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Palaeobiology, ecology, and distribution of stromatoporoid faunas in biostromes of the mid-Ludlow of Gotland, Sweden

OLOF SANDSTRÖM and STEVE KERSHAW



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Six well exposed mid-Ludlow stromatoporoid-dominated reef biostromes in four localities from the Hemse Group in southeastern Gotland, Sweden comprise a stromatoporoid assemblage dominated by four species; *Clathrodictyon mohicanum*, "*Stromatopora*" *bekkeri*, *Plectostroma scaniense*, and *Lophiostroma schmidtii*. All biostromes investigated in this area (of approximately 30 km^2) are interpreted to belong to a single faunal assemblage forming a dense accumulation of fossils that is probably the best exposed stromatoporoid-rich deposit of the Silurian. The results from this comprehensive study strengthen earlier interpretations of a combination of genetic and environmental control on growth-forms of the stromatoporoids. Growth styles are similar for stromatoporoids in all six biostromes. Differences in biostrome fabric are due to variations in the degree of disturbance by storms. The uniformity of facies and the widespread low-diversity fauna support the view that palaeoenvironmental conditions were similar across the area where these biostromes crop out, and promoted the extraordinary growth of stromatoporoids in this shallow shelf area.

Key words: Stromatoporoids, palaeoecology, depositional environment, morphotype, Silurian, Gotland, Sweden.

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Introduction

Recent studies of Palaeozoic stromatoporoids (e.g., Kershaw 1998; Łuczyński 1998, 2003; Sandström 1998; Kershaw and Brunton 1999; Wood 2000) demonstrate that they are important tools in palaeoenvironmental reconstructions. However, a major problem for application of stromatoporoid palaeobiology in palaeoenvironmental analysis is the degree to which growth form of stromatoporoid skeletons is genetically controlled (e.g., Kershaw 1990, 1998; Sandström 1998; Łuczyński 1998; Stearn et al. 1999; a summary of present knowledge is presented by Stock 2001). A key difficulty in solving this problem has been the lack of comprehensive data on stromatoporoid growth form and taxa; such data require large numbers of thin sections (two per specimen), and suitable preservation of growth forms, so that details are known for only a few sites. We address the problem by providing an expanded dataset of taxa and growth forms for stromatoporoid occurrence in one type of setting, stromatoporoid-rich biostromes; such deposits generally contain the most abundant stromatoporoid faunas. Silurian stromatoporoid assemblages were examined in six biostromal deposits in eastern Gotland, Sweden occurring in four sites, across a distance of ca. 12 km (Fig. 1B). All four sites occur in rocks of approximately the same age within the middle Ludlow Hemse Group. This work advances previous investigations by demonstrating palaeobiological variation between the stromatoporoid species across several sites and applying the results to enhance interpretations of palaeoenvironmental setting of stromatoporoid-bearing biostromes.

Two key points emerge: (i) Although there is strong genetic control on the stromatoporoid morphologies of the species in these biostromes (such that low domical growth forms dominate the biostromes), similar strong genetic control is not indicated in all sites, with important implications for interpretations of controls on stromatoporoid growth; (ii) the similarity of stromatoporoid assemblages between the sites suggests that the entire area of 30 km^2 was occupied by a single faunal assemblage, making these deposits all the more remarkable, given the dense accumulation of stromatoporoids in these beds. Furthermore, field evidence indicates that environmental controls, rather than competition among and within species, are interpreted to be key factors controlling faunal diversity and distribution. Ecological and biological studies of reef biostromes are not well-developed; recent examples include work from the Silurian of Gotland (Kershaw 1981, 1990, 1997; Kano 1989, 1990; Calner et al. 2000; Sandström 2000; Kershaw et al. 2006), the Upper Jurassic of central Europe (Insacalo 1996, 1999) and the Miocene of Austria (Riegl and Piller 2000); the current work builds on previous studies on the sites on Gotland, and results in the most comprehensive dataset so far assembled for these deposits.

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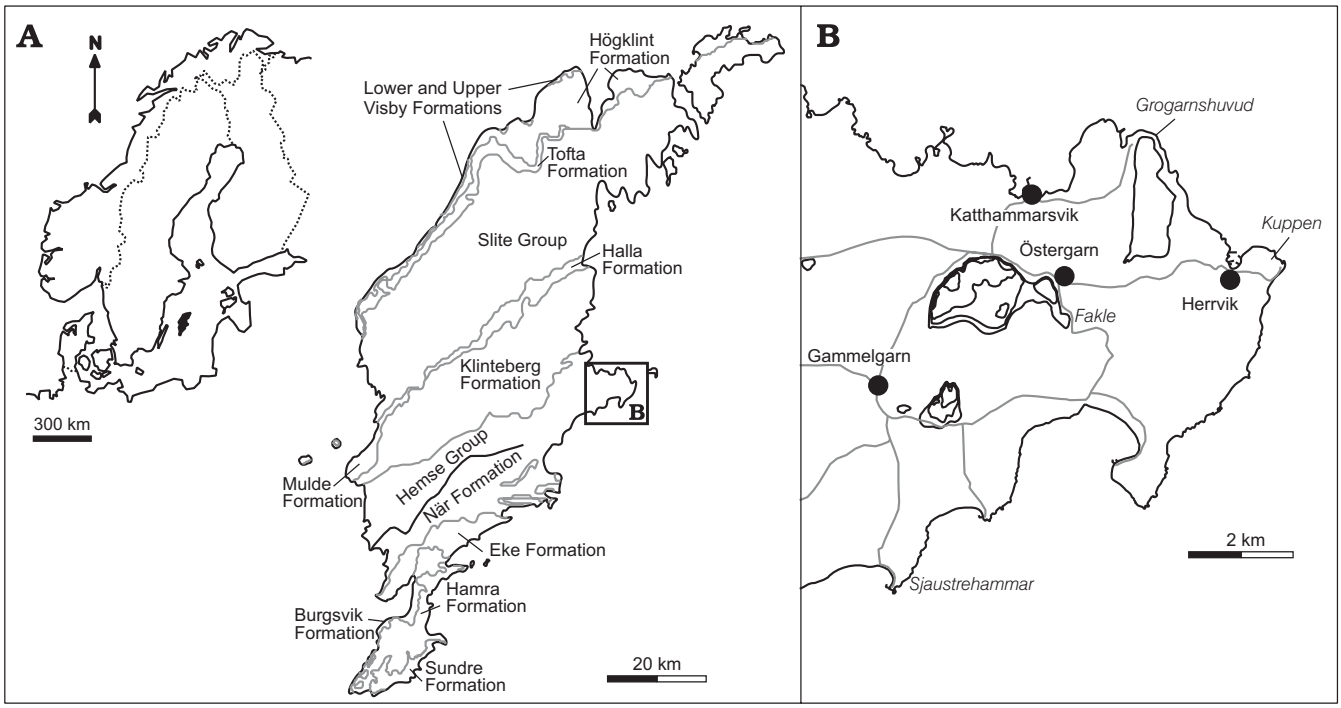


