Palaeoecology of corals and stromatoporoids in a late Silurian biostrome in Estonia

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A middle Ludlow biostrome at Katri, western Estonia, the richest accumulation of corals and stromatoporoids in Estonia, is partly exposed in a coastal section. The fully marine biostrome consists of five fossiliferous layers of carbonate skeletons, grouped into Facies 1 (grainstone-packstone, Layers 1, 3, 5) and Facies 2 (wackestone, interbedded Layers 2, 4). Pressure solution degraded original sedimentary relationships and morphologies of stromatoporoids, tabulates and rugosans which constructed the biostrome, but the two facies have major faunal differences. Facies 1 is rich in stromatoporoids "*Stromatopora*" *bekkeri* and *Plectostroma scaniense* (low to high domical up to ca. 30 cm in basal length); and tabulate *Favosites forbesi* (bulbous to high domical up to ca. 25 cm wide). In Facies 2, all three taxa are less common and much smaller. Instead, the most abundant stromatoporoid is laminar *Syringostromella borealis* up to 30 cm basal length; the most abundant coral is erect branching *Laceripora cribrosa*, as scattered fragments up to 24 cm long. Neither occurs in Facies 1. Six other stromatoporoid taxa, 5 other tabulate and 5 rugosan taxa occur uncommonly in the biostrome, mostly in both facies. The Katri biostrome is slightly younger than, but facially similar to biostromes in the middle Ludlow Hemse Group on Gotland ca. 250 km WSW, with well-known stromatoporoid faunas. Corals are abundant in Hemse biostromes. Several key stromatoporoids occur in both the Hemse biostromes and Katri, but two abundant taxa in Hemse biostromes are absent in Katri and two tabulate corals abundant in Katri are missing in Hemse biostromes. Thus there was a wide distribution of such biostromes in the central Baltic large shallow marine carbonate platform, but with previously unreported variable assemblages presumed due to facies features not recognised in the sediments.

Key words: Anthozoa, Stromatoporoidea, palaeoecology, biostrome, Silurian, Estonia.

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Introduction

Silurian reefs and reef-associated facies in Estonia are well-exposed in low cliffs along the coastline and some inland quarries, and contain abundant faunas of corals and stromatoporoids. Stromatoporoid taxa from Estonia have been described by Nestor (1964, 1966) and coral taxa by Klaamann (1962, 1964). These key workers laid the foundation for taxonomic studies of corals and stromatoporoids in this area, but less is known about their palaeoecology, which is the subject of this paper.

This study selects a particularly abundant co-occurring fauna of late Silurian stromatoporoids and corals in Estonia, and aims to assess the palaeoecology of a suite of coral and stromatoporoid taxa occurring in a well-exposed and easily accessible biostrome at Katri, on the westernmost coastline of Saaremaa Island, Estonia (Fig. 1). Traditionally, corals and stromatoporoids have been studied separately, so the purpose of this co-study of these two important Palaeozoic reef-building organisms, that lived together, is to make a detailed comparison of their growth in a single reef and use this information to (i) enhance understanding of controls on them when they were alive, and (ii) aid facies analysis.

Institutional abbreviations.—KaS, Brunel University, London, UK; GIT, Geological Institute, Tallinn, Estonia.

Geological setting

Estonia is centrally located in a stable platform region of the central Baltic (e.g., Bassett et al. 1989). The Caledonian
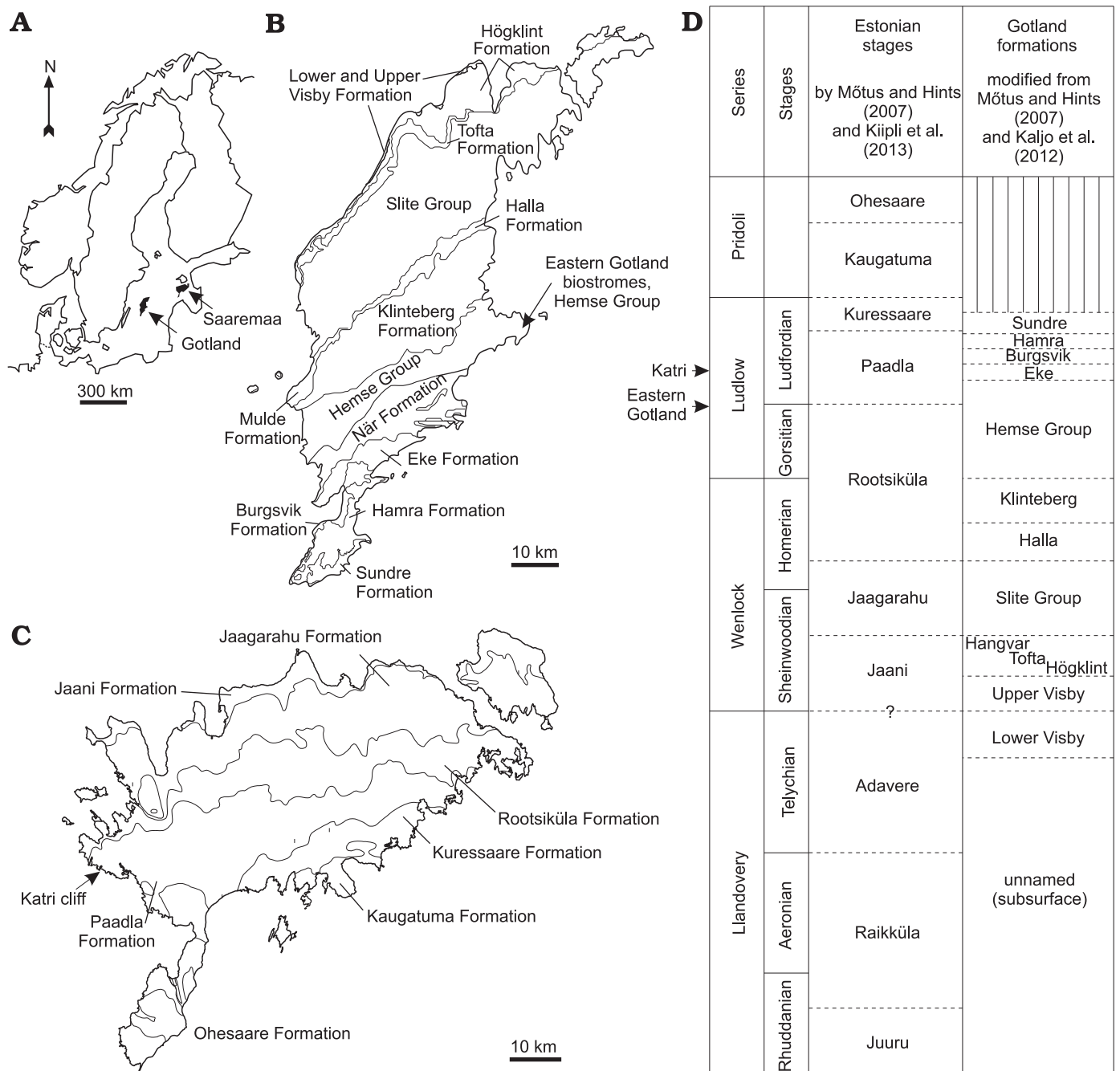
Fig. 1. Location and geology of key sites discussed in this paper. **A**. Map of Baltic region showing location of Saaremaa and Gotland. **B**. Map of Gotland, where similar biostromes occur in the eastern part of the Hemse Group. **C**. General geological map of Saaremaa highlighting Katri in the upper Silurian Paadla Formation, from which stromatoporoids and corals are described in this paper. **D**. Stratigraphic column of Estonia and Gotland (approximate horizons of Katri and the eastern Gotland biostromes are arrowed).

Orogeny produced uplift in Baltoscandia, so the shallow sea of the East Baltic Region narrowed towards the end of Silurian time (Cocks and Torsvik 2005; Nestor and Einasto 1997). Thus the biostrome under study forms part of a carbonate platform system in shallow waters. The Katri site exposes part of the Uduvere Beds of the Paadla Stage of Estonian stratigraphy (Fig. 1) and is dominated by carbonate sediments (Nestor and Einasto 1997). Nestor (1997: 103–104) described the distribution of the Uduvere Beds as consisting of shallow marine "skeletal-, pelletal-, lithoclastic-, oncolitic grainstone, packstone, and rudstone, interbedded with bands of marlstone, coral-stromatoporoid biostromes etc.". Nestor (1997: fig. 73) also showed that reefal deposits occur in boreholes several km east of Katri near the village of Kaugatuma and further east the sequence is principally argillaceous limestone (marlstone). Thus we presume the coarser-grained facies, of which Katri is a part, occurs largely in the western part of Saaremaa Island.

Fig. 2. Cliff exposure of the Katri biostrome, upper Ludlow, Silurian, showing two facies in 5 layers; Layers 1–5 are labelled in each photograph. **A**. General view showing layering of the biostrome. **B**, **C**. Close views of the layers; Facies 1 (Layers 1, 3, 5) forms prominent bands of grey cemented packstone-grainstone comprising comminuted bioclasts of marine shelly fossils; Facies 2 (Layers 2, 4) comprises the intervening bands of wackestone, that are less prominent, but composed of the same material as Facies 1.

The Katri biostrome exposes only ca. 1 m of cliff but is very densely packed with both stromatoporoids and corals for a horizontal distance of ca. 150 m and is the most fossiliferous biostromal deposit in Estonia. Both north and south ends of the biostrome pass laterally along the coastline into bedded limestones containing few corals and stromatoporoids. The exposed biostrome is presumed to be a cross section through a laterally extensive structure. Thus if the biostrome is circular in plan view, it is presumed to be approximately 150 m in diameter.

The Katri biostrome is similar in general appearance to the extensive middle Ludlow stromatoporoid-coral biostromes of the Hemse group on eastern Gotland, Sweden, ca. 250 km WSW of Katri but is age-equivalent to the overlying Eke Formation on Gotland, thus slightly younger than the Gotland Hemse Group (Fig. 1C). Although the Katri site faunas are well known, comparison of their palaeoecology with similar facies on Gotland provides an opportunity to explore the wider facies relationships of these deposits and the stromatoporoid-coral faunas they contain. In this respect, Gotland is a particularly important location for comparisons because the coral and stromatoporoid faunas of the Ludlow of Gotland are largely the same as in Katri, in contrast to more distant stromatoporoid deposits, discussed later.

