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Article

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

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Abstract: The boundary between the Lower and Upper Visby formations on Gotland (Sweden), which roughly correlates with the Llandovery–Wenlock boundary, is characterised by a mass occurrence of the large solitary rugose coral *Phaulactis angusta*. This coral-rich layer can be followed for some 50 km along the north-west coast of Gotland. The mass occurrence coincides with the onset of a pronounced, globally recognised $\delta^{13}C$ and $\delta^{18}O$ excursions in the lower Sheinwoodian. Altogether 31 specimens of *P. angusta* from eight localities were examined. We demonstrate that the corals preferred to grow in an upright position. Attachment structures were not observed, and therefore a liberosessile life strategy is suggested. Some corallites show an abrupt change in growth direction accompanied by a decrease in diameter. These features mostly occur in later growth stages and may be explained by disturbances in the growth due to toppling or tilting of the corals. Many specimens were able to change their growth axes, but finally died after such an event. Most specimens in the outcrops show a flattened upper surface, which is interpreted as a result of post-mortem abrasion. Epibiontic bryozoan encrustation took place mostly while the corals where alive, whereas stromatoporoid encrustation and *Trypanites* borings occurred post-mortem. The repeated growth, tilting and erosion of the corallites of *P. angusta* demonstrate that the *Phaulactis* layer represents a condensed interval, characterised by multiple pulses of sediment accumulation and erosion.

Keywords: Silurian; Gotland; Ireviken event; rugose corals

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Introduction

The Llandovery–Wenlock boundary interval is characterised by a severe extinction event known as the Ireviken Event, which was named after its type locality on Gotland (Jeppsson 1987). The extinction, which mostly affected conodonts and graptolites, but also other groups such as trilobites, acritarchs, chitinozoans, ostracodes, brachiopods and corals (summarised by Calner 2008), can be subdivided into eight datum points by Jeppsson (1987), which can be followed basin-wide, and some of them globally (Molloy & Simpson 2012). The most severe extinctions occurred at datum 2, which corresponds to the Llandovery–Wenlock boundary at the stratotype section (Hughley Brook, United Kingdom; Jeppsson 1997a). The second-most intense reduction of taxa followed at datum 4, which corresponds to the boundary of the Lower and Upper Visby formations on Gotland, and with the onset of a pronounced positive $\delta^{13}C$ excursion (Fig. 1; Samtleben et al. 1996; Bickert et al. 1997; Munnecke et al. 2003).

The Lower Visby Formation yields the small solitary rugose coral *Palaeocyclus porpita* (Linnaeus 1767) which disappeared at the upper boundary with the Upper Visby Formation where a weak but abrupt facies change occurs from regular, fossil-poor limestone-marl alternations to irregular limestone-marl alternations (Samtleben et al. 1996). The lowermost interval of the Upper Visby Formation is called "*Phaulactis* layer" because of the mass occurrence of the eponymous coral (Samtleben et al. 1996). *Phaulactis angusta* (Lonsdale 1839) is a dissepimented large solitary coral with a straight to horn-shaped corallum

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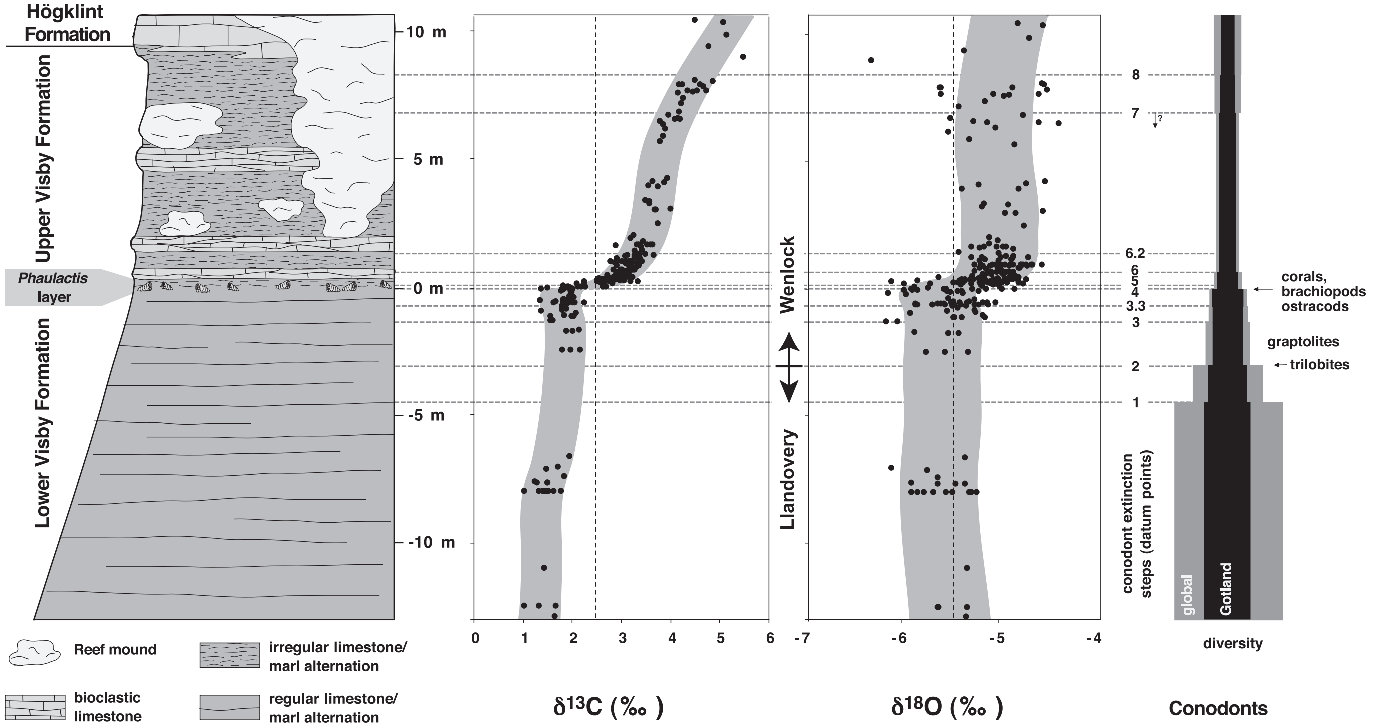

Fig. 1. Schematic weathering profile of the Lower and Upper Visby formations, summarised $\delta^{13}C$ and $\delta^{18}O$ values from brachiopod shells, and conodont extinction events (modified after Munnecke et al. 2003).