Fig. 1. **A**. Map showing the location of Gotland and the current topostratigraphy (after Hede 1960 and Jeppsson 2005). **B**. Detailed map of the investigated area with location names in italics.

Geological setting

The exposed bedrock on Gotland is entirely Silurian and ranges from the latest Telychian to end-Ludlow. The succession is almost entirely platform carbonates and marls, but thin beds of siltstones and sandstones occur as separate units. The strata dip in general less than 1 degree to the south and southeast, resulting in southerly younging of the succession.

The investigated areas (Fig. 1) are all lower Ludfordian (Upper Ludlow; Hemse Group unit d; *Polygnathoides siluricus* Conodont Zone, Jeppsson 1973). This corresponds stratigraphically to the Etelhem Secundo Episode, prior to the Havdhem Primo Episode, in turn followed by the world-wide Lau extinction event (*Pentamerus* event; Jeppsson and Aldridge 2000; Jeppsson et al. 2007). In this unit several reef biostromes (sensu Sandström 2000) crop out, forming a complex of vertically stacked biostromes separated by coarse limestones and erosion surfaces (see photographs in Kershaw 1981, 1990; Sandström 2000; and Sandström and Kershaw 2002 as well as Fig. 2 of this paper). Photomicrographs of stromatoporoid taxa are given by Mori (1970), so it is not necessary to illustrate them here, although two of the species names have changed since Mori's (1970) work, described later.

Materials and methods

This study uses a combination of published results (Kershaw 1990, 1997) from three stromatoporoid-rich biostromes, and new data from three previously undescribed similar biostromes (Fig. 2): 41 from the middle biostrome at Kuppen, 59 from Fakle, and 61 from Sjaustrehammarn, total 161 samples. Vertical height (V) and basal diameter (B) of each specimen were measured in the field if they were clearly displayed. Previously published data are from the Lower Biostrome at Kuppen (Kershaw 1990: 404 specimens), and the lower and upper biostromes at Grogarnshuvud peninsula (Kershaw 1997: 59 specimens). Therefore we have 634 specimens represented in six stromatoporoid-rich reef biostromes distributed across 30 km^2 of the Östergarn area, providing the most comprehensive study on the palaeobiology and ecology of stromatoporoids in biostromal settings. Morphotype classification follows the system outlined by Kershaw (1998; Fig. 3). V/B ratios were divided into laminar ($V/B \leq 0.1$), low domical ($0.1 < V/B \leq 0.5$), high domical ($0.5 < V/B \leq 1.0$), extended domical ($1.0 < V/B \leq 2.0$) and columnar ($V/B > 2.0$). Stromatoporoid taxonomy accords with the latest revision of stromatoporoid classification (Stearn et al. 1999). Limestone classification is according to Dunham's (1962) scheme. Classification of the biostromes is according to the system devised by Kershaw (1994), and the division into different reef types follows earlier definitions from Gotland (see Manten 1971; Riding 1981; Sandström 2000). Locality names in the text refer to the system developed by Laufeld (1974).

The data were analysed using two statistical techniques of diversity indices and rarefaction analysis. Because of the large difference in numbers of specimens between the Lower Biostrome at Kuppen, and the other biostromes sampled, we decided not to use normalising of the datasets. Normalising would introduce the danger of over-emphasising species with small numbers in the other biostromes. Instead we ap-

