SILURIAN RUGOSE CORAL *SCHLOTHEIMOPHYLLUM* SMITH, 1945 FROM THE UPPER VISBY BEDS OF GOTLAND, SWEDEN

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Abstract: A rich (about 60 specimens) collection of *Schlotheimophyllum*, large rugose corals from the Silurian of Gotland, Sweden, was studied. Although the material is mostly fragmentary (beach pebbles), the presence of growth lines, clearly seen in thin sections, provides reliable numerical data. Analyzed were corallum shape, septal numbers, and aspects of coloniality. Uniformity of variability spectra of these parameters indicates that all of the material studied belongs to a single, variable species, which is *Schlotheimophyllum patellatum* (Schlotheim, 1820).

Key words: Rugosa, corals, coloniality, variability, Silurian.

INTRODUCTION

The Silurian deposits of the Island of Gotland, Sweden, are well-known for their abundant fossils, including reefal and non-reefal stromatoporoid and coral faunas (e.g., Wedekind, 1927; Kershaw, 1980, 1990; Adomat *et al*., 2016; Berkowski and Zapalski, 2018; Zapalski and Berkowski, 2019). Among the rugose corals, locally common are representatives of the genus *Schlotheimophyllum* (family Kodonophyllidae Wedekind, 1927), with large and patellate individual corallites (Søiland, 1986). Although they are commonly reported in the literature, actual descriptions and illustrations of these corals are rare. It seems that previous research was based on a few specimens, with the notable exception of the study of Søiland (1986), which regrettably is available only as an unpublished thesis. Below the authors present an analysis of over 50 corallites, which they collected recently, supplemented by literature data and by few loaned specimens. Analysis of over 150 thin sections and many unsectioned specimens, allowed the authors to elucidate growth mode, variability, and finally, the taxonomy of these large and structurally complex corals.

GEOLOGICAL BACKGROUND

The Swedish island of Gotland, located in the central Baltic, displays numerous outcrops of undisturbed (few degrees ESE dips) sediments, originally deposited during the Silurian Period (roughly 443–419 Ma BP) in an extensive, shallow and warm (subtropical) shelf sea embayment (Fig. 1A), at the tectonically stable marginal segment of the Baltica palaeocontinent (Fig. 1B). Excellent outcrops of the Silurian bedrock of Gotland are easily accessible, for the most part at sea front cliffs. All the *Schlotheimophyllum* corals studied here come from the Upper Visby Beds (also referred to as the Upper Visby Formation, see, e.g., Adomat *et al*., 2016), which represent the lower Wenlock (lower Sheinwoodian) and attain about 15 m in thickness. They are exposed in many places along the WNW coast of Gotland (Fig. 1C) and are formed by irregularly bedded limestone-marl alternations, which are considered to have been deposited within photic zone, between the storm wave base and the fair-weather wave base, in a proximal shelf environment. Such a setting is supported by the presence of erosional surfaces, ripple marks and algae (Samtleben *et al*., 1996; Adomat *et al*., 2016).

Limestones of the Upper Visby Beds display thicker bedding towards the top and gradually pass upwards into massive reef limestones, with their associated clastic peri-reef sediments of the Högklint Formation (Fig. 1D), deposited in shallower waters, representing the Sheinwoodian Stage of the Wenlock Series (e.g., Calner *et al*., 2004; Fig. 1E). The underlying Lower Visby Beds, the oldest deposits cropping out on Gotland (topmost Llandovery, Telychian), are lithologically similar to the Upper Visby Beds but have
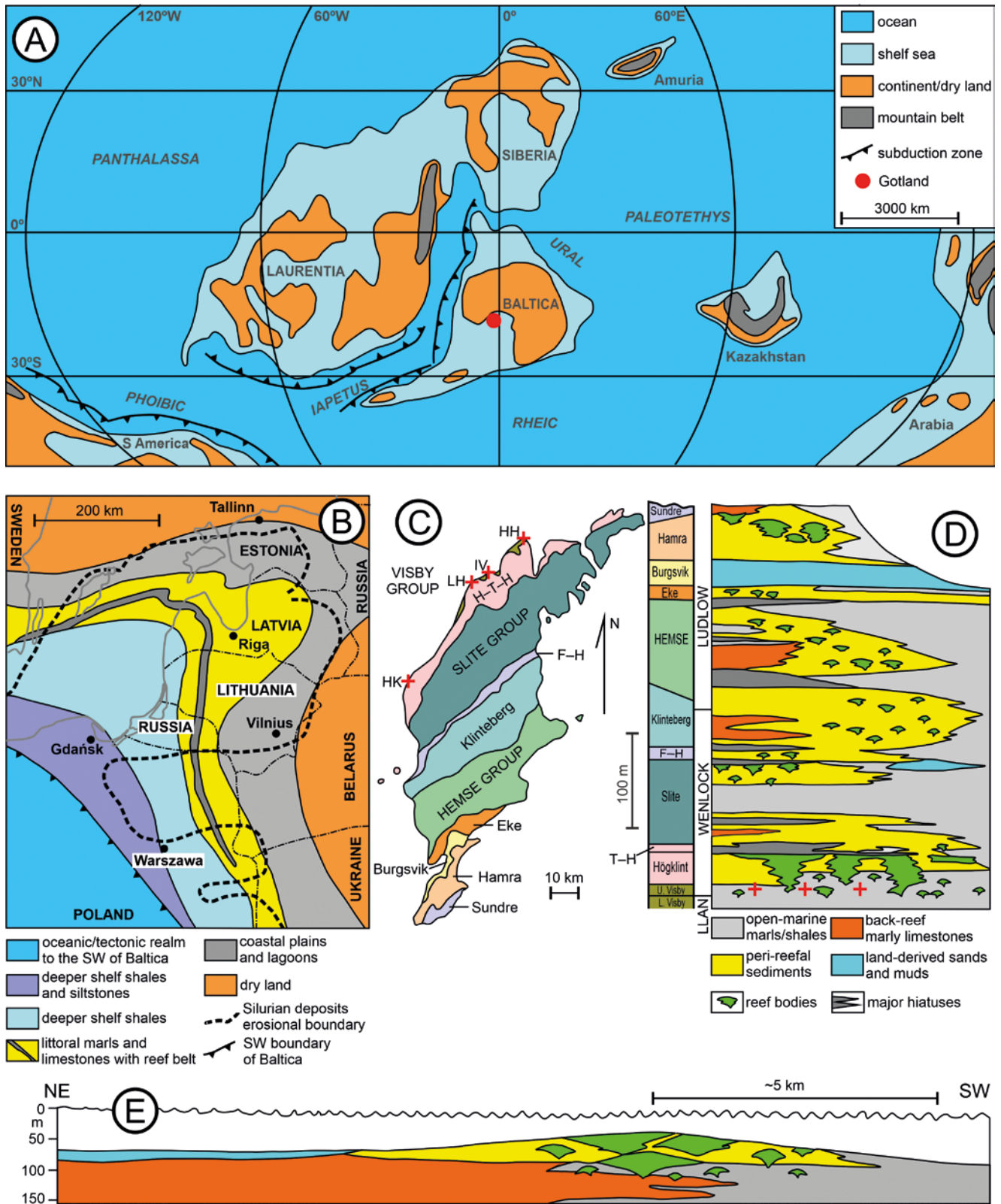
Fig. 1. Location of sampling sites with *Schlotheimophyllum patellatum*, in the lower Wenlock Upper Visby Beds of Gotland, Sweden. **A.** Location of Gotland (about 20°S, marked by red dot) in the Baltic Basin *vs*. Silurian palaeogeography and tectonics, about 425 Ma BP (compiled from Kiessling in Copper, 2002, figs 3, 4A, B, and Golonka, 2002, fig. 8). **B.** Silurian facies distribution in the Baltic Basin (after Lazauskiene *et al*., 2002, fig. 3). **C.** Geological map of Gotland, with lithostratigraphic units (after Bremer, 2017, H–T–H for Högklint, Tofta and Hangvar Formations), marked (+) sampling locations of *Schlotheimophyllum*: IV – Ireviken, HH – Hallshuk, HK – Ygne by Högklint, LH – Lickershamn. **D.** Silurian chrono-, lithostratigraphy and facies of Gotland (after Samtleben *et al*., 2002 and Bremer, 2017); corals of the present authors are from Upper Visby Beds: T–H for Tofta and Hangvar formations; F–H for Fröjel and Halla formations. **E.** Model of facies relationships across the reef belt of Gotland – five major facies are as in Figure 1D (points 1–5).

more regular bedding (Calner *et al*., 2004; Adomat *et al*., 2016; Zapalski and Berkowski, 2019) and, unlike the Upper Visby Beds, are considered to have been deposited in a relatively deep, distal-shelf environment, below the storm wave base and most likely in the aphotic zone (Samtleben *et al*., 1996; Adomat *et al*., 2016; Zapalski and Berkowski, 2019). The Upper and Lower Visby beds are separated by a horizon, rich in the large, solitary coral *Phaulactis* (see Samtleben *et al*., 1996; Adomat *et al*., 2016). Also, at the base of the Upper Visby Beds, a distinct positive $\delta^{13}C$ excursion was noted (Munnecke *et al*., 2003).

Excellent outcrops of the Upper Visby Beds, protected by the massive Högklint strata from above and undercut and renewed by the action of Baltic waves from a NE direction, the abundance of benthic fossils, including corals, but also easy collecting, due to the unconsolidated nature of sediments, make Gotland a paradise for the palaeontologist.

MATERIAL AND METHODS

The material studied here comes from three collections: MB.K, the collection of fossil corals of the Museum für Naturkunde, Berlin, Germany; GIUS, the palaeontological collection of the University of Silesia in Katowice, Sosnowiec, Poland; and PMU, the Paleontological Museum, Uppsala, Sweden. The material comprises 58 specimens (see Supplementary Material), of which the holotype (labelled MB.K) of *Schlotheimophyllum patellatum* (Schlotheim, 1820) was measured from literature illustrations (McLean and Copper, 2013, pl. 39: 1, 2; see also the remarks of the latter authors concerning provenance and holotype status of this specimen at p. 100v). Nine specimens (all uncut) were borrowed from the Museum of Evolution, Uppsala University, Sweden (abbreviated PMU). The majority of corals (48 specimens, abbreviated GIUS) were collected in the field by the present authors and are now deposited at the Institute of Earth Sciences, University of Silesia in Katowice, Sosnowiec. It must be noted that the Gotland shoreline is protected by Swedish state law under Natura 2000 legislation, so the authors collected specimens exclusively from the cliff scree. Two specimens come from Hallshuk (57.929080, 18.733502), 19 specimens come from Högklint (Ygne; 57.586880, 18.178054), 19 specimens (of which two were acquired) come from Ireviken (57.844918, 18.561042) and eight specimens were collected in Lickershamn (57.826867, 18.510237).