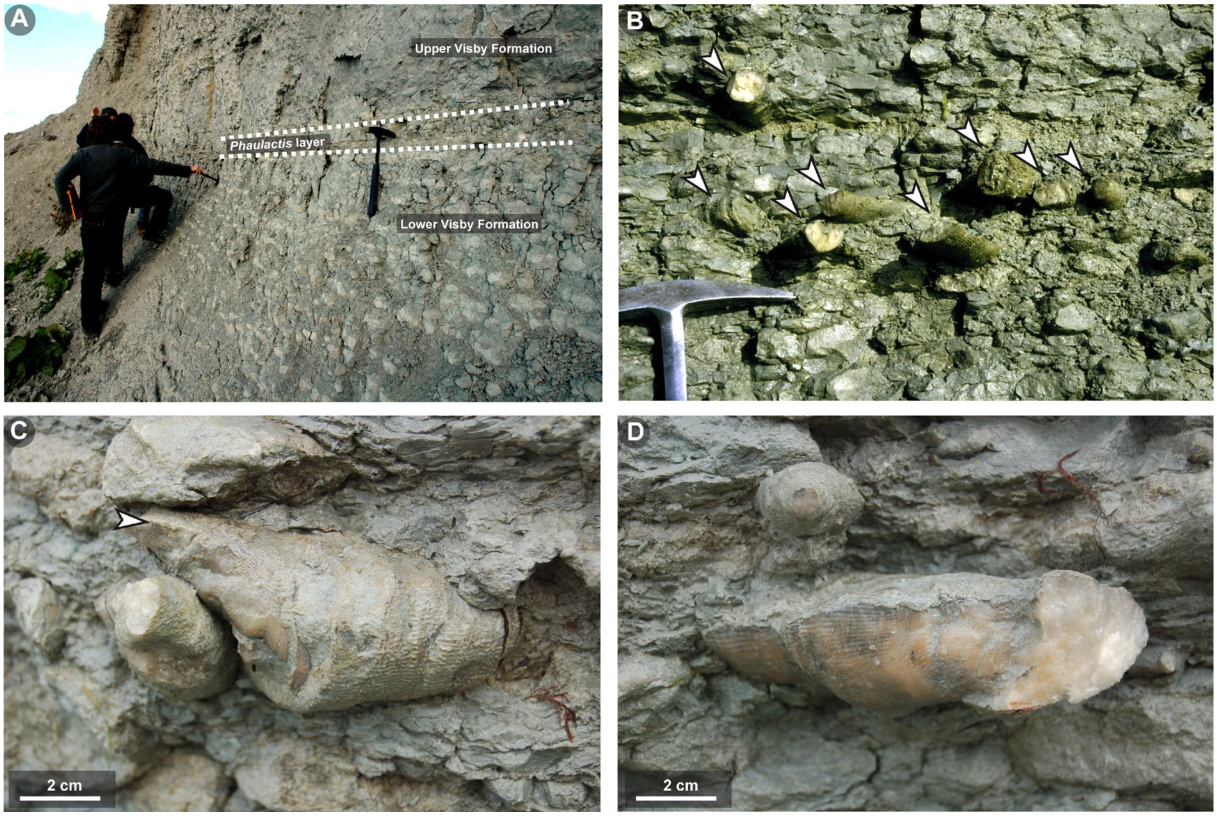

Fig. 2. **A**: Lower and Upper Visby formations near Ygne 3 showing the ***Phaulactis*** layer which represents the lowermost part of the Upper Visby Formation; **B**: ***Phaulactis*** layer ca. 1 km N of Ygne; large specimens of ***Phaulactis angusta*** indicated by white arrows; **C**: two specimens of ***P. angusta*** (locality Sigsarvestrand 3; the same specimen is also figured in Fig. 6/2); note the change in growth direction of the right specimen (arrow); **D**: strongly eroded specimen of ***P. angusta*** (locality Sigsarvestrand 3; specimen figured also in Fig. 6/3).

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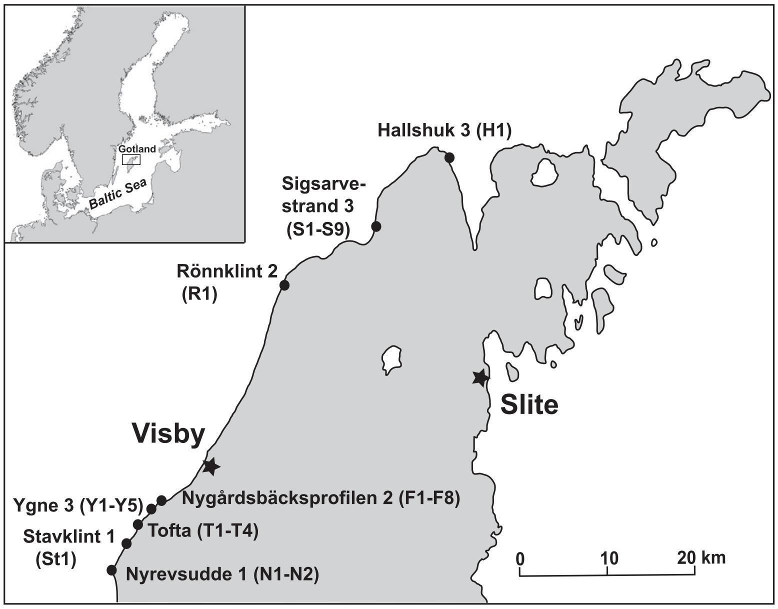

Fig. 3. Map of northern Gotland with sample localities and associated specimen numbers.

reaching up to 30 cm in length. It sometimes formed coral-rich bedding planes with up to 5–10 corals per square metre (Fig. 2). The *Phaulactis* layer, which in most sections has a total thickness of less than 20 cm, was overlooked for a long time. It was first mentioned in the unpublished undergraduate thesis of Mitchell (1990). In the published literature, the layer was first mentioned by Samtleben et al. (1996), who used the base of this layer as a reference horizon for isotopic investigations. The *Phaulactis* layer can be traced for up to 50 km along the northwest coast of Gotland, and shows an increase in thickness from NE to SW (Mitchell 1990; Samtleben et al. 1996; Jeppsson 1997b). All specimens of *P. angusta* were preserved irregularly lying in the sediment, many of them with an abraded side facing upward in the outcrops (Fig. 2B–D). Presently, no specimen has been found in an upright position. The *Phaulactis* layer does not constitute a single horizon consisting only of corals; instead, specimens of *P. angusta* are distributed irregularly within the entire bed forming the *Phaulactis* layer (Fig. 2B).