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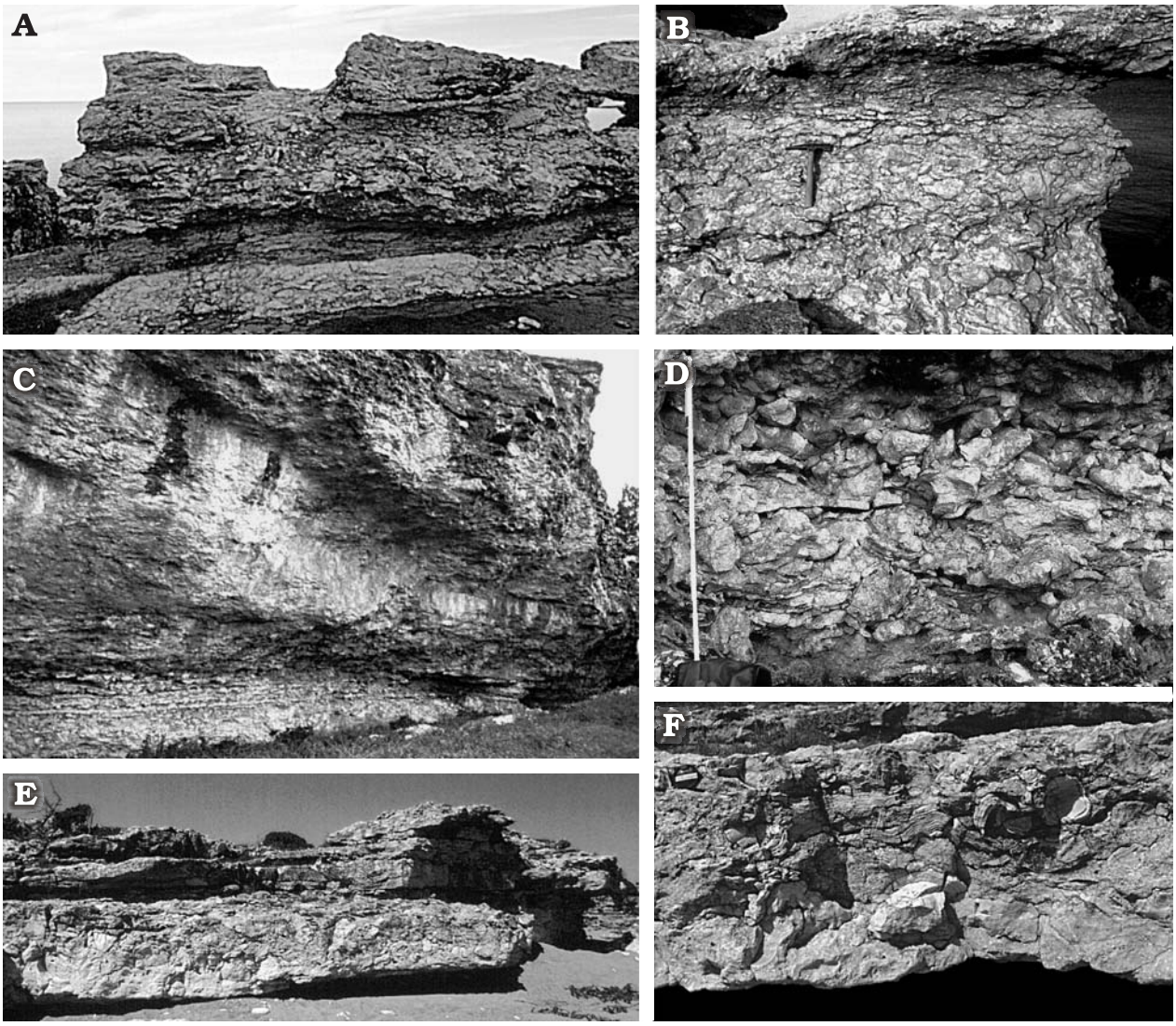


Fig. 2. Photographs of the three previously undescribed stromatoporoid biostromes. **A**, **B**. Kuppen middle biostrome (loc. Kuppen 3). **C**, **D**. The Fakle biostrome (loc. Fakle 1). **E**, **F**. The Sjaustrehammar biostrome (E, loc. Sjaustrehammar 3; F, loc. Sjaustrehammar 4).

plied techniques that would be less sensitive to large differences in sample size. For diversity analysis, the Shannon diversity index was used. The Shannon index (H) weights the most abundant species and thus is not as sensitive to large differences in sample size as other indices are. The Shannon index has been used in previous studies on stromatoporoid diversity (Kershaw 1998). Sample sizes differ a lot between the different biostromes. In order to determine if the number of species found on each site have similar distribution as the largest sample, a rarefaction study was made. This study uses the largest sample (here the sample from the Kershaw 1990 paper) and theoretically predicts the number of species one should expect if smaller samples were taken from this the largest one. The method for this is random picking from the largest sample, thus obtaining a curve of expected amount of species for a certain sample size. For both the diversity and rarefaction analysis methods applied, the PAST-software (Hammer et al. 2001) was used.

Results

The investigated biostromes belong to the Kuppen facies complex (localities Kuppen 1–4; Fig. 2A, B; Laufeld 1974), the Grogarnshuvud complex, the Fakle biostrome (Fakle 1; Fig. 2C, D) and the Sjaustrehammarn complex (Sjaustrehammarn 1–4; Fig. 2E, F). All biostromes except the Sjaustrehammarn biostrome are autoparabiostromes (a mixture of reef-builders which are in place, disorientated, and broken). The Sjaustrehammarn biostrome is a para/allobiostrome, dominated by broken reef-building fossils (terms from Kershaw 1994; more precise descriptions of these sites are in Kershaw 1990 and Sandström and Kershaw 2002). Overall the fauna of all biostromes is low diversity (H = 1.97; Table 1) and comprises the following stromatoporoid taxa, identified following Mori (1970): *Clathrodictyon mohicanum* Nestor, 1966, *Densastroma pexisum* Yavorsky, 1929, *Ecclimadictyon macrotuberculatum* (Riabinin, 1964), *Labechia lepida* Mori, 1970, *Lophio-*

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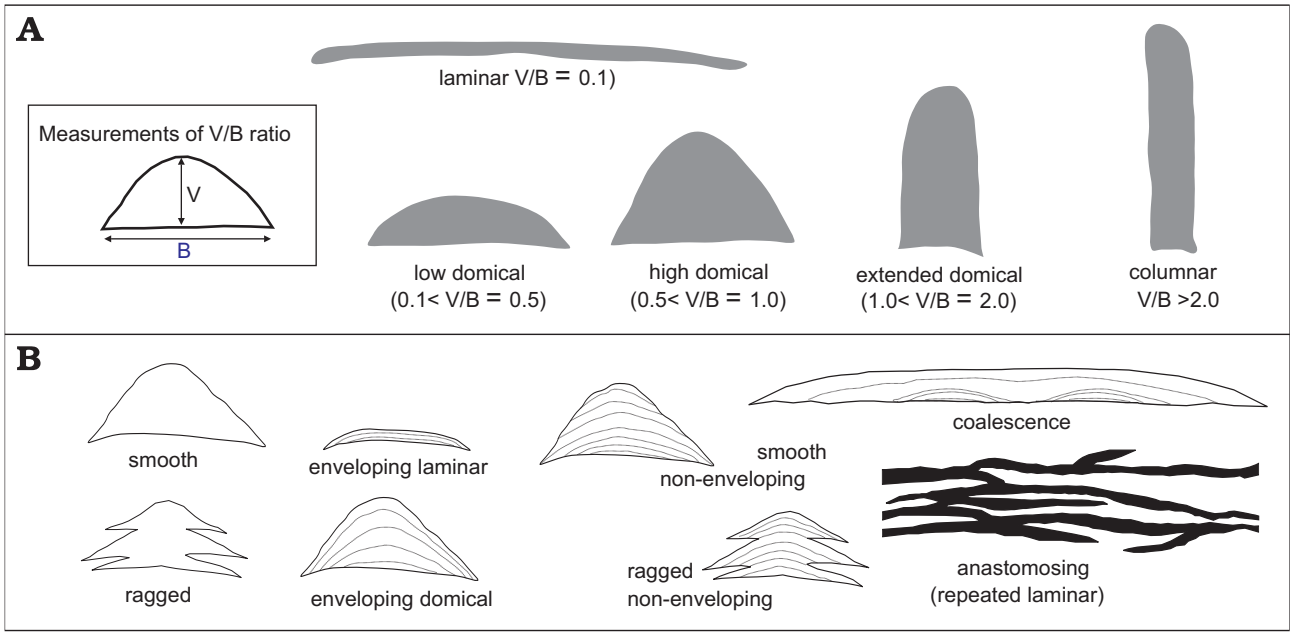


