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Paleoecology of the Paleozoic Stromatoporoidea

Stephen Kershaw

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PART E, REVISED, VOLUME 4, CHAPTER 13: PALEOECOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

Stephen Kershaw

[Institute for the Environment, Brunel University, Stephen.Kershaw@brunel.ac.uk]

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, the reader is directed to *Treatise Online,* Part E, Revised, Chapters 9B (External Morphology: Webby & Kershaw, 2011) and 9F (Functional Morphology: Stearn, 2010), on Paleozoic stromatoporoids. Those 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. 1). Figure 2 shows the full range of results in stromatoporoids of processes that affected the sea floor when stromatoporoids were alive. Figure 3 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*

Kershaw, Stephen. 2012. Part E, Revised, Volume 4, Chapter 13: Paleoecology of the Paleozoic Stromatoporoidea. Treatise Online 31:1–24, 14 fig.

FIG. 1. 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 90º 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 (new).

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 clastics, 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 2–6

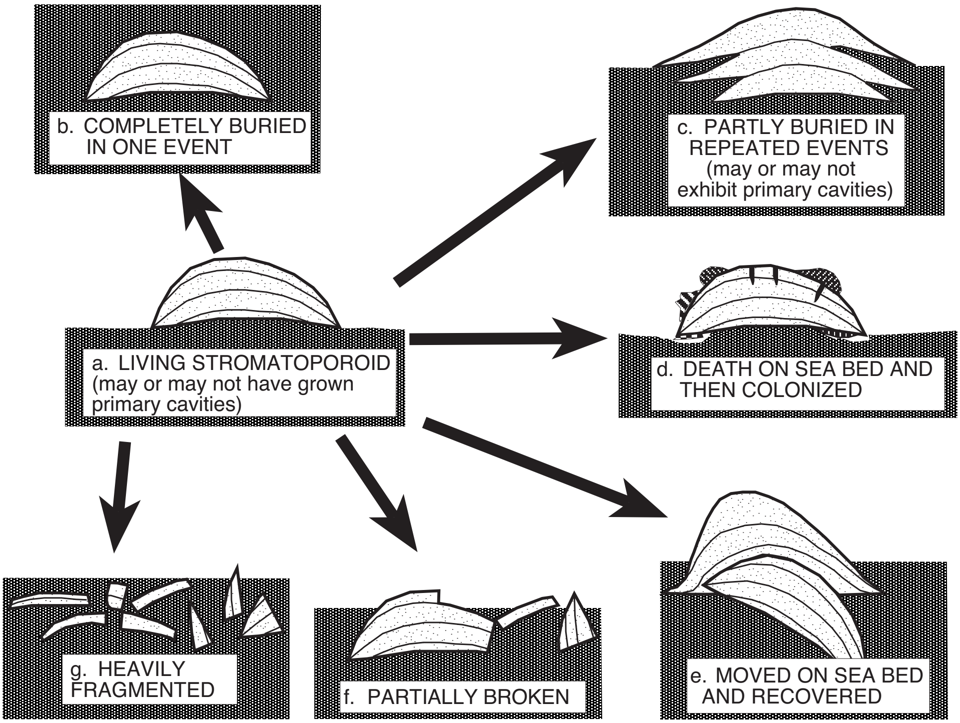


FIG. 2. Fossil stromatoporoid skeleton geometries demonstrating events affecting sea bed during life and in early postmortem, prior to final burial. *a,* Living stromatoporoid prior to burial; *b,* completely buried; *c,* partial burial with flank recovery, but the flanges of skeleton may have grown into the water to form original cavities (see WEBBY & KERSHAW, 2011); *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 (new).

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 WEBBY & KERSHAW, 2011, p. 7). 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 environmental influences is given in Figure 1.

