are underrepresented on the diagram (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

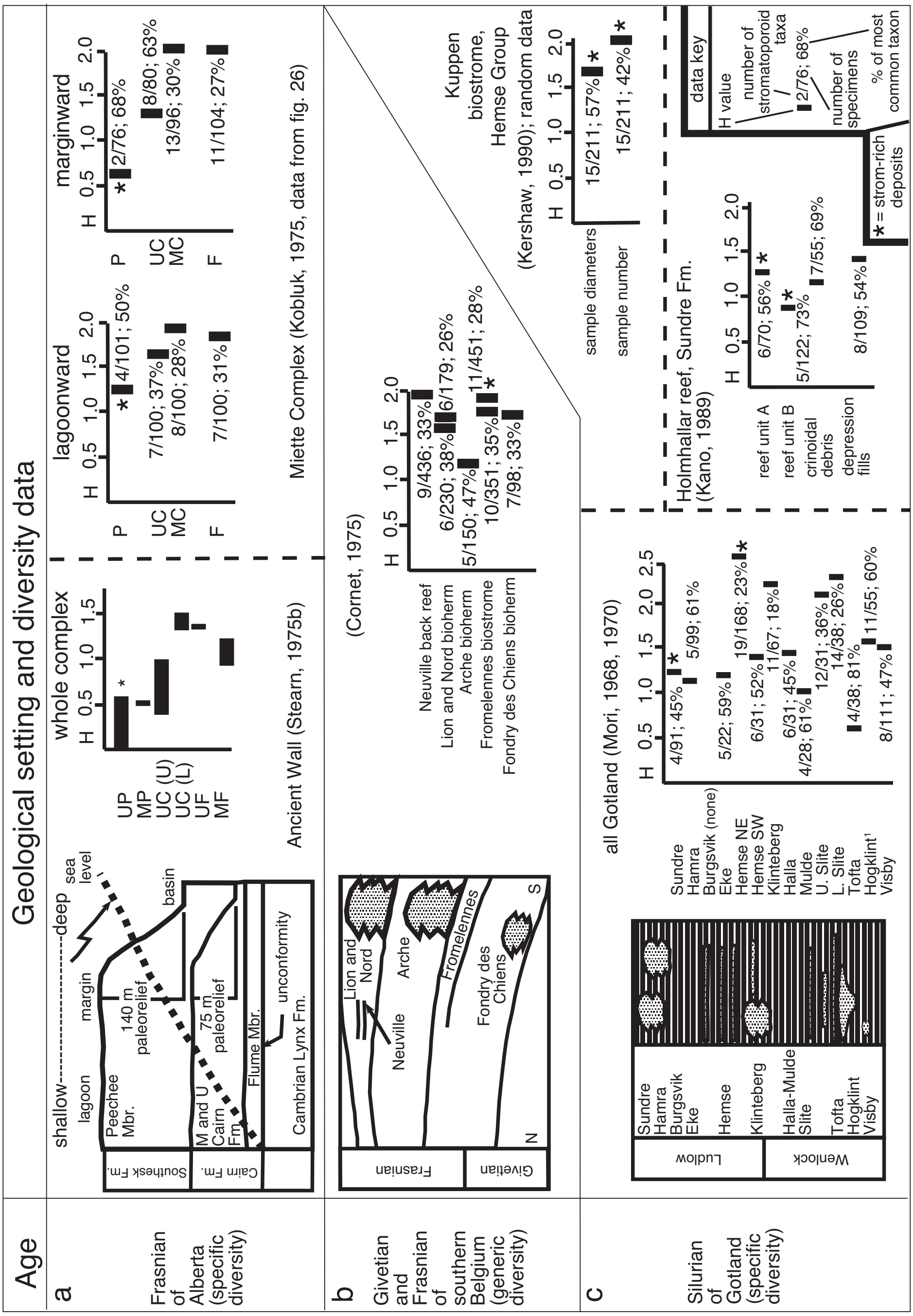


FIG. 378. Shannon-Wiener index (H) for stromatoporoid assemblages from published data for Silurian and Devonian locations. The diversity index is calculated using a combination of numbers of species and numbers of specimens of each species, as explained in the text. *a,* Data were compiled by Kershaw (1998) from the plots of Stearn (1975b, p. 1644) and information in Kobluk (1975, fig. 26)*; F,* Flume Member; *MF,* Middle Flume Member; *P,* Peechee Member; *UF,* Upper Flume Member; *UC(L)* and *(Continued on facing page).*

stromatoporoids. In Figure 378, data from Gotland (Mori, 1968, 1970) show that stratigraphic units dominated by stromatoporoid-rich platform biostromes (Slite, Klinteberg, and Hemse units) have the highest diversities of stromatoporoid faunas, while the lowest values are recorded for very shallow, high stress settings, such as the Tofta Formation (where salinity may have played a part in diversity control), and deeper muddy environments of the Mulde Formation. Kano's (1989) work on the abundant stromatoporoid faunas of the upper Ludlow Holmhällar site, Gotland (where facies are only partly exposed and the reef shape indeterminable), shows diversity differences through the reef complex. Ludlow reefs on Gotland (Fig. 379) are composed almost completely of stromatoporoids (Kershaw, 1981, 1990; Kano, 1989, 1990; Mori, 1970); although diversity of all fossil groups is low, stromatoporoid diversity is high [see Fig. 378c, from Mori's (1970) data, and see the next section on Stromatoporoid Biostromes]. Most are biostromes, implying stable conditions of low sedimentation and possible sea level stillstands (Kershaw & Keeling, 1994; Kershaw, 1994b), in contrast to bioherms (see discussion in Fig. 380). Stromatoporoid faunas mostly comprise large, low profile forms, many coalesced from smaller individuals, and emphasize the competitive advantage of a lateral growth habit, commonly seen in Ordovician to Devonian reef-builders.

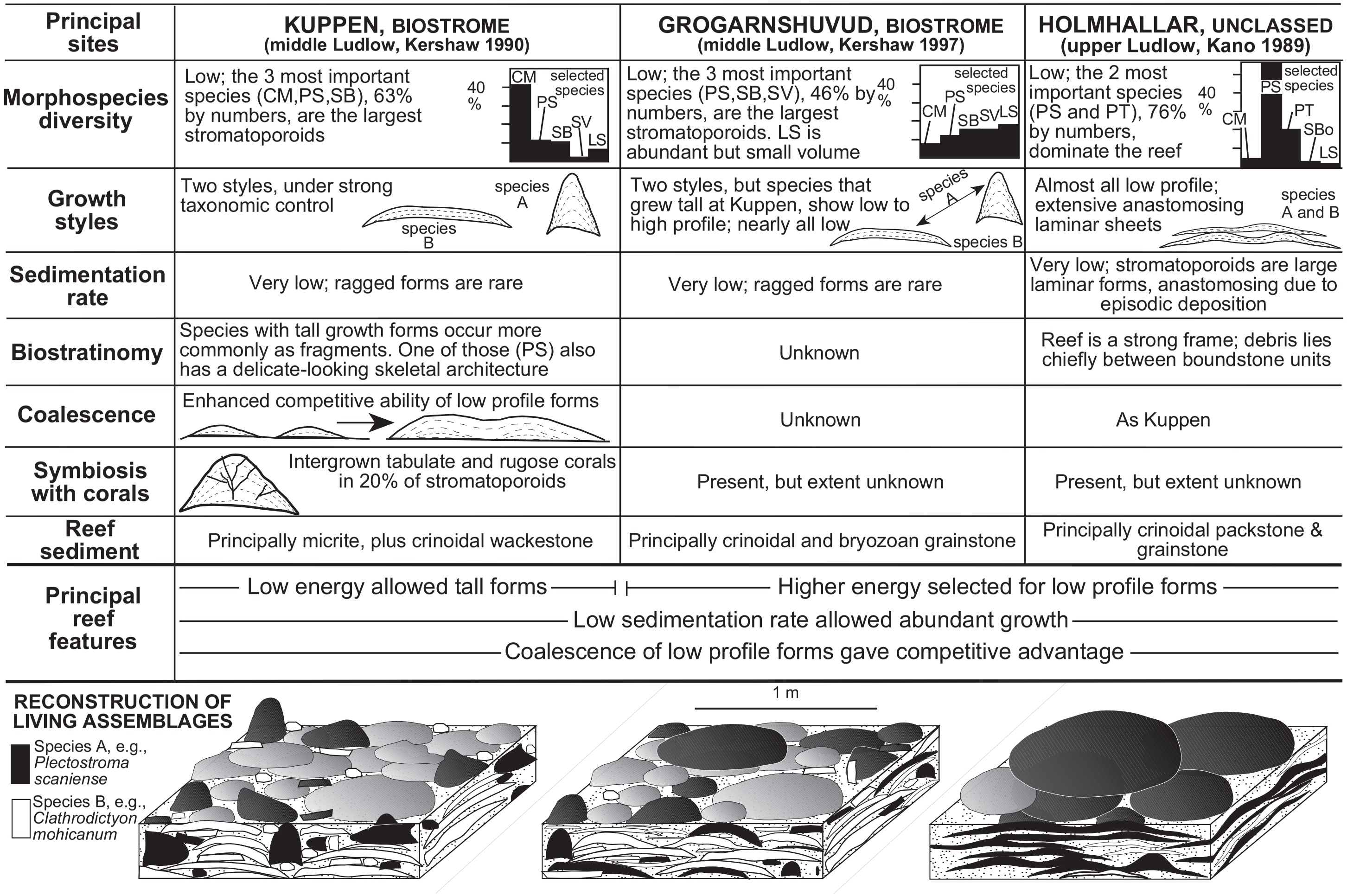
The sum of available data suggests that low stress environments (where platform biostromes were formed) were the optimum settings for stromatoporoids. In a truly random sample, collected using random numbers on a sampling grid (Kershaw, 1990), albeit time-averaged for a single biostrome, stromatoporoid size is emphasized by comparing diversity of the same samples, expressed both as numbers and size (≈basal diameter) of individuals. The use of a diversity index based on a measure of the size of specimens of each species, rather than numbers of individuals of each species, is a novel approach. H is lower for basal diameters than for numbers of specimens, emphasizing the ability of large stromatoporoids to occupy larger areas of sea floor, and suggests that the competitive ability of stromatoporoid taxa is related to the amount of sea floor they were able to occupy.

Stromatoporoid Biostromes

Dense accumulations of stromatoporoids in biostromal deposits occur in Wenlock to Devonian deposits, apparently occurring in platform interior settings. Figure 379 summarizes data from three well-exposed Silurian sites, in order to compare features of the stromatoporoid assemblages. Environmental and stromatoporoid parameters combined to produce dense accumulations of stromatoporoids with a limited range of growth forms. Sample size is, of course, important to gain an accurate picture of diversity. Using a much larger sample than that collected by Mori (1970), two examples studied by Kershaw (1990, 1997) presented in Figure 379 and expanded by Sandström and Kershaw (2008), show that the stromatoporoid assemblages of the Hemse Group biostromes are in fact widely distributed as a low-diversity accumulation, with three species being most abundant.

Work on Devonian examples described later (p. 649; Da Silva, Kershaw, & Boulvain, 2010, 2011b) also supports the need

Fig. 379. Parameters of stromatoporoid-dominated Ludlow reef communities from Gotland, Sweden, with principal reef features highlighted (see two Hemse Group biostromes and an unclassified reef from the Sundre Formation). These reef structures are ideal settings for stromatoporoids because of abundance and diversity of taxa; they formed in ramp-shelf settings. Together with many Devonian stromatoporoid-rich biostromes, they represent platform features not associated with barrier formation at platform margins; platform margin reefs are much less dominated by stromatoporoids. *CM, Clathrodictyon mohicanum*; *PS, Plectostroma scaniense*; *SB, ?Stromatopora bekkeri; SV, Stromatopora venukovi; LS, Lophiostroma schmidti*; *PT, Parallelostroma typicum, SBo, Syringostromella borealis* (Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).