Fig. 3. Terminology used for describing stromatoporoids (from Kershaw 1998). **A**. Outline and general growth forms. **B**. Growth patterns describing surface edges, internal arrangement of lamina and its combinations. Abbreviations: B, basal diameter; V, vertical height.

stroma schmidtii (Nicholson, 1891), *Petridiostroma convictum* (Yavorsky, 1929; previously classified in *Clathrodictyon*), *Plectostroma katriense* (Nestor, 1966), *Plectostroma scaniense* Mori, 1969 (includes *Plectostroma intermedium* [Yavorsky, 1929]), *Pseudolabechia granulata* Yabe and Sugiyama, 1930, *Simplexodictyon yavorskyi* (Nestor, 1966; previously classified in *Diplostroma*), "*Stromatopora*" *bekkeri* Nestor, 1966, *Stromatopora lamellosa* Yavorsky, 1929, *Stromatopora venukovi* Yavorsky, 1929, *Syringostromella borealis* (Nicholson, 1966), *Syringostromella carteri* (Nicholson, 1889). "*Stromatopora*" *bekkeri* is not a *Stromatopora* species (see Stearn 1993) following the taxonomic revision by Stearn et al. (1999). However, because this is clearly a discrete species, we continue to use "*Stromatopora*" *bekkeri*, pending its taxonomic revision.

Kuppen Facies Complex.—The Kuppen site hais one of the most studied biostrome complexes on Gotland (Kano 1990; Kershaw 1981, 1990, 1993, 1994; Kershaw and Keeling 1994; Keeling and Kershaw 1994; Riding 1981; Sandström and Kershaw 2002). The Kuppen Facies Complex (Sandström and Kershaw 2002) is exposed in a curving 3–10 m high coastal cliff, extending for more than 1 km. The facies suite rests on dark mudstones. Basal beds consist of greenish crinoid wackestones and packstones which formed a firm substrate for the initiation of extensive lateral growth of a biostromal reef, presented by a 4 meter-high autoparabiostrome, called the Lower Biostrome. It is terminated by a planar erosion surface (Keeling and Kershaw 1994) that represents a prominent sea level fall, also causing a well-preserved rocky shore environment with conglomeratic beachfaces and preserved palaeo-sea stacks. Such erosive events occurred several times during the formation of the Kuppen Facies Complex (Sandström and Kershaw 2002), giving rise to a facies suite of stacked reef biostromes, eroded at their tops, with lateral facies of stromatoporoid conglomerates and coarse crinoidal rudstones and grainstones. Overlying the Lower Biostrome are crinoid packstones interbedded with more biostromes (including the Middle Biostrome sampled in this study) and with several erosion surfaces (Keeling and Kershaw 1994; Kershaw 1993; Kershaw and Keeling 1994; Sandström and Kershaw 2002). An autoparabiostrome here called the Middle Biostrome was sampled for this study. More than 90% of reef constructors of the Lower Biostrome are stromatoporoids; 14 species were revealed in a sample of 404 specimens with a wide range of stromatoporoid morphologies (Kershaw 1990). High profile stromatoporoids overturned by inferred storm events occur with in situ low-profile forms (Sandström and Kershaw 2002). The stromatoporoid assemblage is dominated by *Clathrodictyon mohicanum*, *Plectostroma scaniense*, and "*Stromatopora*" *bekkeri*, and Shannon index is 1.90 (Table 1; Kershaw 1990). The middle biostrome comprises a range of stromatoporoid growth forms: low-profile forms are mostly preserved in situ and taller forms are found overturned. The degree of transportation seems to be limited. Reef sediments are coarse (skeletal grainstone and rudstone) although occasional pockets of skeletal packstone are evident. Forty one stromatoporoid samples were collected between localities Kuppen 2 and Kuppen 4 comprising seven species, H = 1.49 (Table 1). Only one specimen, a "*S.*" *bekkeri*, showed ragged margins (Table 1). All other specimens display smooth, continuous and enveloping laminae. "*S.*" *bekkeri* and *P. scaniense* both show a wide range of morphologies from laminar through to columnar morphotypes. All the other species show low

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forms (laminar and low domical) except for one specimen of *Clathrodictyon mohicanum* that is high domical (Fig. 4). *Plectostroma scaniense* and "*Stromatopora*" *bekkeri* (Fig. 4) grew both laterally and vertically, but high-profile (high domical to columnar) samples tend to have basal diameters of similar size to the low-profile (laminar and low domical) forms of the same species. Kershaw (1990) showed that the reason for this morphological variation is because the stromatoporoids began growth by establishing a low-profile form, which then developed vertically without much more lateral expansion.

Grogarnshuvud complex.—The stromatoporoid fauna was described by Kershaw (1997), sedimentology by Sandström and Kershaw (2002). Sediments below the complex, displayed at the shoreface of the peninsula were investigated by Sundquist (1982). A general facies succession constructed from these studies begins with argillaceous limestones and marls, interpreted as littoral (Sundquist 1982), overlain by a Kuppen-type autoparabiostrome (sensu Kershaw 1994) described by Kershaw (1997), Sandström (2000) and Sandström and Kershaw (2002); in this lower biostrome, low-profile forms are mostly in place and high profile forms are mostly overturned. Matrix is generally fine-grained, dominated by crinoidal and bryozoan wackestones and packstones. The biostrome is followed by a meter-thick unit of skeletal packstones and grainstones, coarsening upwards into a coarse crinoid grainstone.