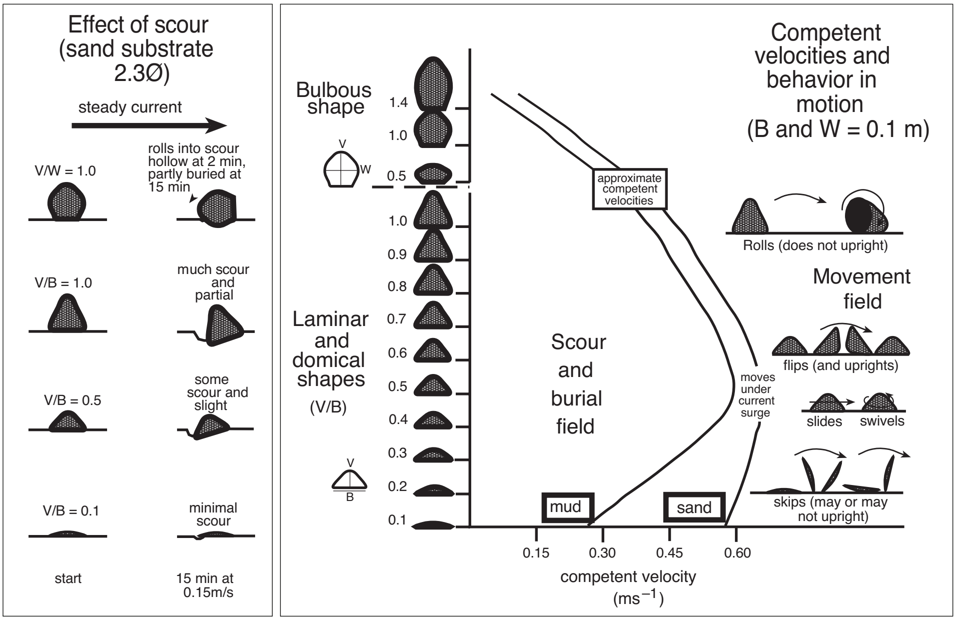


FIG. 3. Results of experimental work on model stromatoporoids illustrating the range of behavior of simple-shaped forms under steady and surge current influence on sand and mud substrates. Models were not fixed to the substrate, emulating fossil stromatoporoids. The data show that stromatoporoids are 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).

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 deep water, laminar stromatoporoids are Ordovician; BOURQUE & AMYOT, 1989, p. 255); laminar shape at depth could have collected more light, as in some modern corals. Arguments favoring algal (=?microbial) symbiosis (e.g., COWEN, 1988) are circumstantial, and papers that record deeper water, laminar forms (KLOVAN, 1964, at Redwater; KREBS, 1974,

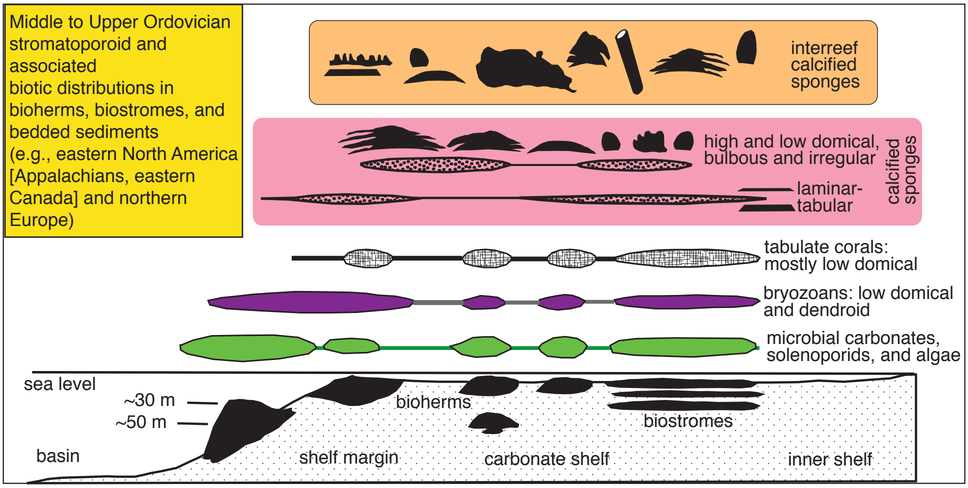


FIG. 4. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Ordovician carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Ordovician labechiid-dominated stromatoporoid morphotypes exhibit a wide range across carbonate 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 and based on the style presented in Kershaw & Brunton, 1999).

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 could not withstand high energy (DE FREITAS, DIXON, & MAYR, 1993). They usually did not build up high 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

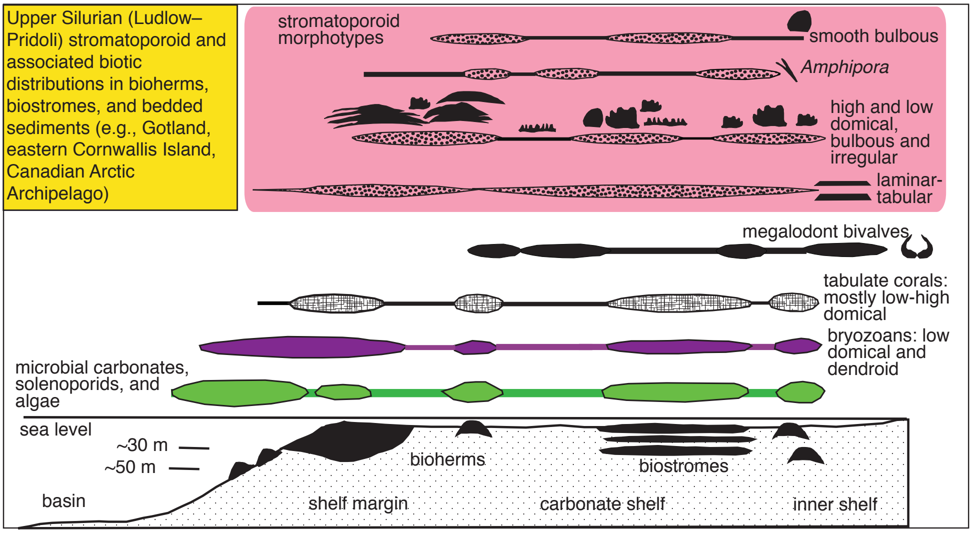


Fig. 5. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Silurian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Late Silurian, predominantly nonlabechiid morphotypes occur in a wider range of niches than 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 and based on the style presented in Kershaw & Brunton, 1999).