The purpose of this study is to describe 31 specimens of *P. angusta* from the *Phaulactis* layer in detail. Taxonomic and taphonomic features are analysed to provide information on the palaeoenvironment and the formation of the conspicuous *Phaulactis* layer.

Geological setting

Gotland is a large island in the Baltic Sea (Fig. 3). A carbonate succession of which approximately 500 m thickness is exposed on the island (Hede 1960) was formed along the margins of the Baltic Basin during the Silurian when Baltica had reached low latitudes (Cocks & Torsvik 2005). The strata dip less than 1° towards the south-east and are tectonically unaltered. The oldest strata are located in the northwest, with progressively younger ones towards the southeast. The Lower and Upper Visby formations, exposed along the northwest coast of Gotland, are the oldest strata exposed (Hede 1960).

The Lower Visby Formation consists of regular, fossil-poor limestone-marl alternations (Fig. 2A), and is of Telychian and lowermost Sheinwoodian age (Jeppsson 1997b). Mud- and wackestones are the dominating lithological textures. The base of the formation is not exposed in the sections along the northwest coast. The small solitary rugose coral *P. porpita* is characteristic of the formation and becomes extinct at datum 4 (Fig. 1). The strata were deposited in an open marine environment below the storm wave base and below the photic zone in a distal offshore shelf environment (Samtleben et al. 1996).

The Upper Visby Formation (Sheinwoodian) also consists of limestone-marl alternations (Fig. 2A), but bedding is less regular than in the Lower Visby Formation, and wacke- to grainstones are more abundant. In addition, the abundance of fossils increases, and numerous reef mounds occur, up to a few metres in diameter, which are built mainly by tabulate corals and stromatoporoids. Sediment structures such as ripple marks and erosional surfaces indicate increased water energy (Samtleben et al. 1996). The strata were deposited in shallower environments than those of the Lower Visby Formation, probably within the photic zone, between storm wave base and fair weather wave base in a proximal shelf environment.

The thickness of the *Phaulactis* layer, which represents the lowermost part of the Upper Visby Formation, increases from a few cm in the north-east to more than 1 m in the south-west, reaching a thickness of at least 1.6 m at Nyrevsudde 1, the southwesternmost locality (Fig. 3). The exact thickness of the *Phaulactis* layer at Nyrevsudde could not be determined because the base is situated below present sea level and the corals occur more sporadically than elsewhere. Hence, the term "mass occurrence" is not appropriate at this locality.

The Ireviken extinction event starts 4.5 m below the *Phaulactis* layer at the locality Ireviken 1, and ends 8.5 m above the *Phaulactis* layer at the boundary between the Visby and the Högklint formations (Jeppsson 1987). Within the *Phaulactis* layer the δ^{13}C values rise rapidly (Fig. 1; Munnecke et al. 2003). In some areas, a thin pyritic horizon is observed at the base of the *Phaulactis* layer (Jeppsson 1997b, p. 489; Calner et al. 2004), which marks

Table 1. Sample numbers, museum collection numbers (Naturhistoriska riksmuseet Stockholm), localities and coordinates of the investigated specimens.

Sample number	Museum collection number	Locality	Coordinates (Swedish Grid)		cp. Fig.
F1	SMNH Cn71803	Nygårdsbäcksprofilen 2	638885	164418	Fig. 9
F2	SMNH Cn71804	Nygårdsbäcksprofilen 2	638885	164418	–
F3	SMNH Cn71805	Nygårdsbäcksprofilen 2	638885	164418	Fig. 4/2A–C; Fig. 9
F4	SMNH Cn71806	Nygårdsbäcksprofilen 2	638885	164418	Fig. 5/2A–C; Fig. 9
F5	SMNH Cn71807	Nygårdsbäcksprofilen 2	638885	164418	Fig. 9
F6	SMNH Cn71808	Nygårdsbäcksprofilen 2	638885	164418	Fig. 9; Fig. 11A, B
F7	SMNH Cn71809	Nygårdsbäcksprofilen 2	638885	164418	Fig. 9
F8	SMNH Cn71810	Nygårdsbäcksprofilen 2	638885	164418	Fig. 7/1A–D; Fig. 8/3
H1	SMNH Cn71811	Hallshuk 3	642560	167480	Fig. 9
N1	SMNH Cn71812	Nyrevsudde 1	638120	163785	Fig. 5/3A,B; Fig. 9
N2	SMNH Cn71813	Nyrevsudde 1	638120	163785	Fig. 9
R1	SMNH Cn71814	Rönnklint 2	641179	165698	Fig. 8/2A–C; Fig. 9
S1	SMNH Cn71815	Sigsarvestrand 3	641860	166685	Fig. 6/1A–C
S2	SMNH Cn71816	Sigsarvestrand 3	641860	166685	Fig. 9
S3	SMNH Cn71817	Sigsarvestrand 3	641860	166685	Fig. 5/1A,B; Fig. 9; Fig. 10A, B
S4	SMNH Cn71818	Sigsarvestrand 3	641860	166685	–
S5	SMNH Cn71819	Sigsarvestrand 3	641860	166685	Fig. 4/4A,B; Fig. 9
S6	SMNH Cn71820	Sigsarvestrand 3	641860	166685	Fig. 4/1A, B; Fig. 9
S7	SMNH Cn71821	Sigsarvestrand 3	641860	166685	Fig. 2D; Fig. 6/3A,B
S8	SMNH Cn71822	Sigsarvestrand 3	641860	166685	Fig. 2C; Fig. 6/2
S9	SMNH Cn71823	Sigsarvestrand 3	641860	166685	Fig. 7/2
St1	SMNH Cn71824	Stavklint 1	638410	163945	Fig. 9
T1	SMNH Cn71825	Tofta military ground	Collected between Stavklint and Ygne along the coast		Fig. 5/4A–C; Fig. 8/1A–G; Fig. 9; Fig. 11C
T2	SMNH Cn71826	Tofta military ground			Fig. 5/5; Fig. 9
T3	SMNH Cn71827	Tofta military ground			–
T4	SMNH Cn71828	Tofta military ground			Fig. 9
Y1	SMNH Cn71829	Ygne 3	638794	164270	Fig. 9; Fig. 11D
Y2	SMNH Cn71830	Ygne 3	638794	164270	Fig. 9
Y3	SMNH Cn71831	Ygne 3	638794	164270	Fig. 4/3A,B; Fig. 9
Y4	SMNH Cn71832	Ygne 3	638794	164270	Fig. 4/5; Fig. 9
Y5	SMNH Cn71833	Ygne 3	638794	164270	Fig. 4/5; Fig. 9

the boundary between the Lower and the Upper Visby Formation (Eriksson & Calner 2005). The succession from the *Phaulactis* layer towards the succeeding Högklint formation is regressive which is typical for prograding platforms during highstand systems tracts (Calner et al. 2004, p. 117).