Following this is an autoparabiostrome of mostly in place laminar stromatoporoids, the upper biostrome, described by Kershaw (1997) as a Grogarnshuvud-type biostrome. Matrix is much coarser than the Kuppen-type biostromes, mainly consisting of crinoid grainstones. The lower biostrome at Grogarnshuvud is texturally and faunally very similar to the Lower Biostrome at Kuppen, and might even be a lateral equivalent to the Kuppen Lower Biostrome (Kershaw 1997). The upper biostrome at Grogarnshuvud differs from all other biostromes in the area because of predominance of low-profile forms even in species that are high profile in the other biostromes. The species suite, however, does not differ from other biostromes (see Table 1). From the upper biostrome, 48 specimens collected by Kershaw (1997) are distributed amongst 10 different species (Table 1).

Fakle biostrome.—This biostrome is situated on top of argillaceous limestones and marls constituting mudstones and wackestones (Sandström 2000; Sandström and Kershaw 2002), and is overlain by coarse bioclastic grainstones, rudstones, and conglomerates. It is a Kuppen-type autoparabiostrome dominated by densely packed high domical to laminar stromatoporoids with laminar forms in growth position, and many domical forms overturned; favositid and syringostromellid corals are present. The biostrome matrix is fine-grained, consisting of skeletal packstones and wackestones. Of 59 stromatoporoid samples, nine species were found (Table 1). All specimens display smooth, enveloping and continuous laminae. The growth style of "*Stromatopora*" *bekkeri* and *Plectostroma scaniense* is similar to that in the middle biostrome at Kuppen (Fig. 4). *Lophiostroma schmidtii* is always laminar and *Clathrodictyon mohicanum* shows mainly low domical forms and are both confined to a lateral style of growth.

Table 1. Summary of measurements and distribution of species. Asterisked results are based on measurements from the shapes of the stromatoporoids (Kershaw 1997: fig. 6).

		Total	Kuppen lower	Kuppen middle	Fakle	Sjaustrehammarn	Grogarnshuvud lower	Grogarnshuvud upper
Number of specimens		634	404	41	59	61	11	48
Composition of shapes	Laminar	56	42	3	9	2	3*	9*
	Low domical	150	112	15	11	12	3*	19*
	High domical	41	25	6	7	3	2*	3*
	Extenden domical	34	23	4	4	3	3*	0*
	Columnar	43	19	7	5	12	0*	1*
Arrangement of latilaminae	Enveloping	231	194	17	14	6	-	-
	Non enveloping	30	17	0	2	11	-	-
Surface	Smooth	363	211	38	58	56	-	-
	Ragged	13	7	1	0	5	-	-
Mean values	B (cm)	-	40.1	23.8	33.5	30.0	-	-
	V (cm)	-	14.9	22.2	13.5	22.4	-	-
	V/B (cm)	-	0.69	0.90	0.40	0.75	0.52*	0.33*
Attitude	in growth position	236	169	17	31	13	6	-
	tilted	168	82	16	20	42	4	4
	V/B>0.5 in growth pos	42	28	6	5	3	0	-
	V/B<0.5 in growth pos	176	132	11	18	9	6	-
Species occurrence	*Clathrodictyon mohicanum*	132	107	2	8	6	5	4
	Densastroma pexisum	6	0	0	2	0	0	4
	Ecclimadictyon macrotuberculatum	1	1	0	0	0	0	0
	Labechia lepida	11	9	0	1	1	0	0
	Lophiostroma schmidtii	42	16	2	12	2	1	9
	Petridiostroma convictum	36	31	0	3	0	0	2
	Plectostroma katriense	2	2	0	0	0	0	0
	Plectostroma scaniense	147	79	14	9	35	4	6
	Pseudolabechia granulata	4	1	3	0	0	0	0
	Simplexodyction yavorskyi	7	2	1	1	1	0	2
	Syringostromella borealis	14	14	0	0	0	0	0
	Syringostromella carteri	14	9	1	1	1	0	2
	"Stromatopora" bekkeri	109	62	11	18	9	1	8
	Stromatopora lamellosa	2	1	0	0	0	0	1
	Stromatopora venukovi	18	10	0	0	0	0	8
	Unidentified	77	60	6	3	6	0	2
Diversity	Shannon index (H)	1.97	1.9	1.49	1.77	1.17	1.16	2.11

Sjaustrehammarn complex.—The lowermost exposed part of the Sjaustrehammarn complex is a bedded limestone of skeletal packstones and grainstones coarsening upwards into skeletal grainstones and stromatoporoid-rich rudstones (Manten 1971; Kershaw 1994; Sandström 2000; Sandström and Kershaw 2002). The top part of the complex constitutes an allo/para-biostrome of almost exclusively stromatoporoids that have been turned over and some fragmented. However, a surprisingly high amount of the stromatoporoids are very little affected, indicating very short transport distance.

Of 61 stromatoporoid biostrome samples seven species were found, dominated by *P. scaniense* (Table 1). Five speci-