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 4–6 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 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 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

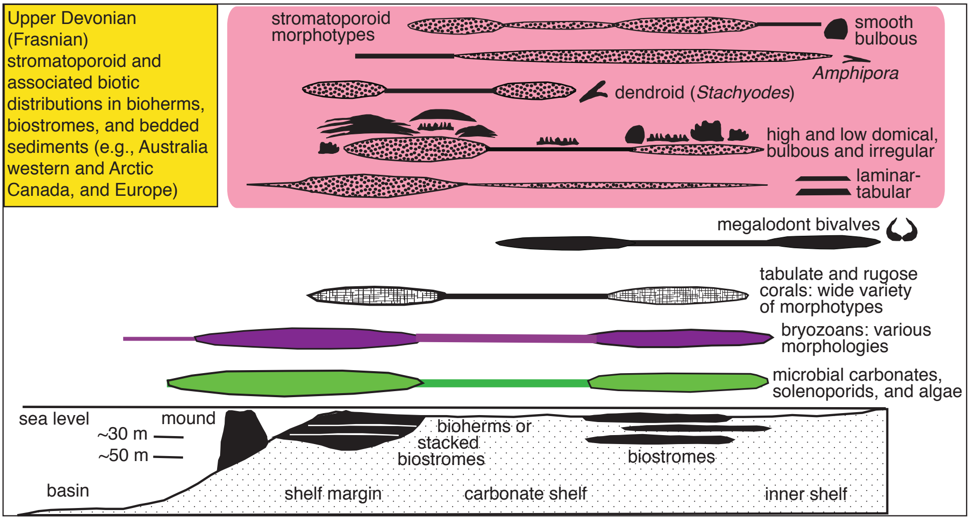


FIG. 6. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Devonian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Upper Devonian, predominantly nonlabechiid morphotypes have the widest range of morphotype 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 and based on the style presented in Kershaw & Brunton, 1999).

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 taxa (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 WEBBY & KERSHAW (2011, p. 7).

PALEOENVIRONMENTAL ANALYSIS

GENERAL RELATIONSHIPS

Growth form was controlled by environmental (extrinsic) and genetic (intrinsic) factors (NICHOLSON, 1892 in 1885–1892, p. 27–29; GALLOWAY, 1957, p. 374; KISSLING & LINEBACK, 1967; FISCHBUCH, 1968, fig. 23; LEAVITT, 1968, p. 323; MORI, 1969, 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. 2), but 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 (1982) 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 given in Figure 7; this figure relates to a diverse range of aspects of stromatoporoid paleoecology, discussed herein and in WEBBY and KERSHAW (2011).

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 4–6.

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 in WEBBY and KERSHAW (2011).

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 Middle Ordovician Crown Point Formation, Lake Champlain area, Vermont, and have a component of taxonomic control on form; *Pseudostylodictyon lamottense* (SEELY) grew