Materials and methods

One of the authors (F.A.) has undertaken field work on Gotland for her diploma thesis (Adomat 2010). From this collection, 28 specimens of *P. angusta* were studied, with an additional three specimens (S7–S9), which were collected subsequently. Specimens were collected from eight different localities along the north-west coast of Gotland: Hallshuk 3 (H1), Sigsarvestrand 3 (S1–S9), Rönnklint 2 (R1), Fridhem (=Nygårdsbäcksprofilen 2) (F1–F8), Ygne 3 (Y1–Y5), Tofta (military training ground, north of Stavklint) (T1–T4), Stavklint 1 (St1) and Nyrevsudde 1 (N1–N2) (Fig. 3). One specimen was not collected *in situ* but was found lying on the beach at Hallshuk 3. Specimens H1 and St1 are embedded in limestone, all others are weathered out and did not require much fossil preparation prior to study. The speci-

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mens are kept in the fossil collection of the Swedish Museum of Natural History, Stockholm (Table 1).

All specimens were cleaned with Rewoquat W 3690 PG, which is a trade name for a concentrate of 75% cationic surfactant 1-methyl-2-oleyl-3-oleyl-amidoethyl-imidazolium methosulfate with 24% propylenglycol. The specimens were whitened with sublimated ammonium chloride (NH_4Cl), photographed, and examined with a binocular microscope. Length of the corallites was measured along the growth axis of the corallite. Diameters of calices were obtained by measuring the longest distance of the calyx. The depths of borings were measured with a wire, which was marked at the "mouth" of the boring. Afterwards, the distance from the tip of the wire to the marking was measured. For analysis of the internal structures of the specimens, 32 transverse acetate peels and 4 longitudinal acetate peels of nine specimens (R1, F4, F5, F8, KL-Y1, KL-Y2, T1, T4 and St1) were prepared.

Synonymy and characteristics of *P. angusta*

Cyathophyllum angustum Lonsdale (1839), p. 690, pl. xvi, fig. 9, Orbigny (1850), p. 47, Milne-Edwards and Haime (1850), p. 281, Tab. LXVI, figs. 4, 4a, Milne-Edwards and Haime (1850), p. 365.

Phaulactis angusta (Lonsdale). Lang and Smith (1927), p. 469, pl. xxxv, fig. 1, text-fig. 10.

The investigated specimens of the solitary coral *P. angusta* vary in size and growth form (Figs. 4–7). The mean length of the corallites is 15.3 cm. The largest specimen reaches 32.5 cm, the smallest one 9 cm in length. The growth form of the corallum is cylindrical, conical, ceratoid or scolecoid. The corallites have mostly subcircular to oval cross section but due to damage caused to some specimens by erosion, exact determination of cross section shape is difficult in some cases. As the peripheral part of the corallites is not completely preserved, maximum corallite diameter of cross sections is measured. Average corallite diameter is 50 mm with maximum up to 57 mm. Septa consist of major and minor ones. The total number of septa ranges between 58 and 98. A maximum total septal number is counted at corallite diameter of 51 mm in specimen KL-Y2. Seven cross sections of the specimen T1 show the increasing total septal number from 58 to 82 between corallite diameters of 21 and 47 mm (Fig. 8/1A–G). Major septa extend to axial area in the neanic to ephebic growth stages. Length of minor septa is about two-third to four-fifth of major septa (Fig. 8/1A–G). The specimens F5, F4, T1, KL-Y1, KL-Y2, F8 and St1 show septal dilation during these growth stages in the tabularium and some cases around the boundary between the tabularium and dissepimentarium. From the cross section of some specimens, we observed that often only few septa thicken in one quarter part of the corallite (Fig. 8/1A–C). Apart from the dilated parts of septa, major and minor septa show similar thickness in the dissepimentarium. The axial ends of some major septa are fused. Counter septum is long and reaches to the axial part of the corallite. A distinctive cardinal fossula is observed when the total number of septa ranges from 58 to 91. It is formed by open space between the shortened cardinal septum and the axial end of adjacent major septa (Fig. 8/1A–C). In this ontogenetic stage, bilateral symmetry in the transverse section is produced. In specimens T1 and F8, which have curved coralla in the early growth stage, the cardinal septum develops on the concave side of the corallite. Specimen F5 that shows a change of growth form, from cylindrical shape to horn shape, in a later growth stage has also the cardinal septum on the concave side. In the specimens F4, KL-Y1 and KL-Y2, which have conical-shaped coralla in the earlier growth stage and change to horn-shaped coralla in the later growth stage, the cardinal septum lays on the convex side of the corallite. The peripheral wall is not preserved. The tabularium is narrow with incomplete tabulae, which are divided into two series; inclined towards dissepimentarium or weakly concaved periaxial series and concaved axial series (Fig. 8/3). In periaxial and axial series of the tabularium ca. 7 tabulae occur in vertical distance of 5 mm when corallite diameter is about 30 mm in specimen F8. The corallite has concentric dissepiments. In the longitudinal section, the wide dissepimentarium is composed of small globose and elongate dissepiments (Fig. 8/2A–C). They incline moderately or steeply toward axial part of the corallite (Fig. 8/2B). Some specimens show different width of dissepimentarium between the concave and convex sides of the corallite; in the specimen R1, the dissepimentarium is wider on the concave side compared to the convex side of the corallite (Fig. 8/2A). In addition, dissepiments develop more densely, but smaller on the concave side and those in the other side are stretched. External morphology shows indications for rejuvenescence (Fig. 5/1,3,5; Fig. 6/3B,C). In the specimen R1, the calyx is 14 mm deep with 34 mm of corallite diameter at the calice base and 43 mm at the calical rim (Fig. 8/2A). Calyx floor is horizontal.