The Katri coastal section consists of five distinguishable layers, numbered 1 to 5 upwards (Fig. 2). The layers are shown in a schematic log in Fig. 3, together with representative morphologies of the constructing organisms. Layers 1, 3, 5 are very similar in sediment and fossil type and are here grouped as Facies 1. Facies 1 comprises packstone-grainstone of comminuted marine bioclasts with abundant larg-
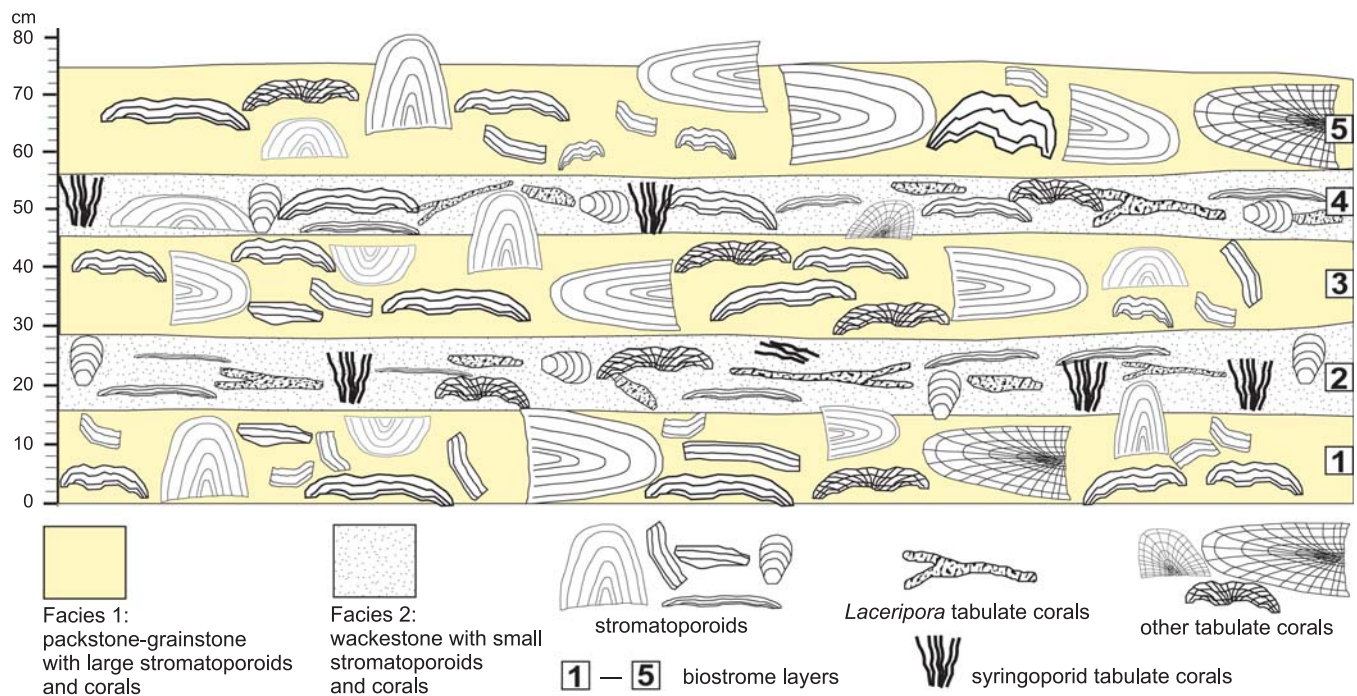
Fig. 3. Schematic log of Katri biostrome, upper Ludlow, Silurian, showing the distribution of constructing fossils in five layers. Layers 1, 3, 5 form Facies 1; Layers 2 and 4 form Facies 2. Note the differences in stromatoporoid and coral growth forms and sizes between Facies 1, 2.

er-sized stromatoporoids and corals (Fig. 4). The interleaved Layers 2 and 4 (Figs. 5, 6) are also similar to each other (but different from 1, 3, 5) and are here grouped as Facies 2, a wackestone of the same material as Facies 1. Facies 2 contains smaller stromatoporoids and corals, and has a greater abundance of branching corals than Facies 1. The biostrome base lies below beach level and its top is eroded as the modern erosion surface. Remnants of further biostrome layers above Layer 5 indicate the sequence continued upwards, but the entire thickness and number of biostromal layers is not preserved.

The biostrome is heavily affected by pressure solution so the original sedimentary contacts between the five layers are not preserved (Fig. 3). Furthermore the margins of corals and stromatoporoids are stylolitised (Figs. 4, 5), such that the original full sizes and morphologies are not preserved; exact measurements of the morphologies cannot be made. Furthermore, because margins of stromatoporoids and corals are stylolitised, the relationships between their growth and the accumulation of sediment cannot be established. Thus it has not been possible to determine whether the corals and stromatoporoids were buried as they grew (constratal) or grew on the substrate and were subsequently buried (superstratal; see Insalaco 1998 for full description of these two terms). Nevertheless, the overall morphology of individual stromatoporoid and coral samples is clear, so that laminar, low to high domical, and bulbous shapes can be easily distinguished. The assemblage is thus suitable for a study of the stromatoporoid and coral taxa in relation to their growth forms and enclosing facies, to investigate the palaeoecology of the faunas.

Material and methods

A suite of stromatoporoids (84 specimens) and corals (70 specimens) collected from Katri in August 2012 is considered sufficient to represent the assemblage based on the numbers of taxa collected in other studies (e.g., for stromatoporoids; Kershaw 1997). Taxa in each sample were identified in thin section, and combined with growth form measurements (noting the imprecision caused by pressure solution destruction of fossil margins) and sedimentological information from associated facies. This paper therefore employs light microscope work to characterize the faunas and facies. Minor additional information was obtained from cathodoluminescence.

Results

Taxonomic issues in stromatoporoids and tabulate corals.—Most stromatoporoids in Katri are relatively easy to identify (Fig. 7), but the taxon currently called "*Stromatopora*" *bekkeri* (Mori, 1970) remains unassigned formally to a genus (Fig. 8). This taxon is common in the Ludlow of Gotland (Kershaw 1990; Mori 1970) where it has the same appearance as in Katri. Its skeletal structure has overlap, in different samples, and sometimes parts of the same samples, with the genera *Parallelostroma*, *Coenostroma*, and *Habrostroma*, yet does not satisfactorily fit into any of these genera. Thus "*S.*" *bekkeri* is considered to be a separate taxon and in most specimens is easily recognizable, thus we keep it as "*S.*" *bekkeri* until such a time as its identification is resolved. *Favosites pseudoforbesi*
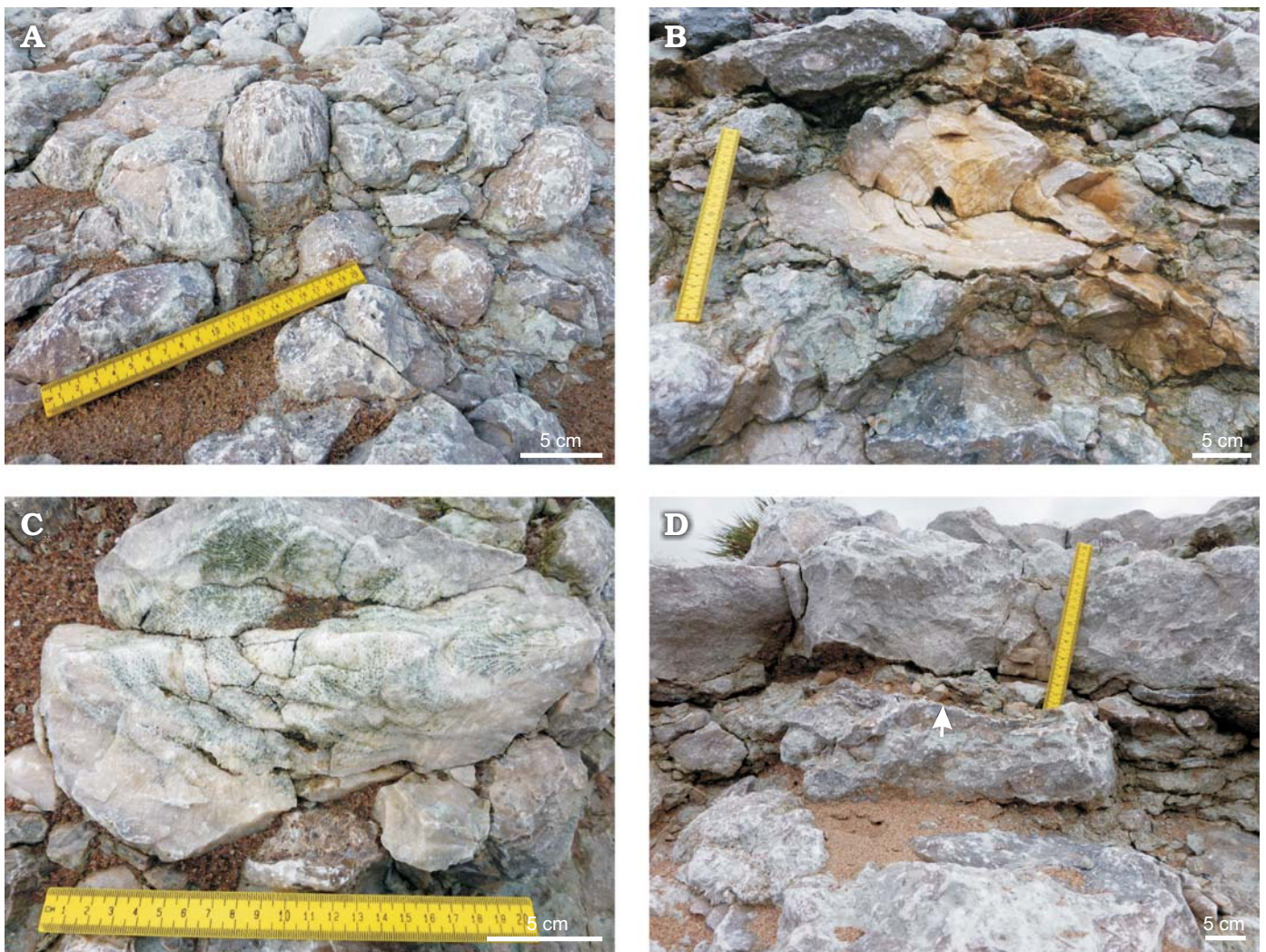
Fig. 4. Field photographs of Facies 1 in Katri biostrome, upper Ludlow, Silurian. **A**, **B**. Stromatoporoids. **C**. Corals. **D**. Differences between Facies 1 (Layers 3, 5 are the solid limestone beds) and Facies 2 (Layer 4 is the ca. 5 cm-thick band of less consolidated rock directly above white arrow, centre) are distinguishable, but pressure solution resulted in compaction of the beds and removal of detailed sedimentary relationships between the successive layers. Note that the margins of the stromatoporoids and corals are degraded, affecting accurate measurement of their growth forms.

pseudoforbesi was described from Katri by Klaamann (1962). It was synonymised with *Favosites forbesi* by Stel (1978). Otherwise the coral taxa are distinct.

Distribution of stromatoporoids and corals.—As noted above, Facies 1 (Layers 1, 3, 5) contains densely packed large stromatoporoids and corals, in contrast to Facies 2, which has smaller specimens and some differences in taxa. The percentage volume of the facies occupied by stromatoporoids and corals is not determinable because of the pressure solution. Furthermore, because pressure solution has the capability of removing small samples, we are unable to assign percentages to the relative abundance. However, we estimate that stromatoporoids were slightly more abundant than corals.

In Facies 1, larger low to high domical stromatoporoids and corals occur, and some of the corals form into bulbous shapes. The most abundant stromatoporoid taxa are "*Stromatopora*" *bekkeri* and *Plectostroma scaniense*, formed as morphotypes of low to high domical form and di-

mensions of 2.5–30 cm basal length. Other stromatoporoids in Facies 1 are: *Plectostroma atterdagi*, *Petridiostroma convictum* (always containing symbiotic syringoporids, and often rugosans, as in the Ludlow of Gotland), *Plexodictyon katriense*, and *Simplexodictyon yavorskyi*. The most abundant coral in Facies 1 is the tabulate taxon *Favosites forbesi* (Fig. 9A–D), which has average width 13 cm and height 12 cm (larger than samples in Facies 2); most samples of this coral are found lying on their sides. Other tabulates in Facies 1 also occur in Facies 2, including symbiotic *Syringopora affabilis* (Fig. 9K), *Aulopora amica* (Fig. 10F) and *Favosites forbesi*. Rugose corals in Facies 1 comprise taxa *Stauria* (Fig. 10G) and *Cystiphyllum* (Fig. 10H).