Principal sites	**KUPPEN, BIOSTROME** (middle Ludlow, Kershaw 1990)	**GROGARNSHUVUD, BIOSTROME** (middle Ludlow, Kershaw 1997)	**HOLMHALLAR, UNCLASSED** (upper Ludlow, Kano 1989)
Morphospecies diversity	Low; the 3 most important species (CM,PS,SB), 63% by numbers, are the largest stromatoporoids	Low; the 3 most important species (PS,SB,SV), 46% by numbers, are the largest stromatoporoids. LS is abundant but small volume	Low; the 2 most important species (PS and PT), 76% by numbers, dominate the reef
Growth styles	Two styles, under strong taxonomic control	Two styles, but species that grew tall at Kuppen, show low to high profile; nearly all low	Almost all low profile; extensive anastomosing laminar sheets
Sedimentation rate	Very low; ragged forms are rare	Very low; ragged forms are rare	Very low; stromatoporoids are large laminar forms, anastomosing due to episodic deposition
Biostratinomy	Species with tall growth forms occur more commonly as fragments. One of those (PS) also has a delicate-looking skeletal architecture	Unknown	Reef is a strong frame; debris lies chiefly between boundstone units
Coalescence	Enhanced competitive ability of low profile forms	Unknown	As Kuppen
Symbiosis with corals	Intergrown tabulate and rugose corals in 20% of stromatoporoids	Present, but extent unknown	Present, but extent unknown
Reef sediment	Principally micrite, plus crinoidal wackestone	Principally crinoidal and bryozoan grainstone	Principally crinoidal packstone & grainstone
Principal reef features	Low energy allowed tall forms	Higher energy selected for low profile forms	
	Low sedimentation rate allowed abundant growth		
	Coalescence of low profile forms gave competitive advantage		

RECONSTRUCTION OF LIVING ASSEMBLAGES

FIG. 379. *(For explanation, see facing page).*

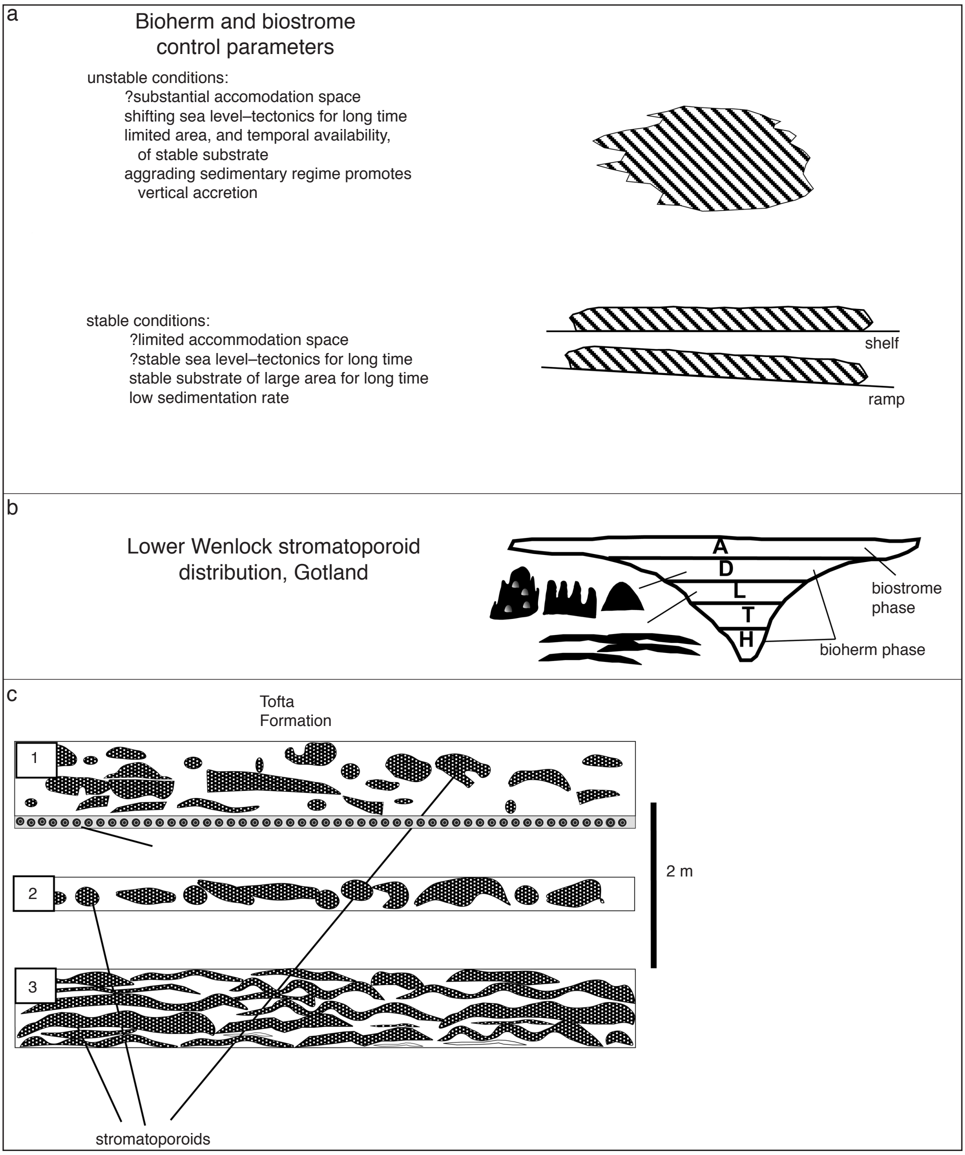


FIG. 380. Application of concepts of bioherm and biostrome in Silurian stromatoporoid reef facies. *a,* Form differences between bioherms and biostromes, demonstrating the dimensions in vertical section. Note that within these two forms, the constructing biota may consist of in-place frames, eroded debris, or a mixture of the two. Thus the biostrome and the bioherm are simply geometric objects without implication of their constructors; *b,* schematic vertical section of Högklint reef from the lower Wenlock of Gotland, Sweden, showing vertical change in form from bioherm upward into biostrome, within the same reef mass. Stromatoporoid general growth forms are added, illustrating the environmental change (relative sea-level fall) throughout the history of the reef; *H,* halysitid tabulate corals most abundant; *T,* tabulate corals of all types most abundant; *L,* laminar stromatoporoids most abundant; *D,* domical stromatoporoids most abundant; *A,* calcified algae most abundant (Kershaw, 1998; reproduced with kind permission from the Palaeontological Association); *c,* stylized examples of three biostromes from the lower Wenlock of Gotland, Sweden, showing the constructors, stromatoporoids and corals (not differentiated); *1,* contains a mixture of debris and in-place constructors; *2,* contains only debris; *3,* contains laminar-frame constructors. These illustrations demonstrate the range of constructional elements within biostromes, thereby showing that some biostromes are most appropriately classified as reefs (based on data from Kershaw, 1994b).

for large sample size in stromatoporoid studies. Biostromes are probably the richest stromatoporoid faunas, representing ideal conditions for their growth, characterized by low sedimentation rates and, presumably, widespread availability of suitable substrate.

Devonian Reef Communities and Barrier Reefs

Stromatoporoids are very abundant in Devonian reef systems, where *Amphipora* is the most abundant volumetrically (e.g., Cockbain, 1984). Although Middle Devonian reefs contain the first interpreted barriers and reef systems, and the best known of these are the occurrences in the Canning Basin (Playford & Lowry, 1966; Playford, 1980) and western Canada (e.g., Klovan, 1964; Jamieson, 1969), these mainly lack evidence of an identifiable reef core: for example, the Miette complex of Alberta (Noble, 1970, p. 540; see Fig. 378a), and the southern Belgium bioherms (Monty, Bernet-Rollande, & Maurin, 1982). Devonian reef crests typically contain relatively small numbers of stromatoporoids, with other elements, such as *Renalcis*, being equally or more important reef constructors. In the Canning Basin, the crest zone is narrow, 100–200 m wide (Wilson, 1975, p. 137), and without biozonation; whereas fore-reef slopes of up to 30° were generated by microbial constructors (Playford & Lowry, 1966, p. 71), compared to 5° slopes where reefs are not present on platform margins.

Sporadic efforts have been made using taxonomic and growth form data to apply an integrated approach to illustrate aspects of stromatoporoid community ecology (e.g., Cornet, 1975; Hoggan, 1975). Kobluk (1975) attempted a community reconstruction using crude statistical measures of association between growth forms and species, but his data did not relate species to growth forms and environments. He noted (p. 243) that some stromatoporoid morphologies occur together and others do not. Kobluk (1975, p. 259) extended life-table analysis to stromatoporoids using basal diameter as a proxy for relative age in the Devonian Miette Reef complex in Canada. Data were time-averaged within a bed, growth forms rather crudely classified, and although species/growth form data were not available, the results produced the broad conclusion that most stromatoporoids are small, with a relatively low chance of growing large. This observation is consistent with studies in other sites and ages, presumably largely attributable to fluctuating energy levels and sediment deposition rates. A feature of stromatoporoids influenced by such processes is that, as their skeletons grew, their forms commonly changed from an initial laminar shape to domical, then sometimes to bulbous, so it is important to plot growth form against size (e.g., basal diameter, see Kershaw, 1990). If this can be related to taxa, then there is a much more useful data set available for the interpretation of controls on stromatoporoid growth form, although little information is yet available.

In the most comprehensive survey so far attempted of Frasnian stromatoporoids of Belgium (Da Silva, Kershaw, & Boulvain, 2010, 2011b), the branching stromatoporoid *Stachyodes* was shown to represent approximately half of the assemblage, measured both by numbers of samples and by area of the rock occupied in vertical rock faces. Ten genera were found altogether, but only one or two genera are abundant in any one bed. These results emphasize not only the relatively low diversity of stromatoporoid assemblages, but also their importance in development of Devonian reef facies.

REGIONAL AND GLOBAL SCALE SYNECOLOGY

Stromatoporoids in Devonian Global Facies Patterns

Although reef facies may be difficult to unravel in tectonically complex terrains (Scrutton, 1977b), Devonian reefs formed mostly at platform margins (e.g., Playford, 1980, in the Canning Basin; and Scrutton, 1977a, in the United Kingdom). Significant buildups worldwide contain similar fossil assemblages (across all phyla) (e.g., Belgium, Germany [Eifel region], Alberta, Canning Basin; WILSON, 1975, p. 119). STOCK (2005) recorded provincialism of earlier Devonian stromatoporoid faunas, changing to cosmopolitanism at genus level through the Frasnian, and restriction in the Famennian. Furthermore, STOCK (2005) noted a decrease in generic diversity in the Frasnian, interpreted by him as caused by sea level rise, allowing mixing of faunas by submerging of barriers; PROSH and STEARN (1996) recognized Devonian stromatoporoid cosmopolitanism commencing earlier in the Emsian, and migration being facilitated by Early Devonian transgression across epeiric shelves. Rapid widespread migration also promotes the use of stromatoporoids as biostratigraphic tools, due to more restricted stratigraphic ranges (PROSH & STEARN, 1996), in contrast to the traditional view that stromatoporoids lack stratigraphically restricted ranges.

Stromatoporoid growth forms aid recognition of facies patterns in the Devonian Iberg reef in Germany (GISCHLER, 1995); the patterns suggest influence of southeastern trade winds and provide interpretation of the reef as an atoll. Although GISCHLER (1995, p. 185) suggested that the southeast-facing (windward) portion containing massive stromatoporoids and bulbous corals was wave-resistant, the reef rim itself is hardly preserved. Wave resistance on the constructor organisms of Devonian reefs is relatively low, so early cementation (BURCHETTE, 1981; MOUNTJOY & RIDING, 1981; WATTS, 1988b; GISCHLER, 1995) and microbial stabilization were important features. Care is therefore required in interpreting wave resistance in Devonian reef systems; the analogy between modern coral reefs and their Devonian counterparts is not reliable. KOBLUK's (1978) application of the Waltherian concept to the Miette reef near Jasper, Alberta, using statistically constrained stromatoporoid assemblages, is affected by taphonomic disturbance of the reef biota, even locally (e.g., FISCHBUCH, 1970), and reconstruction of the original assemblages is difficult.

Stromatoporoid Reefs and Sea Level Change

Stromatoporoid reefs are generally assumed to indicate shallow waters. While this is normally true for rimmed shelves and patch reef bioherms, distinguishing between ecological upward reef growth and sea level change to generate reef aggradation cannot always be achieved, and controls on biostromes remain problematic. Stromatoporoids in sequence stratigraphic analysis of Middle Devonian platform sediments of the Great Basin, United States, suggest that biostromes could grow in both transgressive and regressive settings (ELRICK, 1996, p. 403–405), which adds to the debate outlined by BRUNTON and COPPER (1994, p. 74) that reefs grow better in trangressive regimes than in regressive settings.