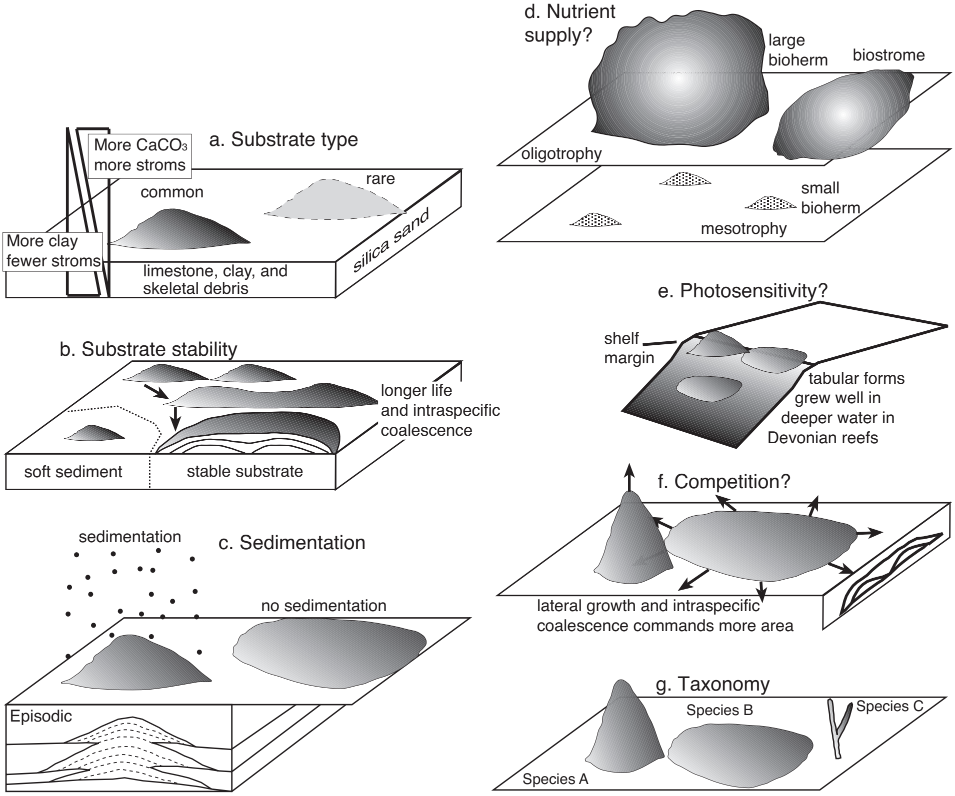


Fig. 7. Diagram summarizing stromatoporoid growth controls, which encompass the range of environmental boundaries that may be expected to have operated on Paleozoic stromatoporoids. *a,* Stromatoporoids are found mostly associated with calcareous sediments low in clay and are rare in coarser siliciclastic 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).

into high domical shapes (see Webby & Kershaw, 2011, fig. 15), 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 Webby & Kershaw, 2011, fig. 14–15) 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. 8; and see WEBBY & KERSHAW, 2011, fig. 14.1); early growth showed lateral expansion with some enveloping latilaminae, then upward growth was apparently stimulated by episodic sedimentation to generate ragged forms (see WEBBY & KERSHAW, 2011, fig. 14.2–14.3, fig. 15).

Specimens may be closely spaced, less than one meter apart (KAPP, 1974), and commonly asymmetrical (Fig. 8; and see WEBBY & KERSHAW, 2011, fig. 14.2), 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, therefore, give considerable information about stromatoporoid paleobiology and autecology but also raise questions about the controls of form.

Silurian Level Bottom Stromatoporoids, Gotland, Sweden

Figure 9 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 WEBBY & KERSHAW, 2011, p. 6), 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 uprighted following disturbance (Fig. 3); 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 killed them (Fig. 10).

Upper Devonian Bioherm, Lion Quarry, Southern Belgium

Figure 11 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 (1975) 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 (1975) 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 Shannon-Weaver Function. As an

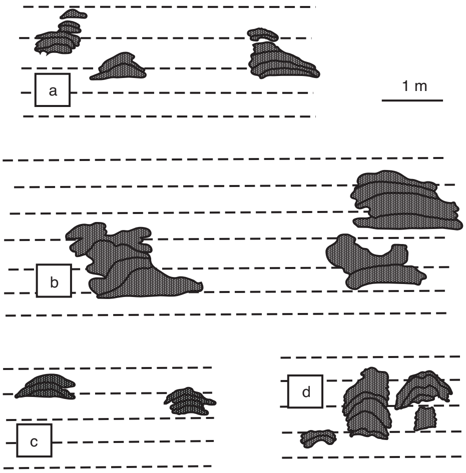
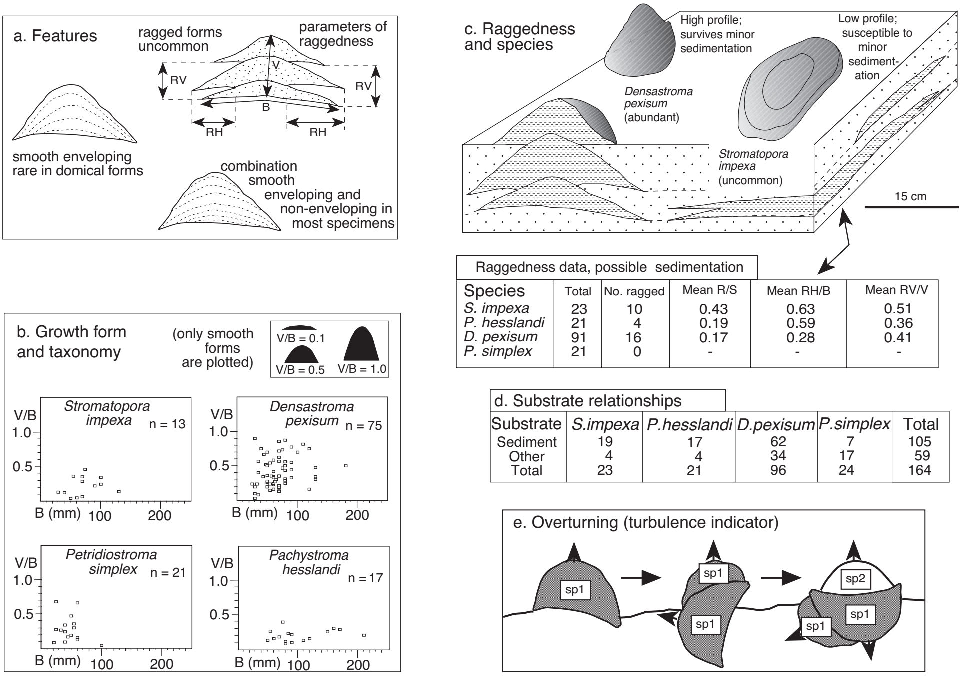


FIG. 8. Sketches of stromatoporoid vertical sections. Growth was apparently principally on soft sediment; individuals began growth at different levels and have ragged margins, suggesting that episodic sedimentation controlled growth initiation and development. Growth is biased in left or right directions. *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. 9. 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 its upturned base by species 2. 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).

attempt to demonstrate its utility, Figure 12 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 (1975), in order to attempt to compare diversities of different stromatoporoid assemblages, using the same index. However, in the examples of Figure 12, 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 a general guide to stromatoporoid diversity.