Facies 2 comprises laminar and small domical-bulbous stromatoporoids, predominantly laminar. The most abundant is *Syringostromella borealis*, which occurs in only Facies 2, forms laminar shapes 15–30 cm basal length (Figs. 5A, 7B). All the stromatoporoid taxa noted in the previous paragraph
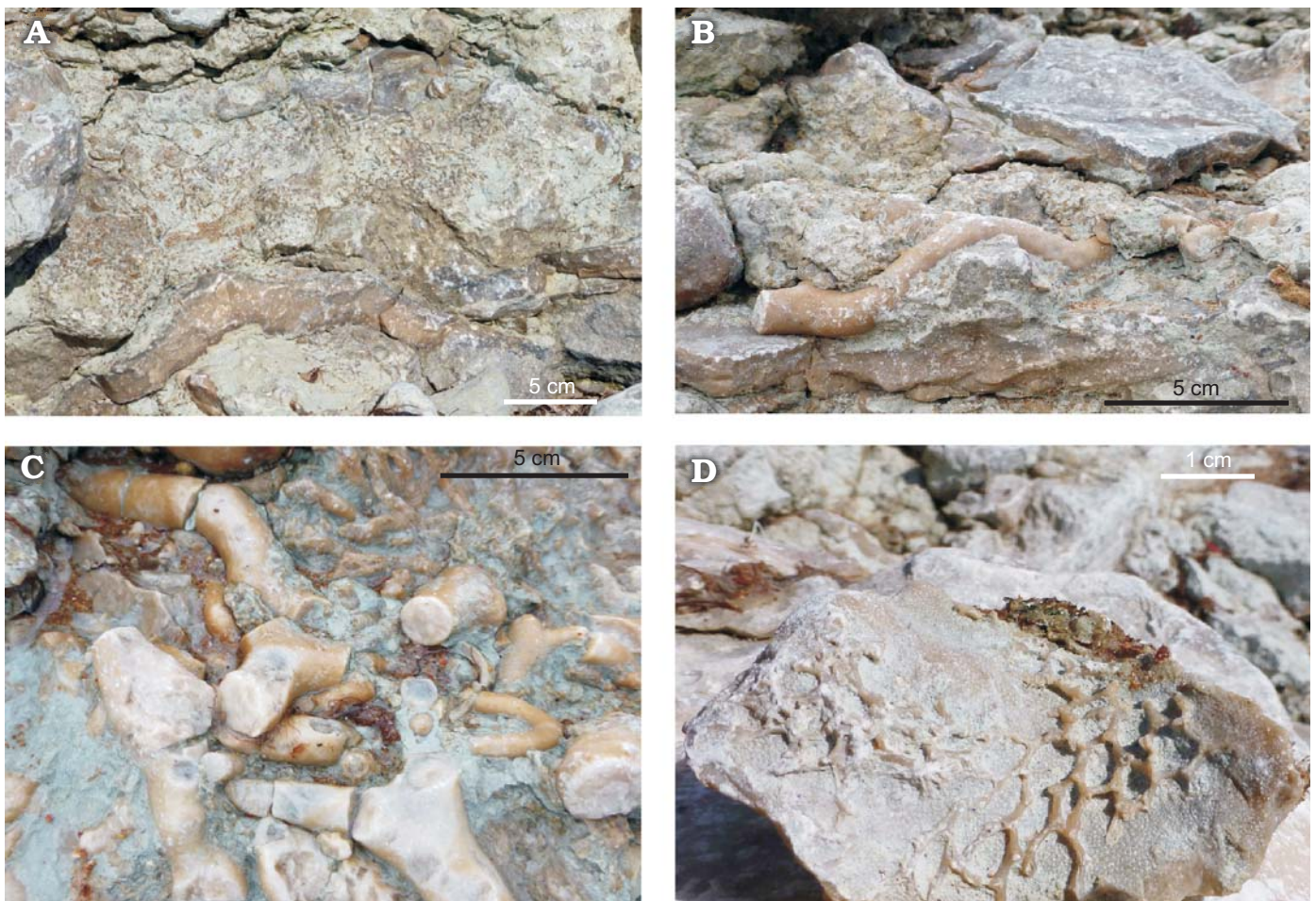
Fig. 5. Field photographs of Facies 2 in Katri biostrome, upper Ludlow, Silurian. **A**. Laminar *Syringostromella borealis* Nicholson, 1891 in lower centre of photo, surrounded by grey-green wackestone. **B**. Broken stem of *Laceripora* in centre, with laminar stromatoporoids above and below it. **C**. Fragmented *Laceripora*, and the edges of two small bulbous stromatoporoids at the top of the photo. **D**. Encrusting auloporid tabulate on the upper surface of a laminar tabulate coral.

for Facies 1 are also present in Facies 2 but as smaller specimens. In addition, *Stromatopora antiqua* is present in only Facies 2. The most abundant tabulate coral taxon, which also occurs in only Facies 2, is *Laceripora cribrosa* (Fig. 9I, J), as exclusively erect-form branching structures, but in all cases found lying horizontally. These are obviously erect forms because they have corallites all around the surface of the stems of coral, so did not grow lying on their sides. However, coralla of *Laceripora* are not fully preserved, occurring as broken pieces with maximal lengths up to 24 cm and no samples were found attached to their substrates in our study. Only three specimens of *Laceripora* with bases have been found at Katri, by Klaamann (1962: fig. 9J). Facies 2 also contains tabulates *Syringopora multifaria*, both symbiotic (within stromatoporoids) and non-symbiotic occurrences (Fig. 10A, B), *Kitakamiia callosa* (Fig. 9G, H) and *Thecia swinderniana* (Fig. 9F). Some corals show corallites that grew in different directions, thereby producing adjacent dome-shaped forms within individual coral specimens (Fig. 9A). *Favosites forbesi* has smaller coralla in Facies 2 (average 8 cm width and 9 cm height) than in Facies 1, but the

growth styles of *F. forbesi* are similar in both facies. Rugose corals in Facies 2 include *Hedstroemophyllum* (Fig. 10C, I), *Stereoxylodes* (Fig. 10D) and *Entelophyllum* (Fig. 10E).

Other fossils.—Study of our samples shows other fossils are present in the Katri biostrome. Literature reports reveal the presence of brachiopods (*Quadrithyris sinuata* Rubel, 1970, see Rubel 1970; *Didymothyris katriensis* Rubel, 1967, see Rubel and Modzalevskaya 1967; *Stegerhynchus diodontus*, was reported but not formally identified, see Rubel and Rozman 1977), ostracods (*Calcaribeyrichia katriensis* Sarv, 1968, see Sarv 1968), trilobites (*Proetus pulcher* Nieszkowski, 1857, see Männil 1981; *Cheirurines balizoma* in the collections of Tallinn Institute, but without references, see http://sarv.gi.ee for access to the Tallinn fossil database that has the details) and unidentified crinoids (as debris) and nautiloids (rare). However, confirmed calcareous algae and microbial carbonates were not found in thin sections, a feature in common with the Hemse Group biostromes on Gotland discussed later. Nevertheless, rare occurrence of a possible alga, referred to by Kõrts (1991) as *Parachaetetes*,
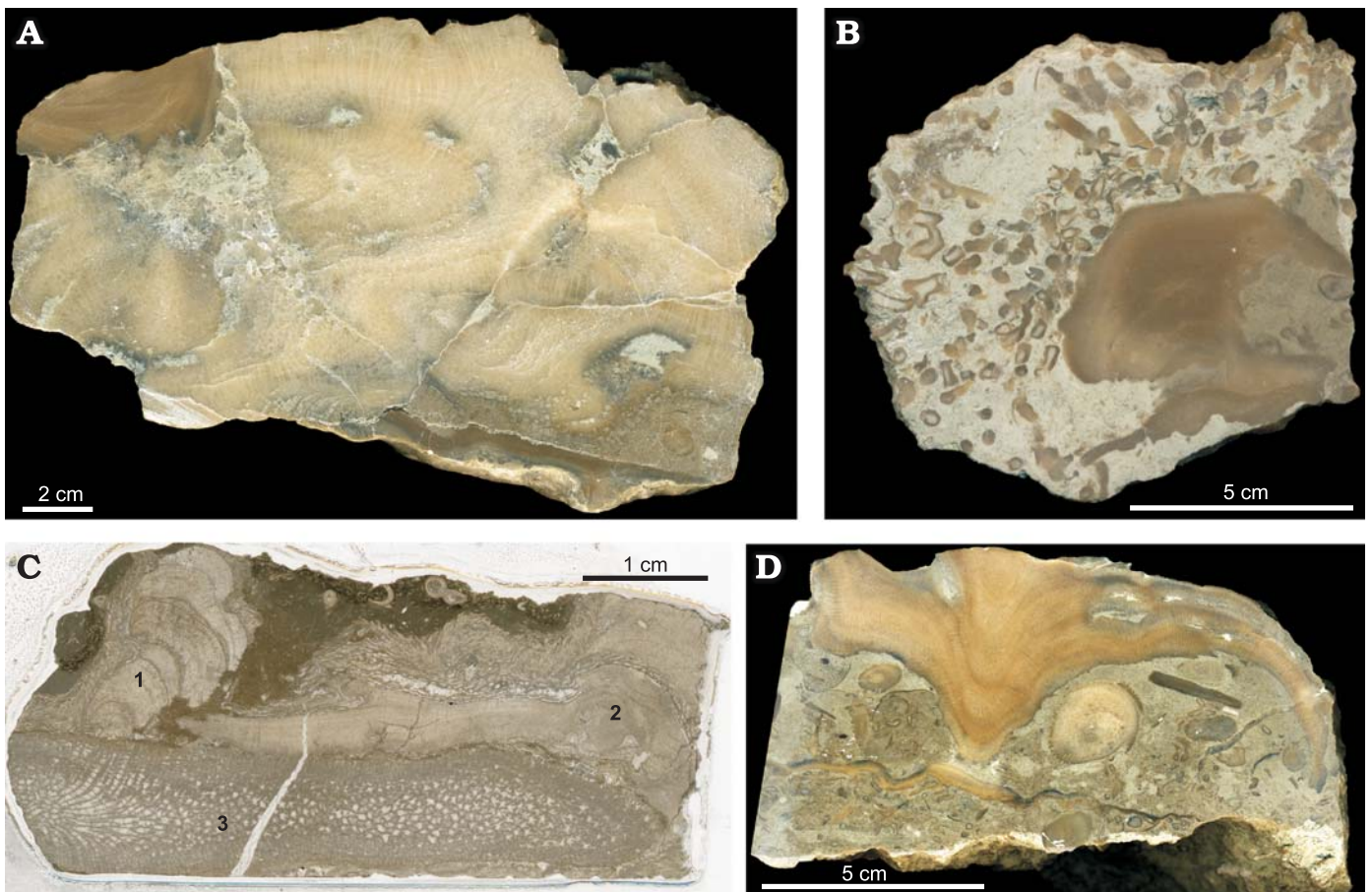
Fig. 6. Photographs of examples of details of fossils and fabrics, in Katri biostrome, upper Ludlow, Silurian. **A**. Polished block showing complex domical growth of *Favosites*, with stromatoporoids upper left and lower right, separated from the coral by stylolites, making the detailed original growth relationships impossible to determine. **B**. Polished block of stromatoporoid with encrusting syringoporid tabulate (*Syringopora multifaria* Klaamann, 1962). **C**. Thin section showing complex multiple overgrowth of corals (*Laceripora cribrosa* Eichwald, 1854 [3], *Kitakamiia callosa* Klaamann, 1964 and stromatoporoid *Plectostroma scaniense* Mori, 1969 [2]), and a columnar growth of a possible alga, resembling *Parachaetetes*, see Kõrts (1991) [1]. **D**. Corals *Thecia swinderniana* Goldfuss, 1829, thin laminar stromatoporoid, and bioclasts in wackestone matrix.

occurs in some thin sections (see Fig. 6C). Also two samples of fossils that resembled stromatoporoids in the field were revealed to be composed of layered peloids (Fig. 6C, D), and are considered here as peloidal stromatolites, presumed of microbial origin. Overall the fossil assemblage of corals, stromatoporoids, and other fossils establishes both Facies 1 and 2 as being fully marine stenohaline.