In total, 31 specimens were cut and about 150 thin sections and a few acetate peels were obtained for the present study. Twenty-seven specimens were left uncut, and only their exteriors were studied.

Measurements and septal counts were made for both unsectioned and sectioned material. As a major part of the GIUS specimens were more or less abraded beach pebbles, the measurements were often made on growth lines, clearly seen in thin sections, here presented mostly in enlarged fragments of larger thin sections, in Figures 10–13. The data obtained are presented in Supplementary Material, with the following information: ID# is the identification label of a specimen; ID#a is an abbreviated version of the former,

used in numerical analyses; here indexes a, b, c, etc. (if present) indicate various transverse sections of a given specimen, whereas indexes x, y, z indicate various measurements taken from growth lines of a single longitudinal section; dia/dia/h are the external measurements of specimens, with minimum diameter/maximum diameter/height (in mm); as pebbles or rock fragments were measured, these values must be interpreted as minimum. S1 is the counted number of the first order septa. Some errors are to be expected, as the septa are fused and lack the sharp septal edges at the periphery and are twisted and connected by tabular segments in the tabularium. For some uncut specimens, the number was counted as a fraction of the perimeter, then recalculated to the entire specimen (e.g., in specimen MB.K.861). TAB is the measured diameter of the tabularium (in mm). The tabularia are typically oval in transverse sections, which may but must not indicate some deviation of the cutting plane from the ideal orientation, i.e., perpendicular to corallite elongation. We give here the minimum value, this may introduce an error, we can only hope it is of minor importance for the present analysis. ANG is the measured angle (in degrees) between the "horizontal" plane (i.e., perpendicular to the corallite axis) and the peripherical plane of the calicular platform. Positive values indicate outwardly sloping platforms, which are typical, zero is for horizontal septal platforms, and negative values are for inwardly sloping peripheral platforms (rare). Measurements were taken either from matrix-free specimens or from the growth lines in sections. As typically opposite parts of a peripheral platform display various inclinations, an average value of the two was listed.

To find correlations between measured parameters, the data from Supplementary Material were analyzed using the PAST software (Hammer *et al*., 2001). The results are presented graphically in Figure 2.

RESULTS

Figure 2A, B indicates that the corals measured: 1) grew upward, with rapid septal insertion in the initial growth stages, then rapidly expanded in external diameter (less so in tabularium diameter), accompanied by very slow septal insertion. Septal expansion, of various types, can be observed in many other, unrelated tetracorals (e.g., in the Late Devonian endophyllid *Hankaxis* Birenheide, 1978, or in disphyllid *Diffusolasma* Wrzołek, 1993); 2) distinction of two species of *Schlotheimophyllum* in the Upper Visby Beds material from Gotland (Søiland, 1986, cited by Neuman and Kershaw, 1991) is not confirmed by the data of the present authors, as the correlation lines cut across the lines of Søiland; 3) shapes of correlation lines are somewhat dubious, as the measurements presented here are scarce; especially noteworthy is the concavity of some curves in Figure 2B, which, if confirmed by further study, might indicate various growth patterns in the present material, possibly indicating the presence of more than one species.

Figure 2C shows the presence of 1) a fairly uniform batch of initial growth stages, with steep-walled, funnel-shaped calyces, followed by 2) a stage with initial expansion of the calicular platform, attained usually by
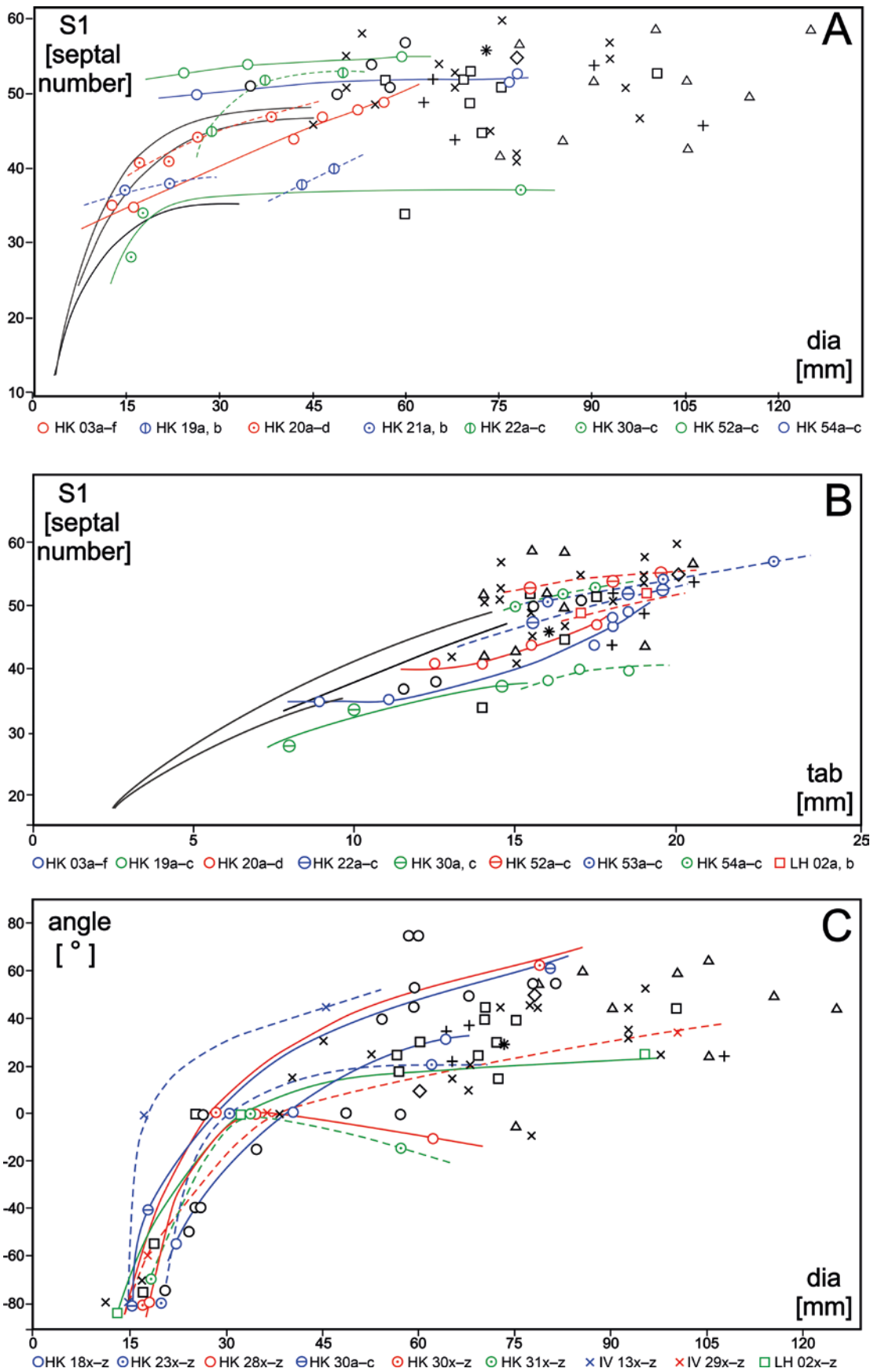
Fig. 2. Plotted numerical data for *Schlotheimophyllum patellatum*, Upper Visby Beds, Gotland, Sweden. **A.** Number of first-order septa (S1) *vs* corallite diameter (dia). **B.** Number of first-order septa (S1) *vs* tabularium diameter (tab). **C.** Angle of calicular platform (angle) *vs* number of first order septa (S1). ∗ – MBK specimen, ◇ – Hallsuk, o + – Högklint (Ygne), ✕ – Ireviken, □ – Lickershamn, △ – PMU collection; black lines in Figures 2A, B are from Søiland (1986, fig. 54a, b explained in text); colour lines link series obtained for some specimens.

a corallite diameter of 20 to 40 mm, and followed by 3) large-sized stages, with various calicular platform angles, ranging from low-negative (weakly funnel-shaped) to sub-horizontal (flat-topped) to positive or strongly positive values (discoid to dome-shaped) calicular platform angles in adult corallites. Part of the material of the present authors indicates that such a diversification may reflect not genetic, but rather environmentally induced, fenotypic effects. Here, the present authors would like to direct the readers' attention to the longitudinal sections of LH19 (Figs 11C, 12B), with various and in some places abruptly changing angles of growth lines at the corallite periphery, indicating that the polyps were capable of remodeling their skeletons in response to changing environmental parameters – possibly to waxing and waning sediment influx. Actually, the authors can see numerous expansions/contractions in many specimens (Figs 6, 7B, 8B, 9B, 12A, C). This indicates oscillation of environmental conditions (e.g., turbulence and/or sediment influx) during the life of the corals in times of sedimentation of the Upper Visby Beds.

External morphology analysis of the material studied is hindered by fragmentary preservation, as complete specimens are represented by a minority (about 20%) of the whole sample; most of these are the PMU specimens, mentioned above. All the other specimens are more or less fragmentary, so their original morphology must be reconstructed,

either from "complete" sections, and/or from the analysis of growth lines. Indeed, it would be difficult or even impossible to find in the present collection a specimen, which would not display one or more fracture(s), or abrasion surfaces, indicated by the truncation of corallite structures/growth lines at their periphery. Potentially, much evidence from these specimens, even from those that are best preserved (e.g., Fig. 3A with fractures at corallite periphery) can be missing.