Results

Morphology

In *Phaulactis* specimens with changes in growth direction, the degree of curvature varies (Fig. 9). Curvature of the growth axis is reflected by a change in growth direction accompanied by growth lines and a calyx which are oblique to the original growth axis. Where the epitheca is not preserved, septal grooves and septal ridges show changes in growth direction. Curvature occurs either continuously (Fig. 5/1A,B) or abruptly (Fig. 5/5). Geniculation, which means a sharp change in growth direction, was observed. In S8 an angle of up to 70° to the original growth axis was formed (Fig. 7/2). The corallites of 15 specimens show distinct changes in growth direction in the last growth interval. Of these, the calices of six specimens (F1, S3, S5, S6, T2 and N1) are oriented towards the abraded side in this last growth interval (Fig. 9). Some specimens have straight as well as curved intervals. However, even seven predominantly straight corals (F1, F3, F5, F6, S5, Y3 and Y4) show beginning of curvature in the last growth interval (Fig. 9).

The diameter of corallites in 13 specimens (F1, F3, F5–F7, S2, S3, S5, S6, St1, Y5, T2 and N1) decreases in the last stage of development, associated with changes in growth direction (Fig. 9; see also Fig. 2C). The diameter in these terminal growth stages reaches lower values than the diameter of previous adult growth stages. In S5, the decrease of diameter is 40% (Fig. 4/4A). In few specimens, the decrease in calyx diameter appears to have happened in several steps, for example in S6 and F3, showing a decrease of 78% and 30%, respectively (Fig. 4/1A, 2A,B). In six specimens (R1, F3, Y3, T1, T4 and N2), calices show no changes in diameter. The mean diameter of these calices is 5 cm. The base of the calyx is either flat or slightly concave. The calyx walls are steep, in some cases slightly convex.

Externally most specimens have rhythmically developed macroscopic growth bands, which are separated by constric-

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Fig. 4. ***Phaulactis angusta***; **1**: S6 (SMNH Cn71820); **1A**: calyx; dislocation of growth axis towards the abraded side (in the figure below); stepwise decrease in diameter; **1B**: lateral view of predominantly cylindrical corallite; constriction (short-term decrease in diameter) and slight bend in growth direction (at the level of bryozoan encrustation, white arrow); the latest growth interval shows better preservation than previous growth stages; **2**: F3 (SMNH Cn71805) with preserved apex (white arrow); **2A**: calyx; dislocation of growth axis towards the abraded side; stepwise decrease in diameter; **2B**: lateral view of the abraded side of the corallite; decrease in diameter in later growth stages; **2C**: lateral view of the non-abraded side; better preserved side of the predominantly straight corallite; preservation of apex (white arrow); **3**: Y3 (SMNH Cn71831); **3A**: calyx; slightly abraded side oriented downwards; **3B**: lateral view; conical corallite; beginning curvature in the latest growth interval; **4**: S5 (SMNH Cn71819); **4A**: lateral view of the abraded side with decrease in diameter of the corallite during the latest growth interval; **4B**: lateral view of the opposite, also slightly abraded, side; later growth stages show better preservation than earlier growth stages; **5**: Y4 (SMNH Cn71832) and Y5 (SMNH Cn71833); lateral view; conical–cylindrical growth form; change of growth direction during the latest growth interval; Scale bar is 1 cm.

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Fig. 5. ***Phaulactis angusta***; **1**: S3 (SMNH Cn71817); **1A**: lateral view of un-abraded side; ceratoid growth form; the later growth stages are better preserved than earlier growth stages; **1B**: lateral view of abraded side; decrease in diameter and change in growth direction towards the abraded side during the latest growth interval; big boring in the upper third of the corallite (white arrow); **2**: F4 (SMNH Cn71806) with apex preserved; **2A**: lateral view of the less-abraded side; conical growth form in the lower part of corallite changing to curved growth shape in the upper part; preservation is better in the later growth stages; preservation of apex (white arrow); **2B**: lateral view of the abraded side; short-term decrease in diameter after initial of curvature, thereafter increase in diameter; **2C**: calyx; **3**: N1 (SMNH Cn71812); **3A**: lateral view of less-abraded side; latest growth interval of corallite is better preserved than earlier growth intervals as it keeps epitheca; **3B**: lateral view of abraded side with distinct constrictions and change in growth direction after the early growth stages; decrease in diameter and dislocation of the growth axis towards the abraded side during the latest growth interval; **4**: T1 (SMNH Cn71825); **4A**: lateral view of non-abraded side; ceratoid growth form; slight bend of growth axis; **4B**: lateral view of abraded side; **4C**: calyx; **5**: T2 (SMNH Cn71826); lateral view; scolecoid growth form; multiple changes in growth direction with regularly spaced constrictions and rejuvenescence; epitheca is preserved in the upper part of the corallite. Scale bar is 1 cm.