According to STEARN (1975), 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 *i*th species of the sample (Table 1).

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 using a spreadsheet, and an example is given below, for the marginward Peechee Member stromatoporoid assemblage collected by KOBLUK (1975), plotted on

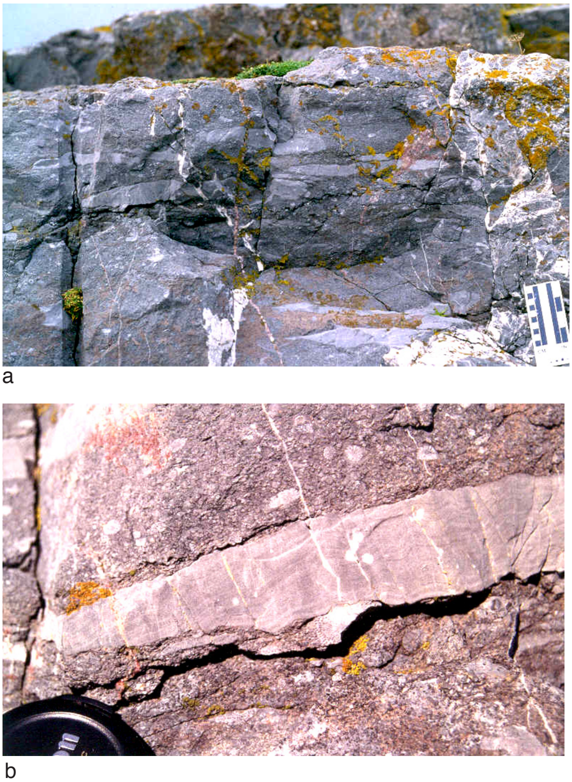


FIG. 10. *a–b,* Laminar stromatoporoids at Hope's Nose, Givetian, South Devon, United Kingdom. Growth of low profile stromatoporoids on mobile substrates made of crinoidal debris suggests a stabilizing effect provided by the stromatoporoids. The stromatoporoids probably grew in low-moderate energy conditions, because laminar forms are readily overturned by current flow (see Fig. 3). The lower photo shows that margin of stromatoporoid is modified by pressure solution, visible part of lens cap is 4 cm wide (new).

Figure 12, 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 12, the point plotted in relation to Table 1 is accompanied by text (2/76; 68%) that summarizes the data relating to that point, explained also in the key (Fig. 12, lower right when viewed in a horizontal orientation). The remainder of Figure 12 was constructed using spreadsheets, as above. Data plotted from STEARN (1975, p. 1644) were taken from his summary. Diversity index data depend on sampling procedure, but also on quality of taxonomy; in the Höglint Formation of Gotland, for example, many stromatoporoids are so strongly recrystallized that they are unidentifiable (MORI, 1969), reducing the utility of the diversity index for that formation in comparison with others.

In Figure 12, only data for stromatoporoids are given, and total biotic diversity

TABLE 1. Example of method of calculation of species diversity H index, used in Figure 12. 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