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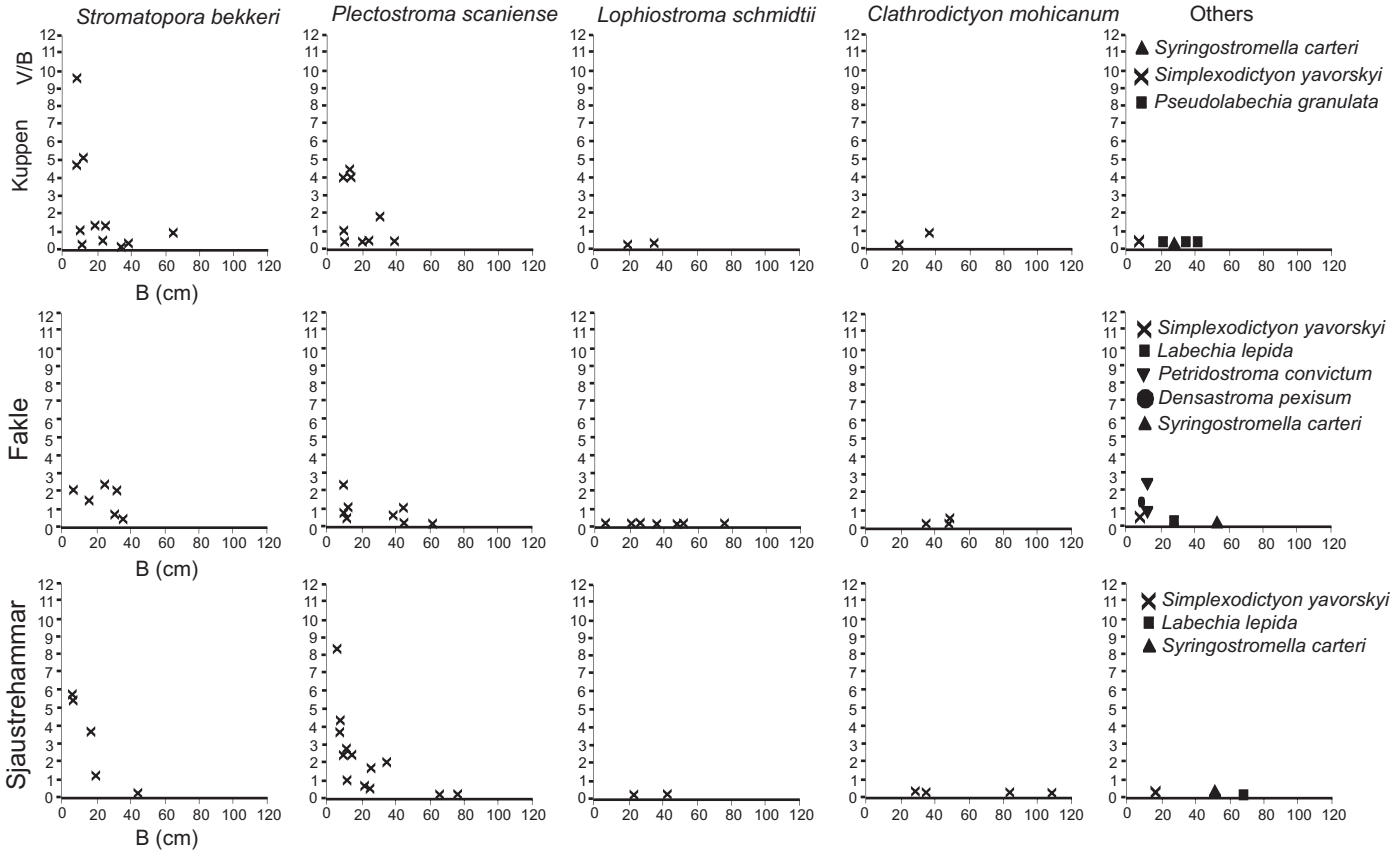


Fig. 4. Diagrams (V/B versus B) showing growth-strategies of different stromatoporoid species from the three biostromes Kuppen Middle Biostrome, Fakle Biostrome and Sjaustrehammarn Biostrome. Abbreviations: B, basal diameter; V, vertical height.

mens show ragged margins (Table 1). Apart from these, all specimens display smooth, enveloping and continuous laminae. As in Kuppen and Fakle, at Sjaustrehammarn *P. scaniense* and "*S.*" *bekkeri* show a wide range of growth forms (low domical to columnar; Fig. 4). *Lophiostroma schmidtii* is always laminar and *C. mohicanum* is low domical (Fig. 4). All the less numerous species in the sample are low domical. *P. scaniense* grows either laterally or vertically (Fig. 4). Intermediate growth habits are only represented in species with a base less than 0.4 m in diameter. Growth styles in "*S.*" *bekkeri* are harder to determine as there are fewer measurable specimens. However, overall, "*S.*" *bekkeri* exhibits growth styles similar to those in *Plectostroma scaniense* (Fig. 4). All other species show a lateral mode of growth.

Biometry.—Examination of the species suite shows that there are few differences between the sites (Table 1). All display low diversity assemblages, with domination of one or few species. Rarefaction analysis (Fig. 5) also supports that the studied sites have the same or similar distribution of species, all sites are within the 95% confidence interval of having the same distribution as the largest sample (here Kuppen Lower Biostrome). This is a strong support of our hypothesis that these different biostromal sites are parts of one very large complex of stacked biostromes, belonging to one faunal assemblage of stromatoporoids.

All sampled sites have diversities comparable to other investigations on stromatoporoid diversity (see examples in Kershaw 1998), ranging from 1.16 in the Grogarnshuvud lower biostrome to 2.11 in the Grogarnshuvud upper biostrome. Diversities in stromatoporoids are generally low, and the results obtained for this study seem to be fairly normal for a typical stromatoporoid reef.

Discussion

Fauna and diversity.—From Gotland, Mori (1968, 1970) described 64 stromatoporoid species from latest Telychian to late Ludlow times, spanning several different carbonate facies from deep marls to shallow reef and beach limestones. In the Hemse Group, Mori (1970) found 19 species belonging to the NE limestone facies and 6 species from the marl facies to the SE (equals the När Formation, sensu Jeppsson 2005), with only two species common to both areas. Applying diversity statistics to Mori's results, Kershaw (1998) found a diversity of ca. 2.5 on the Shannon Index, for the Hemse NE stromatoporoid assemblage (Kershaw 1998: fig. 14). Comparison with several stromatoporoid faunas from Silurian and Devonian rocks shows that diversities generally lie between 1 and 2 on this index. Those results demonstrate that

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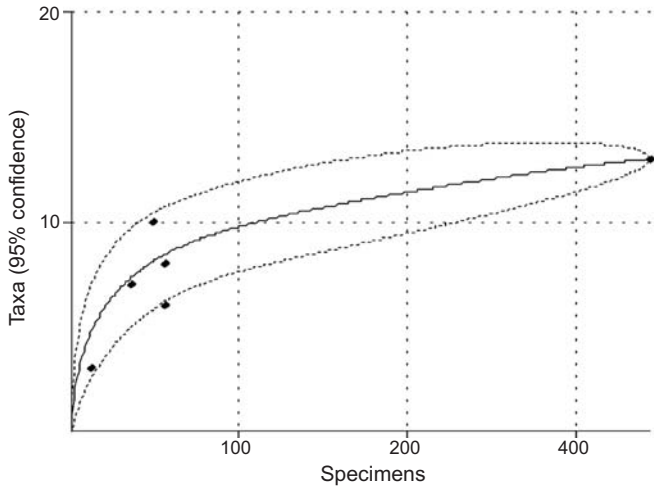