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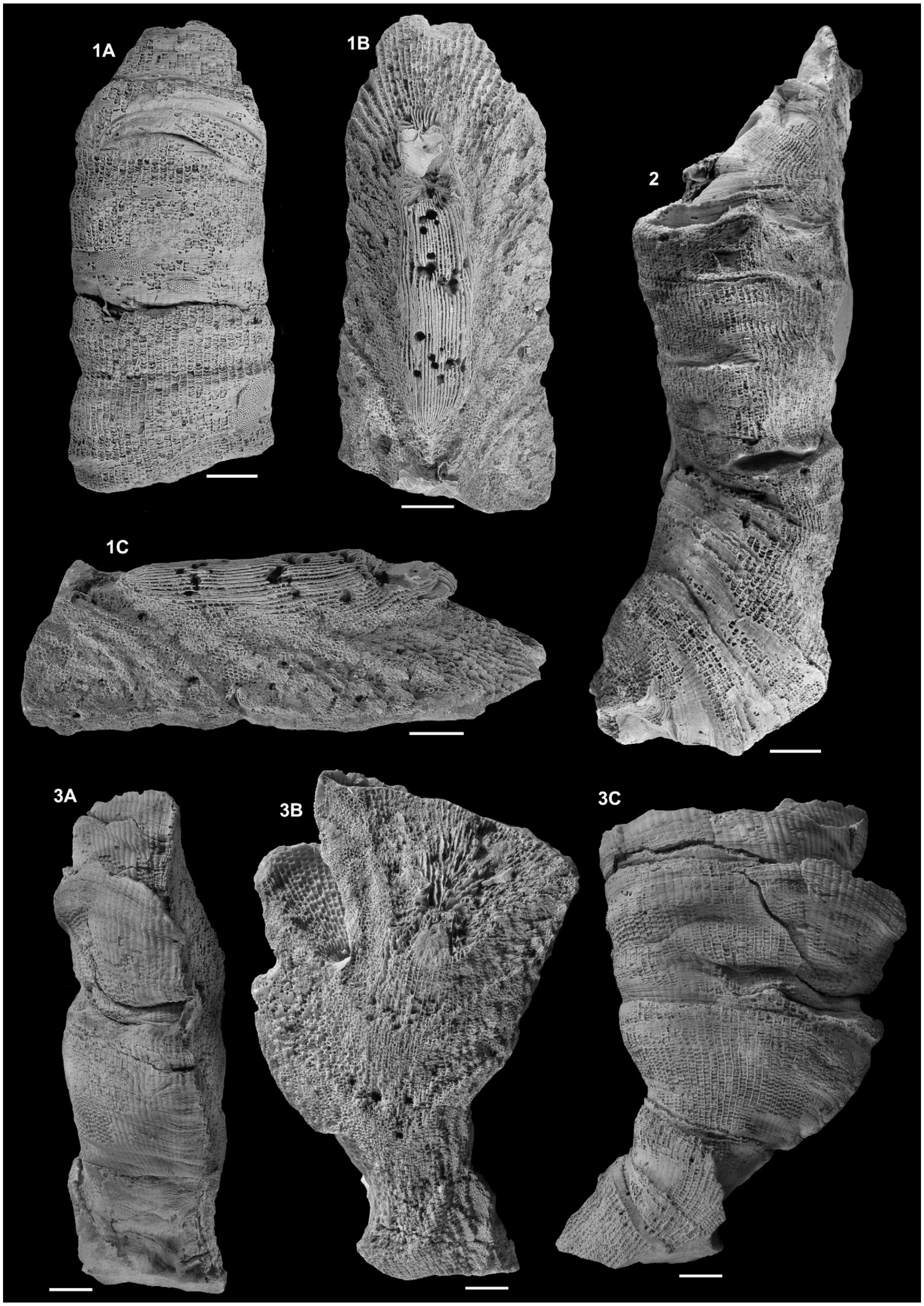

Fig. 6. ***Phaulactis angusta*** with borings and epizoans; all specimens in lateral view; **1**: S1 (SMNH Cn71815); **1A**: less abraded side of fragmented corallite with epitheca partly preserved; constriction and curved growth lines; **1B**: strongly abraded side with exposed columella and numerous borings; **1C**: lateral view; **2**: S8 (SMNH Cn71822); lateral view, with abraded side on the right; scolecoid growth-form; multiple changes in growth direction; **3**: specimen S7 (SMNH Cn71821); **3A**: lateral view of convex side; **3B**: lateral view of abraded side; change in growth direction in later growth stages; **3C**: lateral view of the less-abraded side. Scale bar is 1 cm.

tions. The intervals between successive growth bands differ in size between specimens (Fig. 4/1B, 2B, C, 4; Fig. 5/1, 2A,B, 3, 4A,B, 5), except in Y5 where they are regular (Fig. 4/6). The thickness of the growth bands is 0.4–4.0 cm. The thickness of the growth bands within a single specimen ranges from 1.04 cm (F7) to 2.4 cm (S2), with a mean value of 1.65 cm. Where the epitheca

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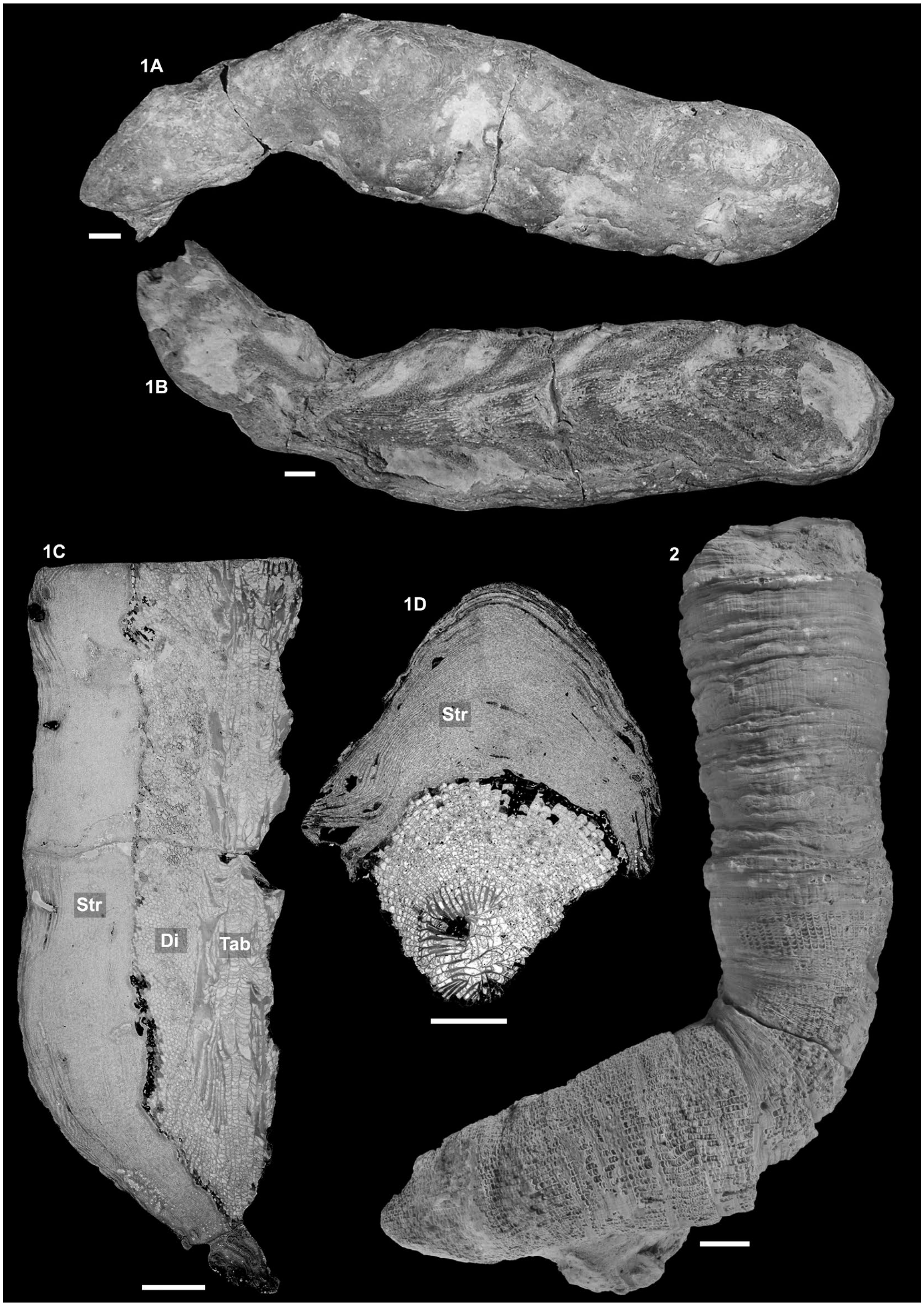