Fig. 11 shows, schematically, the range of growth forms of stromatoporoids and corals described in this paper, and a data table of taxa and growth forms is given in Fig. 12. Figs. 13 and 14 show reconstructions of the appearance of the coral and stromatoporoid assemblages in Facies 1 and 2, respectively.

Discussion

Interpretation of Katri biostrome

The recognition of two interlayered facies in the Katri biostrome indicates repeated change from one environmental condition to the other. The limited outcrop means that only three layers of Facies 1 and two layers of Facies 2 can be recognized, and that the beds underlying and overlying the biostrome are largely unknown. Thus the extent to which the setting is repeated between the two facies is of course unknown, but there are enough data to make some important new interpretations about the ecology of these Ludlow corals and stromatoporoids.

Stromatoporoids in Facies 1 are larger and their domical forms are commonly overturned, indicating a low energy growth period followed by sudden high energy, presumably by storms, as interpreted for the Hemse Group biostromes in the similar, slightly older, deposits (Fig. 1C) on Gotland (Kershaw 1990). In contrast, the presence of abundant branching coralla of *Laceripora* in Facies 2 at Katri is evidence of a lower energy environment than Facies 1. However, because no samples of *Laceripora* were found as complete specimens, nor were any in place, it is clear that the environment of Facies 2 was subject to high-energy pulses too.

Overall, we interpret Facies 1 to have developed in higher energy than Facies 2, but both were relatively low energy most of the time, interspersed with storms. The alternation
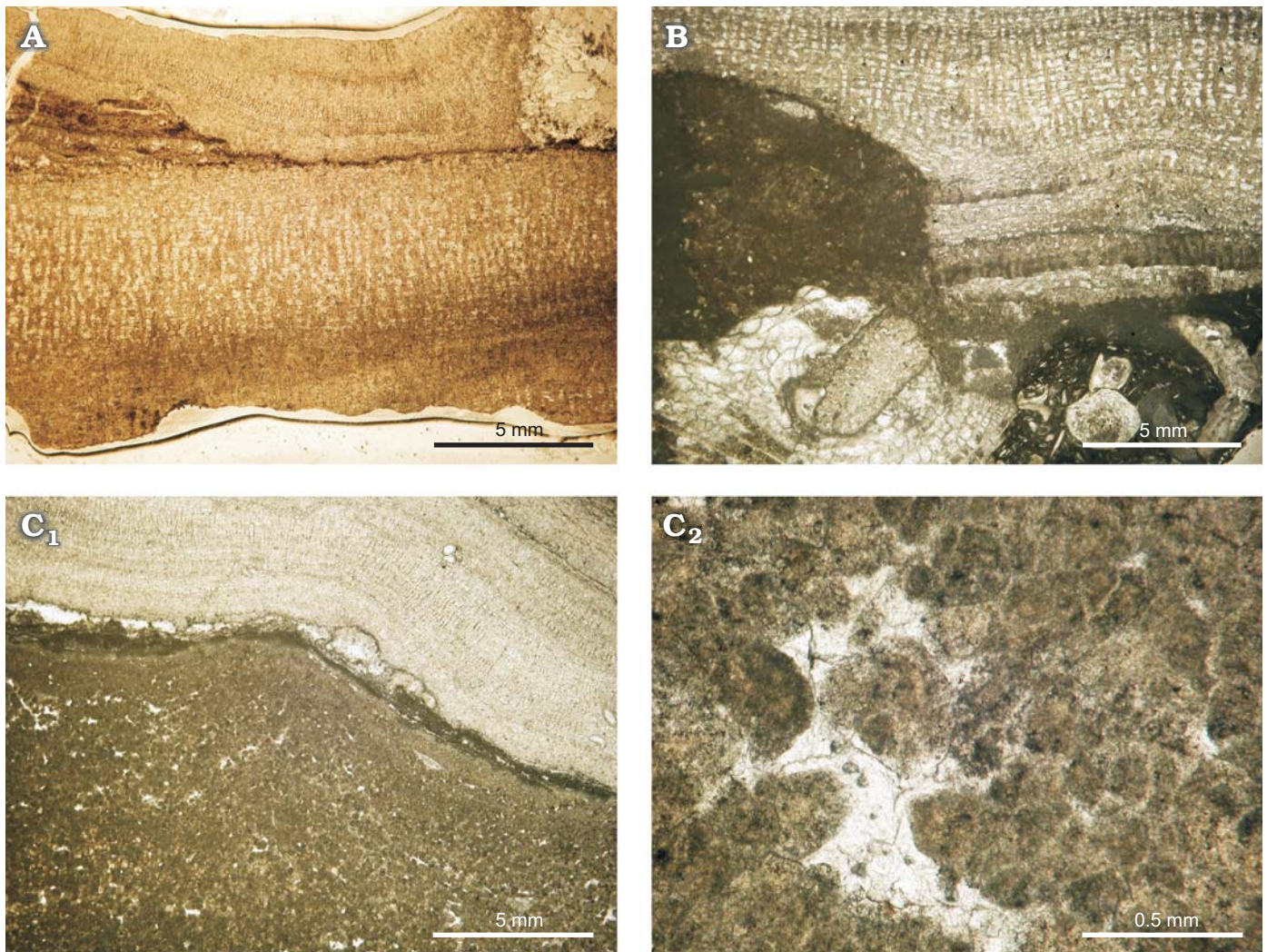
Fig. 7. Thin section photographs of some stromatoporoids from Katri biostrome, upper Ludlow, Silurian, showing details of growth relationships. **A**. *Plectostroma scaniense* Mori, 1969 grew on *Syringostromella borealis* Nicholson, 1891, KaSE-GIT656-191. **B**. *S. borealis* in wackestone of Facies 2, KaS46-GIT656-151. **C**. *P. scaniense* grew on a layered structure composed of peloids (enlarged in C_2), that is presumed to be a stromatolite, KaS39-GIT656-144. See Mori (1970) for photographs of other stromatoporoids, listed in Fig. 12.

of facies at Katri is most easily interpreted as controlled by minor sea-level changes, with shallower, more turbulent water for Facies 1 and quieter, likely deeper, water for Facies 2. Alternatively the facies represent different energy regimes at different times within the same water depth, which implies climatic changes without sea-level change. However, since climate change essentially equates to at least regional, if not global, temperature change, sea-level fluctuation is an inevitable consequence of climate shifts. In a limited outcrop not readily correlated to other places, identification of controls on climate change is not realistic. Nevertheless, the primary control on Facies 1 and 2 by sea-level change (regardless of what caused sea level to change) can explain the facies variations.

Because of the biostromal nature of the deposit, topography of the sea floor was likely to be low profile for both facies; the overall similarity of the sediment in each facies suggests relatively little environmental shift (perhaps sea level change of only a few metres) led to the alternate nature of the faunal assemblage. Differences in fauna and growth form characteristics of the corals and stromatoporoids between the two facies demonstrates sensitivity of these particular corals and stromatoporoids to changing environmental conditions, such that they are essentially facies-controlled assemblages. Thus there are corresponding differences between the coral and stromatoporoid taxa in the two facies that match the growth forms (e.g., branching *Laceripora* and laminar *Syringostromella* are more delicate, in Facies 2, than the domical *Favosites*, "*Stromatopora*", and *Plectostroma* in Facies 1).

Silurian stromatoporoid faunas elsewhere in Baltica

As noted earlier, the Katri biostrome is similar in appearance, and contains a comparable stromatoporoid fauna, to those in the middle Ludlow Hemse Group on Gotland 250 km to WSW, although the Katri biostrome is slightly younger,
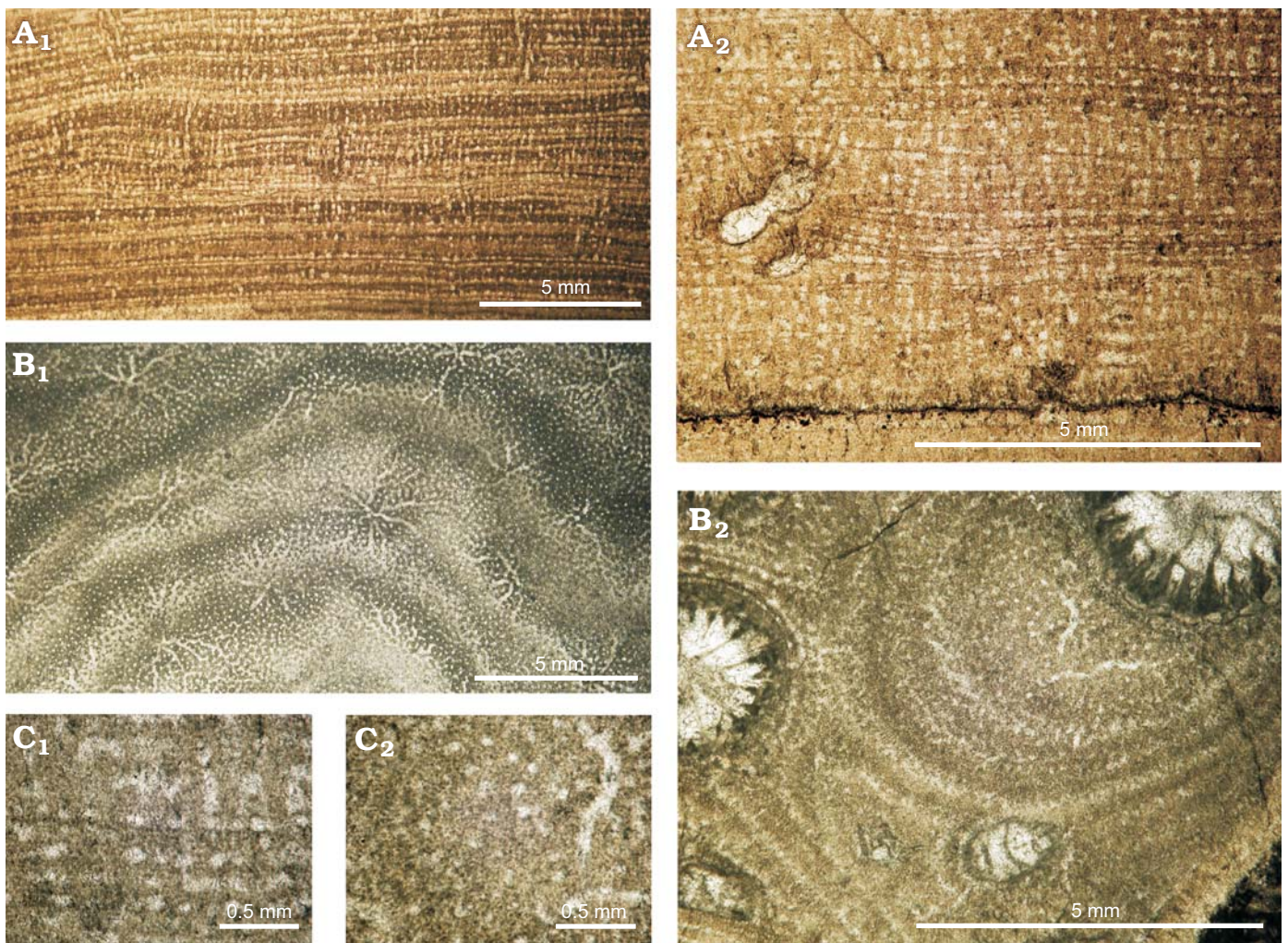
Fig. 8. Vertical (A_1–C_1) and transverse (A_2–C_2) views of "*Stromatopora*" *bekkeri* Nestor, 1966, Katri biostrome, upper Ludlow, Silurian, showing its range of structure. This taxon has not been satisfactorily assigned to a genus, see text for more details. Other stromatoporoids in the Katri site are well-established taxa, described and illustrated by Nestor (1966), with identical taxa on Gotland described and illustrated by Mori (1970), to which the reader is referred for more details. **A**. KaS59-GIT656-164. **B**. KaS37-GIT656-137. **C**. KaS45-GIT656-150.