Fig. 5. Rarefaction analysis of the biostromes compared to the species distribution of the largest sample size, in this case the Kuppen Lower Biostrome. All investigated biostromes fall inside the 95% confidence interval of the distribution at the Kuppen Lower Biostrome.

diversity of the stromatoporoid reef biostromes obtained from this study are higher than diversities in most of the other stratigraphic units on Gotland. In comparison with modern reefs, Palaeozoic stromatoporoid communities are very low diversity. The overall low diversity of stromatoporoid-rich communities is puzzling, considering their status as the main reef constructing biota for the upper half of the Silurian and most of the Devonian (Stock 1990; Brunton et al. 1998). Although arguments for convergence of stromatoporoid higher taxa have been presented which are counter to the traditional classification of stromatoporoids, consistent differences between most stromatoporoid skeletal structures that define species, promotes confidence that the separation of species based on skeletal structure represent real biological differences. Recent revisions of stromatoporoid genera have also made use of multivariate techniques in order to further discriminate very similar species (e.g., Stock and Burry-Stock 2001). Thus we consider that stromatoporoid diversities really are quite low in the preserved components of Palaeozoic assemblages, in contrast to those in modern scleractinian reefs.

The stromatoporoid assemblages from the eastern Hemse Group reef-biostromes comprise the same species suite, and display a similar distribution that compares well with the Lower Biostrome at Kuppen (16 species, Kershaw 1990). The study of the latter (404 samples) is more than eight times the number of samples from any other investigated biostrome in the area. Due to this, the diversity may only seem to be higher in the Lower Biostrome (Table 1), as very rare species could be undetected in the other biostromes in the area due to fewer samples. However, the Shannon diversity index weights the most abundant species, so that the effect of rare species on the index is reduced. Within the most abundant species, biostromes of this study include the same number of species, present in similar proportions (Table 1). Therefore, we propose a common fauna for all biostromes in the area (this includes Sjaustrehammarn, Fakle, the Kuppen complex and Grogarnshuvud). Further south, at the Rudvier quarry (Kano 1990) a thin biostrome is visible in the upper parts, which contains a fauna similar to that from the Grogarn area. Even the relative abundance of species seems to agree, with three species dominating (*Clathrodictyon mohicanum*, "*Stromatopora*" *bekkeri*, and *Plectostroma scaniense*; Kano 1990). The Hemse Biostromes are all low-diversity in overall biotic components, and because they are biostromes show lateral growth, but lack in internal zonation. No studies have been made so far on the non-biostrome stromatoporoid fauna, so any non-stromatoporoid faunal differences are unknown.

There is little variation of abundance of stromatoporoid species between localities, except for the Lower Biostrome at Kuppen (Kershaw 1990) which has a greater abundance of *C. mohicanum*. We attribute this to local variation of distribution of stromatoporoid faunas, perhaps due to recruitment, and do not regard the Lower Biostrome at Kuppen as fundamentally different from the other sites, because the same species suite is present in all sites.

Comparison between sites, and assessment of environmental factors.—The six biostromes show clear differences in the fabric of biostrome construction. The fauna of the Fakle biostrome shows the least damage both to original orientation and to fragmentation. The most damaged is the Sjaustrehammarn biostrome where most specimens are disorientated, and very few are unaffected by fragmentation and/or abrasion, at least to some degree. These differences show the effect of physical changes in the environment on the final appearance of these biostromes. At Sjaustrehammarn, the area was exposed to storms and hurricanes more than the other sites, yielding a total demolition of the original texture and skeleton orientation. At Kuppen and Fakle, on the other hand, storms and hurricanes did not have a strong impact on the final appearance of the reefs, and only tall forms of stromatoporoid specimens were subjected to orientation changes (Sandström and Kershaw 2002). Similarly, in the Lower Biostrome at Kuppen, tall forms were overturned by storms while low-profile forms were relatively unaffected (Kershaw 1990), although there is a lot of stromatoporoid debris in the Lower Biostrome which is attributable to storm action. In the upper biostrome at Grogarnshuvud, low-profile forms dominate and the intra-reef sediment is much coarser than in the Kuppen-type biostromes. This biostrome type developed in a shallower and/or higher energy setting than the Kuppen-type (Kershaw 1997), but taphonomically it shows similar patterns of disorientated high-profile forms and low-profile forms in growth attitude.

Broad comparisons between the Silurian biostromes and modern coral reefs add to our interpretation of the biostromes, although ecological differences mean that exact parallels cannot usefully be drawn. For example, in modern reef areas, windward reefs are generally better developed than leeward reefs, primarily due to greater exposure to moderate wave energies that keeps oxygenation and nutrient lev-

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els at an optimum (see Hubbard et al. 1990; Grigg 1998). However, in Hawaii the thickest reef accumulation (i.e., in situ accretion) is in wave-sheltered embayments and in localities sheltered by adjacent islands (Grigg 1998). Leeward in situ accumulations are comparable with the model for biostrome formations in the studied sites on Gotland (Sandström and Kershaw 2002). The sum of field evidence from a range of localities indicates that the seaward-facing biostrome margins are on the southerly sides of the biostromes. The Belize backreef areas contain patch reefs that are suggested as a possible modern equivalent to the Hemse Biostromes (Sandström and Kershaw 2002). These patch reefs are developed in a lateral growth mode (Mazzullo et al. 1992; Burke et al. 1998), producing tabular reef structures (= biostromes; sensu Kershaw 1994). Coral species diversity in these biostromal reefs is low, with only ten coral species reported from the "Elmer Reef" (Mazzullo et al. 1992) with one species, *Monastrea annularis*, dominating the actual reef biota, and one other species, *Acropora cervicornis* dominating the off-reef facies. The Elmer Reef at Belize is also biologically zoned in leeward and windward biotic zones (Mazzullo et al. 1992), however, in another studied patch reef area at Mexico Rocks, to which the Elmer Reef belongs, no internal zoning was found at any studied site (Burke et al. 1998). At Mexico Rocks a slightly richer fauna was collected, with 17 coral species found, but is otherwise very similar to the Elmer Reef study with *M. annularis* dominating the fauna by 83% (Burke et al. 1998). Burke et al. (1998) did also show that diversity was highly correlated to patch reef size, with an increased diversity together with increased patch reef surface area as predicted by the island theory presented by MacArthur and Wilson (1967).