The specimens of the present authors are either individuals (solitary?, Figs 3A, B, 4A, 5–8), or colonies (Fig. 3C, D: aggregate of individuals?; Figs 4B–F, 9, 13). It is possible that the individuals represent in fact fragmented colonies, or solitary polyps, which did not give rise to offsets. The individual corallites are generally of patellate aspect (for corallite shapes and colony types, see Hill, 1981, F9–11), i.e., they rapidly expand in diameter in maturity, with resulting broad basal part (Fig. 3B). The earlier growth stages are represented by small, ceratoid, proximal parts of corallites and are rarely preserved (Fig. 3B, compare with Fig. 6; both represent similar corallites). The distal parts of corallites can be dome-shaped (Fig. 3A, C), but also flat-topped or broadly funnel-shaped (cf. Fig. 2C, see also Figs 8B, 11B). Septal edges, as seen at the periphery are broad and smooth, with shallow furrows between the septa (Fig. 3A–C, also Figs 6A, 10A, 12A), while at the marginarium/tabularium boundary the septal edges are sharp, interseptal furrows are
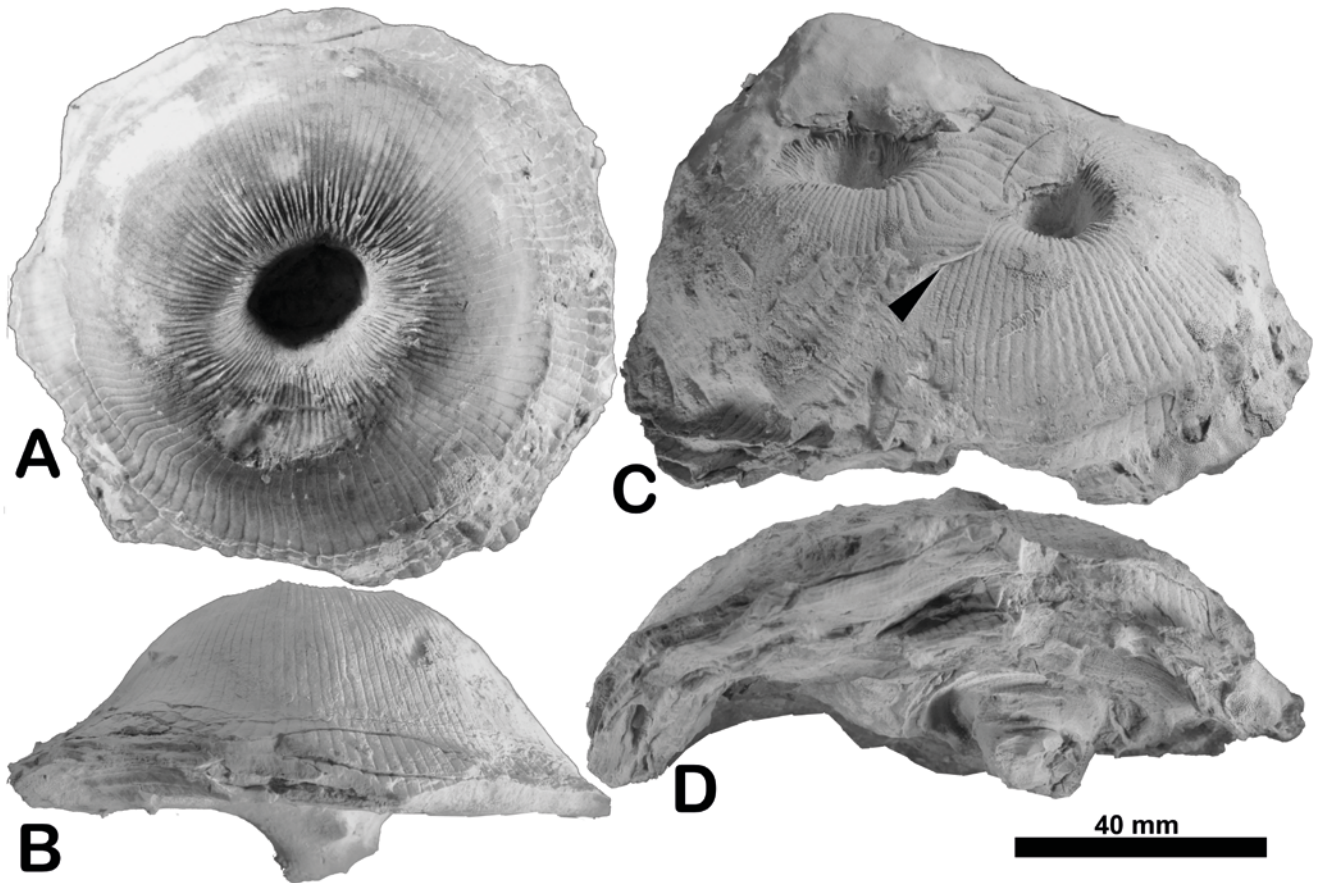

Fig. 3. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. External views of complete specimens with strongly convex distal parts. **A, B.** Solitary, mushroom-shaped specimen PMU W01 in distal (A) and in side view (B). **C, D.** Colonial (aggregate?) specimen PMU Got3, besides being colonial, quite similar to the former specimen, distal (C) and side view (D); septal discontinuity in Figure 3C (arrowed) indicates overgrowing of the right corallite by the left one. Locations unspecified. Length of scale bar for all figures.
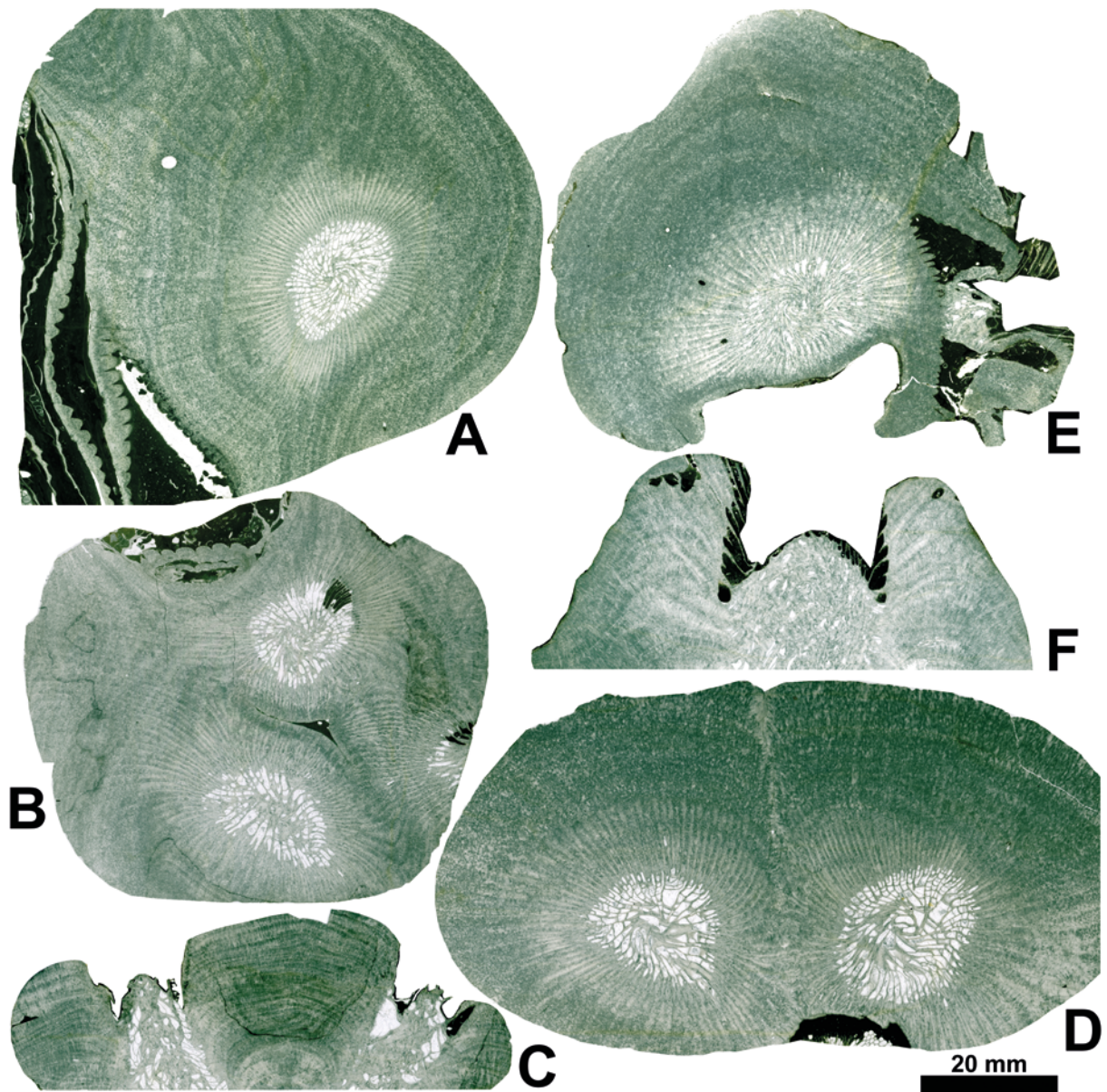
Fig. 4. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Thin sections of pebbles (A–D) and of complete specimens (E, F) from Högklint (Ygne) (A, D–F) and Ireviken (B, C). **A.** GIUS 3691 HK 27_2, transverse section of a very large individual with undulating calicular platform extensions on the left. **B**, **C.** GIUS 3691 IV 03, transverse and longitudinal section of abraded colony, with three corallites. **D.** transverse section of an abraded fragment of GIUS 3691 HK 27, a colony with some discontinuity of septa between its corallites seen in centre. **E**, **F.** GIUS 3691 HK 54, "complete" large individual with a marginal offset seen in transverse section (E), established just outside of the highly arched saddle of the calicinal platform. Length of scale bar for all figures.

deeper, and the minor septa are slightly thinner and less elevated than the major septa (Figs 3A, 4E: at the base of an offset; Fig. 12B). Calices are located axially, they have steep walls (Fig. 3A) and thin sections indicate the presence of calicular bosses (e.g., Figs 4C, F, 6B, 7B, 11B).

Ontogeny can be deduced from observations of external morphologies (see above) and also from series of transverse thin-sections obtained for a few specimens (Fig. 5): in proximal parts, the corallites are thin-walled, with major septa reaching the axis and minor septa present only at the tabularium periphery (Fig. 5A, B); in the subsequent sections (Fig. 5C, D), expansion of the corallite periphery, to a lesser degree also of the tabularium diameter, can be seen.

The sectioned material typically displays growth lines, which indicate the external shape of the original corallum, sometimes even in very fragmentary specimens. The minimum fragment, useful for the present study, is with preserved axis and internal and central parts of marginarium – this would allow for the measurement of angles and tabularium diameter, making septal counts, establishing minimum size of diameter, thus adding points to the data (Supplementary Material).