equivalent approximately to the Eke Formation on Gotland (Fig. 1). These Gotland biostromes vary in composition; few have been studied in detail (Kershaw 1990; Sandström and Kershaw 2008) but most are rich in stromatoporoids and relatively poor in corals. However, some biostromes are richer in corals than stromatoporoids, in particular favositids and some heliolitids, together with a lesser abundance of solitary and colonial rugose corals (SK unpublished observations; taxonomic work was published by Klaamann 1982, detailed below). Furthermore, variations in morphology of some stromatoporoids between different biostromes were interpreted by Kershaw (1997) to be due to facies differences between individual biostromes of the Hemse Group, revealing considerable variation that is yet to be fully described and discussed in relation to environmental controls. It is important to emphasise that the Katri biostrome facies strongly resemble the Hemse Group biostromes, being fully marine yet poor in algae. For the stromatoporoids, there are notable differences between the Hemse biostromes on Gotland and the Katri biostrome in Estonia, and elsewhere in Baltica, described in the following three sections.

Stromatoporoid taxa variations in relation to both facies and stratigraphy.—Stromatoporoid taxon *Lophiostroma schmidti* is abundant throughout the Ludlow of Gotland (Kershaw 1990; Mori 1970; Sandström and Kershaw 2008), not only in the Hemse Group but also in later parts of the Ludlow of Gotland; however this stromatoporoid is missing in Katri. Also, two very abundant stromatoporoids in the Hemse biostromes on Gotland, *Clathrodictyon mohicanum* and "*Stromatopora*" *bekkeri*, were reported by Mori (1970) as being limited stratigraphically to only the Hemse Group, although Kano (1989) reported *C. mohicanum* from the Holmhällar locality in the upper Ludlow of southern Gotland, implying that it occurs rarely (but not absent) above the Hemse Group, and emphasises the importance of large sample sizes in stromatoporoid research. Thus the discovery by Kano (1989) of *C. mohicanum* at Holmhäller raises the possibility that *C. mohicanum* may indeed be present
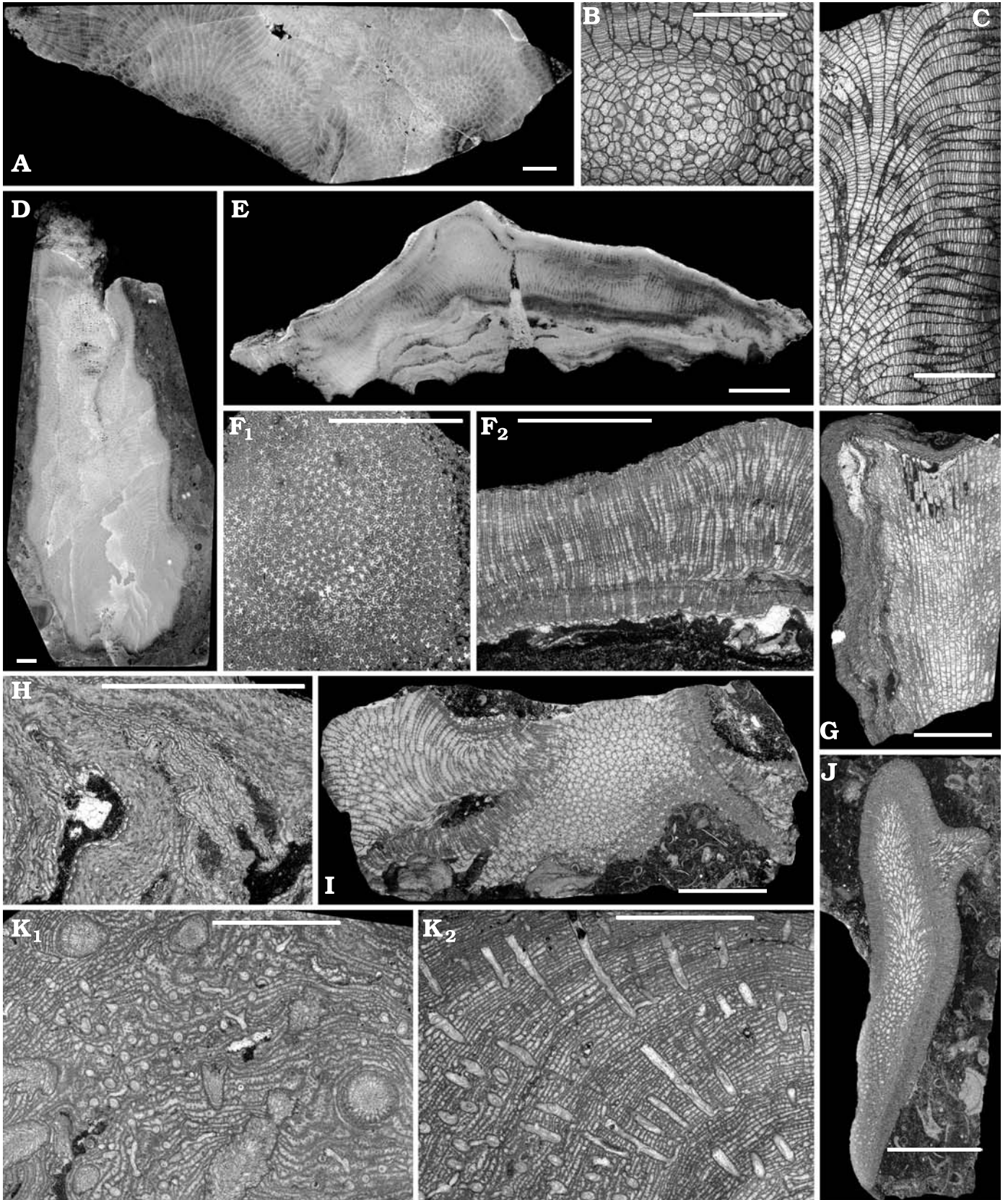
Fig. 9. Slab and thin section photographs of tabulate corals from Katri biostrome, upper Ludlow, Silurian, showing the identifications of taxa. **A–D**. *Favosites forbesi* Milne-Edwards and Haime, 1851. **A**. GIT656-27, vertical polished slab of bulbous corallum showing different growth centres. **B**. GIT656-17, transverse thin-section. **C**. GIT656-54, vertical thin-section. **D**. GIT656-56, vertical slab of columnar corallum in sediment. **E**, **F**. *Thecia swinderniana* Goldfuss, 1829. **E**. GIT656-20, vertical slab of tabular corallum. **F**. GIT656-62, transverse (F_1) and vertical (F_2) thin-sections. **G**, **H**. Thin- →
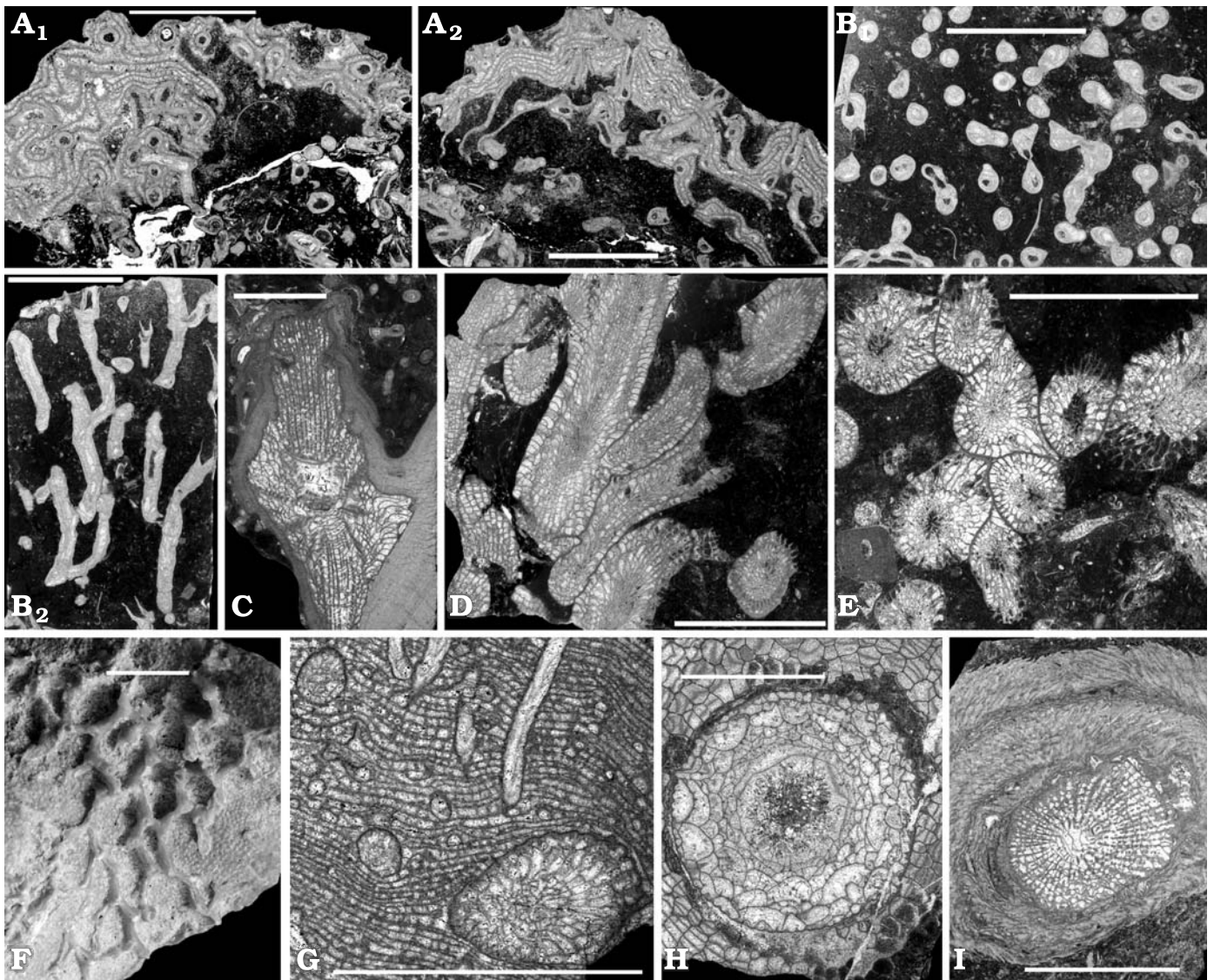
Fig. 10. Thin section photographs of tabulate and rugose corals from Katri biostrome, upper Ludlow, Silurian, showing the identifications of taxa. **A**. *Syringopora multifaria* Klaamann, 1962 in symbiosis with stromatoporoid *Petridiostroma convictum* Yavorsky, 1929, GIT656-51, transverse (A_1) and vertical (A_2) sections. **B**. *Syringopora multifaria*, GIT656-105, transverse (B_1) and vertical (B_2) sections. **C**. Vertical section of *Hedstroemophyllum* growing on stromatoporoid, GIT656-16. **D**. Different sections through corallites of *Stereoxylodes*, GIT656-50. **E**. Different sections through corallites of *Entelophyllum*, GIT656-41. **F**. *Aulopora amica* Klaamann, 1962 encrusting another coral, GIT656-62. **G**. Transverse section of *Stauria* in symbiosis with stromatoporoid *Petridiostroma convictum*, GIT656-47. **H**. Transverse section of *Cystiphyllum* in tabulate *Favosites forbesi* Milne-Edwards and Haime, 1851, GIT656-72. **I**. Transverse section of *Hedstroemophyllum* encrusted by *Kitakamiia callosa* Klaamann, 1964, GIT656-60. Scale bars 10 mm.