Fig. 7. ***Phaulactis angusta***; **1**: F8 (SMNH Cn71810); **1A**: lateral view of one side which is entirely covered by a stromatoporid; **1B**: lateral view of the opposite side; **1C**: longitudinal section (acetate peel); the stromatoporoid (Str) is visible on the left; the dissepimentarium (Di) on the non-overgrown side is abraded (Tab = Tabularium); **1D**: transverse section (acetate peel); no epitheca preserved between stromatoporoid and coral; sediment is present between the corallum and the stromatoporoid; **2**: S9 (SMNH Cn71823); growth stages which formed after change in growth direction are better preserved than early growth stages; in latest growth interval change of growth direction towards the abraded side (oriented backwards). Scale bar is 1 cm.

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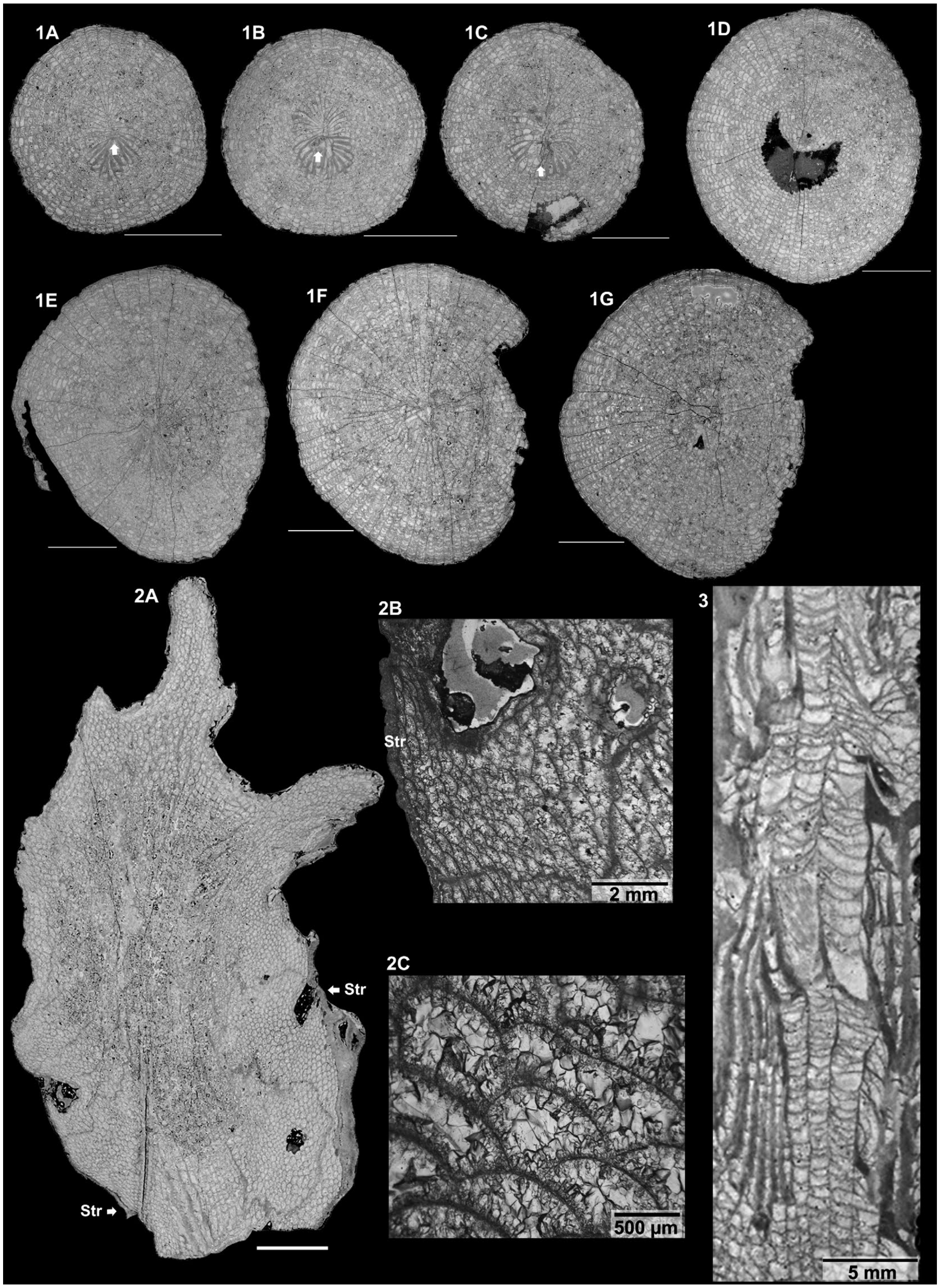

Fig. 8. Acetate peels of ***Phaulactis angusta***; **1**: T1 (SMNH Cn71825); **1A–G**: serial transverse sections of the specimen with the convex side facing downwards; arrows in **1A**, **1B** and **1C** indicate the position of the cardinal fossula; **2**: R1 (SMNH Cn71814); **2A**: longitudinal section; arrows indicate stromatoporoid (str) overgrowth; **2B**: detail of dissepimentarium; **2C**: dissepiments; **3**: detail of longitudinal section of the specimen F8 (SMNH Cn71810) showing the tabularium (same specimen as Fig. 8/1). Scale bars for **1A** and **2A–G** indicate 1 cm.

is preserved growth ridges can be observed (Fig. 10A, B). The thickness of these growth ridges ranges from 40 to 350 µm, with the number of ridges ranging from seven to nine per millimetre, in a few cases up to twelve. The number of growth ridges per dissepiment is also variable and occurs in a range of three to five (Fig. 10B).