In the present material, a few morphotypes may be distinguished. Mushroom-shaped specimens are those with the proximal part in the form of a ceratoid (slenderly conical) corallite, subsequently expanding to a dome-shaped
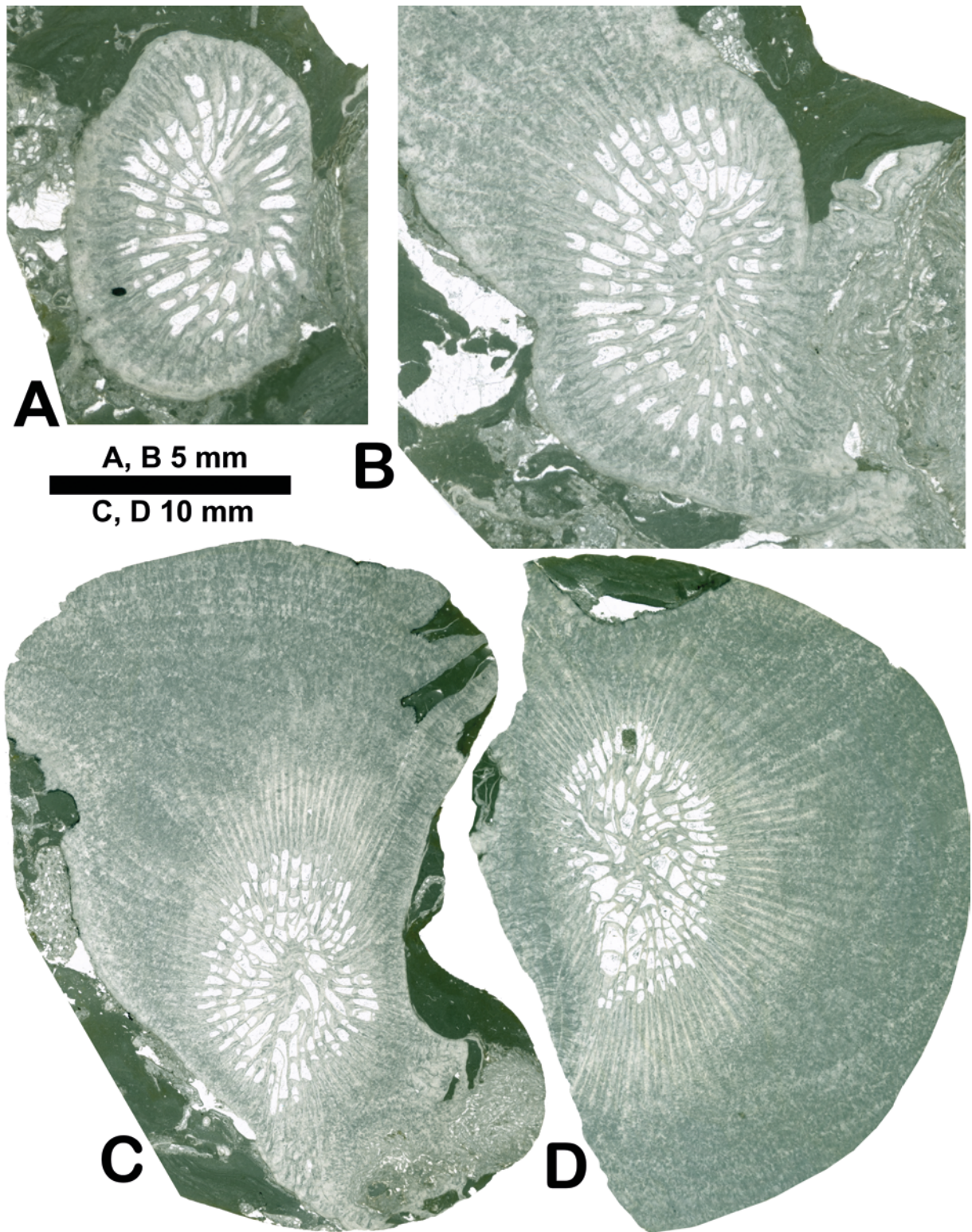
Fig. 5.   *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Series of transverse thin sections to illustrate ontogeny in the specimen GIUS 369l HK 03 from Högklint (Ygne). **A–D.** Sections HK 03a to HK 03f, cut at the proximal, ceratoid part of corallite (A – HK 03a), then at its more and more distal, expanded patelloid parts (B–D, HK 03b, e, f).