in the Eke Formation, but has not yet been discovered. *C. mohicanum* and "*S.*" *bekkeri* form a significant percentage of the stromatoporoid assemblage of the Hemse biostromes (Sandström and Kershaw 2008); for example these two taxa comprise 40% and 11%, respectively, of all stromatoporoids in the lower biostrome at Kuppen, see Kershaw (1990). However, they are both absent from the Eke Formation on Gotland, equivalent in age to Katri, but only *C. mohicanum* is absent from Katri; "*S.*" *bekkeri* is abundant in Katri. Nestor

(1966) found *C. mohicanum* in the Paadla Stage (K_2, the second part of lower Ludlow) in Estonia. Although this older stratigraphy is imperfect, the Paadla Stage beds in Estonia are approximately equal in age to the Hemse biostromes but lower than the Eke Formation (Gotland) and Katri (Estonia). Stratigraphically therefore, the absence of *C. mohicanum* in the Eke Formation on Gotland is consistent with its absence at Katri, but palaeoenvironmentally it would be expected in the Katri biostrome because of the apparent environmental

sections of *Kitakamiia callosa* Klaamann, 1964. **G**. GIT656-98, vertical section through rugosan with *K. callosa*. **H**. GIT656-90, transverse section. **I**, **J**. Thin-sections of *Laceripora cribrosa* Eichwald, 1854. **I**. GIT656-29, vertical section through the base of corallum. **J**. GIT656-10, vertical section through the branching corallum. **K**. Symbitoic *Syringopora affabilis* Klaamann, 1962 within stromatoporoid *Petridiostroma convictum* Yavorsky, 1929, GIT656-38, transverse section (K_1), which also has rugose corals within the stromatoporoid; vertical section (K_2). Scale bars 10 mm.
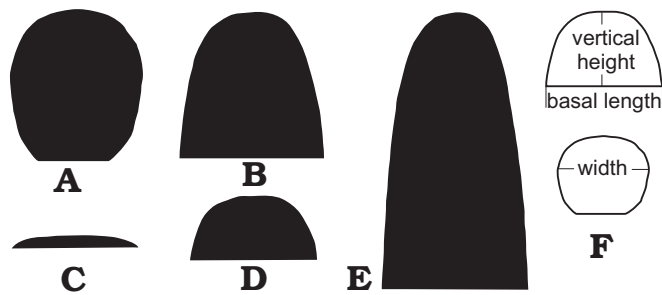
Fig. 11. Silhouettes of bulbous (**A**), laminar (**C**), and domical (**B**, high; **D**, low; **E**, extended) coral and stromatoporoid morphologies, showing the range of form in Katri. Outline diagrams (**F**) show the measurements collected from the fossils, noting that these are minimum values because of the pressure solution. In addition to these forms is the branched structure of the tabulate *Laceripora*, found only as broken specimens, encrusting auloporids, and branched syringoporids that occur both as free-living forms and symbiotic growths inside stromatoporoids, illustrated in other figures in this paper.

similarity to the Hemse biostromes of Gotland, also noting the abundance of "*S.*" *bekkeri* and *P. scaniense* in both Katri and the Hemse biostromes. Thus we infer a characteristic of the environment at Katri, not recognised in the sediments, that allowed the presence of "*S.*" *bekkeri* and *P. scaniense* but prevented *C. mohicanum* growing there.

Syringostromella borealis, which is abundant in Facies 2 at Katri, does not occur in the Eke Formation, but occurs sparsely higher in the Gotland sequence (see Mori 1970: 31). Thus it too exhibits an environmental sensitivity, with an apparent preference for the biostrome environments.

In contrast to the restricted stratigraphic distribution of *C. mohicanum* and *S. borealis*, other stromatoporoids abundant in the Hemse Group biostromes (e.g., *Plectostroma scaniense, Parallelostroma typicum, Petridiostroma convictum,*) are also abundant in all the reef deposits above the Hemse Group on Gotland, implying that they were less environmentally constrained.

Facies distribution of stromatoporoids in biostromes.— On Gotland, all the stromatoporoid taxa in the Hemse biostromes studied in detail by Kershaw (1990, 1997) are found together in one facies, in contrast to their facies separation in Katri. Kershaw (1990, 1997) noted that many stromatoporoids in the Hemse biostromes are fragmented and the biostromes interpreted as having been affected by storm action. Thus the facies separation of specific stromatoporoid taxa in Katri may indicate that these taxa were actually quite sensitive to environmental conditions, but in the Hemse biostromes the possibility exists that this sensitivity is masked by taphonomic mixing by storm action. Alternatively, it is also possible that the Hemse biostrome stromatoporoid taxa occurred all together in life prior to taphonomic movement; in that case the facies controls on the Hemse Group stromatoporoids on Gotland was less discriminatory on the stromatoporoids than in Katri. Consequently the stromatoporoid assemblage at Katri is very important in developing understanding of environmental sensitivity amongst Ludlow stromatoporoids and

our results therefore demonstrate features of the distribution of stromatoporoids that have not previously been reported. Further work is required to explore the alternative interpretations presented here.

Stromatoporoid distribution beyond central Baltica.— Mori (1969) described three stromatoporoid taxa in the (undifferentiated) Upper Ludlovian of Scania (southern Sweden), including *Plectostroma scaniense*, present as "irregularly massive" fossils, thereby indicating this taxon had a wide distribution across Baltica. The other two taxa in Scania (*Plexodictyon*? *irregulare* and *Parallelopora ornate*) are somewhat different from stromatoporoids in Katri.

Further away from Estonia, but still within Baltica, Mori (1978) described stromatoporoids from the Oslo area, where Llandovery, Wenlock, and Ludlow stromatoporoids occur. Mori (1978) noted some similarity between Llandovery and Wenlock stromatoporoids of the Oslo area with both Gotland and Estonia, consistent with mixing of faunas between these ares. Unfortunately there are few occurrences of Ludlow stromatoporoids around Oslo and no useful conclusions can be drawn in relation to this study.

The above variations in stromatoporoid occurrence reveal a surprising control on stromatoporoid distribution that has not been previously identified; these results demonstrate that stromatoporoids were quite sensitive to facies controls, but there is no information yet recorded in the sedimentary rocks that indicate what caused these differences.

Silurian stromatoporoid faunas outside Baltica.—Nestor and Webby (2013: figs. 10, 11) noted that, in the Ludlow, *Clathrodictyon* is a geographically cosmopolitan genus (see Fig. 15), which raises the question as to why is it apparently so sensitive to environments in Gotland and Estonia, as indicated by our results. *Lophiostroma* was limited in distribution in the Wenlock to Laurentia, but then spread to western Baltica in the Ludlow, yet continued to have a restricted distribution, During the Ludlow *Lophiostroma* was in only Gotland, Estonia (but missing in Katri), Ukraine in Baltica; and Turkey in Gondwana, with the Rheic Ocean separating Turkey from Baltica (Nestor and Webby 2013: figs. 10, 11), see Fig. 15. Nestor (1966) recorded *Lophiostroma* in a stratigraphically lower level of the Paadla Stage on Saaremaa Island (where Katri is situated), but neither his work nor our sampling revealed any specimens in the Katri biostrome. It is worth pointing out here that *Lophiostroma* is a very distinctive stromatoporoid with prominent papillae on the upper surface, and is unusual amongst stromatoporoids because it is easily recognisable in the field in hand specimen; thus it is unlikely to have been overlooked in collecting, so its recorded distribution is likely to reflect its real distribution. Nestor and Webby (2013: figs. 10, 11) demonstrated that other abundant stromatoporoid genera in Katri (*Parallelostroma, Petridiostroma, Syringostromella*) also have cosmopolitan distribution in the Ludlow; they include *Stromatopora* as a cosmopolitan genus in their compendium, but because of the taxonomic problem of "*Stromatopora*" *bekkeri*, we can-
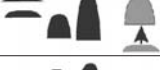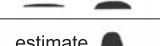
Low-level taxa	Number	Basal length/width range: mean	Shape	Facies
Syringostromella borealis	20	15–30: 19		2
Plectostroma scaniense	18 + ?3	2.5–30: 14		1-large 2-small
Parallelostroma typicum/ "*Stromatopora*" *bekkeri*	18 + ?1	4–28: 16		1-large 2-small
Plectostroma atterdagi	7 + ?1	3–25: 14		1-large 2-small
Pteridostroma convictum	5	6–10: 8		1 + 2
Plexodictyon katriense	4	20–30: 26		1 + 2
Simplexodictyon yavorskyi	3	fragments	estimate	1 + 2
Parallelostroma typicum	1 + ?1	21 + fragm.		1-whole 2-fragm.
Stromatopora antiqua	1	25		2
Favosites forbesi	20	2–24.5: 19		1-large 2-small
Laceripora cribrosa	15	fragments		2
Kitakamiia callosa	9	n/a		2
Aulopora amica	7	n/a		1 + 2
Syringopora multifaria	5	fragments 1 symbiotic		2
Syringopora affabilis	3	symbiotic		1 + 2
Thecia swinderniana	4	5.5–13: 8.8		2

Fig. 12. Growth form plot of shapes of the various taxa of stromatoporoids in Facies 1 and 2 at Katri (upper Ludlow). Low-level taxa, traditionally referred to as species (these taxa are the lowest level of identification possible using the calcareous skeleton, whether or not they are biological species is undetermined). Number, number of specimens of each low-rank taxon ("?", too poorly preserved to give unequivocal identification). Basal length/width range: mean (in cm); left-hand figures give the range of the widest measurable dimension, which is either the basal length of laminar to domical forms, or the width of a bulbous form at its widest point; the right-hand figure is the mean of widest dimensions, providing an indication of overall size of the fossils; fragments, means that the taxon was found only as fragments so that numbers (and therefore morphologies) are uncertain. It is important to note that because of pressure solution (see also Figs. 2, 4, 6), the full dimensions of the fossils are not preserved, so this figure provides a general record of the dimensions, lacking the precision of outcrops unaffected by pressure solution; "n/a" (not applicable), means that growth form measurements were not appropriate in these encrusting taxa. Shape, diagrams illustrate silhouettes of growth form seen in vertical section through the skeleton (silhouettes in brackets are uncommon, silhouettes in gray indicate that these taxa began growth as laminar forms and grew into domical forms as they developed as individual specimens), determined from vertical sections of entire stromatoporoids. Facies, this records which facies the taxon occurs in. Most taxa occur in both facies, but note that *Syringostromella borealis* and *Stromatopora antiqua* occur in only Facies 2. "1-large, 2-small" indicates that in Facies 1 that taxon is larger size than in Facies 2. "1 and 2" indicates that the taxon is similar size in both facies. The results show the taxonomic separation of the layers reflecting facies relationship with stromatoporoid taxa. Note that corals *Syringopora multifaria* and *S. affibilis* are symbiotic branching structures within stromatoporoids and dimensions are not obtainable. *Laceripora*, and abundant branching coral in the Katri faunas, occurs only in Facies 2.

not include that in this discussion. The key point is that the absence of *Lophiostroma* in the Katri biostrome suggests an environmental control, not recorded in the sediments, that prevented this taxon from reaching that environment. In contrast, the restriction of *Syringostromella* to Facies 2 in Katri is interpreted in this paper as due to a need for less turbulent conditions.