If stromatoporoid biostromes formed in transgressive (as well as regressive) settings, then water depth (=accommodation space), as long as sea level rise was not fast, was probably not as important as the nature of the substrate in controlling their occurrence with low sedimentation rate. Availability of suitable substrate also controlled individual stromatoporoid development, and because stromatoporoid substrate tolerance is so broad (see p. 419–480 and p. 555–567), perhaps it is not surprising that biostromes provide the richest stromatoporoid faunas. Some stromatoporoid biostromes are demonstrably shallow; two examples are: approximately 10 m water depth suggested for many European Devonian examples (BURCHETTE, 1981, p. 119); and 10–30 m water depth for upper Llandovery of Michigan (JOHNSON & MCKERROW, 1991, p. 156) and the Upper Ordovician of southern China (JOHNSON, RONG, & FOX, 1989, p. 47). In contrast, coral-dominated Silurian biostromes form in deeper water, prior to shallowing

(Desrochers & Bourque, 1989), and stromatoporoids and corals aided stabilization of steep off-reef slopes in lower Silurian biostromes of Greenland during pauses in subsidence (Sønderholm & Harland, 1989, p. 361–365), further illustrating that conditions of stability favored biostromal growth. Nestor (1995) also noted that stable environments promoted development of flattened lenticular bioherms and biostromes in the Silurian of Baltica, as in Devonian biostromes in Belgium (Tsien, 1974). There is much work to do here, because although some reefs apparently formed in regressive settings, others present conflicting data. Middle Ludlow biostromes of southeastern Gotland have been regarded as exhibiting shallow water characteristics (low mud, abundant grainstones, abundant syntaxial cement on crinoid grains, eroded biostrome tops, stacked rocky shorelines; Keeling & Kershaw, 1994; Kershaw & Keeling, 1994). However, these biostromes contain almost no algae, otherwise common in shallow Silurian facies; that they may have grown in deepening water on flooding surfaces and acquired their shallow water features during later regression is supported by the recognition of an oceanic S-state during this interval (Jeppsson, 1990; Jeppsson, Aldridge, & Dorning, 1995), one feature of which is slightly higher sea level. Clearly, no reliance can be placed on biostromes as general indicators of regressive systems. Whether stromatoporoid-rich deposits can be related to suggestions of orbitally forced sea level change for the Givetian and Frasnian (e.g., Marshall, Rogers, & Whiteley, 1996, p. 461) is another topic requiring further study.

CONCLUSIONS

Though stromatoporoids have complex paleoecological aspects, they are valuable tools in paleoenvironmental interpretation, at various scales. There is much more detailed work required to fully realize their potential, but the information presented here should provide a basis for investigators to apply stromatoporoids in their analyses of paleoenvironments.

ACKNOWLEDGMENTS

Steve Kershaw's work on stromatoporoids began under supervision from Robert Riding. Discussions on various aspects of calcified sponge paleobiology and their facies, with Ron West (Manhattan, Kansas), Colin Stearn (Montreal), Lennart Jeppsson (Lund), Mike Keeling (ex-Brunel), Frank Brunton (Kingston, Ontario), and Barry Webby (Macquarie, NSW) have substantially enhanced ideas presented here. Field work on Gotland was facilitated by the Allekvia Field centre, now sadly closed, and its administrators at Lund University are warmly thanked.

PALEOBIOGEOGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

CARL W. STOCK, HELDUR NESTOR, and B. D. WEBBY

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 herein (Labechiida, p. 709–754; Clathrodictyida, p. 755–768; Actinostromatida, p. 769–779;

Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida, and Genera With Uncertain Affinities, p. 781–836).

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), and see Webby in Nestor and Webby (2013). Also Bogoyavlenskaya and Lobanov (1990), Bogoyavlenskaya (2001a), 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, Cooper, & 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, 1984a). 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, 1984a, 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 paleogeographic reconstructions, based on paleomagnetic 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 on p. 582–583).

Bogoyavlenskaya (2001a) 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

TABLE 33. Geographical distribution of stromatoporoid (labechiid only) assemblages in the Darriwilian Stage (Middle Ordovician). The seven middle Darriwilian–upper Darriwilian sites are represented in Figure 381 by *black circles* (numbered as indicated here); †genera that were the only forms that apparently did not survive into the Late Ordovician (Stock, Nestor, & Webby, 2012).

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							+

Ashgill coral and stromatoporoid associations and local reefs occur (BOL'SHAKOVA & ULITINA, 1985), were anomalous. Overall, the spread of Ordovician stromatoporoids has been found to be within limits of near 30° N and S of the paleoequator (WEBBY, 1980). KIESSLING (2001a) 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, and the latest published global maps of TORSVIK and COCKS (2013a, fig. 12, and 2013b, fig. 2.12, 2.14, 2.15), which show representations of north China, south China, and Tarim as discrete, peri-Gondwanan island-type continental blocks that occupy positions in low paleolatitudes, even straddling the paleoequator, rather than having a close association with Gondwana. Perhaps it is also significant that these offshore, paleoequatorial, peri-Gondwanan sites exhibit somewhat more diversified Middle–Late Ordovician stromatoporoid faunas.

The geographical distribution of the Ordovician stromatoporoid genera is compiled in three tables, representing the late Middle Ordovician (mid–late Darriwilian) associations (Table 33), the early Late Ordovician (Sandbian) assemblages (Table 34), and the latest Late Ordovician (Katian and

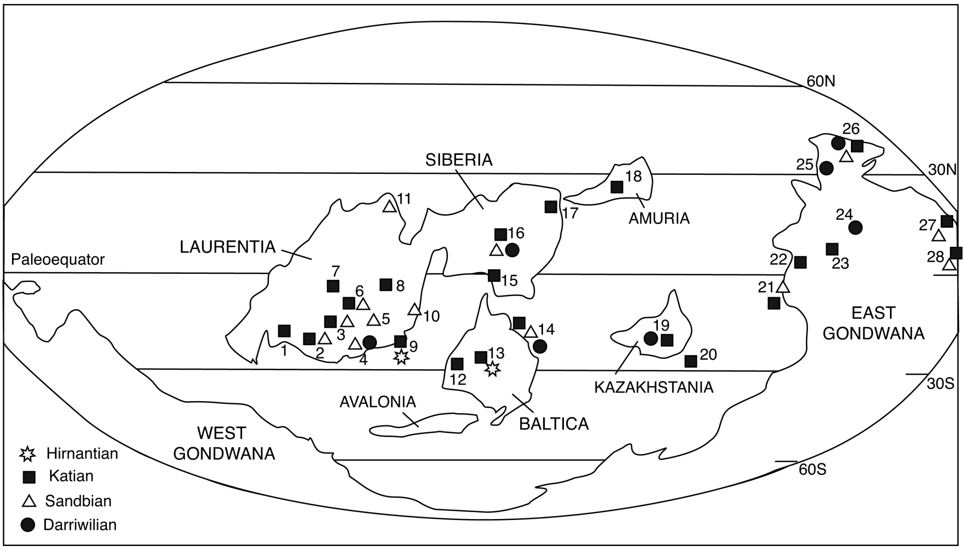


FIG. 381. Ordovician paleobiogeographic map based on GOLONKA's (2002) reconstruction showing the distribution of Middle Ordovician–Upper Ordovician stromatoporoid assemblages. Note the clustering of Ordovician sites in low paleolatitudes, mainly between 30° N and S. Nevertheless, GOLONKA's "East Gondwana" is not likely to have been part of such a large, undivided block through Ordovician time, given that some parts, such as North China, South China, and Tarim, now seem to be confirmed (e.g., TORSVIK & COCKS, 2013) as remaining discrete, peri-Gondwanan blocks throughout this time interval. Key to symbols: *black circles,* mid–late Darriwilian; *open triangles,* Sandbian; *black squares,* Katian; *open, seven-pointed stars,* Hirnantian; localities: *1,* Texas and New Mexico; *2,* Alabama, Kentucky, and Tennessee; *3,* Ohio, Indiana, Iowa, and Michigan; *4,* Vermont, New York, and Pennsylvania; *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 (Stock, Nestor, & Webby, 2012).

Hirnantian) associations (Table 35). The distribution of the stromatoporoid localities is plotted on the simplified base map (Fig. 381).

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 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 33]), involving the differentiation of five of the seven known families of labechiids and containing more than half of the known genera (WEBBY, 2004b; and see Early Evolution of Ordovician Paleozoic Stromatoporoidea, p. 575–589).

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. 381, 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. 381, site no. 24) were earlier suggested to have a pre-Chazyan Whiterockian age (Wongwanich & others, 1983; Stait & Burrett, 1984). However, more complete correlation

TABLE 34. 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 381; *genera that made their first appearances in the Sandbian (Stock, Nestor, & Webby, 2012).

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*					+	

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

Three other middle Darriwilian–late Darriwilian sites have been recorded in Eurasia (Table 33), 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, COOPER, & others, 2004; see also p. 575–592). 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).

TABLE 34 (*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*							

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 further discussion on p. 575–589). *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, 2004b). The global distribution of Sandbian genera is shown in Table 34. 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 Stromatoceriidae, 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 34 and Fig. 381), 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, COOPER, & 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 34 and Fig. 381). 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. 381), 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 on p. 575–590). 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. 381). 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 Maliecikan 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 8 myr, which is much longer than the preceding Sandbian Stage (GRADSTEIN & others, 2004, 2012). The global distribution is represented by the occurrences of genera from 22 sites, shown in Table 37 and Figure

TABLE 35. 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 381 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 Fig. 381 by *open, seven-pointed stars);* genera that made their first appearances in the Katian and Hirnatian are indicated with an asterisk (*) and hash mark (#), respectively (Stock, Nestor, & Webby, 2012).

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		+	+		+	+	+				
#*Quasiaulacera*							+				
**Alleynodictyon*											
Cryptophragmus											
Ludictyon											
Thamnobeatricea											
Lophiostroma											+
Dermatostroma		+	+								
Clathrodictyida											
**Clathrodictyon*					+		+	+	+	+	
**Stelodictyon*											+?
**Ecclimadictyon*				+	+			+		+	+?
Camptodictyon											
Plexodictyon											
Labyrinthodictyon											
Actinostromatida											
**Plumatalinia*									+		

381, 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. Three clathrodictyid genera, *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* 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 also p. 575–592). 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 appearance also of the genus *Plumatalinia* may mark the beginnings

TABLE 35 (*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	+										+	+	
#*Quasiaulacera*												+	
**Alleynodictyon*									+	+	+		
Cryptophragmus	+												
Ludictyon			+										
Thamnobeatricea											+		
Lophiostroma	+		+			+							
Dermatostroma													
Clathrodictyida													
**Clathrodictyon*			+					+	+	+	+	+	+
**Stelodictyon*								+		+?			+
**Ecclimadictyon*				+?	+?		+	+	+	+	+	+	+
Camptodictyon		+								+			
Plexodictyon										+?			
Labyrinthodictyon												+	
Actinostromatida													
**Plumatalinia*													

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 on p. 589–590).

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). 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, 1979c), 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 on p. 837). 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, 1977a). 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. 381), 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 (1960c), 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. amzassense,* 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, 1971b), 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 (1992) concluded 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 on p. 575–592). 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 37) 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, 1964a, 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

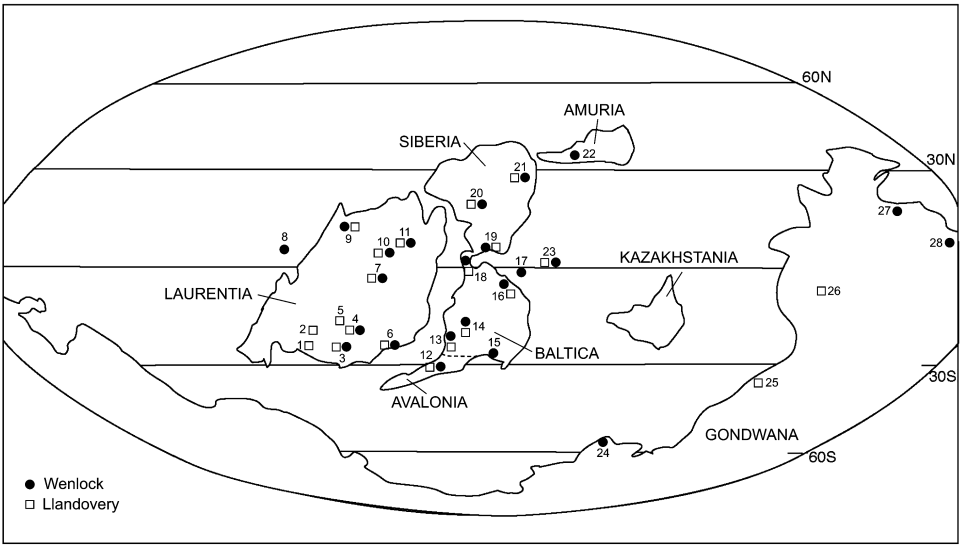


Fig. 382. Geographical distribution of stromatoporoids in the lower Silurian (Llandovery, Wenlock). The names of the localities are shown in Tables 37 and 38; *dashed line* separates cratons of Avalonia and Baltica (Stock, Nestor, & Webby, 2012).

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).