form, growing over the subhorizontal plane (Figs 2A, B, 6), although the last of these specimens is in fact fragmentary. The fractures are evident at the margins of transverse sections (Fig. 6A, C) and at the top of longitudinal section (Fig. 6B), which is without calice: the distal part in this section represents probably a fracture along some growth discontinuity zone, comparable to those seen at the right side of Figure 6B. The latter section is notable also, as it displays small, dissepiment-like peripheral tabellae in the left part of the tabularium, seen only in this specimen in the entire collection studied. Enlarged details of the same specimen are presented in Figures 10A, 11A.
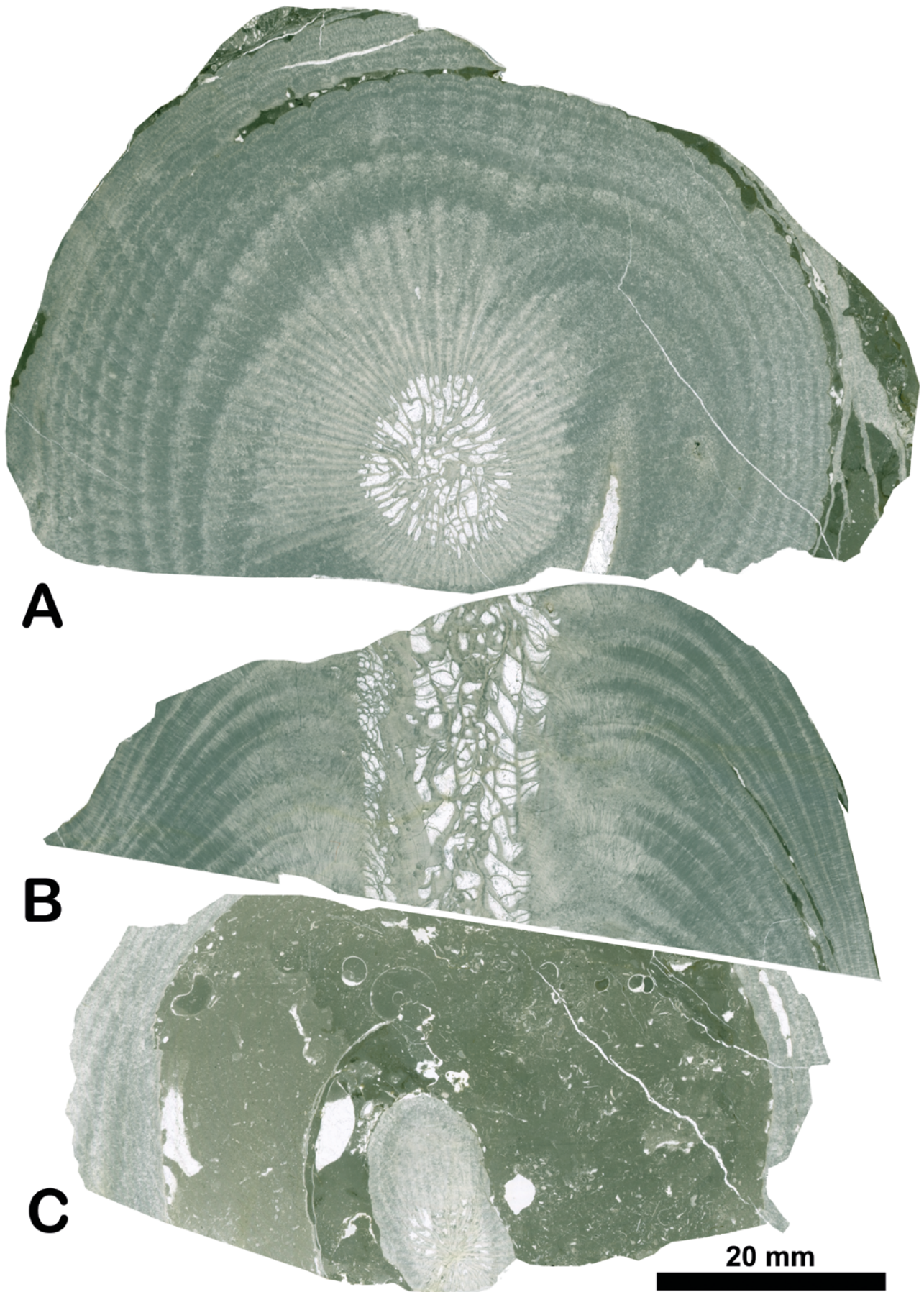
Fig. 6. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Thin sections of mushroom-shaped individual corallite GIUS 369l HK 30 Högklint (Ygne), with dissepiment-like small tabellae in the left part of its tabularium. **A–C**. Thin sections: HK 30_3 (distal-transverse), HK 30_6 (longitudinal); HK 30_1 (proximal-transverse). Length of scale bar for all figures.
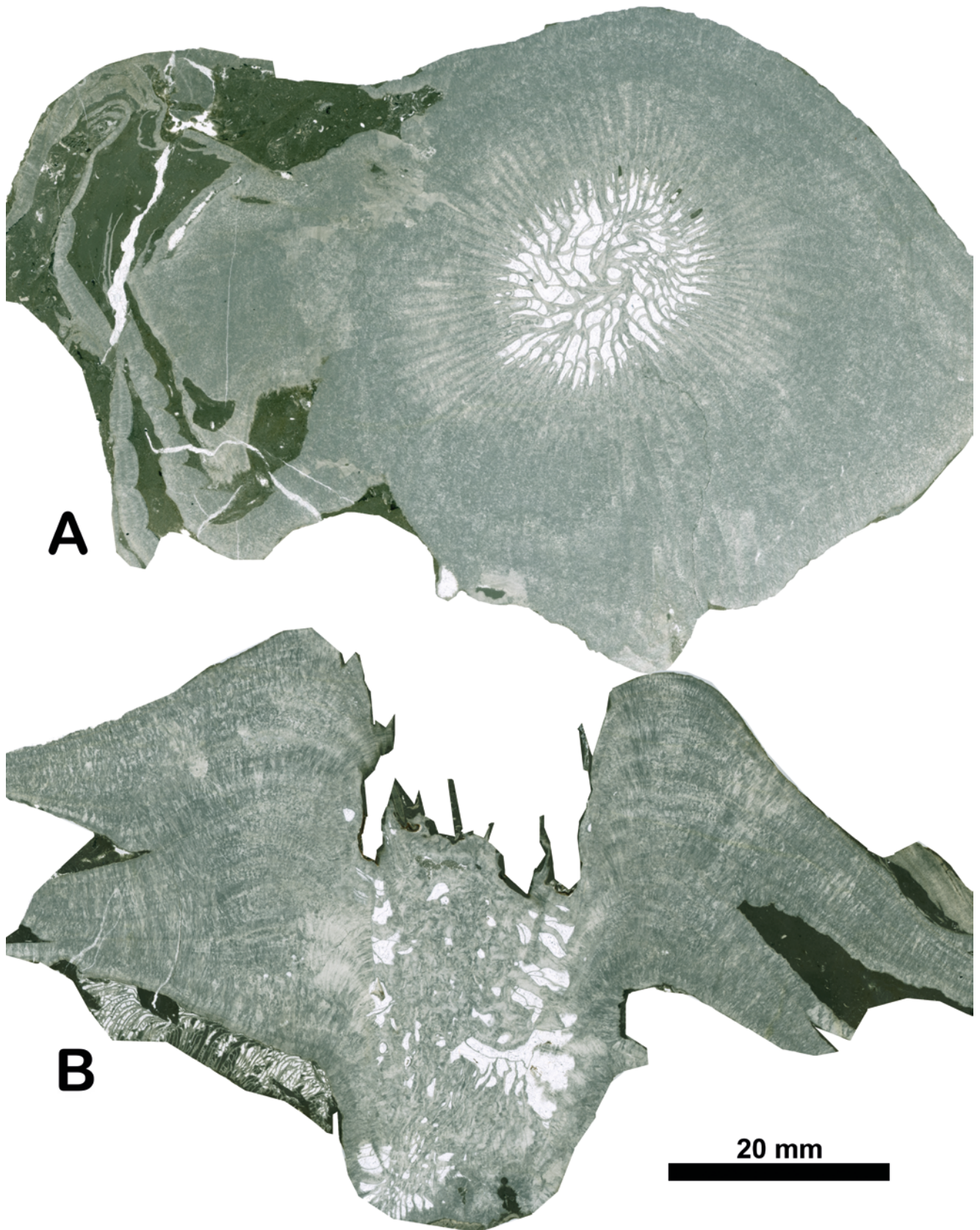
Fig. 7. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Thin sections of complete discoid individual corallites from Lickershamn (A) and Ireviken (B). **A.** Transverse section of GIUS 3691 LH 02, locally with irregular, thin corallite expansions at periphery. **B.** Longitudinal section of GIUS 3691 IV 29, with irregular expansions and contractions at periphery. Length of scale bar for all figures.
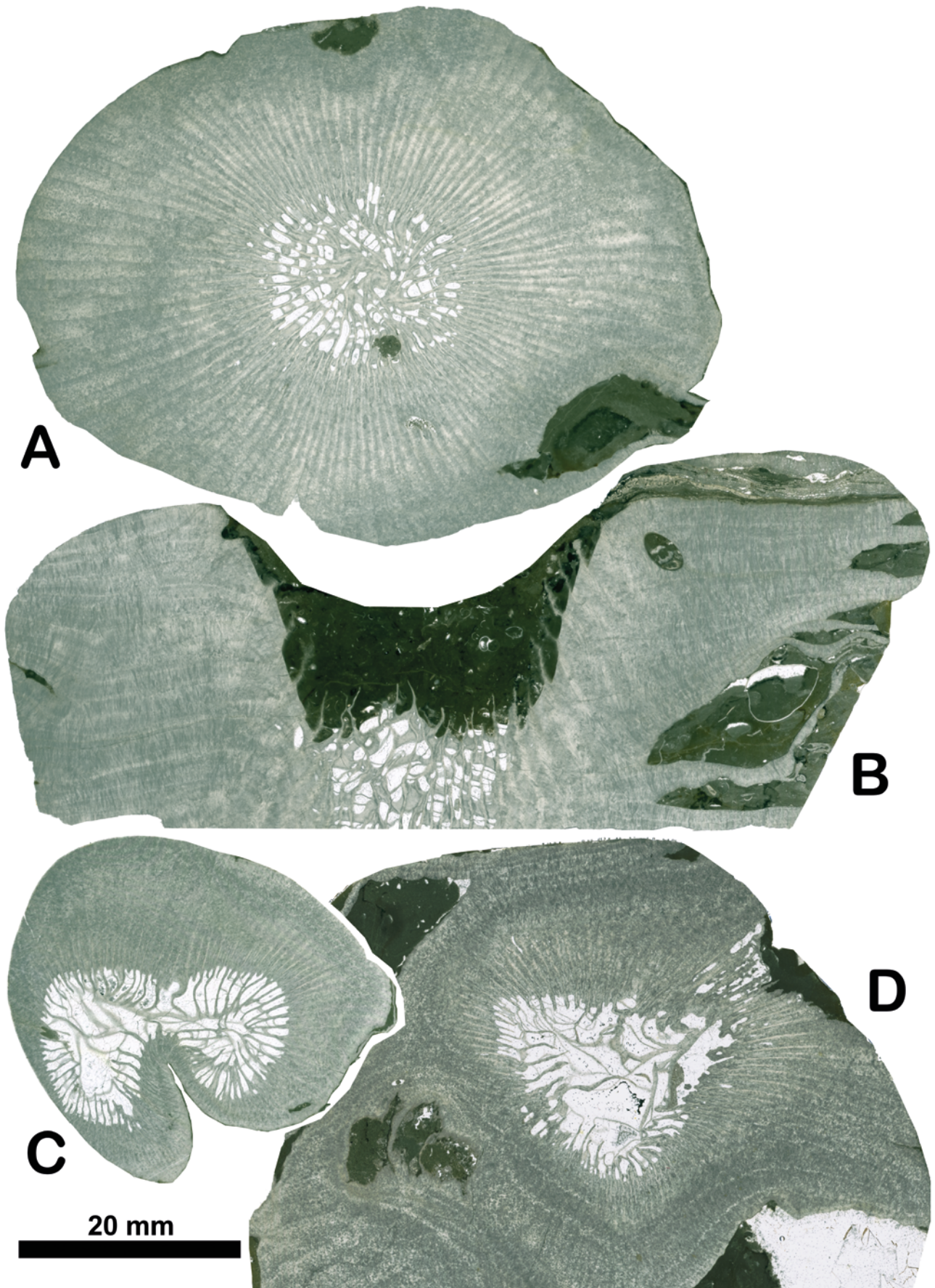
Fig. 8. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Flat-topped corallites from Högklint (Ygne). **A**, **B**. Specimen GIUS 3691 HK 31, thin sections HK 31_2 and HK 31_6c. **C**, **D**. Two transverse sections of a specimen GIUS 3691 HK 28, with anomalous, triangular shape of tabularium, possibly indicating aborted fission. Length of scale bar for all figures.
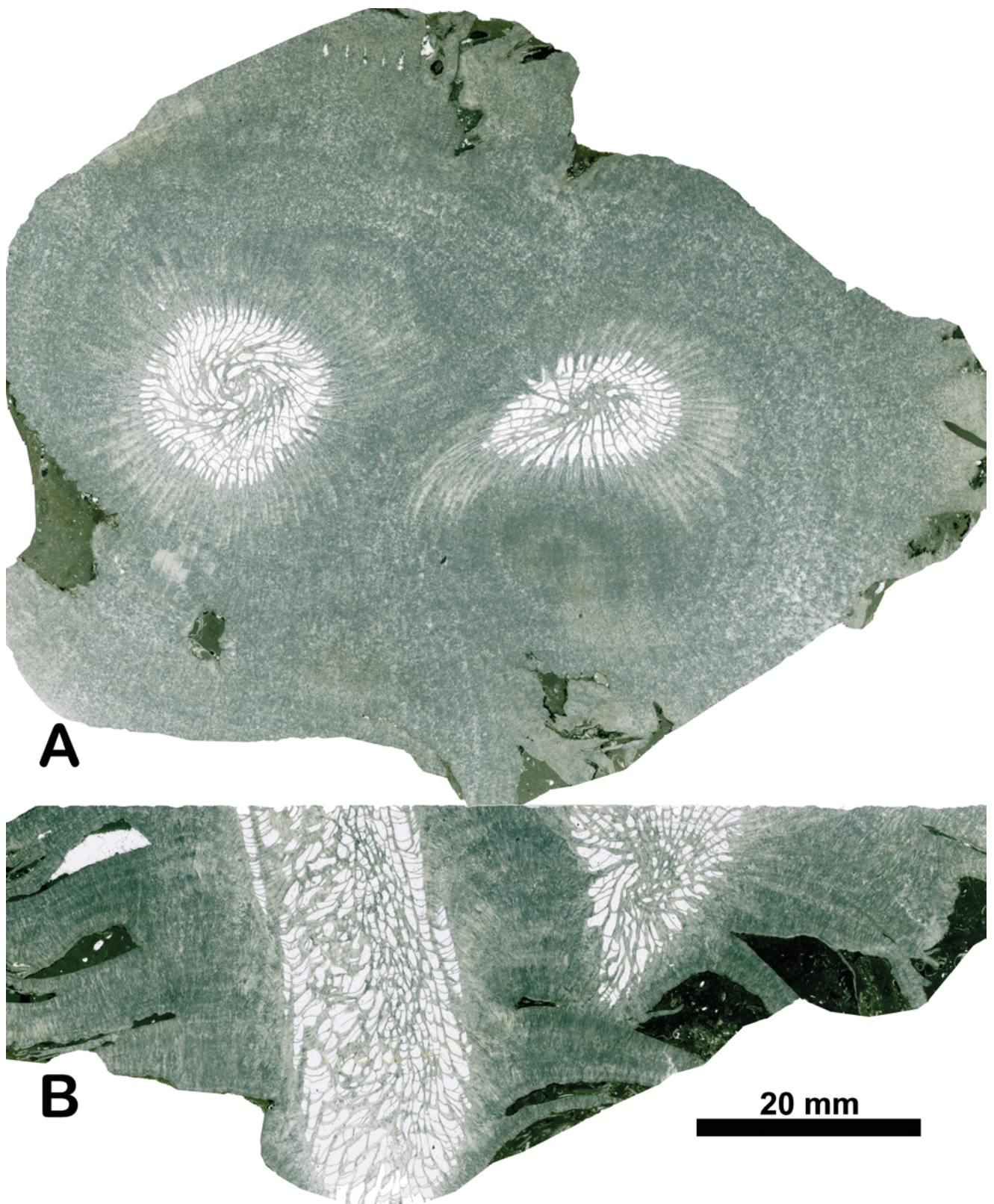
Fig. 9.   *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Complete colony from Lickershamn, GIUS 3691 LH 01. **A.** Transverse section with two subequal-sized corallites, with continuous septal structures between the two. **B.** Longitudinal section demonstrating parent (to the left) and offset (to the right), the latter was initiated in mid-part of the parent's expanded calicular platform. Length of scale bar for all figures.
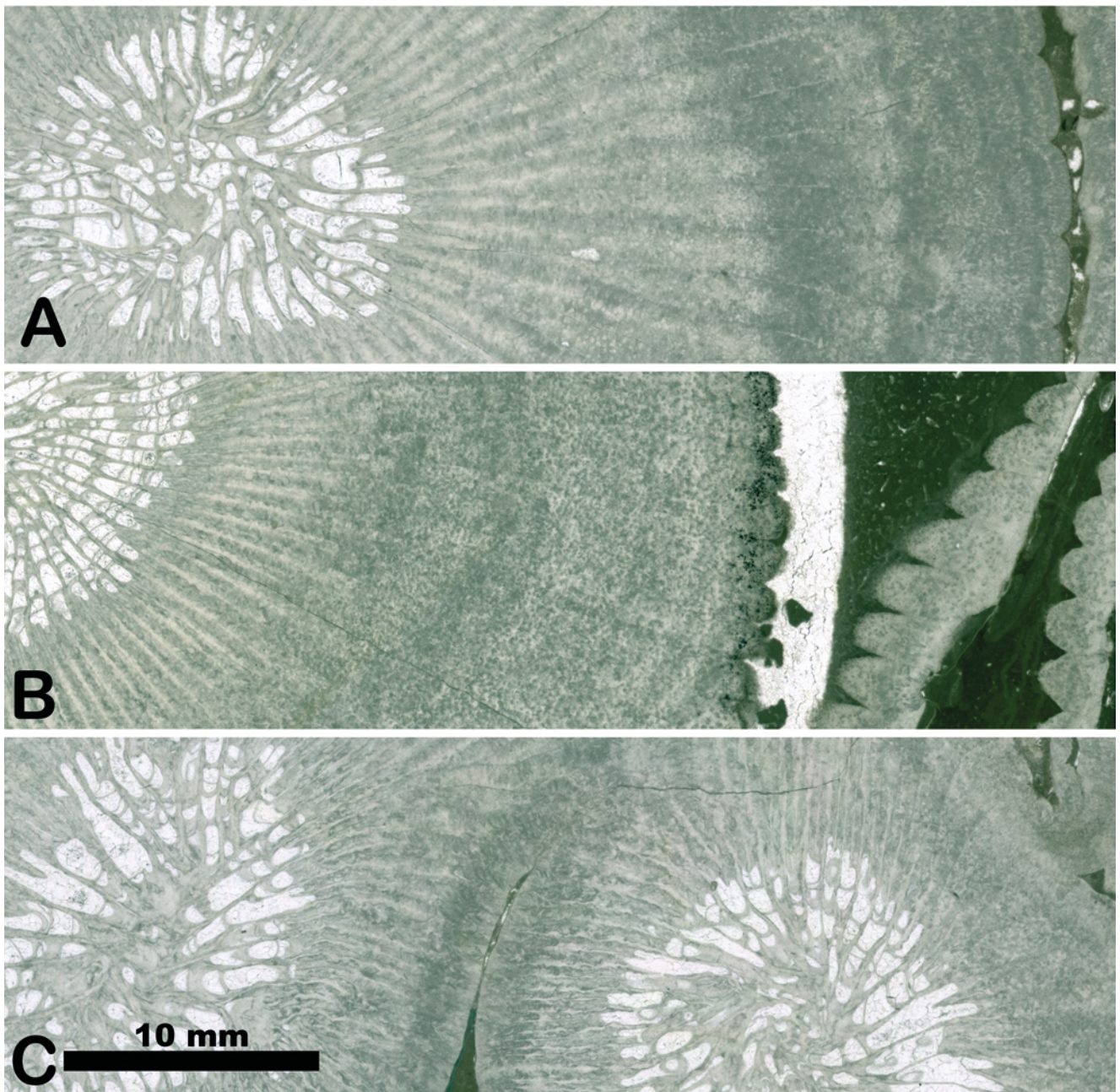
Fig. 10. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Details of septal structure and arrangement in transverse thin sections of specimens from Högklint (Ygne) (A, B) and Ireviken (C). **A.** GIUS 3691 HK 30_3, with centrifugal growth at periphery (see also Fig. 6 above). **B.** GIUS 3691 HK 27_2, with centrifugal growth changing to adaxial one in peripheral corallite extensions. **C.** GIUS 3691 IV 03 T, two corallites of a colony, separated by corallite walls in central part, so with adaxial growth, also with centrifugal growth pattern visible in upper-right part of the right corallite. Length of scale bar for all figures.