Stock (1979: 318) reported *Parallelostroma typicum* in shallow marine biostromes of the upper Silurian (Pridoli) Rondout Formation of New York (Laurentia), together with some stromatoporoids not recorded in Baltica. Stock (1979: 318–320) recorded "*S.*" *bekkeri* as a rare taxon restricted to eastern New York State, but is reported from deeper facies, not the shallow biostromes. Stock (1979: 320) records *Densastroma pexisum* in shallow marine facies in the Rondout; but this taxon also occurs in the Wenlock and Ludlow of Baltica, but is a deeper water stromatoporoid abundant in calcareous muddy facies (see Kershaw 1984). These differences in apparent depths of water in which stromatoporoids grew indicate a potential variation in controls on growth of stromatoporoids in different continents.

In an unpublished M.Sc. thesis, Pope (1986) described stromatoporoids from the late Silurian West Point Formation in Gaspé Peninsula, southeastern Canada. Her work revealed several genera in common with the Baltic region, with two identified as *Ecclimadictyon macrotuberculatum* and *Plexodictyon katriense*, both of which occur in the Hemse biostromes on Gotland (Kershaw 1990); *P. katriense* also occurs in Katri (it was of course named for Katri by Nestor 1966). These two taxa presumably occur in both Laurentia and Baltica due to ocean current transport. However, the other abundant low-rank taxa of stromatoporoids described in this paper in the Ludlow of Estonia and Gotland are not present in Pope's (1986) study. In particular, *Parallelostroma typicum* and "*Stromatopora*" *bekkeri*, both described in the upper Silurian in New York by Stock (1979) and present both in Katri and through the Ludlow of Gotland, were not found in Gaspé by Pope (1986), despite its proximity to the other areas (Fig. 15).

The information from Laurentia cited above is a further indication of facies control in stromatoporoids due to the incomplete occurrence of taxa in Laurentia and Baltica, but an important caveat must be taken into account: the taxonomy of Palaeozoic stromatoporoids, based on the calcareous skeleton, is regarded by sponge workers as being a secondary feature of no value in higher level taxonomic classification. In contrast, Kershaw (1997, 2013) argued that the low-rank (genus and species) differences between skeletal architectures of different taxa are of sufficient magnitude to allow their acceptance as biologically different, at least at genus level. This is a contentious issue because of the implication of the possibility of overlap between the skeletal architecture of different stromatoporoid biological taxa, such that the genera and species easily recognisable in one area may not necessarily be the same biological taxa in another area. Consequently we warn that interpretations regarding the

Facies 1: packstone-grainstone
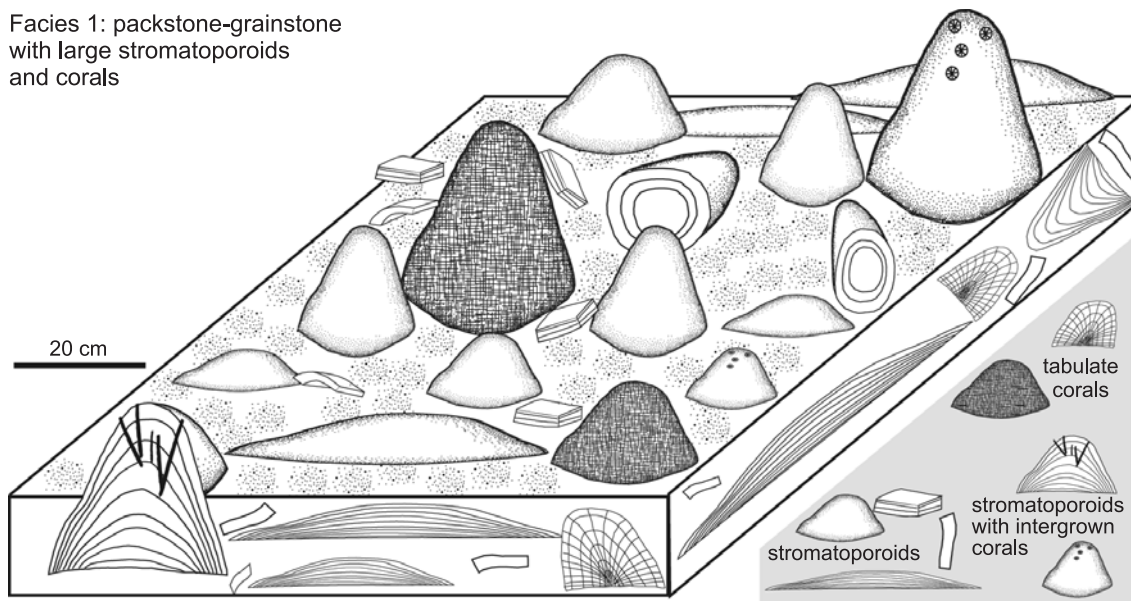with large stromatoporoids
and corals

20 cm

tabulate
corals

stromatoporoids
with intergrown
corals

stromatoporoids

Fig. 13. Interpreted recon-
struction of faunas and
sea-floor appearances of
Facies 1 at Katri, repre-
sented by Layers 1, 3, 5.

large-distance geographic distribution of Palaeozoic stro-
matoporoids (taxa defined by architecture of the calcare-
ous skeleton) across oceans separating continents and even
different regions of the same continent, in contrast to the
shorter distances in one shallow marine platform, may not
be fully reliable indicators of transport and survival of taxa
in shallow marine shelves.

Silurian coral faunas elsewhere

Klaamann (1982) noted that coral assemblages analogous to
Katri are found in the Hemse Group of Östergarn Peninsula
and in Linde parish of eastern Gotland where the biostromes,
discussed above, are abundant. As stated above, these inter-
bedded biostromes and bioclastic limestones contain mostly
stromatoporoids and lesser numbers of tabulates. Klaaman
(1982) identified the tabulate taxa *Favosites forbesi*, *Para-
striatopora coreaniformis*, and *Laceripora cribrosa*. *Paleo-
favosites* is found in bioclastic limestones. The Hemse
Group limestone also contains *Favosites similis*, *Favosites
subgothlandicus*, *Syringopora multifaria*, *Barrandeolites*,
and *Riphaeolites lamelliformis*. All named representatives
of *Favosites* and also *Parastriatopora coreaniformis* may
be conspecific to *Favosites forbesi*, because their biometrics
overlap, drawing attention to the problems of determin-
ing taxonomic biodiversity of the corals. However, import-
ant species in the Katri biostrome (*Thecia swinderniana*
and *Kitakamiia callosa*) are missing in the Hemse Group
on Gotland; nevertheless, *Thecia* occurs in the Hamra
Formation (late Ludlow) on Gotland (Stel and de Coo 1977),
thus does not disappear from the Gotland sequence after the
Hemse Group. Young and Scrutton (1991) described in de-
tail digitate forms of the tabulate *Stelliporella parvistella* in
the Lau Backar locality on Gotland, in the Eke Beds, closely
stratigraphically equivalent to Katri. Lau Backar site is a
non-reefal calcareous mudstone containing abundant small
corals and stromatoporoids, and is clearly a quieter water

facies than the Katri biostrome. Thus the facies difference is
presumed to have prevented the growth of *S. parvistella* in
Katri. Nevertheless, *Stelliporella* is a widespread genus of
the heliolitid tabulates; heliolitids (including *Stelliporella*)
are well-known as open shelf and carbonate bank inhabitors,
and occur in a range of facies, including eastern Canada on
the Laurentian continent during the late Silurian (Young
and Noble 1990). Furthermore, in the Gaspé area of east-
ern Canada, Young et al. (1991) described upper Silurian
halysitids and auloporids that grew in place in calcareous
shale, silt and sandstone, but in deeper water facies from
those studied at Katri. Halysitids and heliolitids, common in
the Ludlow of Gotland, are missing in the analogous strata
of Estonia, interpreted by Klaamann (1982) to be due to
shallower sea than on Gotland.

The coral data therefore show the existence of facies
sensitivity amongst the coral taxa, although the reasons for
the variation in distribution are not yet determined, as in
stromatoporoids.

Symbiosis between stromatoporoids and corals

The intergrowth of syringoporid tabulates and some rugose
corals and stromatoporoids in the Silurian is well known
(Kershaw 1987). Most stromatoporoid taxa can host rugose
corals, but such intergrowths are not common. However,
all specimens of one stromatoporoid taxon at Katri,
Petridiostroma convictum, contain syringoporids and some
specimens also contain some branching rugose corals. This
arrangement is identical to the Gotland faunas; all samples
of *P. convictum* found in this study and by Kershaw (1990)
contain syringoporids and the syringoporid taxon is always
Syringopora affabilis. Furthermore, *P. convictum* is abun-
dant in the Katri biostrome and the Hemse biostromes on
Gotland, thus was apparently well-suited to that environ-
ment, yet has not been found in other levels of the Ludlow
(Mori 1970: 31). Kershaw (1987) interpreted the relation-

Facies 2: wackestone with
small stromatoporoids
and corals

Laceripora
tabulate coral

syringoporid
tabulate corals

other
tabulate
corals

rugose
corals

20 cm

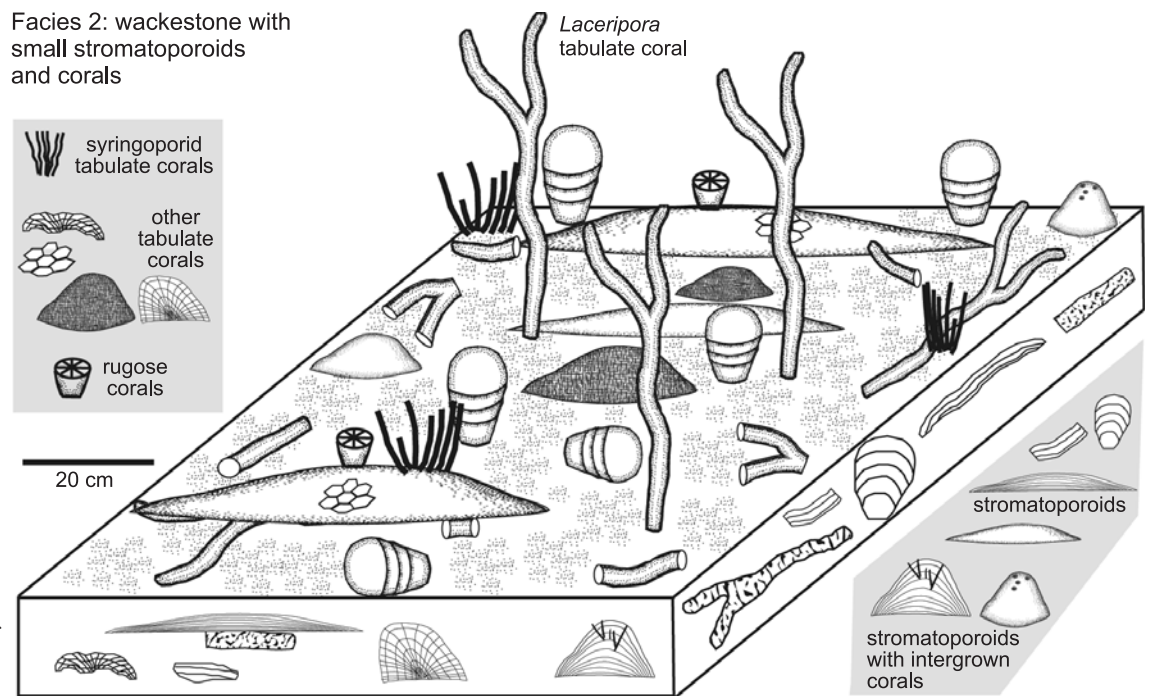stromatoporoids

stromatoporoids
with intergrown
corals

Fig. 14. Interpreted reconstruction of faunas and sea-floor appearances of Facies 2 at Katri, represented by Layers 2 and 4.

ship as a mechanism by which the corals gained protection from the environmental energy, the stromatoporoid neither gaining nor losing from the relationship. However, in the Silurian of eastern Canada (Young and Noble 1989) syringoporids grew in symbiosis with stromatoporoids in open shelf environments, but not in high-energy settings, which therefore allows for an interpretation that the symbiosis was a biologically mutual intergrowth. Thus there is growing evidence of an obligate relationship between these two fossils in the late Silurian, regardless of facies. Consequently, *P. convictum* may be a facies-limited fossil for the Hemse and Katri biostromes, but always provides a host for *S. affabilis*.