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, 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, 1886a, 1889, 1891a, 1892); Ireland (Nestor, 1999a); Norway (Mori, 1978); Gotland Island (Mori, 1968, 1970); Estonia (Riabinin, 1951; Nestor, 1964a, 1966a, 1990b); Podolia (Riabinin, 1953; Bol'shakova, 1973; Bogoyavlenskaya, 1969a; Bogoyavlenskaya in Tsegelnjuk & others, 1983); Bohemia (May, 2005); Urals (Bogoyavlenskaya, 1973a, 1976); Novaya Zemlya (Nestor, 1981b, 1983); Siberian Platform (Nestor, 1976; Khromykh in Tesakov & others, 1980, 1985); Altai and Salair (Khalfina, 1961b); Tuva (Bogoyavlenskaya, 1971b, 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, 1978b; 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 on stromatoporoids from Severnaya Zemlya (NESTOR's data from 1983) and from Alabama, Ohio, Oklahoma, Iowa, and northern Michigan (STOCK and NESTOR's data from 1998–1999) are also used in the present review.

The main districts of stromatoporoid occurrences are plotted on the simplified base maps of GOLONKA (2002) (Fig. 382–383). Geographical distribution of the Silurian stromatoporoid genera is represented in Tables 36–39.

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. 382) 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

TABLE 36. 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; *quotation marks,* questionable occurrences) (adapted from Stock, Nestor, & Webby, 2012).

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										
Tarphystroma						+				
Clathrodictyida										
Actinodictyon							x		x	
Camptodictyon						+				
Clathrodictyon	x	+	+	+	+	+			+	+
"Clavidictyon"				+	+	+				
Desmidodictyon						+				
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"										

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 stromatopo-

TABLE 36 (*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				+
Tarphystroma											
Clathrodictyida											
Actinodictyon											
Camptodictyon			+								
Clathrodictyon		+	+		+	+	+	+	+		+
"Clavidictyon"							+				+
Desmidodictyon											
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				

roid 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.

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

TABLE 37. Distribution of stromatoporoid genera in the Wenlock (+, occurrences of Wenlock genera; ?, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

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 37 (*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			+	+	+						+

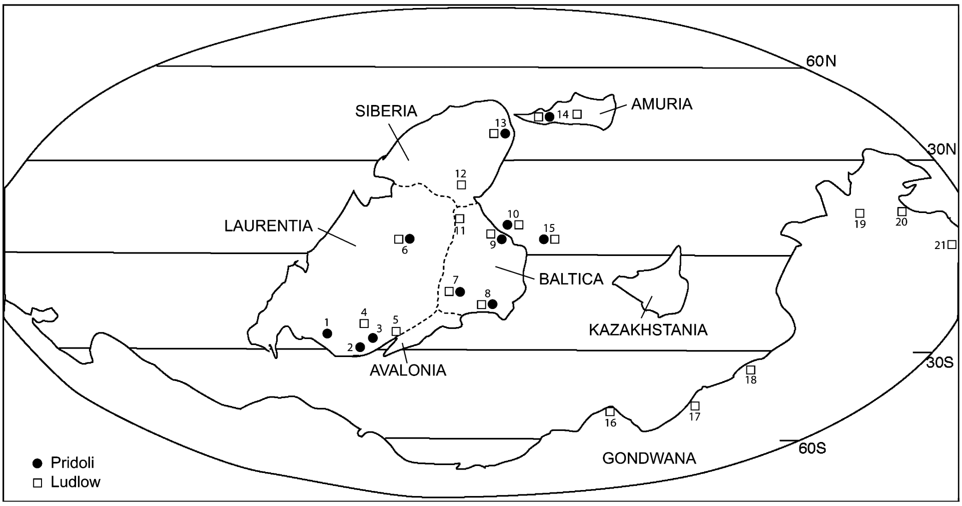


FIG. 383. Geographical distribution of stromatoporoids in the upper Silurian. The names of the localities are shown in Tables 39 and 40; *dashed lines* separate named cratons that during the late Silurian were merged to form the Laurussia paleocontinent (Stock, Nestor, & Webby, 2012).

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 TORSVIK and COCKS (2013b), however, show a more convincing Wenlock relationship, with Bohemia in a more northerly position (27–28° S) (see also NESTOR & WEBBY, 2013, fig. 7.10), almost connected to a part of the African margin of Gondwana.

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 37). 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 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 *Plecto-*

stroma 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. 383): 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 Torsvik and Cocks (2013b) are employed.

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 sensu stricto (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 sensu lato (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

TABLE 38. Distribution of stromatoporoid genera in the Ludlow (+, occurrences of Ludlow genera; *?*, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

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"				+				
Parallelostroma		+		+	+	+		+
Amphiporida								
Amphipora s.l.			+	+			+	
Clathrodictyella					+		+	+
Uncertain affinities								
Clavidictyon s.s.								
Praeidiostroma							+	

recorded from North America, Siberian, and eastern European platforms. Third, the genus *Lophiostroma* (order Labechiida, family Lophiostromatidae) reappears in the Ludlow of Gotland, Estonia, Podolia, and Bosporus district of Turkey, although this genus had only been present previously in the Ordovician.

TABLE 38 (*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										

PRIDOLI

In the Pridoli, the regressive trend of development continued in many parts of the world, and occurrences of stromatoporoids became less common (Fig. 383). Stromatoporoids have not been described from the Pridoli of the Gondwana supercontinent or the Siberian craton, except Salair. In North America,

TABLE 39. Distribution of stromatoporoid genera in the Pridoli (+, occurrences of Pridoli genera; ?, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

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								+			

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

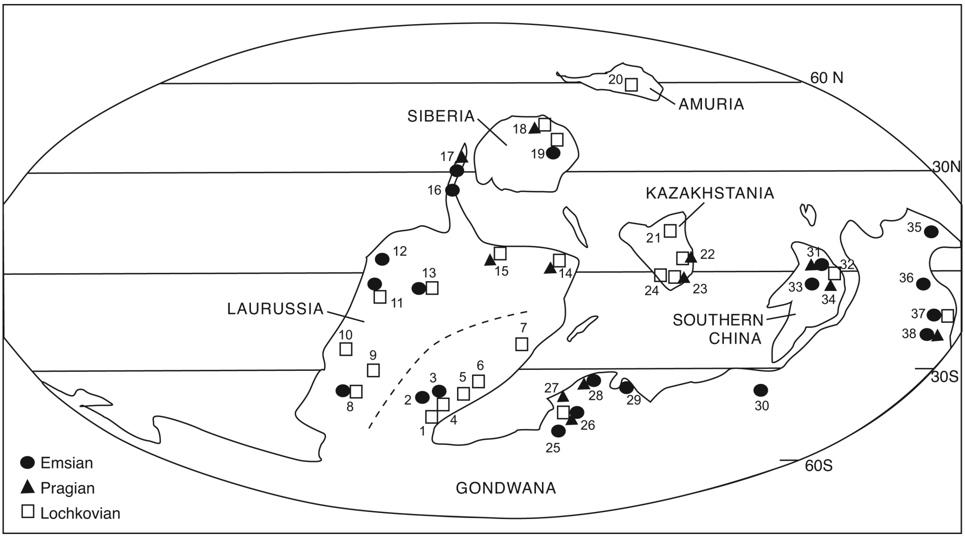


FIG. 384. Geographic distribution of Lower Devonian stromatoporoids; *dashed line* separates the two realms; localities 1–7 are in the Eastern Americas Realm, and localities 8–38 are in the Old World Realm. Key to localities: *1,* Virginia; *2,* Michigan; *3,* southern Ontario; *4,* New York; *5,* Maine; *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 (Stock, Nestor, & Webby, 2012).

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.

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

TABLE 40. 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
Clathrodictyida								
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 40 (*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

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 (see Clathrodictyida, p. 755–758) or may derive from a different line of descent from post-Devonian stromatoporoid-type hypercalcified sponges (see p. 193–208). Generic diversity peaked in the Eifelian but was high from the Emsian through Frasnian (Table 40).

In Devonian paleogeography, a new tectonic plate developed. 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 40.

The southernmost occurrence of Lochkovian stromatoporoids is in Virginia (Fig. 384, no. 2), and the northernmost is in Mongolia (Fig. 384, no. 17), for a range of 105°. The Pragian range is 90°, with extremes in northern Spain (Fig. 384, no. 23) and Altai-Sayan and Salair (Fig. 384, no. 15). The range remained at 90° in the Emsian, but shifted slightly southward, with southern Spain being southernmost (Fig. 384, no. 22) and the Ulachan-Sis Range and the Kuznetsk Basin being equally northernmost (Fig. 384, no. 14, 16).

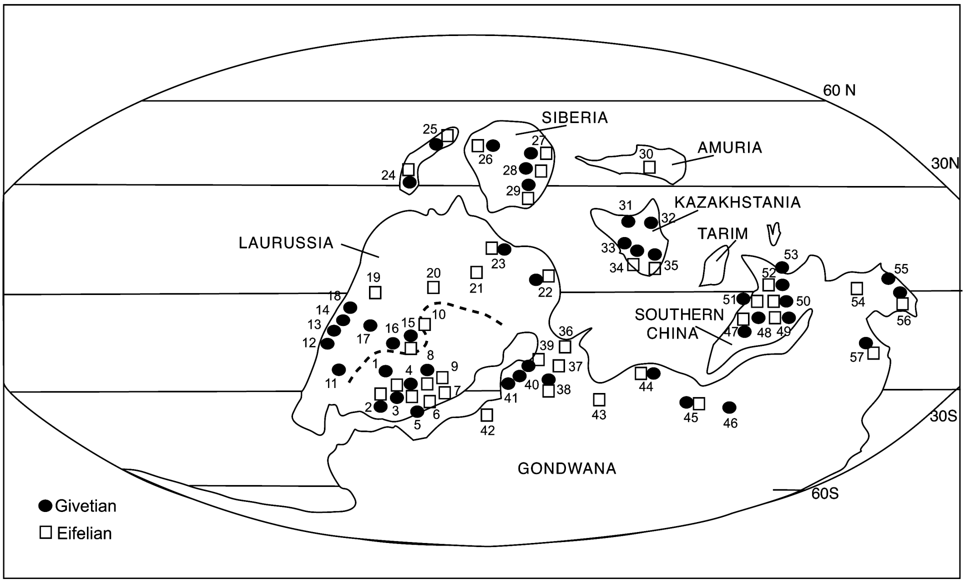


Fig. 385. Geographic distribution of Middle Devonian stromatoporoids. The *dashed line* separates the two realms; localities 1–10 are in the Eastern Americas Realm, and all the known localities (11–57) worldwide are in the Old World Realm. Key to localities: *1,* Iowa; *2,* Missouri; *3,* Illinois; *4,* 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 (Stock, Nestor, & Webby, 2012).

Eifelian stromatoporoids range from Morocco (Fig. 385, no. 40) to the Ulachan-Sis and Sette-Daban Ranges (Fig. 385, 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. 385, 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. 386, no. 16) and the southernmost occurrence being in both Nevada and Afghanistan (Fig. 386, no. 2, 43). The southern extent of Famennian stromatoporoids was limited to Germany (Fig. 386, 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 41 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

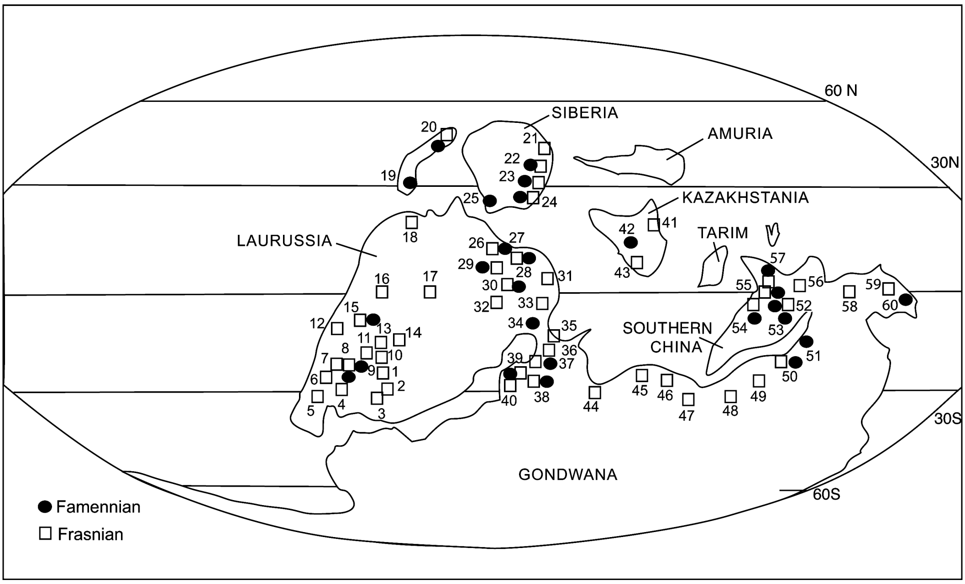


FIG. 386. Geographic distribution of Upper Devonian stromatoporoids. Key to localities: *1,* Nebraska; *2,* Iowa; *3,* Missouri; *4,* New Mexico; *5,* Sonora; *6,* Arizona; *7,* Nevada; *8,* Utah; *9,* Wyoming; *10,* North Dakota; *11,* Montana; *12,* Washington; *13,* Saskatchewan; *14,* Manitoba; *15,* 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 (Stock, Nestor, & Webby, 2012).

of the tropical and subtropical climates in which the stromatoporoids dwelled. He also suggested 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 41 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,

TABLE 41. Paleolatitudinal ranges of Devonian stromatoporoids by stage (Stock, Nestor, & Webby, 2012).