In Hawaii, community structure and coral reef accretion seems to be primarily controlled by wave energy, i.e., annual and/or decennial disturbances that cause enough damage to prevent reef accretion in exposed and shallow enough areas (Grigg 1998). In sheltered areas, in situ accretion takes place with a mean annual growth of approximately 2 mm. Coral species diversity is significantly lower in areas where accretion is limited or absent. Modern coral communities in wave-exposed environments undergo constant turnover that can be associated with mortality and recruitment (or regrowth of fragmented corals). In Hawaii, such communities are seldom thicker than a single living colony (Grigg 1998), thus in areas exposed to heavy disturbances, taphonomic feedback is one vital factor for the sustainability of reef growth (see Kershaw and Brunton 1999; Sandström and Kershaw 2002).

Results from this study serve to strengthen the argument that the Hemse biostromes comprise a low diversity assemblage, together with an important genetic control on growth forms, but the degree of genetic control varies. In some species the control seems to be very strong (e.g., *Lophiostroma schmidtii*), in others it is weaker (e.g., *Plectostroma scaniense* and "*S.*" *bekkeri*) such that in some sites the growth form range is greater than others. *P. scaniense* and "*S.*" *bekkeri* show a dominance of vertical over lateral growth in all sites except for the upper biostrome at Grogarnshuvud, where these species exhibit a dominantly lateral growth (Kershaw 1997), implying that environmental control may override the genetic influence. Thus, these data show that the growth form of stromatoporoids is controlled by both genetic and environmental factors.

Raggedness in modern corals that can be directly attributed to sedimentation stress is not commonly reported. Recently, however, hurricane Marilyn in 1995 caused an extensive movement of sediments around Buck Island (St Croix, Virgin Islands), revealing ragged margins on heads of the modern coral *Diploria strigosa* (Hillis and Bythell 1998). These ragged margins were the response to repeated events of sediment removal by hurricanes, and inter-hurricane sedimentation stress. In contrast, for the Hemse biostromes, although sedimentation is a key factor in the distribution of growth forms in an assemblage, in these three biostromal settings on Gotland, the evidence suggests very low sedimentation stress. The large laminar stromatoporoids and the very high-profile forms are dominantly smooth, non-enveloping forms.

All features often attributed to sedimentation events such as raggedness, sediment inclusions, and non-overlapping lamina are almost completely missing from these biostromes. They may instead have been net exporters of sediment to other areas of the carbonate ramp. For instance, ca. 10 km south of Sjaustrehammarn the Folhammar locality has a stromatoporoid assemblage affected by episodic sedimentation (Riding 1981; Kano 1990; Sandström 1998, 2000). The sedimentary conditions are interpreted to have restricted development of the complex (Sandström 1998). At Folhammar, evidence for sediment influence is based on the presence of abundant ragged stromatoporoids with associated sediment inclusions in stromatoporoid skeletons, and laminar forms with an anastomosing character. Episodic sedimentation is attributed to storm transportation, thus making the Folhammar area an area of net sediment accumulation. We have found no evidence that the raggedness of these stromatoporoids was due to growth of laminae into the water to create original growth cavities.

The role of competition seems to be of lesser importance for the control of the assemblage. No features that can be directly addressed to competition were found from any of the investigated biostromes. Very few indications of competition are evident from Palaeozoic reefs (Fagerstrom et al. 2000). On the other hand, there are several examples of non-competitive strategies among reef builders in the mid-Palaeozoic, by means of symbiosis (Kershaw 1987; Zhen and West 1997), coalescence (Kershaw 1990; Sandström 1998) and niche partitioning (Watkins 2000), all aimed to avoid direct competition. Throughout the upper part of the Hemse beds, both symbiosis and coalescence are common features, and in all three investigated biostromes both of these features were observed, thus implying that competition was not an important factor. Predation pressures do also

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seem to be of very little importance in controlling the growth characters and the faunal assemblage of the Hemse Biostromes. There is no evidence found of grazing or endolithic weakening of stromatoporoid skeletons from the three biostromes. Most of the boring and grazing activities on stromatoporoids so far reported from the Silurian have a post-mortem origin (Kershaw 1980; Fagerstrom et al. 2000; Lebold 2000).

Conclusions

- Biostromes in the eastern Hemse Group (Ludlow) on Gotland are low-diversity assemblages dominated by three stromatoporoid species ("*Stromatopora*" *bekkeri*, *Plectostroma scaniense*, and *Lophiostroma schmidti*).
- A genetic control on growth forms, suspected in previous work at one site (Kershaw 1990), is not evident for some of the species (*P. scaniense* and "*S.*" *bekkeri*) in all the investigated biostromes. This suggests that while the controls of growth form of stromatoporoids across this area are mainly genetic, some species like *P. scaniense* and "*S.*" *bekkeri* show a greater level of morphological plasticity presumed due to environmental differences.
- This study serves to emphasize the value of relating growth form and taxa in stromatoporoids for palaeoenvironmental interpretation. Both the uniformity of facies and the widespread low-diversity stromatoporoid-bearing biostromes reveal that there was a similar set of palaeoenvironmental conditions across the area where the biostromes crop out. Variations in exposure to wave energy is proposed as the principal reason for growth form variation in certain species, while other species are under such strong genetic control that the growth form is conservative and thus, may be limited to certain environments.
- Comparisons with modern environments serve to strengthen the argument that the role of frequent disturbances to reef environments is a key factor in controlling the final appearance of a reef and to the growth forms of reef-constructing organisms, in this case the stromatoporoids.

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