Discoid specimens (Fig. 7) are those with a low dome-shaped distal part and with a broad apical angle. It seems that there is a continuum of shapes, in this case of the angles of peripheral platforms, so there is gradation of high domes into low domes, then into flat-topped and funnel-shaped specimens. Moreover, the irregular expansions at the corallite periphery (Fig. 7A, to the left) indicate that lamellar frills (comp. with Fig. 12A) are a common structure, often abraded or broken-off in the material derived from a scree.

Flat-topped specimens (Fig. 8A, B) are those with sub-horizontal calicular platforms; this specimen is with the calical part preserved, also with epibionts, but its proximal part is missing.

Among the flat-topped corallites recorded is an anomalous specimen (Fig. 8C, D) with triangular shape of the tabularium. In the most proximal section available (Fig. 8C), there are two partly connected tabularia; the corallum outline is, correspondingly, with a deep indentation at the periphery (Fig. 8C, bottom). More distal sections are also of irregular outline, but the peripheral indentation is lost and a single corallite lumen, triangular in outline, appears (Fig. 8D). We think this specimen may present record of aborted fission.
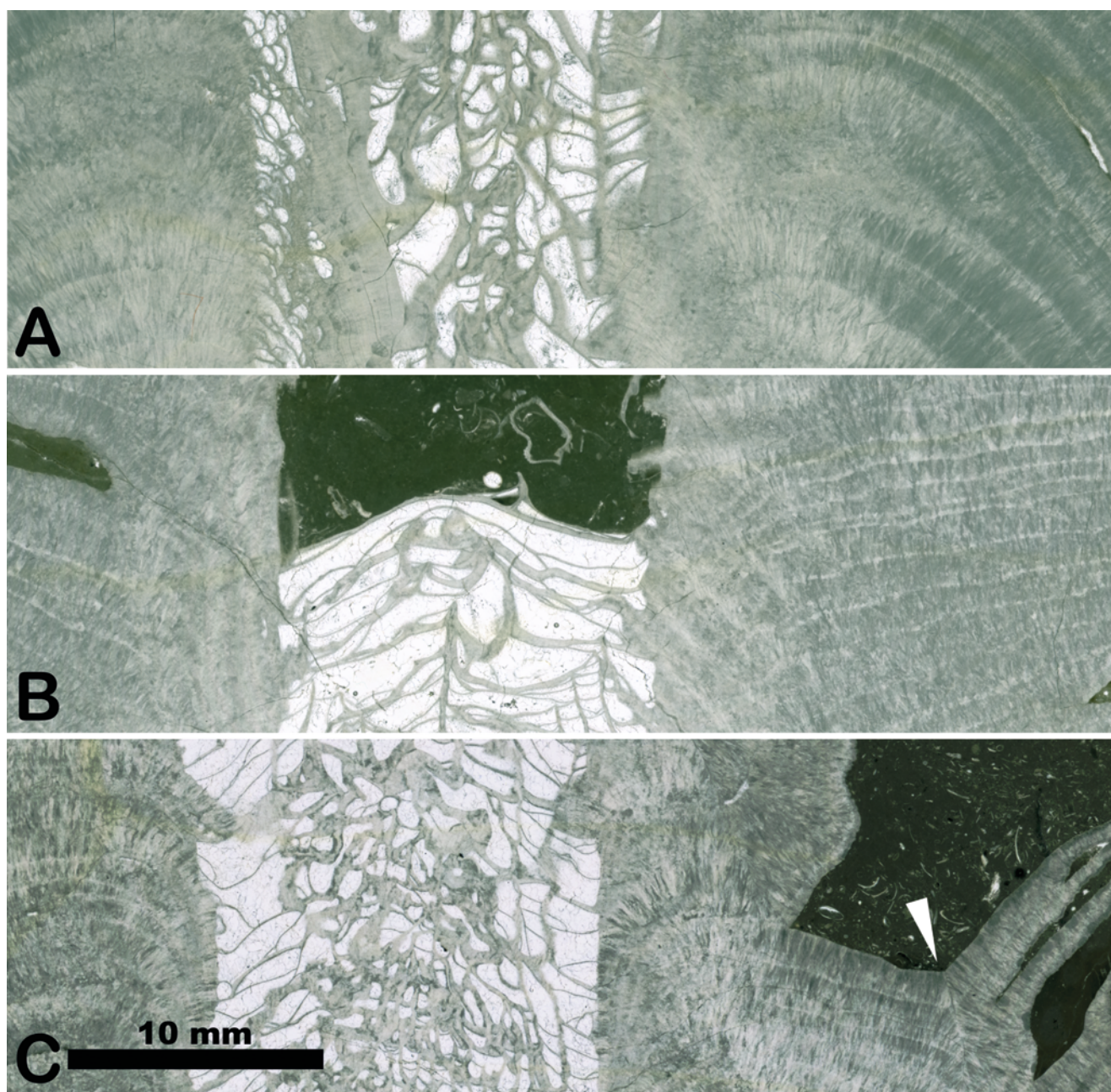
Fig. 11. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Structural and microstructural details in longitudinal axial thin sections of specimens from Högklint (Ygne) (A, B) and Lickershamn (C). **A.** GIUS 3691 HK 30_6 with a zone of irregularly bulbous dissepiments at left part (enlarged fragment of Fig. 6B). **B.** GIUS 3691 HK 28_06a, flat-topped corallite with straight, slightly upturned growth lines in marginarium. **C.** GIUS 3691 LH 19 L1a, a dome-shaped corallite, locally with sharply upturned corallite extensions in its right part – arrowed is zone of converging septal fibers. Length of scale bar for all figures.

Coloniality (Fig. 9, also Figs 3C, D, 4B–E, 10C, 13) is evident in about 25% of the present material, but this ratio is a minimum, as the studied specimens are fragmentary, so they may represent also "solitary" fragments of originally larger colonies. The colonies of the present authors (colony fragments) display 2 or 3 corallites, with intervening septal structures lacking discontinuities (thamnasterioid habit, Fig. 9A), or, rarely, indicating upfolding of basal soft tissue between some polyps (Fig. 4B, enlarged in Fig. 10C). Some of the thin sections represent equal-sized corallites (Figs 4B–D, 9A), whereas there are some other specimens,

with a large parent and a small, single marginal offset (Fig. 4E), established in the mid-parts of the everted calicular platform of the parent (see also the discussion on colonies – paracolonies – aggregates, provided below).