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°

due at least in part to the onset of glaciation (e.g., CROWELL, 1999). Thus, the latitudinal 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. 382–384) with a collision (an accretion event) of the Siberian, Baltica, Avalonian, and Laurentian cratons by the Ludlow, and then in the Early Devonian, the Siberian craton was 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. 385)—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, 1997b). In addition, on the Gondwanan margin of Morocco, stromatoporoids invaded the region for a comparatively short time in the Middle Devonian (Eifelian) (see Fig. 385). A noticeable 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. 384–386).

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. 384–385) 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 EAR, 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 40). 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 40).

The Frasnian–Famennian extinction profoundly affected the stromatoporoids; a total of 24 Frasnian genera became extinct before the Famennian (Table 40). During the Famennian, stromatoporoids were absent from the area of the former EAR; Stock (1997b) concluded that the influx of siliciclastic sediments produced during the Acadian Orogeny and global cooling contributed to this absence.

Table 42. Degrees of endemism of stromatoporoid genera through the Devonian; *OWR,* Old World Realm; *EAR,* Eastern Americas Realm; *NA,* not applicable, as stromatoporoids absent from area of EAR (Stock, Nestor, & Webby, 2012).

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

During the Famennian, stromatoporoids retreated from many areas of Laurussia and Gondwana (Fig. 386). 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 (1982a) 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 Extinction Patterns of the Paleozoic Stromatoporoidea, p. 600, Table 30; 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 (1982a) 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 42 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 42). 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 40).

CONCLUSIONS

CARL W. STOCK, HELDUR NESTOR, & B. D. WEBBY

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 (see p. 681). 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 (28° S; Anticosti Island); and western Baltica (30° S; Estonia) (Fig. 381). 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, 2004b).

The second is the complete absence of stromatoporoids from Gondwana during the Pridoli (Fig. 383), and the third is the complete disappearance of stromatoporoids from the Eastern Americas Realm during the Pragian (Fig. 384). 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 (see p. 686).

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. 381) 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 (see p. 681), 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 (see p. 686).

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TECHNIQUES OF STUDY: COLLECTION, PREPARATION, AND ANALYSIS OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

FIELD OBSERVATIONS AND COLLECTING

COLLECTING IN CARBONATES OF THE REEF FACIES

Most stromatoporoids are preserved in carbonate sediments formed within a reef environment. They are, therefore, most common in unbedded or poorly bedded limestones and dolomites of the reef facies, or in bedded carbonates deposited in adjacent lagoonal or foreslope deposits. In such carbonates, the fossils do not weather free of the matrix and must be extracted, usually in fragments, by breaking the rock. Where the rock is broken in fragments in quarrying, this may not be difficult, but in natural outcrops where the unbedded reefal facies commonly forms smooth-surfaced domes, it may be almost impossible with a geologist's hammer. Where a specimen must be extracted to satisfy a sampling scheme, a portable circular saw with a cement-cutting blade can be used to make grooves around the sample and allow a cold chisel to chip it out. The saw, however, generates much rock dust, therefore the operator should wear a protective mask. Generally, in such host rocks, the collector must be satisfied with fragments that will provide enough material for the two thin sections required for identification.

In many reef outcrops, the shapes of stromatoporoids can be observed only in a random cross section. Because the whole specimen can rarely be collected, the impression of shape that such sections allow should be recorded in notes or by taking photographs before collection. The study of stromatoporoids in cores from reef reservoirs in the subsurface involves similar problems, although the regularity of the core surface may make estimates of shape in three dimensions easier. Samples must be cut from the core with a rock saw. Core storage agencies will generally allow only a small sample to be cut out of the core (for example, a cubic inch every linear foot or 15 ml/0.3 m).

In areas of cold climate, such as high altitudes and latitudes, carbonate outcrops are commonly covered with a thin tufa that obscures fossils. Fresh rock faces recently exposed by frost wedging that show the rock texture better can usually be found in these areas, but the surface may have to be broken with a hammer to reveal the fossils within. Reef textures and fossils are most clearly revealed in outcrops repeatedly abraded by flooding rivers, tides and waves, and winds charged with sand.

COLLECTING IN FOREREEF SLOPES

The carbonates deposited at the margins of Paleozoic reef complexes are commonly affected by pervasive dolomitization that reduces stromatoporoids to so-called ghosts. The faunas of these margins are commonly much better preserved in debris blocks that have slumped from the steep reef front onto the forereef slope (MOUNTJOY & others, 1972; CONAGHAN & others, 1976). Reef blocks several meters across may have traveled several kilometers downslope into basinal deposits and now constitute beds of megabreccia. Well-preserved stromatoporoid faunas have been described from such debris flow deposits (SCRIVASTAVA, STEARN, & MOUNTJOY, 1972; POLAN & STEARN, 1984).

The depositional slope on which benthic organisms (such as stromatoporoids in position of growth) grew can be estimated by measuring growth axes. If it is assumed that the growth axis of domical and dendroid stromatoporoids is on average vertical (that is, they are geotropic or phototropic), then the divergence between the axis and a line perpendicular to the bedding will indicate the slope on which they grew. The orientation of the growth axis can be determined if the stromatoporoid is exposed in more than one plane and its pole measured with a simple device. A dowel that can be oriented along the growth axis and fixed at one end temporarily with plasticine is attached at right angles at the free end to a flat disk whose strike and dip can be measured with a Brunton compass. From these data, the poles of the bedding and growth axes can be plotted on a stereonet. In deformed beds, the post-depositional tilt of the beds must be compensated for by modifying the poles of growth by the strike and dip of the bed using a stereonet.

ORIENTATION

Kobluk (1974) measured the azimuths of dendroid stromatoporoids on bedding planes in the Miette Reef Complex in Alberta, Canada. He analyzed the results by a chi-square test to show that the stems had a preferred northwest orientation. Kobluk, Bottjer, and Risk (1977) measured the proportion between domical stromatoporoids of various sizes that were in growth position and those that were disoriented. They found no difference in mean size between those that were turned over and those in growth position. The toppled or upright position of stromatoporoids has also been measured by Kershaw (1981) at the Kuppen biostrome in Gotland, Sweden, and by Kershaw and Riding (1980) in Devon, England.

MARLS

In argillaceous limestone successions (marls), stromatoporoids may weather free or be easily extracted from the soft matrix. Such successions are found in the Silurian rocks of Scandinavia and Britain. There the growth forms of stromatoporoids are much easier to study, and surfaces of the skeletons can be examined in detail. Many of the studies of the relationship of growth form, environment, and taxonomy have been made in these areas (for example, Kershaw 1981, 1984, 1993; Kershaw & Keeling, 1994) and are discussed elsewhere (see External Morphology of Paleozoic Stromatoporoids, p. 419–486).

STATISTICALLY CONTROLLED SAMPLING

Although various research workers have advocated a statistical approach to the study of the distribution of stromatoporoid taxa or shapes in reefs, local conditions rarely make random sampling, a requirement of most statistical tests, possible over a large area. Stromatoporoids on extensively exposed horizontal bedding planes have been divided into quadrats and surveyed as to shape and size over areas of several tens of square meters. Quarry faces and mountain cliffs may expose large vertical sections of a reef deposit but are only rarely accessible for random sampling over extensive horizontal or vertical distances.

Estimates of the proportion or density of various growth forms or types of organisms on a face or bedding plane can be made by drawing random lines, or stretching strings randomly, across a face. The constituents along the line are identified. Either the total length of the line lying upon each constituent is summed, or the line is marked at a regular interval (e.g., every 5 cm), the constituent beneath each mark is recorded, and the number of occurrences is taken as a measure of the relative abundance of each constituent. The latter method, a form of point counting, is the quicker of the two (Polan & Stearn, 1984). Line intercept transects were also used by Edinger and others (2002) in their survey of Onandaga reefs. Sandström (1998) drew sketches of outcrops on Gotland at 1:5 scale and point counted these sketches to quantify the identity and shape of the stromatoporoids. Because stromatoporoids can rarely be identified taxonomically on external appearance alone, methods like these that depend on identification without collection and processing do not give information for plotting the distribution of species in a reef.

MAPPING

Detailed maps of the distribution of stromatoporoid shapes and taxa on small representative areas of biostromes and bioherms have been made by many investigators. Only studies in which the occurrence of stromatoporoids is essential, rather than incidental, are mentioned here. Kershaw (1984, 1990) and Kano (1989, 1990) have published maps showing the distribution of stromatoporoids in the reefs of Gotland. Schneider and Ausich (2002) have mapped the distribution of various framebuilders, including stromatoporoids, in the lower Silurian Brassfield Formation of Ohio, USA. Fagerstrom and Bradshaw (2002) drew maps of the distribution of Early Devonian stromatoporoids in the reef facies at Reefton, New Zealand. Stromatoporoids are prominent in the maps of Late Ordovician patch reefs in Alabama presented by Stock and his colleagues (Stock & Benson, 1982; Crow & others, 2001).

GENERAL

The usual precautions of labeling and cataloguing that apply to all fossils are not discussed here. Because specimens broken from carbonates rarely are complete or show details of surfaces, wrapping of individual specimens is usually unnecessary, but pieces broken from a single large specimen should be kept together if an approximation of the abundance of the individual taxa in a collection is to be obtained from the contents of the collection bag.

A collection of papers on various laboratory techniques for preparation of fossils published as Paleontological Society Special Publication 4 (Feldman, Chapman, & Hannibal, 1989) contains descriptions of many procedures relevant to stromatoporoids. A similar collection of papers was assembled earlier by Kummel and Raup (1965).

THIN SECTIONS

SIZE AND THICKNESS

Since Nicholson introduced the method about 1875, stromatoporoid workers have used thin sections viewed in transmitted light to identify these fossils (Wells in Feldman, Chapman & Hannibal, 1989). Two sections are required to define the skeletal elements in three dimensions; one parallel to the growth surface (tangential) and the other perpendicular to it (longitudinal). Large thin sections are better than small ones, because they show the local variation of structural elements in the various phases of the skeleton. Lecompte (1951–1952) studied sections that were up to 5 cm × 10 cm. However, such large sections are very difficult to make uniformly thin enough to show microstructure clearly. Such sections are also difficult to store. The most useful size for thin sections is 44 mm × 75 mm, as commercially available cabinets for storing 22 mm × 75 mm slides can be modified to hold them. Sections ground to standard petrographic thickness of 30 µm are too thin to show structural elements clearly. The appropriate thickness of the section can only be determined experimentally as it depends on the particular type of preservation but should be such that the structural elements are translucent, their microstructure is clear, their edges are in sharp focus in photographs at ×10 magnification, and the crystal boundaries in the galleries are sharp. Most illustrations that appear out of focus are taken of thin sections that are too thick. Unfortunately, sections of the holotypes of older taxa are commonly too thick to show microstructure clearly.

ADHESIVES

Until the middle of the 20th century, thin sections were made exclusively with Canada Balsam (a resin made from balsam firs). If the adhesive is properly cooked, such sections are archival, and many in collections of the late 1800s are in pristine condition. In the 1950s, thermoplastics, such as Lakeside 70, were used to cement the specimen to the slide. These were convenient but were difficult to clear of bubbles. Covering agents used at this time included the commercial product Permount, which proved unsatisfactory because it became opaque after about 20 years. Beginning about 1960, epoxy cements such as Araldite became the choice of many preparators, as, once set, they were impervious to heat or chemicals. Plastic solutions that were allowed to flow over the surface and set were also used to form a clear membrane on the thinned specimen in place of a cover glass. About 1990, adhesives that set by the action of ultraviolet radiation became generally available and proved to be a great convenience for thin-section preparation. The adhesive film between the specimen and glass slide is set by ultraviolet light shone through the glass slide for a few minutes. It sets only under the specimen where not exposed to the air and the excess cement around the specimen can be wiped off with methanol. If the cover glass is to be permanently attached, the same adhesive can be used. Canada Balsam remains the most reliable, long lasting, and easily removable cement for cover glasses.