Wider aspects of stromatoporoid and coral characters

The stromatoporoid fauna at Katri has one aspect that is consistent with all other detailed studies of stromatoporoids in recent years: a small number of taxa at Katri are much more abundant than all the other taxa. This feature of stromatoporoid assemblages has been recognized also in case studies of parts of: (i) the Wenlock of Gotland (Kershaw 1984), (ii) the Wenlock of England (Kershaw and Da Silva 2013 and unpublished material by SK and Da Silva), (iii) the Ludlow of Gotland (Kershaw 1990; Kano 1990) and (iv) the Middle Devonian of Belgium in both mounds and platform settings (Da Silva et al. 2011, 2012). Thus the Katri stromatoporoid assemblage reinforces the view that Palaeozoic stromatoporoid assemblages in general were of relatively low diversity, with only a few species abundant in any particular environment. Evidence assembled so far, in the case studies listed above, shows this pattern to be true regardless of geological age, facies, taxonomic composition and growth forms of the stromatoporoid assemblage. Stromatoporoid communities in general, therefore had a relatively simple structure. Coral distributions are less well understood and further work is needed to characterise the taxonomic distribution within assemblages.

Comparisons with modern faunas

Problems exist in drawing close analogies between modern and ancient sponge-coral faunas because ancient stromatoporoid sponges were large reef-building fossils, likely to have grown quickly, in contrast to their slow growth in modern environments (see Kershaw 1998 for a review). It is interesting to note that modern coral reefs tend to be dominated by a small number of taxa (e.g., *Acropora palmata* in the reef crest of most modern reefs), which has parallels in Palaeozoic stromatoporoid communities as discussed in the previous section. However, there is some indication of variable distributions amongst corals and sponges. The existence of two major modern coral provinces (Atlantic and Indo-Pacific, with the Red Sea as a minor additional province), with taxonomic differences between Atlantic and Indo-Pacific corals, are well-known; Indo-Pacific corals are significantly more diverse than Atlantic corals, and the diversity of Indian Ocean corals remains approximately the same across the Indian Ocean (Veron 1995). The centre of Indo-Pacific coral diversity is the Coral Triangle in the southwest Pacific. However, distributions of sponges are less well-researched, but there are some published reports that show differences existing between coral and sponge distributions. Wulff (1996), working in the Panama Canal region of central America, noted that sponges in the eastern Pacific side of the Panama Isthmus were indistinguishable in morphological characters from those on the Caribbean
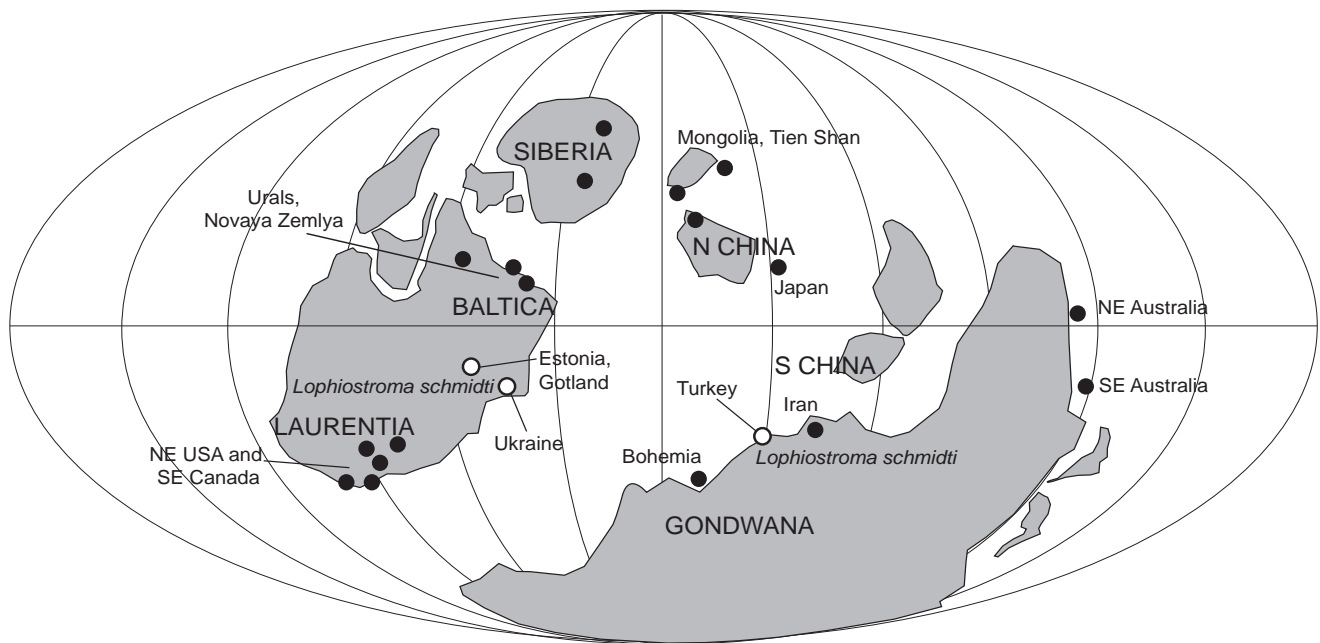
Fig. 15. Palaeogeographic map of the Ludlow Epoch, showing the distribution of stromatoporoid genera according to the compilation by Nestor and Webby (2013: figs. 10, 11). Estonia is labelled in Baltica as part of the combined Laurentia-Baltica continent. Dots mark the positions of stromatoporoid discoveries, showing their cosmopolian distribution in the Ludlow, see Nestor and Webby (2013: fig. 11, table that lists the stromatoporoid genera and global sites). White dots mark localities where unusually-restricted stromatoporoid *Lophiostroma schmidti* is present: Gotland and Ukraine in Baltica, and Turkey on the coast of Gondwana, separated by the Rheic Ocean.

side, yet coral faunas are different; this implies controls on distribution of the two groups were different. In an analysis of sponges of the Indian Ocean, Thomas (1983) demonstrated that the three sponge groups (demosponges, hexactinellids, and calcareans) in the Indian Ocean all had comparable amounts of similarity with neighbouring southern hemisphere regions, yet there was considerable species-level variation of geographic distribution between the Indian Ocean and other areas (Australian, Pacific, Atlantic, Red Sea, Mediterranean, Arctica, and Antarctic Oceans); the Indian Ocean has the greatest similarity with the Australian region (35.4% of Indian species occur in the Australian area; Thomas 1983: table 1). Thomas drew attention to the potential importance of Indian Ocean currents to carry larvae the long distances to effect such similarity although the Indian sponge populations had little overlap with Antarctic sponges. Downey et al. (2012) concluded that sponge distribution in the high latitudes of the Southern Ocean is governed by the Antarctic Circumpolar Current, thereby preventing migration from that region, and emphasising the control exerted by ocean currents on sponge distribution.

Returning to the Silurian, the small overlap at low-rank taxonomy between stromatoporoid taxa of the Gotland-Estonia carbonate platforms and Laurentia, discussed earlier, may relate to ocean currents. Indeed recent work on Silurian ostracods (Perrier and Siveter 2013) proposes that ostracod distribution is related to whether they had pelagic or benthic larvae, and demonstrate that the Avalon/

Baltic continent had a distinctive faunal assemblage, not mixed with the remainder of the Laurentian Plate, but the reasons are unclear, noting that the Avalon/Baltic region was merged with Laurentia by Silurian time (see Fig. 15). Thus there are parallels here with the stromatoporoid and coral distributions; despite the cosmopolitan aspect of many Ludlow stromatoporoids (Nestor and Webby 2013), low-rank taxa in the central Baltic show only limited overlap with Laurentian sites, drawing attention to potential complexities in the palaeobiology of different stromatoporoid and coral taxa that require more detailed studies to fully characterise. Our study at Katri demonstrates that there is a long way to go before the palaeobiology and palaeoecology of Palaeozoic stromatoporoid and coral faunas are comprehensively investigated.

Conclusions

Corals and stromatoporoids from a ca. 1-m exposure of Ludlow (upper Silurian) biostrome at Katri, western Estonia, are facies-controlled at small scale, to produce two distinct faunal assemblages in two alternating facies, demonstrating environmental preference not recorded before in upper Silurian platform limestone.

The corals and stromatoporoids at Katri show environmental sensitivity that is here interpreted to have been caused primarily by changing sea-level, to produce differences in faunal assemblages between two different facies.

Sea-level change may have been due to wider controls of climatic shifts, but this aspect has not been investigated here because of the limited outcrop of Katri.

In contrast to the Katri faunas, similar biostromes in the slightly older eastern Hemse Group (middle Ludlow) of Gotland, 250 km WSW of Katri, were shown by Kershaw (1990) to not have separation of facies preference in the preserved assemblages because all the stromatoporoid taxa are mixed within individual biostromes. Thus the differences in coral-stromatoporoid faunas between Facies 1 and 2 at Katri may have preserved the environmental sensitivity of the taxa that either did not exist in the Gotland sites, or has been lost due to taphonomic mixing in Gotland.

The presence/absence of particular taxa in Katri compared to eastern Gotland demonstrates uneven distribution of these benthic taxa across the sea-floor in the central Baltic area. Katri lacks key stromatoporoid taxa (*Lophiostroma schmidti* and *Clathrodictyon mohicanum*) common in similar biostrome facies on Gotland, suggesting that environmental differences between the two areas prevented them from spreading into the Katri area. Katri has two tabulate species, *Thecia swinderniana* and *Kitakamiia callosa*, that are missing in the analogous Ludlow biostromes on Gotland. However, environmental differences that may have controlled the stromatoporoid and coral assemblages are not recorded in the facies, thus the reasons for the faunal differences between the eastern Hemse Group on Gotland and Katri are currently unknown.

Elsewhere in the Silurian world, coral and stromatoporoid faunas show that some are cosmopolitan while others are more geographically restricted, but there is insufficient published information to allow broad conclusions of controls on their distribution. Thus this study at Katri highlights the need for further detailed studies in the future, that can build the database of environmental response in these two co-existing fossil groups.

Acknowledgements

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