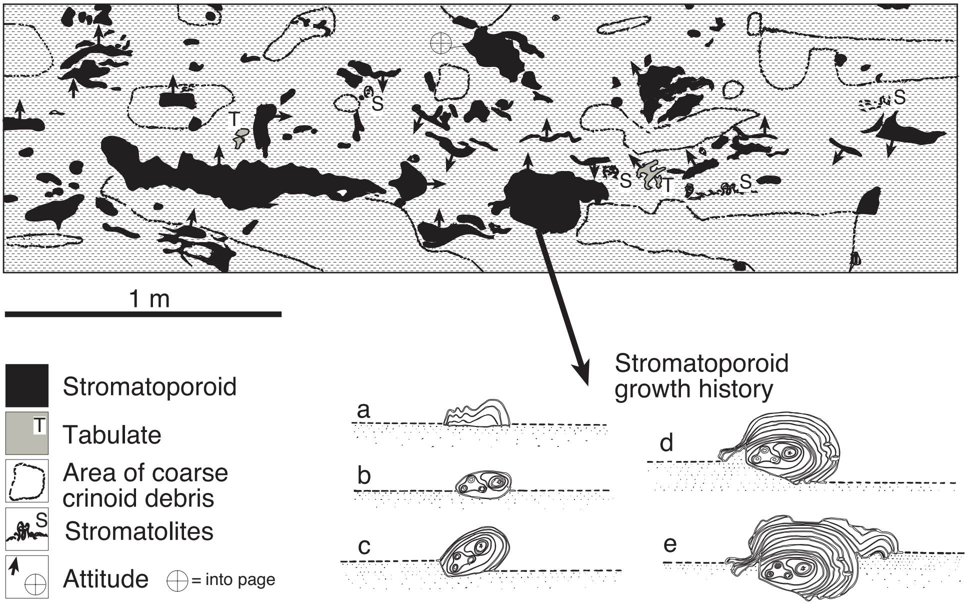


FIG. 11. Small area of vertical surface of reef, Lion Quarry, Frasnes, southern Belgium. A mixture of whole and fragmented stromatoporoids appear to occur in rhythms separated by coarser debris; stromatoporoids demonstrate growth on a probable loose substrate, with a prominent lateral growth aspect. 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 WEBBY & KERSHAW, 2011). In the *Attitude* symbols, *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).

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 (1975, 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. 12). 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 stromatoporoids. In Figure 12, data from Gotland (MORI, 1969, 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

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Fig. 12. *(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 (1969, 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).

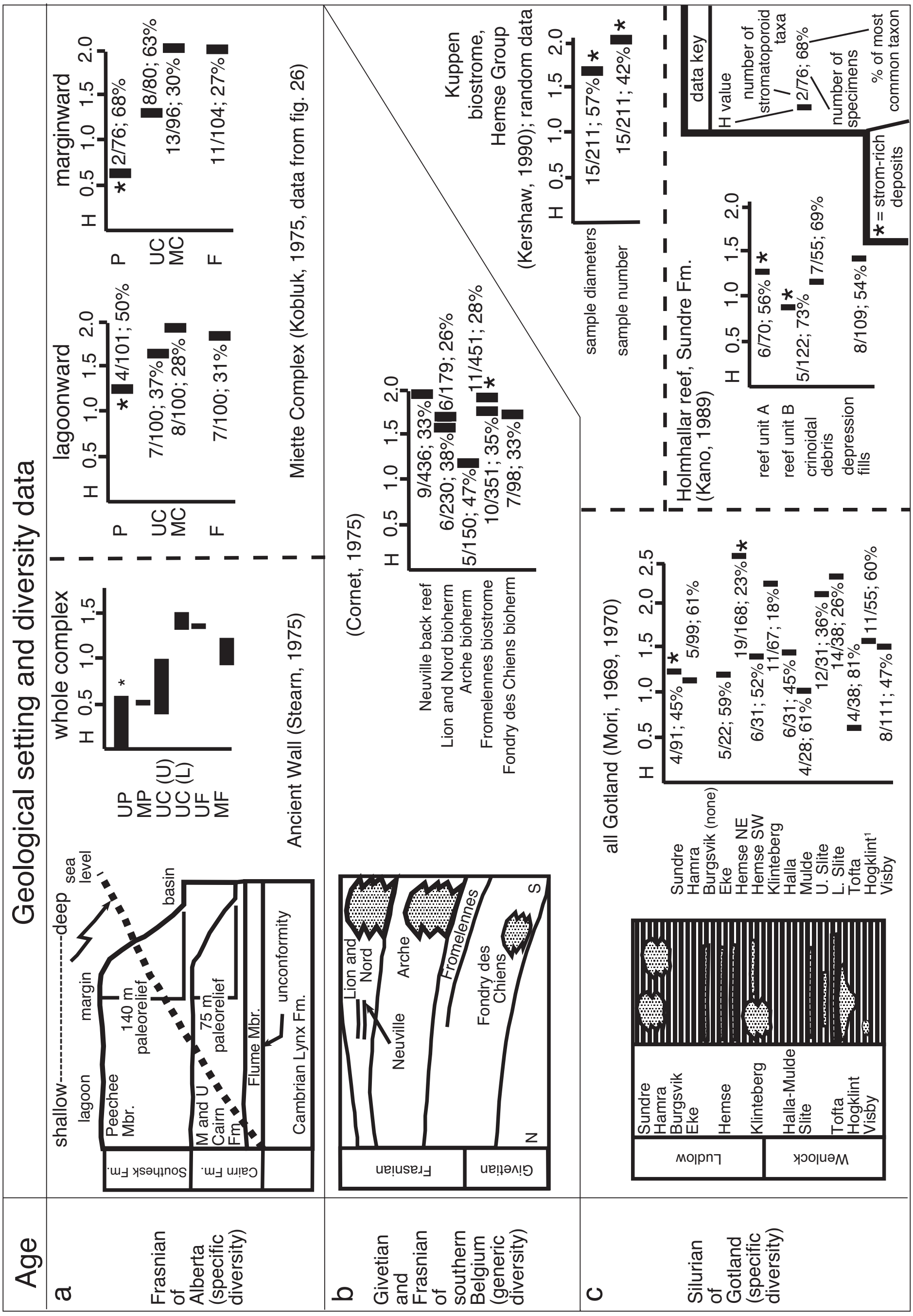


FIG. 12. Shannon-Wiener index (H) for stromatoporoid assemblages from published data for Silurian and Devonian locations. The diversity index is calculated using a combination of numbers of species and numbers of specimens of each species, as explained in the text. *a,* Data were compiled by KERSHAW (1990) from the plots of STEARN (1975, 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).*

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. 13) 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. 12c, from Mori's (1970) data, but also 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, 1994), in contrast to bioherms (Fig. 14). 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.