Structural and microstructural details (Figs 10–13) are presented here in enlarged fragments in thin sections. They represent very small, oriented fragments of original specimens (about 1,5 by 6 cm each). In transverse sections (Fig. 10), usually one can see distally convex septal edges at the periphery (Fig. 10A), indicating dome-shaped corallites; in less common specimens with flat or upturned peripheries,
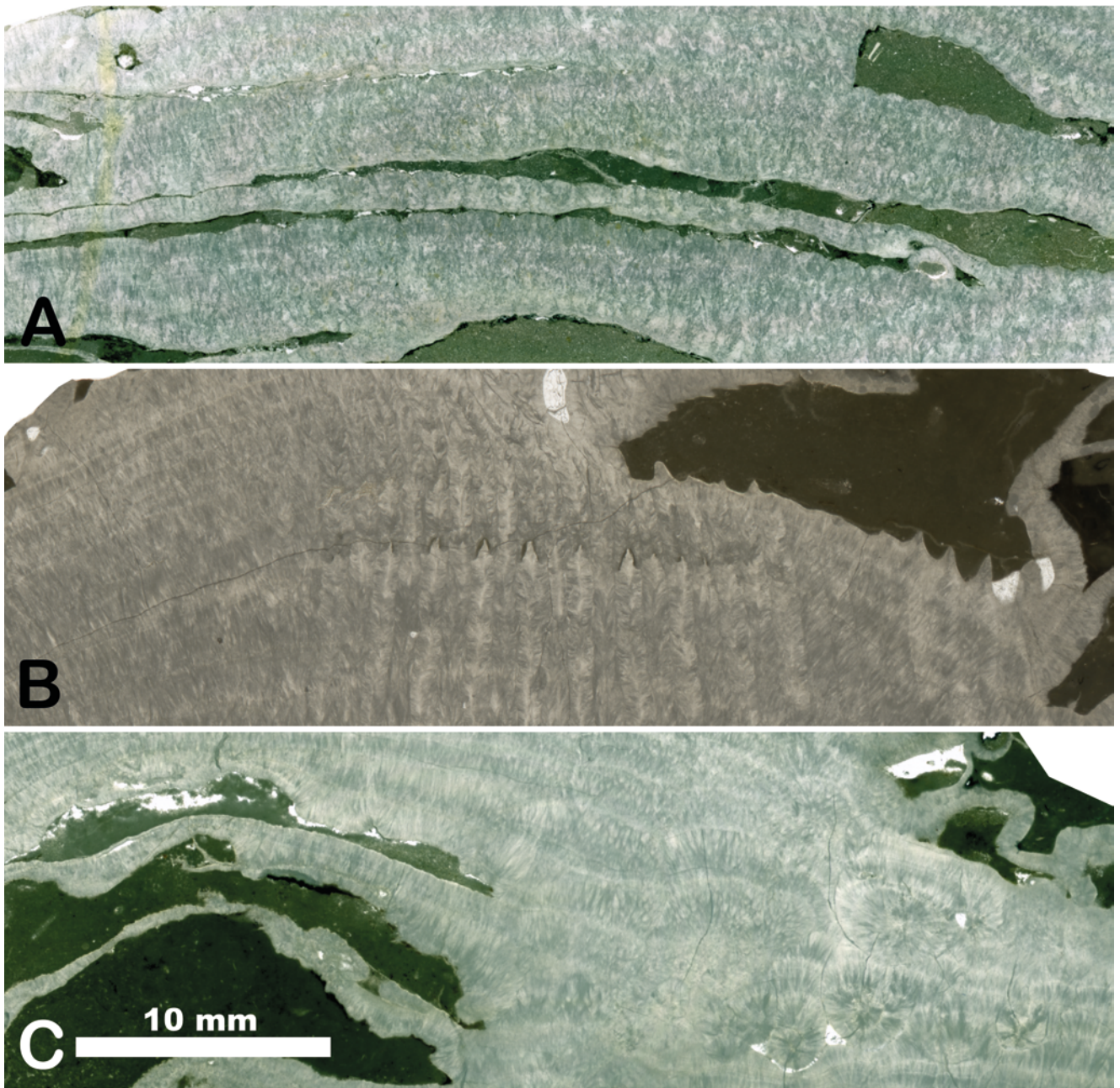
Fig. 12. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Structural and microstructural details in longitudinal-tangential thin sections of specimens from Lickershamn (A, B) and Ireviken (C). **A.** GIUS 3691 LH 01 L4 with numerous lamellar corallite extensions of distally gently convex septal segments. **B.** GIUS 3691 LH 19 Ltgl, cut close to tabularium/marginarium boundary, with serrated appearance of growth lines, corresponding to septal margins sharper than in former section – moreover, growth disruptions occur in every second septum (minor septum?). **C.** GIUS 3691 IV 33 Ltgl, with compound trabecular structures in lower right corner. Length of scale bar for all figures.

the convexity changes to adaxially directed at the periphery (Fig. 10B). Also, combinations of different growth directions can be observed in various radial segments in a single corallite (Fig. 10C: centripetal growth at left of the right corallite, centrifugal growth at its upper-right part). Transverse sections also display major/minor septa relationships, as described above in the case of external morphology.

Longitudinal axial sections (Fig. 11) are with the tabularium in its axis, axially with dome-shaped tabellae and sections of septa, and with massive, peripheral parts of corallites, forming a marginarium of expanded septa with variously shaped growth lines, indicating that corallites are dome-shaped, flat to broadly funnel shaped, or with upturned peripheral platforms (Fig. 11A–C). Exceptional are dissepiment-like, small, peripheral tabellae (Fig. 11A, see also Fig. 6B), seen only in a single specimen in the whole collection studied.

Longitudinal tangential sections (Fig. 12), if cut at the far periphery, often present the isolated horizontal segments of calicular platforms, indicating growth interruptions (Fig. 12A).
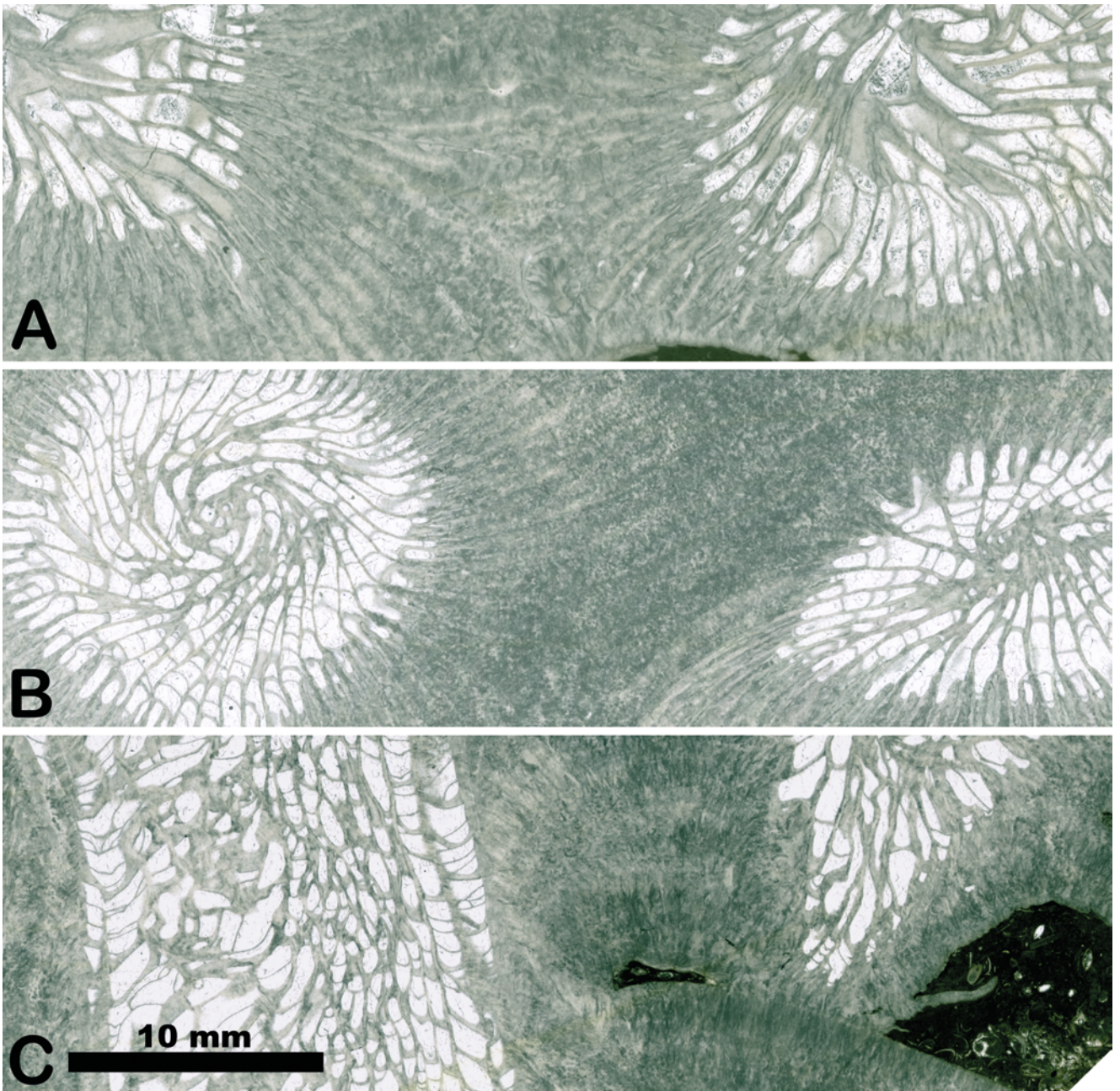
Fig. 13. *Schlotheimophyllum patellatum* from the Upper Visby Beds of Gotland. Structural and microstructural details in thin sections of colonies from Högklint (Ygne) (A) and Lickershamn (B, C). **A.** GIUS 3691 HK 29 T1, transverse section of two large corallites with their zone of contact (see Fig. 4D for whole view). **B**, **C.** Transverse and longitudinal sections (GIUS 3691 LH 01 T2 and GIUS 3691 LH 01 L1) of parent and a marginal offset in a thamnasterioid colony (see Fig. 9A, B for whole views). Length of scale bar for all figures.

It is noteworthy that such corallites with lamellar expansions will quickly disintegrate, when abraded, leaving the more compact axial part of corallite intact. In peripheral, tangential sections, septal edges/growth fronts, display broad, gentle, distally convex aspect (Fig. 12A). In longitudinal, tangential sections, cut closer to tabularium (Fig. 12B), septal growth lines are serrate, indicating sharp septal edges (see also Fig. 4E, at the base of an offset). In some tangential sections (Fig. 12C), otherwise of a quite typical aspect (as in Fig. 12A), there are some compound, trabecular cylindrical(?) structures, of diameter 2–3 mm, indicating horizontal growth and septal reorganization, at least locally.

Colonial coralla (Fig. 13) display microstructural continuity between parents and offsets, both in transverse and in longitudinal sections. On the other hand, aggregated individuals, as suggested for *Schlotheimophyllum* by Weyer (2016, p. 65, pl. 1l), would develop as separate corallites, only subsequently fusing into paracolonies (Weyer's term), with structural continuity between corallites, due to low or nil genetic difference between the individuals. The continuity would be present in the distal parts of the paracolony, whereas its proximal parts would be with numerous individual (proto)corallites. The key factor, in the opinion of the present authors, is genetic difference between individuals

derived from various planulae, produced in course of sexual increase. The authors would rather expect the aggregates to display sharp structural discontinuities. They would get easily broken, when eroded/abraded, and so they would be, if present, underrepresented in the samples of beach pebbles. In the present material, one can rather see continuity of septal structures (com., Fig. 13A, B), indicating the presence of corallites of the same true colony, confirmed by some longitudinal sections (Fig. 13C, the same specimen as in Fig. 13B, see also Fig. 9 for complete sections of this colony). The present authors might add here, that the colonial cerioid rugose corals, although compound, retain their individual external walls. Even the presence of structural discontinuities between neighbouring corallites does not prove they are parts of a single colony; the distinction between colony and aggregate can be seen in the longitudinal sections with and without any indication of offsetting processes, respectively.