IMPREGNATION

In stromatoporoids that have been dolomitized, the galleries and pores of the stromatoporoid skeleton are empty, and they trap air bubbles and abrasive in the cements used in making thin sections. The pores must be filled before the specimen is cemented to the glass to exclude these undesirable contaminants. In the traditional method, the specimen is immersed in a low-viscosity, slow-setting epoxy treated with hardener and is placed in a chamber in which pressure can be reduced by a vacuum pump (Wells in Feldman, Chapman, & Hannibal, 1989, gave trade names of products). As ambient pressure is reduced, the air escapes from the pores, and the epoxy takes its place. Unfortunately, the low pressure produced by the vacuum pump may evaporate the more volatile constituents of the epoxy mixture, and the proper proportions of hardener and resin that ensure setting may be modified. If the pores are not interconnected, the impregnating epoxy may fail to reach them all. Stearn (1996) proposed a method using melted paraffin wax to fill the pores on the polished surface and diamond-faced laps to eliminate loose abrasive. Excess wax is scraped from the surface with a blade, and the specimen is cemented to the glass with an ultraviolet-setting adhesive such as Locktite.

SERIAL SECTIONS

Successive, parallel, thin sections or polished surfaces cut through a fossil specimen allow it to be reconstructed in three dimensions. Computer programs are available to assist in combining the multiple images into a three-dimensional reconstruction. This technique may involve the destruction of the specimen by grinding it away to produce the successive polished surfaces, or closely spaced thin sections may be prepared by repeatedly cementing the specimen to a microscope slide and slicing it off as close to the slide as possible. The spacing of the sections is as close as the thickness of the blade. This latter procedure was used by Stearn (1997c) to prepare a set of serial thin sections to act as neotypes for *Amphipora*. Another method of preparing three-dimensional reconstructions of large specimens of corals that could be applied to stromatoporoids was described by Hammer (1999). He placed successive polished sections of the tabulate coral *Catenipora* on a scanner and used a computer program to produce a three-dimensional image of its growth.

A nondestructive technique using computer tomography to delineate the interior of a stromatoporoid has been tested by Beuck and others (2008). The C-T scan allowed the authors to reconstruct the trace of a boring in a stromatoporoid skeleton from Gotland in three dimensions. Differences between the physical properties of the boring and stromatoporoid skeleton allowed its reconstruction, but the method does not reveal the internal structure of the stromatoporoid.

REFLECTED LIGHT

Nearly all thin sections of stromatoporoids are best observed in transmitted light at magnifications of ×10 to ×50, but some dolomitized specimens show much more detail in reflected light against a white background. Lights are directed at the thin section surface, about 45° from the plane of the section. Photography under these conditions is difficult, as the level of the light reflected and contrast are low.

ULTRATHIN SECTIONS

In sections of several tens of micrometers thickness, the high birefringence of calcite makes resolution of the crystal boundaries within the structural elements difficult. To examine this aspect of the microstructure of corals, Lafuste (1970) introduced the technique of polishing the face of the specimen that is to be adhered to the slide and grinding it carefully to a thickness of two or three micrometers. At this thickness, the interference colors of calcite under crossed polars are grey and yellow. Lafuste's work in the 1970s and 1980s was largely applied to tabulate and rugosan corals and convinced him that his slides showed the preservation of original biocrystals. Many of the elongate calcite crystals had a shape he referred to as dented (*bosselure*) with small embayments down their length. The technique was applied to stromatoporoids by Stearn and Mah (1987) to investigate the nature of the specks in structural elements (see Fig. 335.2). Mistiaen (1994) illustrated many ultrathin sections of stromatoporoids in his discussion of the density of the skeleton.

STATISTICAL EVALUATION OF TAXONOMIC DIFFERENCES

Relatively little work has been done on specifying the variability of the stromatoporoid skeleton statistically or on using the parameters that define this variability to distinguish between species or other taxa. Fagerstrom and Saxena (1973) used statistical tests to assess whether the variability within a single section of *Syringostroma sherzeri* was representative of the whole of the skeleton. Fagerstrom (1982) made extensive measurements of the structural elements of specimens and calculated similarity coefficients to distinguish between and to group taxa of stromatoporoids from the Detroit River Group. Stearn (1989b) recorded the intraspecific variability of stromatoporoids and related organisms in terms of Simpson's coefficient of variability. The most extensive use of statistics to distinguish between species has been by Stock and Burry-Stock (Stock & Burry-Stock, 1998, 2001; Stock, 1991, 1997a) who have applied multivariate procedures to separate species in large collections from the Lower Devonian of New York. They used cluster analysis in an exhaustive study of 103 specimens of *Habrostroma* to distinguish the two species, *H. centrotum* and *H. consimile,* and to rate by canonical correlation analysis which of the skeletal features were most useful in distinguishing them (Stock & Burry-Stock, 2001). Research into stromatoporoid phylogeny using concepts of cladogenesis has been limited, probably owing to the small number of skeletal characters that these fossils present for analysis. The only cladogram of stromatoporoid genera published so far is based on 16 characters of the labechiids (Webby, 1994). Wolniewicz (2010) has used an image analysis computer program that performs measurements of skeletal elements of stromatoporoids, distinguishing the structures from the sparry calcite filling galleries. The program's software allows rapid analysis of the measurements taken from photographs and is more objective than traditional measurements taken by an operator using a microscope. He has also written on the value of the usual measurements for stromatoporoid taxonomy (Wolniewicz, 2013).

CATHODOLUMINESCENCE

If thin sections are uncovered, their microstructure can be investigated under the microscope by cold cathode luminescence. This technique is particularly suitable for assessing the degree of alteration of the skeleton and delineating the crystal boundaries (Kershaw, 1994a). The reasons why certain calcite crystals luminesce with different colors is still unclear, but most carbonate workers believe it is due to slight impurities in their crystal lattices. Kershaw's studies (1994a) confirmed that different stromatoporoids secreted skeletons of aragonite or high magnesium calcite with various proportions of magnesium.

Attempts (by this author) to detect organic matter within the skeleton of stromatoporoids by stimulating fluorescence in ultraviolet light under the microscope showed no response from thin sections. Stromatoporoids, like scleractinian corals, seem to have been able to secrete skeletal carbonates free of organic matter. However, Clark (2005) reported organic matrix dispersed through a stromatoporoid skeleton.

SCANNING ELECTRON MICROSCOPY

The relationship between the arrangement of crystals and the structure and microstructure of the stromatoporoid skeleton can be studied on polished surfaces that have been etched or on broken surfaces with the scanning electron microscope (SEM). The technique was described by Stearn (1977). Although other workers polished the specimen highly and etched it with weak acids such as acetic or formic, Stearn (1977) found that good results were obtained by grinding with 600 grain silicon carbide and etching with 10% hydrochloric acid for 10 seconds. The specimen surface is then coated with a metallic film (usually gold-palladium) or carbon and placed in the SEM. The relief produced by the differential etching is imaged by the microscope at magnifications up to the tens of thousand times, but for most microstructural studies, magnifications of a few hundred times are most useful (see Fig. 335.1; Fig. 344–348). To test whether textures seen in etched specimens are artifacts of the preparation process, specimens may be fractured and the broken surface examined. Some investigators, to insure that the fracture is random and not guided by fine pores and cracks, have soaked the specimen in a penetrating liquid of very low viscosity (such as ethyl ether) and immersed it in liquid nitrogen to freeze the liquid before fracturing the specimen (Stearn & Mah, 1987).

Direct comparison of transmitted light images with scanning electron micrographs of the same part of the specimen is difficult. Stearn (1977) described a technique of cutting a disk about 5 mm in diameter from a thin section with an abrasive jet charged with alumina, such as those used to excavate small fossils. The disk is photographed at high and low powers in transmitted light and marked with a reference mark (such as a scratch or depression) that will appear in the electron microscope. It is then prepared for the SEM in the usual way, and the area that was photographed at high power is located in the scanning electron image by reference to the mark. However, comparison of light microscope and SEM images is not easy, because the specimen in the SEM is tilted at an angle, chosen by the operator, to the electron beam, foreshortening its image in the direction of tilt, and the photograph is an inverted mirror image of the scanning electron micrograph. Scanning electron micrographs of stromatoporoids have been published by Stearn (1977, 1989b), Stearn and Mah (1987), and Rush and Chafetz (1991).

GEOCHEMISTRY

The original skeletal composition of Paleozoic stromatoporoids and related living hypercalcified sponges has been studied through analysis of the structural elements for strontium, magnesium, lead, and rare earth elements. Results of these studies are further discussed in the section on skeletal microstructure and mineralogy (see p. 521–542). The results have been obtained largely through microprobe x-ray fluorescence and laser-ablation plasma mass spectrometry.

Biologically secreted aragonite is enriched in strontium and may contain up to 9000 ppm Sr^{2+}. RUSH and CHAFETZ (1991) supported their conclusion that the original mineralogy of Devonian stromatoporoids was high magnesium calcite with microprobe analyses of Sr^{2+} and Mg^{2+}. MALLAMO (1995; MALLAMO & STEARN, 1991) made cross plots of Sr^{2+} and Mg^{2+} from microprobe analyses of living corals, recently calcitized corals, and stromatoporoids of various ages. He found that high values of Sr^{2+} in the structural elements of Ordovician labechiids relative to that of the gallery cements justified the conclusion of an original aragonite mineralogy. Younger stromatoporoids do not show the elevated Sr^{2+} and probably secreted high magnesium calcite.

ROSENHEIM and others (2004) found that the strontium-calcium ratio in living *Ceratoporella* was an indication of the temperature at which the aragonite skeleton was secreted, but this method has not been applied to fossils. WEBB, WORHEIDE, and NOTHDURFT (2003) measured the distribution of rare earth elements (REE) in stromatoporoids from the Devonian of the Canning Basin, Australia, and the living sponge *Acanthochaetetes*. The proportion of REE in the stromatoporoid was similar to that of sea water and suggested that its skeletal composition was originally calcite. LAZARETH and others (2000) measured lead in recent *Ceratoporella* to assess its relationship to environmental changes.

Identification of microdolomite by morphology in scanning electron micrographs as an indication of original magnesium calcite composition in Ordovician stromatoporoids has led to contradictory results (YOO & LEE, 1993; TOBIN & WALKER, 1998).

ISOTOPE STUDIES

NORRIS and CORFIELD (1998) collected a series of papers on the use of isotopes in paleontology.

To isolate a carbonate sample for isotope analysis of the skeleton from that of the galleries, a micropositioning stage driven by stepping motors and connected to a computer is used (DETTMAN & LOHMANN, 1995). A structural element in a polished thin section is drilled out with a dental drill 20 µm wide to a depth of 50 µm. To get a sample large enough for the mass spectrometer (10 µg), about 4 mm along the length of the structural element (e.g., a lamina) must be drilled out.

MALLAMO (1995) has applied analyses of oxygen and carbon isotopes in the stromatoporoid skeleton to the problem of whether the organisms were photosymbiotic. Because photosynthesis preferentially fixes ^{12}C, it increases the $^{13}C/^{12}C$ ratio in the skeleton but has only a minor effect on the oxygen isotopes (SWART, 1983). FRYKMAN (1986) plotted the C and O isotopes in stromatoporoids from Gotland but did not discuss the significance of the results for these fossils.

The proportion of O isotopes in the skeletons of modern corals is sensitive to temperature, and changes in the ratio of $^{18}O/^{16}O$ across the growth axis have been used to define annual increments. BOEHM and others (2000) have applied this technique to the skeletons of living hypercalcified sponges, but so far application of this technique to stromatoporoids to determine paleotemperatures has not been reported.

PHOTOGRAPHY

In 19th century works, the illustrations are engravings produced by lithography. While most of these illustrations are fair representations of the thin sections from which they were drawn, writers (e.g., STEARN, 1993) have commented that they cannot find the part illustrated in the plate in the type thin sections. In some publications (e.g., PARKS, 1936; GALLOWAY & ST. JEAN, 1955, 1957; GALLOWAY, 1960), the photographs are retouched, typically by whiting out details that the author decided were of secondary origin. The microstructures of such illustrations are rarely accurate representations of the nature of the specimen and in worst cases are misleading. Such retouching has not been practiced in recently published papers.

Standard methods of photomicrography have been used in illustrating stromatoporoids. Although various magnifications have been used, the standard magnification of 10 for macrostructure and 25 for microstructure has been widely adopted and allows easy comparison between taxonomic descriptions. To increase depth of focus and uniformity of focus across the picture, the thin section can be placed in an enlarger and projected onto film. The image from the enlarger can best be captured on slow orthochromatic emulsions (for example, the now unobtainable Kodak 7302 or 5302), but such products are now difficult to find as manufacturers are discontinuing production of black and white films. To increase depth of focus in producing the negative, the initial magnifications should be kept low, typically ×3, and the ×10 image produced by enlarging the negative ×3.3 onto paper. To save effort, some paleontologists have published negative prints produced by projecting the thin section directly onto printing paper rather than film. To compare such illustrations with those produced as photomicrographs, one must make a mental adjustment that the darker areas on the photograph would be lighter (less opaque) when the section is seen under the microscope.