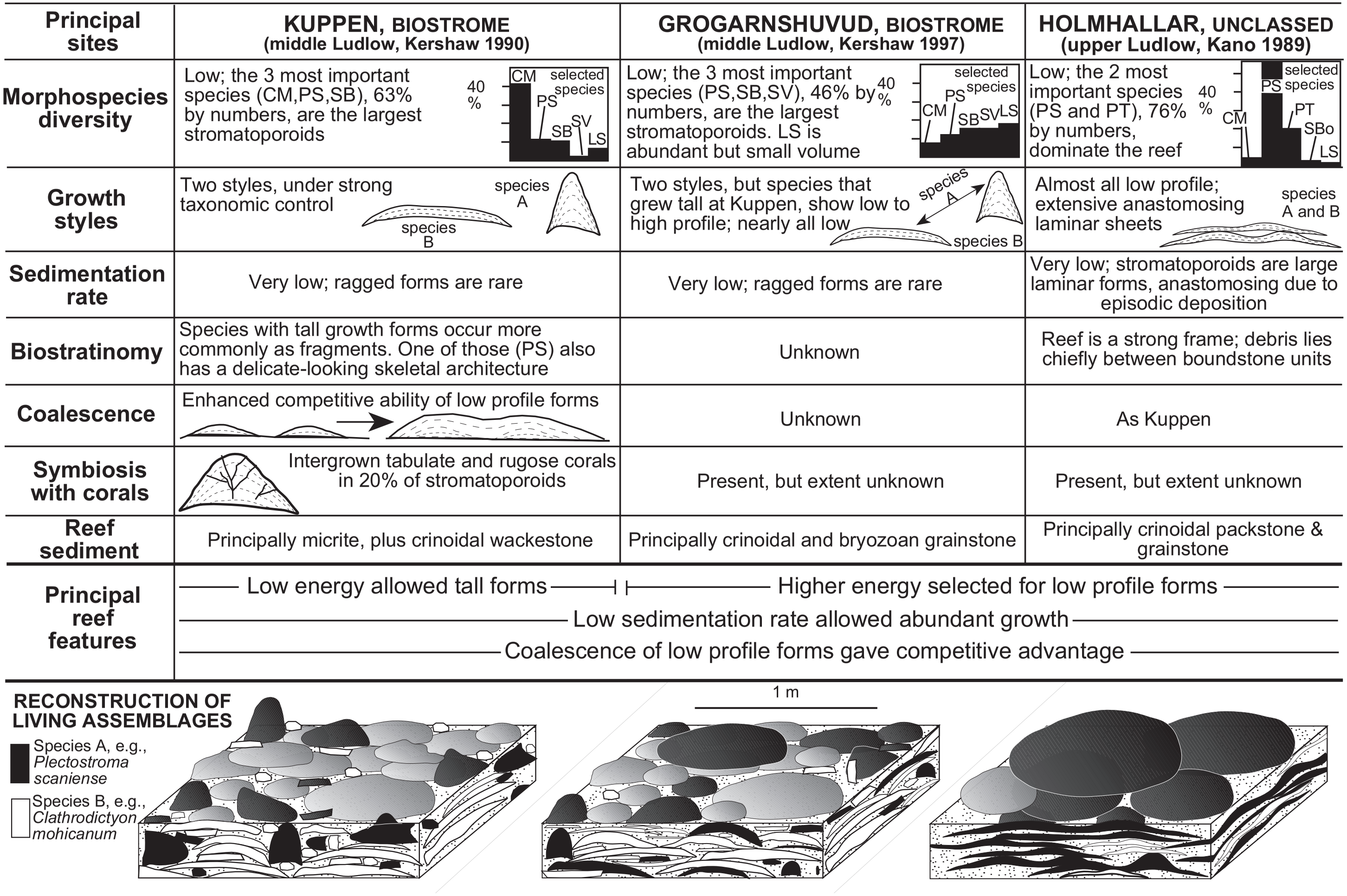
Stromatoporoid Biostromes

Dense accumulations of stromatoporoids in biostromal deposits occur in Wenlock to Devonian deposits, apparently occurring in platform interior settings. Figure 13 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 13 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. 19 herein; Da Silva, Kershaw, & Boulvain, 2010, 2011) also supports the need 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*

Fig. 13. Parameters of stromatoporoid-dominated Ludlow reef communities from Gotland, Sweden, with principal reef features highlighted. The reefs 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		