SYSTEMATIC PALAEONTOLOGY

Family Kodonophyllidae Wedekind, 1927
Genus *Schlotheimophyllum* Smith, 1945

Type species: *Fungites patellatus* Schlotheim, 1820.

Schlotheimophyllum patellatum (Schlotheim, 1820)
Figs 2–13

partim 1820   *Fungites patellatus* – Schlotheim, p. 347.

      1927   *Chonophyllum patellatum* Schlotheim, 1820 – Wedekind, p. 42, pl. 7, fig. 1.

      1945   *Schlotheimophyllum patellatum* (Schlotheim) – Smith, p. 18, pl. 32, fig. 1.

      1991   *Schlotheimophyllum patellatum* (Schlotheim, 1820) – Neuman and Kershaw, pl. 43 [partly redrawn from Wedekind, 1927].

      2013   *Schlotheimophyllum patellatum* (Schlotheim, 1820) – McLean and Copper, pp. 99–101, pl. 39, figs 1–6.

      2016   *Schlotheimophyllum patellatum* (Schlotheim, 1820) – Weyer, p. 65, pl. 11, figs 1, 2.

Holotype: MB.K.861, uncut specimen from Schlotheim's collection, Humboldt University, Museum für Naturkunde, Berlin (recognized as holotype by Weyer, noted by McLean and Copper, 2013, p. 100; pl. 39, figs 1, 2; measured here from these illustrations), presumably from the lower Wenlock Upper Visby Beds of Gotland.

Additional material: Besides the holotype, 48 specimens (acronymed GIUS) were studied, mostly comprising reworked beach pebbles, found below the cliffs of the Upper Visby Beds of Gotland; also examined were nine specimens loaned from Uppsala University (PMU) for the study of associated sclerobionts (for details see Zatoń *et al.*, 2020). The studied specimens, although not precisely dated, are of fairly well-established and uniform geographical and stratigraphical provenance, namely from the lower Wenlock Upper Visby Beds of WNW Gotland. Some advantages of such a scree collection over specimens collected from bedrock are,

firstly their abundance, and secondly some time-averaging, giving insight into the morphological range, characteristic for the Upper Visby time interval as a whole. On the other hand, some biases can be expected in this material, as the beach pebbles contain abraded coralla, with reduced external measurements and with some external structures (proximal corallite parts, external frills, details of surface) lacking. Also overrepresented may be the robust coralla or their relatively compound, axial parts, more resistant to wave action than the delicate forms/fragments, which may be more abundant in the primary bedrock.

Diagnosis: Kodonophyllid tetracorals with individual corallites discoid to patellate, proximally ceratoid, with narrow calices and broad, everted to subhorizontal peripheral platforms in mature stages, usually with numerous growth interruptions; corallite periphery (marginarium) compact (without dissepiments), of expanded, multitrabecular septa; tabularium profile dome-shaped, with depressed margins; in axis vortically twisted major septa, minor septa present only in tabularial periphery; common are colonies with few marginal corallites developing at calicular platforms of their parents.

Discussion: As presented in the section above, in the opinion of the authors, the entire collection studied represents a single, variable species, *Schlotheimophyllum patellatum* (Schlotheim, 1820). *Schlotheimophyllum canadense* (Billings, 1862) from the topmost Jupiter Fm and Chicotte Fm (mid- to late Telychian) of Anticosti Island, Canada (McLean and Copper, 2013), is a large, solitary species, with very high, raised rim around the calicinal pit; also, its septa display more distinct trabeculae than those in *S. patellatum*, though this may be the result of differences in diagenesis and/or different weathering patterns. The other species considered as representing the genus *Schlotheimophyllum*, are recorded from the mid-Silurian of Kentucky (USA), Telychian of Ringerike (Oslo Graben, Norway), Lower Silurian(?) of Iran, Upper Silurian of Inner Mongolia (China), and Lower Silurian of Guizhou (China; records taken from McLean and Copper, 2013, p. 101), although, as noted by the latter authors, all of these findings are in need of more detailed study to confirm their taxonomic position. Moreover, McLean and Copper (2013, pp. 101–102) list numerous other, still more dubious findings, which were, in their opinion, erroneously attributed to the genus *Schlotheimophyllum*.

Occurrence: *Schlotheimophyllum patellatum* occurs in the Upper Visby shales and limestones, and possibly also in the lower part of the overlying Högklint limestones, of the Isle of Gotland, Sweden.

CONCLUSIONS

The analysis of a rich collection of specimens of the Silurian rugose coral *Schlotheimophyllum* from Gotland showed that they represent a single species, *Schlotheimophyllum patellatum* (Schlotheim, 1820). This coral species is characterized by wide morphological variability of corallites, ranging from discoidal to mushroom-shaped morphologies. Extensive morphological variability can be seen not only in various specimens, but commonly within individual

corallites, thus indicating these are rather fenotypic but not genetic effects. Abruptly changing angles of growth lines at the corallite periphery may indicate responses to changing sediment influx and/or water turbulence. Quasi-colonial (aggregate) aspects have not been detected in the material studied. Instead, continuity of septal structures between neighbouring corallites and continuity of growth lines between parents and offsets, indicate that they belong to the same colony and thus demonstrates true coloniality.

REFERENCES

Adomat, F., Munnecke, A. & Kido, E., 2016. Mass occurrence of the large solitary rugose coral *Phaulactis angusta* at the boundary Lower/Upper Visby Formation in the Silurian of Gotland, Sweden: palaeoecology and depositional implications. *GFF*, 138: 393–409.

Berkowski, B. & Zapalski, M. K., 2018. Large dwellers of the Silurian biostrome: rhizosessile life strategies of cystiphyllid rugose corals from the Llandovery of Gotland. *Lethaia*, 51: 581–595.

Billings, E., 1862. New species of fossils from different parts of the Lower, Middle and Upper Silurian rocks of Canada. *Geological Survey of Canada, Palaeozoic Fossils*, 1: 96–185. [Section on corals published in 1862, other fossils in 1865.]

Birenheide, R., 1978. *Rugose Korallen des Devon. Leitfossilien, begründet von Georg Gürich* 2. Gebrüder Borntraeger, Berlin-Stuttgart, 265 pp.

Bremer, O., 2017. *Silurian Vertebrates of Gotland (Sweden) and the Baltic Basin*. Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 1544. Acta Universitatis Upsaliensis, Uppsala, 61 pp.

Calner, M., Jeppsson, L. & Munnecke, A., 2004. The Silurian of Gotland – Part I: Review of the stratigraphic framework, event stratigraphy, and stable carbon and oxygen isotope development. *Erlanger Geologische Abhandlungen, Sonderband*, 5: 113–131.

Copper, P., 2002. Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages. In: Kiessling, W., Flügel, E. & Golonka, J. (eds), *Phanerozoic reef patterns*. *SEPM Special Publication*, 72: 181–238.

Golonka, J., 2002. Plate-tectonic maps of the Phanerozoic. In: Kiessling, W., Flügel, E. & Golonka, J. (eds), *Phanerozoic Reef Patterns*. *SEPM Special Publication*, 72: 21–75.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D., 2001. paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4: 1–9.

Hill, D., 1981. Rugosa and Tabulata. In: Teichert, C. (ed.), *Treatise on Invertebrate Paleontology*, *Pt. F, Supplement 1*. University of Kansas Press, Boulder and Lawrence, pp. I–XI + F1–F762.

Kershaw, S., 1980. Cavities and cryptic faunas beneath nonreef stromatoporoids. *Lethaia*, 13: 327–338.

Kershaw, S., 1990. Stromatoporoid palaeobiology and taphonomy in a Siluran biostrome, Gotland, Sweden. *Palaeontology*, 33: 681–705.

Lazauskiene, J., Stephenson, R., Šliaupa, S. & van Wees, J.-D., 2002. 3-D flexural modelling of the Silurian Baltic Basin. *Tectonophysics*, 346: 115–135.

McLean, R. A. & Copper, P., 2013. Rugose corals from the Early Silurian (Late Rhuddanian–Telychian) post-extinction recovery interval on Anticosti island, eastern Canada. *Palaeontographica Canadiana*, 33: 1–263.

Munnecke, A., Samtleben, C. & Bickert, T., 2003. The Ireviken Event in the Lower Silurian of Gotland, Sweden – relation to similar Palaeozoic and Proterozoic events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195: 99–124.

Neuman, B. & Kershaw, S., 1991. *Gotland/Sweden: Silurian Reefs and Coral Bearing Strata. Excursion Guidebook of the VI. International Symposium on Fossil Cnidaria including Archaeocyatha and Porifera.* International Association for the Study of Fossil Cnidaria and Porifera, Münster, 111 pp.

Samtleben, C., Munnecke, A., Bickert, T. & Pätzold, J., 1996. The Silurian of Gotland (Sweden): facies interpretation based on stable isotopes in brachiopod shells. *Geologische Rundschau*, 85: 278–292.

Schlotheim, E. V., von, 1820. *Die Petrefactenkunde auf ihren jetzigen Standpunkte durch die Beschreibung seines Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert.* Becker'sche Buchhandlung, Gotha, 437 pp.

Smith, S., 1945. Upper Devonian corals of the Mackenzie River region, Canada. *Geological Society of America, Special Paper*, 59: 1–126.

Søiland, G. V., 1986. *Noen kodonophyllide rugose koraller fra Gotlands og Oslofeltets Silur*. Unpublished M.Sc. Thesis. Bergen University, Bergen, 92 pp. [In Norwegian.]

Wedekind, R., 1927. Die Zoantharia Rugosa von Gotland (bes. Nordgotland). *Sveriges Geologiska Undersökning Avhandlingar och uppsatser, Ser. Ca*, 19: 1–95, 30 pls.

Weyer, D., 2016. Solitary and/or colonial growth in the Palaeozoic superorder Heterocorallia Schindewolf, 1941 (Eifelian–Serpukhovian). *Freiberger Forschungshefte*, C550: 59–101.

Wrzołek, T., 1993. Rugose corals from the Devonian Kowala Formation of the Holy Cross Mountains. *Acta Palaeontologica Polonica*, 37: 217–254.

Zapalski, M. K. & Berkowski, B., 2019. The Silurian mesophotic coral ecosystems: 430 million years of photosymbiosis. *Coral Reefs*, 38: 137–147.

Zatoń, M., Wrzołek, T. & Ebbestad, J. O. R., 2020. Patterns of sclerobiont colonization on the rugose coral *Schlotheimophyllum patellatum* (Schlotheim, 1820) from the Silurian of Gotland, Sweden. *Lethaia*, 53: 486–499.