Recording images with a digital camera or scanning photographs produced from film and paper allows the image to be stored in various memory devices, such as hard disks, zip drives, compact discs, or memory cards and manipulated for size, brightness, and contrast on a computer. As a result, these digital techniques have largely replaced film and paper methods, and all the illustrations in this volume have, at some stage, been digitized, although many were originally recorded on film and later scanned. So far, paleontologists have not confronted the problem that electronic manipulation of images may mislead readers as to the true state of the specimens, to the same extent that retouching photographs could mislead an earlier generation.

CLASSIFICATION OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

INTRODUCTION

The Paleozoic stromatoporoids have been considered, among other groups, to be an order of the class Hydrozoa (e.g., NICHOLSON, 1886a; LECOMPTE, 1956; BOGOYAVLENSKAYA, 1969b, 1984), a subphylum of the phylum Porifera (e.g., STEARN, 1972), and a class of the Porifera (e.g., STEARN & others, 1999; and p. 707–836). Recently, the most commonly adopted rank for this group has been a class of the Porifera.

BASIS OF CLASSIFICATION

In sorting or classifying fossils, the paleontologist decides which of the features of morphology or life history of the group are important, and which are trivial. An important influence on classification has been the living group to which the fossil group has been assigned. Although the first writers describing the stromatoporoids suggested they were sponges (see Morphologic Affinities, p. 543–549), the consensus from the 1870s to the 1970s was that they were Hydrozoa and that the morphology of that living group should be the guide to assessing the relative importance of features of the fossil for classification. Thus NICHOLSON's classification (1886a), which was followed for a century by many writers, was based on the division of the fossils of the four families into groups that resembled the living hydroids *Hydractinia* (Hydractinoidea) and those that resembled *Millepora* (Milleporoidea). Comparison with these living hydroids also influenced the classification used by LECOMPTE (1956) in volume F of the *Treatise on Invertebrate Paleontology* and KÜHN (1939b). TRIPP (1929), BOGOYAVLENSKAYA (1984), and BOGOYAVLENSKAYA and YELKIN (2011) made detailed comparisons between living hydroids and fossil stromatoporoids.

The selection of a single morphological feature as the basis for classification has appealed to several paleontologists. HEINRICH (1914b) divided stromatoporoids into families in which the microstructure was homogeneous (Actinostromatidae) and in which it was porous or tubular (Stromatoporidae). The sensitivity of the skeleton to diagenesis has discouraged other writers from reliance on microstructure for classification (LECOMPTE, 1956; STEARN, 1966). BOGOYAVLENSKAYA (1965b, 1969b) proposed that the form of the astrorhizae should be the basis of major divisions of the stromatoporoids, but she did not use this criterion in practice. Other classification schemes have been based on the overall morphological similarity of the groups rather than a single feature. STEARN (1980, p. 881–882) called such schemes phenetic and explained that in them the higher taxonomic groups (for instance, orders) ". . . are conceived as being groupings of lower taxa (e.g., families) which share more morphological features in common than they share with taxa (other families) of another higher taxon (another order)." While it is easy to formulate diagnoses for higher taxa distinguished by single or few distinguishing features, it may be difficult to diagnose higher taxa based on overall similarity.

The methods grouped as cladistics depend on a compilation of a series of character states that together express overall similarity and comparison of these states to an outgroup. For the stromatoporoids, cladistics has been applied only to the labechiids. WEBBY (1994) used 16 derived characters to produce a cladogram and division of the order into 4 families. The small number of morphological features of the stromatoporoids that can be factored into cladistic analysis appears to have limited the further application of this methodology.

The ideal classification will faithfully reflect the phylogeny of the Paleozoic stromatoporoids. Ideally each higher taxon should be monophyletic, that is, derived from a single ancestor. Many taxonomists assume that overall similarity of morphology is a reliable guide to ancestry (like begets like). Textbooks discuss exceptions to this principle caused by convergent evolution. STEARN's (1993, fig. 4) revision of the order Stromatoporida is an example of a classification based on overall similarity as a guide to a reconstructed phylogeny.

TREATISE CLASSIFICATION

The classification used in this volume has been slightly modified from that published by STEARN and others (1999). The main changes in higher taxa from that classification are as follows.

1. Addition of the family Platiferostromatidae.
2. Deletion of the subfamilies Pseudolabechiinae and Plumataliniinae from the family Pseudolabechiidae.
3. Substitution of the name Coenostromatidae for Syringostromatidae in the order Syringostromatida.
4. Introduction of a new family to the Clathrodictyida: the Anostylostromatidae.
5. Transfer of the family Pulchrilaminidae from the class Stromatoporoidea and order Labechiida to the separate class Uncertain and order Pulchrilaminida (see below).

The classification is based on the overall similarity of structural elements in the skeletons but emphasizes microstructures of these elements and phylogeny of the taxa. The authors assume and hope that the major groups are monophyletic, but monophyly is difficult to prove.

- Phylum Porifera GRANT, 1836
  - Class Stromatoporoidea NICHOLSON & MURIE, 1878
    - Order Labechiida KÜHN, 1927
      - Family Rosenellidae
      - Family Labechiidae
      - Family Stromatoceriidae
      - Family Platiferostromatidae
      - Family Stylostromatidae
      - Family Aulaceratidae
      - Family Lophiostromatidae
    - Order Clathrodictyida BOGOYAVLENSKAYA, 1969b
      - Family Clathrodictyidae
      - Family Actinodictyidae
      - Family Gerronostromatidae
      - Family Tienodictyidae
      - Family Anostylostromatidae
      - Family Atelodictyidae
    - Order Actinostromatida BOGOYAVLENSKAYA, 1969b
      - Family Actinostromatidae
      - Family Pseudolabechiidae
      - Family Actinostromellidae
      - Family Densastromatidae
    - Order Stromatoporellida STEARN, 1980
      - Family Stromatoporellidae
      - Family Trupetostromatidae
      - Family Idiostromatidae
    - Order Stromatoporida STEARN, 1980
      - Family Stromatoporidae
      - Family Ferestromatoporidae
      - Family Syringostromellidae
    - Order Syringostromatida BOGOYAVLENSKAYA, 1969b
      - Family Coenostromatidae
      - Family Parallelostromatidae
      - Family Stachyoditidae
    - Order Amphiporida RUKHIN, 1938
      - Family Amphiporidae
    - Order and Family Uncertain
  - Class Uncertain
    - Order Pulchrilaminida WEBBY, 2012a
      - Family Pulchrilaminidae

Seven of the formally named orders unite stromatoporoids of similar, but not unique, skeletal architecture and microstructure that can reasonably be considered to be a clade. The labechiids are characterized by an architecture based on cyst plates but include forms that also incorporate laminae and pillars. Their early appearance in the Middle Ordovician and the persistence of conservative morphologies in the order to the end of the Devonian suggest that they are the basic stock from which the other orders evolved. In the Late Ordovician, they grade into the actinostromatids, whose skeletal network is based on pillars of a range of sizes giving off colliculi to form lacy laminae. The clathrodictyids appeared after the labechiids in early Late Ordovician time, possibly from noncalcified ancestors, and built skeletons of single-layer, compact laminae, combined with a wide variety of pillars that spanned the spaces between them. The stromatoporellids had laminae that are more complex, typically thick and divided into layers. STEARN and PICKETT (1994) suggested that they, and the clathrodictyids, may have formed their skeleton in modules like that of the sponges informally grouped as sphinctozoans. The stromatoporids arose at the end of early Silurian time, probably from clathrodictyid ancestors, and were characterized by amalgamate skeletons formed of pachysteles and pachystromes of cellular microstructure. *Eostromatopora*, which is of obscure microstructure, may have been an ancestor. Structural elements with cellules are not confined to the stromatoporids, however; elements of similar microstructure also occur in the stromatoporellids. The syringostromatids are typically a Devonian group but are believed to have evolved in middle Silurian time from the actinostromatids. They built skeletons of pachysteles, pachystromes, and columns typically of microreticulate microstructure. NESTOR and STOCK (personal communication, 2006) are of the opinion that the order Syringostromatida should be divided into an order with clinoreticular microstructure derived from the Pseudolabechiidae and an order with orthoreticular microstructure derived from the Actinostromellidae or Densastromatidae. The amphiporids are a small group of abundant fossils, most of which are digitate, columnar, or dendritic in form, and composed of a network of compact, fibrous, or vacuolate elements. The order Pulchrilaminida is a small, independent, Early to Mid-Ordovician group of hypercalcified sponges assigned to class Uncertain (see Early Evolution of the Paleozoic Stromatoporoidea, p. 575–592; and Class Uncertain, Order Pulchrilaminida, p. 837–844).

HISTORICAL REVIEW
1826–1980

The classifications of Paleozoic stromatoporoids published before 1980 have been reviewed by LECOMPTE (1956) and STEARN (1980); no purpose would be served by repeating these summaries of older work. Few papers have been published that cover the whole class and provide diagnoses of each higher taxon. The literature on classification since 1980 will be discussed in the following section.

LECOMPTE's (1956) critiques of previous viewpoints on classification were based on his convictions that: (1) the stromatoporoids were hydroids; (2) microstructures were of little value in their classification; and (3) the Mesozoic stromatoporoid-like forms should be integrated into the families of Paleozoic stromatoporoids. None of these convictions are held by the writers of this section of the volume (see p. 417–836). He outlined the classifications used by NICHOLSON (1886a), HEINRICH (1914b), DEHORNE (1920), STEINER (1932), and KÜHN (1939b) before proposing a new classification of 10 families (plus an uncertain group). He also included in the stromatoporoids the Cambrian forms (YAVORSKY, 1932) of the former Soviet Union that have generally been excluded from the Stromatoporoidea by most specialists (e.g., NESTOR, 1966b; and see p. 575–577). LECOMPTE's classification was criticized (ST. JEAN, 1957) and then largely ignored by paleontologists. Its neglect was partly owing to the publication soon after of GALLOWAY's 1957 classification, which proved more acceptable to those working with this group, including YANG and DONG (1962), who used it in their first comprehensive survey of Chinese stromatoporoids. YAVORSKY, who contributed five major monographs on stromatoporoids of the former Soviet Union through the 1950s and 1960s, also found it difficult to use LECOMPTE's classification, preferring to use a simpler scheme for the Paleozoic forms (YAVORSKY, 1962) based on NICHOLSON's four original families: Actinostromatidae, Labechiidae, Stromatoporidae, and Idiostromatidae.

STEARN (1980) also briefly reviewed the history of classification of the Paleozoic stromatoporoids from the beginning and proposed a modification of the GALLOWAY (1957) classification to include the many new genera proposed from the Soviet Union. His classification was based on overall similarity and minimized the influence of microstructures in defining higher taxa. Major modifications of STEARN's (1980) classification made in this *Treatise* involve the giving of a larger place to microstructure in the criteria of classification, as well as the following modifications.

1. Splitting off of the Stylostromatidae and Stromatoceriidae from the Labechiidae.
2. Removing the Lophiostromatida as an order to a family of the Labechiida.
3. Removal of the Ecclimadictyidae as a family and placing some of these genera in the family Actinodictyidae.
4. Recognition of the families Gerronostromatidae, Atelodictyidae, and Anostylostromatidae in the Clathrodictyida.
5. Removal of the Syringostromatidae from the Stromatoporida to a separate order with new families Coenostromatidae, Parallelostromatidae, and Stachyoditidae.
6. Recognition of the amphiporids as a separate order and removal from the Clathrodictyida.

1980–2009

An extensive analysis of stromatoporoid morphology, interpretation, and classification from a Soviet Union perspective was published in 1984 by BOGOYAVLENSKAYA, based on earlier papers (BOGOYAVLENSKAYA, 1969b, 1974). This was followed in 1985 by a catalogue of genera and species of the stromatoporoids by BOGOYAVLENSKAYA and KHROMYKH. BOGOYAVLENSKAYA compared the classifications of NICHOLSON (1886a), KÜHN (1939b), LECOMPTE (1956), GALLOWAY (1957), and KHALFINA and YAVORSKY (1973) in a table. BOGOYAVLENSKAYA's own classifcation reflected her belief that the stromatoporoids were hydrozoans and that the Mesozoic stromatoporoid-like fossils should be included in the subclass. Her classification of 1984 did not include Mesozoic genera, however. She formulated a phylogeny diagram showing an interpretation of the relationship between the taxa. The following is a summary of her higher taxa.