FIG. 13. *(For explanation, see facing page).*

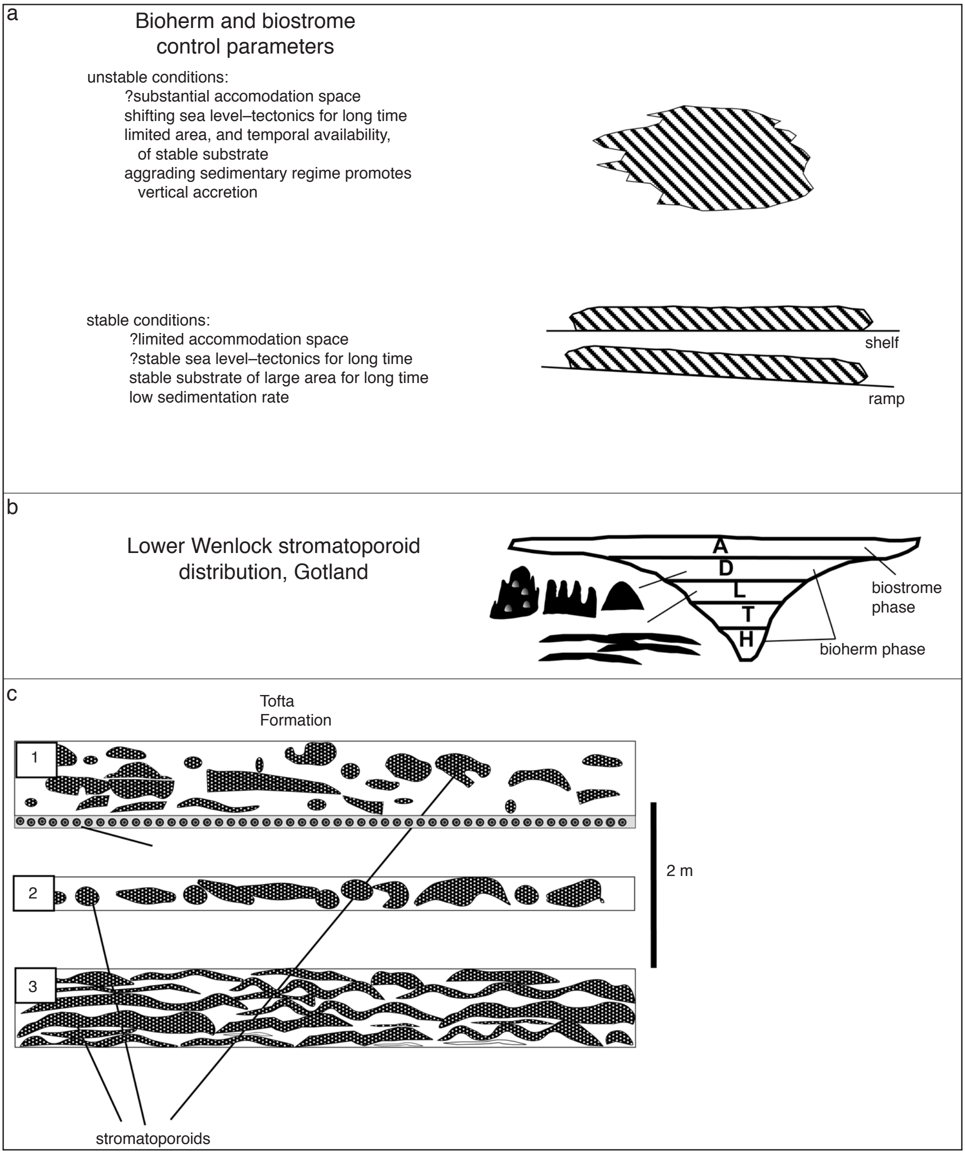


FIG. 14. Application of concepts of bioherm and biostrome in Silurian stromatoporoid reef facies. *a,* Form differences between bioherms and biostromes, demonstrating the dimensions in vertical section. Note that within these two forms, the constructing biota may consist of in-place frames, eroded debris, 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; *A,* calcified algae most abundant; *D,* domical stromatoporoids most abundant; *H,* halysitid tabulate corals most abundant; *L,* laminar stromatoporoids most abundant; *T,* tabulate corals of all types 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, 1994).

is the most abundant volumetrically (e.g., Cockbain, 1984). Although Middle Devonian reefs contain the first interpreted barriers, of which the Canning Basin (Playford & Lowry, 1966; Playford, 1980) and western Canadian (e.g., Klovan, 1964; Jamieson, 1969) systems are best known, many lack an identifiable reef core (e.g., the Miette complex of Alberta, Noble, 1970, p. 540, and data from Kobluk, 1975 [see previous page, Fig. 12a]; 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, 2011), 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 (PROSH & STEARN, 1996), in contrast to the traditional view that they are insufficiently stratigraphically restricted.

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 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 differentiated, 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 STEARN, 2010; WEBBY & KERSHAW, 2011), 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 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 characters (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 awaiting further work.

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.

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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.

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