Subclass Stromatoporata
  Order Labechiida
      Family Aulaceratidae
      Family Stratodictyidae
      Family Tuvaechiidae
      Family Labechiidae
      Family Stromatoceriidae
  Order Clathrodictyida
      Family Clathrodictyidae
      Family Plexodictyidae
      Family Actinodictyidae
      Family Stromatoporellidae
      Family Coenellostromatidae
  Order Actinostromatida
      Family Plumataliniidae
      Family Pseudolabechiidae
      Family Densastromatidae
      Family Actinostromatidae
      Family Atelodictyidae
  Order Gerronostromatida
      Family Gerronostromatidae
      Family Simplexodictyidae
      Family Tienodictyidae
  Order Syringostromatida
      Family Parallelostromatidae
      Family Clathrocoilonidae
      Family Pichiostromatidae
      Family Syringostromatidae
      Family Hermatostromatidae
  Order Stromatoporida
      Family Stromatoporidae
      Family Ferestromatoporidae
  Order Incertae Sedis
      Family Cleifdenellidae [*sic*]
      Family Amphiporidae
      Family Lophiostromatidae

As might be expected, many of BOGOYAVLENSKAYA's higher taxa are recognized in the classification adopted here. The major changes for the *Treatise* classification are as follows.

1. Removal of the Tuvaechiidae as a separate family.
2. Recognition of the Stromatoporellida as a separate order, not a family.
3. Placing of the Gerronostromatida as a family in the Clathrodictyida.
4. Placing of the Simplexodictydae in the Stromatoporellida, with the exception of *Anostylostroma,* which is a clathrodictyid.
5. Reinterpretation of the Syringostromatida based on the typical genus and removal of the genera grouped in the Clathrocoilonidae and Hermatostromatidae to the Stromatoporellida.
6. Assignment of the genus *Pichiostroma* to the Actinostromellidae and removal of the family.
7. Removal of the Cliefdenellidae from the Stromatoporoidea (WEBBY & LIN, 1988).
8. Recognition of the Amphiporida as a separate order.
9. Assignment of the Lophiostromatidae to the Labechiida.

BOGOYAVLENSKAYA and LOBANOV (1990) reviewed the morphological relationships, phylogeny, and paleogeography of many genera of the labechiids. They proposed another family be established in this order, the Cystostromatidae, to include the genera *Cystostroma* and *Pachystylostroma.*

WEBBY (1979a, 1986, 1993) has written extensively on the early history of the stromatoporoids and the classification and phylogeny of the labechiids. In 1979, he reviewed the genera of the labechiids and clathrodictyids that accompany them in Ordovician rocks and the speculations of GALLOWAY (1957), NESTOR (1966b), BOGOYAVLENSKAYA (1969b), and KAŹMIERCZAK (1971) that the former gave rise to the latter in Late Ordovician (Katian) time. WEBBY (1979a) considered the labechiiids to be an undivided family, but later (WEBBY, 1986) recognized a division of the labechiids into the Rosenellidae, Aulaceridae, Lophiostromatidae, and Labechiidae and speculated on the origin of the group from *Pulchrilamina* (which he included in the Labechiidae) and part of the Cambrian Khasaktiidae, which he included in the Stromatoporoidea (WEBBY, 1986, fig. 10). By 1993, WEBBY had increased the number of families in the order Labechida to six with the addition of the Pulchrilaminidae (doubtfully assigned) and the Stylostromatidae (WEBBY, 1993, 1994). WEBBY's evolving views on the classification of the labechiids are recorded by his doubtful inclusion of the pulchrilaminids in the labechiids (STEARN & others, 1999) and his later exclusion of them from the order to an indeterminate position (WEBBY, 2004b). They are now separated in this *Treatise* volume into a small, independent order of hypercalcified sponges of stromatoporoid-like appearance with uncertain phylogenetic relationships (see p. 837–844). NESTOR (in STEARN & others, 1999, p. 60) regarded two of the khasaktiid genera as being possibly parts of archaeocyath holdfasts. In this volume, the family Khasaktiidae does not have a relationship with members of the class Stromatoporoidea; see discussion of the family Khasaktiidae (p. 576–577).

WEBBY (1994, p. 379) noted that the morphological gradations between first-appearing clathrodictyid (Late Ordovician) genera—*Clathrodictyon* on the one hand and *Ecclimadictyon* and *Plexodictyon(?)* on the other—do not support the differentiation of these genera into separate families during their early developmental history. WEBBY, STEARN, and ZHEN (1993) used the classification of STEARN (1980) in their description of non-labechiid Lower Devonian stromatoporoids from the state of Victoria, Australia.

The Chinese viewpoint on classification has been formulated largely by DONG, who wrote numerous reports on Chinese Paleozoic stromatoporoids during the 1980s and 1990s. In 1983, he recognized nine different pillar microstructures and described the form of pillars of many genera. In 1987, DONG presented an extensive summary of the group, including sections on the significance of morphologic features, microstructures, and principles of classification. This handbook reviewed the classification of NICHOLSON (1886a), KÜHN (1927), LECOMPTE (1956), GALLOWAY (1957), BOGOYAVLENSKAYA (1965b, 1969b), and KHALFINA and YAVORSKY (1973). DONG's (1987) classification is basically a modification of STEARN's (1980) classification with the following differences.

1. The family Platiferostromatidae was established within the Labechiida to receive, in most part, Famennian stromatoporoid genera from China.
2. The family Gerronostromatidae was established within the Actinostromatida to receive genera, which are regarded herein, largely on the basis of microstructure, as being of different orders (e.g., *Atopostroma* [Syringostromatida], *Amnestostroma* = *Hermatostromella* [Stromatoporellida], *Clathrostroma* = *Gerronostromaria* [Clathrodictyida]).
3. The family Cubodictyonidae in the Actinostromatida was established to contain the single genus *Cubodictyon*. NESTOR (in STEARN & others, 1999) placed the genus provisionally in the Clathrodictyida (family Atelodictyidae) and suggests it may not be a stromatoporoid.
4. The new order Idiostromatida was established to accommodate three families: Idiostromatidae, Amphiporidae, and Stachyoditidae. This is an unwarranted return to the concept of NICHOLSON (1886a) and GALLOWAY (1957) that digitate, columnar, and dendroid growth forms can be used as a criterion for separation of higher taxa.

The same classification was presented by DONG in 1988. The stromatoporoids were placed in the phylum Porifera, STEARN's (1980) classification was criticized, and the modifications listed above proposed. Diagnoses of the various taxa were formulated in which little significance is given to microstructure as a guide to taxonomic affinity. In DONG's (2001) monographic treatment of the stromatoporoids of China, these same higher taxa are used in the classification.

STEARN (1993) revised his classification of the order Stromatoporida by dividing it into two orders separated by microstructure and phylogeny by splitting off the Syringostromatida. The stromatoporids were postulated to have arisen from clathrodictyid or labechiid ancestors in late early Silurian time, while at a similar time, the syringostromatids evolved from actinostromatids, from which they derived their microreticulate microstructure. Only a single family was recognized in the Syringostromatida.

The section on Paleozoic stromatoporoids in *The Fossil Record 2* (RIGBY & others, 1993) is based on the classifications of LECOMPTE (1956) and STEARN (1980) and does not introduce new taxa.

In 1994, STOCK reviewed the origin, evolution, and classification of the Actinostromatida. The phylogeny of the order is traced from the Late Ordovician genus *Plumatalinia* through the early Silurian *Plectostroma* to its diversification in middle Silurian time. Although suggesting that not all genera fit into these divisions, he recognized only three families in the order: Pseudolabechiidae, Actinostromellidae, and Actinostromatidae.

NESTOR has published several versions of his classification of Paleozoic stromatoporoids as phylogenetic diagrams without diagnoses. In the first series of these, which appeared in 1974, the main divisions were recognized as the superfamilies Labechiacea, Clathrodictyacea, Actinostromacea, and Stromatoporacea. This classification differed from his subsequent ones, largely in the inclusion of the Stromatoporellidae and Hermatostromatidae in the clathrodictyids and the Syringostromatidae in the actinostromatids. In his monograph on the Silurian of the Moiero River, NESTOR (1976) removed the lophiostromatids to the superfamily Lophiostromatacea, recognized the Actinodictyidae and Synthetostromatidae in the clathrodictyids, and the Yavorskiinidae in the Stromatoporacea. In a diagram of 1994, NESTOR recognized the superfamilies as orders and proposed the following subdivisions of these orders.

- Order Lophiostromatida
  - Family Lophiostromatidae
- Order Stromatoporellida
  - Family Hermatostromatidae
  - Family Synthetostromatidae
  - Family Stromatoporellidae
- Order Clathrodictyida
  - Family Clathrodictyidae
  - Family Amphiporidae
  - Family Tienodictyidae
  - Family Ecclimadictyidae
- Order Labechiida
  - Family Rosenellidae
  - Family Aulaceratidae
  - Family Stromatoceriidae
  - Family Plumataliniidae
- Order Actinostromatida
  - Family Pseudolabechiidae
  - Family Actinostromatidae
  - Family Densastromatidae
  - Family Actinostromellidae
- Order Stromatoporida
  - Family Pseudotrupetostromatidae
  - Family Yavorskiinidae
  - Family Stromatoporidae

In NESTOR's 1997 paper and his contribution to the classification of the clathrodictyids in 1999 (in STEARN & others, 1999), he substituted the name Actinodictyidae for the Ecclimadictyidae, added the Gerronostromatidae and Atelodictyidae, and removed the Amphiporidae. In the classification adopted herein, he also added the new family Anostylostromatidae.

In 1996, KHROMYKH outlined his concept of the clathrodictyids, emphasizing the similarity of structural elements in various higher taxa and the necessity to maintain the uniformity in microstructure of such taxa. He reintroduced from his 1974 paper (see KHROMYKH, 1974b) the superfamily Cystostromacea, which no other paleontologists have used, and divided it into various families, one of which, the Clathrodictyidae, is subdivided in the 1996 paper into the subfamilies Clathrodictyinae, Tienodictyinae, Ecclimadictyinae, and Actinodictyinae. Although NESTOR (1997) used the term Actinodictyidae as a substitute for the Ecclimadictyidae, KHROMYKH (1996)regarded the two groups of genera as separate entities.

In the *Systema Porifera*, no attempt was made by COOK (2002) to present a classification of the Paleozoic stromatoporoids.

Taking account here of the classification of BOGOYAVLENSKAYA and YELKIN (2011) and incorporating their higher taxa in synonymies of the taxonomic sections of the *Treatise* is not practical owing to fundamental differences in the bases of their taxonomy and that of the *Treatise* authors. BOGOYAVLENSKAYA and YELKIN based their wide-ranging revisions on assumptions that the Paleozoic stromatoporoids (and the disjectoporids and Mesozoic stromatoporoid-like genera) were Hydrozoa and that the astrorhizae, whose form they used as defining characterisitics of higher taxa, housed polyps rather than being canal systems of sponges. See discussion herein of the interpretation of the astrorhizae and their significance in taxonomic definitions in sections on internal morphology and functional morphology (p. 487–520 and p. 551–573).

PALEOZOIC STROMATOPOROIDEA

C. W. Stearn, B. D. Webby, Heldur Nestor, and Carl W. Stock

Class STROMATOPOROIDEA Nicholson & Murie, 1878

[Stromatoporoidea Nicholson & Murie, 1878, p. 241] [=class Stromatoporoidea Stearn & others, 1999, p. 11; =subphylum Stromatoporata Stearn, 1972, p. 385; =subclass Stromatoporata Nestor, 1978, p. 18; Bogoyavlenskaya, 1984, p. 66]

Invertebrate organisms of poriferan affinities with calcareous, basal skeletons, of laminar, domical, bulbous, branching to columnar form; internally composed of regular, continuous network of tangential and longitudinal structural elements; normally without preserved spicules; either interconnected laminae or cyst plates and pillars; or an amalgamated network in which tangential, longitudinal, and oblique elements are poorly differentiated; skeletons may be interrupted by a system of astrorhizae: canal-like voids that branch between structural elements and converge toward centers on growth surfaces. [Almost complete unanimity exists among contemporary stromatoporoid workers for the use of Nicholson and Murie's (1878) prior taxonomic name, the Stromatoporoidea, and the informal group name stromatoporoids. Bogoyavlenskaya (1984, 2001a) and Bogoyavlenskaya and Yelkin (2011), however, have preferred to maintain Stearn's (1972) term Stromatoporata and the informal term stromatoporates for the group.] *Middle Ordovician (Darriwilian)–Lower Carboniferous (Serpukhovian), ?Triassic.*