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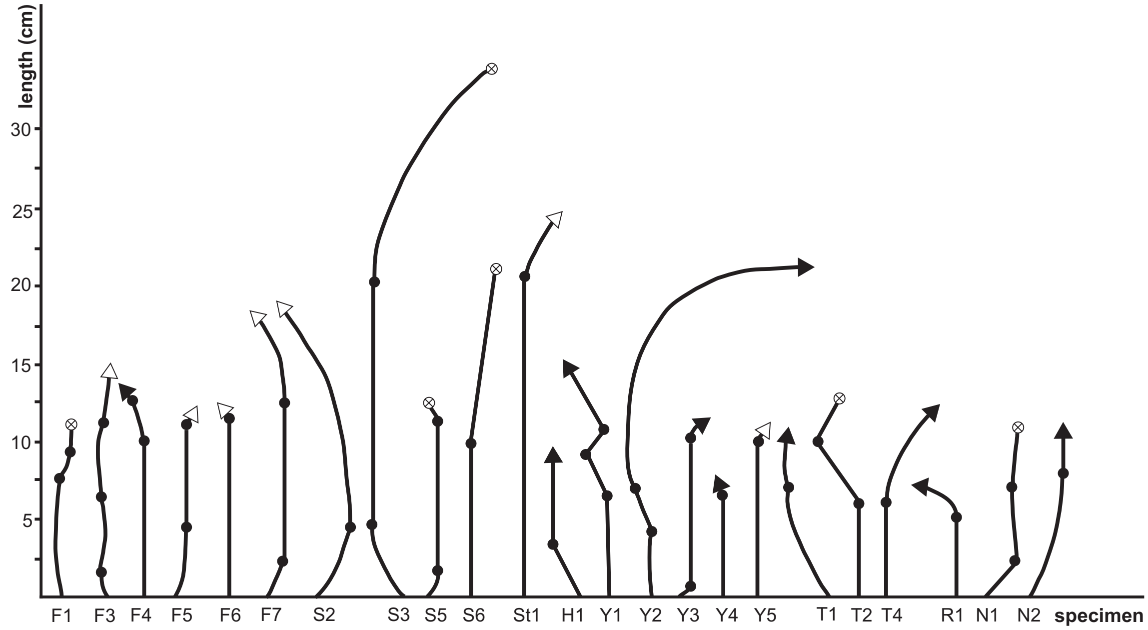

Fig. 9. Schematic illustration of changes in growth directions of ***Phaulactis angusta***; abraded side of the corallites oriented backwards; each dot marks a change in growth direction of the respective corallum; each cross marks a change of growth direction towards the predominant abraded side associated with a decrease in diameter; white arrows indicate a decreased diameter during the last growth interval; black arrows indicate an unchanged diameter during the last growth interval.

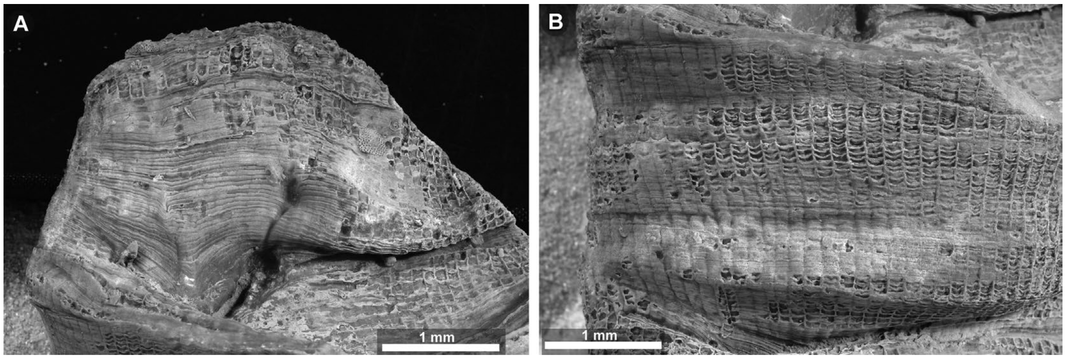

Fig. 10. S3 (SMNH Cn71817); **A**: growth ridges are preserved in un-abraded parts of the corallum (detail of specimen figured in Fig. 5/1a); **B**: the dissepiments are visible in abraded parts of the corallum.

Preservation

Rugose corals consist primarily of calcite and therefore are usually well preserved. Some corallites are broken, whereby breakage mostly affected the apical and calical portions. Three specimens (F3, F4 and Y4) are completely preserved from the apex to the calyx (Fig. 4/2, 5(Y4); Fig. 5/2A,B). The apex is preserved only in these specimens. No specimen shows a completely preserved epitheca, but all specimens have at least some epitheca preserved. In poorly preserved specimens the only part of the epitheca present is in protected areas such as constrictions of the corallite or underneath epifaunal bryozoans.

The most significant difference in preservation is between the upward and downward facing side of the corallites, as found in the outcrop. Many specimens where found lying on their sides, with the side they had come to lay on being un-abraded and the upwards-facing side abraded, often to a degree that this part of the specimen appeared polished and almost flat (Fig. 2B, D). 26 out of 31 specimens show strong evidence of mechanical or chemical erosion on the upward facing side (for example, Fig. 4/2B, 4A; Fig. 5/1B, 2B, 3B, 4B; Fig. 6/1B,C, 3A,B). In those corallites with strong abrasion the epitheca and parts of the stereozone were removed. The degree of abrasion is variable among the specimens. In three specimens the epitheca and large parts of the dissepimentarium were removed and the columella exposed (Fig. 6/1B,C; Fig. 7/1D). However, abrasion not only affected one side of the coralla, but is less pronounced on other sides.

In twelve specimens the proximal part of the corallite is more abraded than the distal part (for example, Fig. 4/4B; Fig. 5/2A; Fig. 7/2). Straight and slightly curved corallites mostly show equal preservation in both proximal and distal parts of the corallum, and only small differences in preservation between their convex and concave sides. Comparison of the preservation be-

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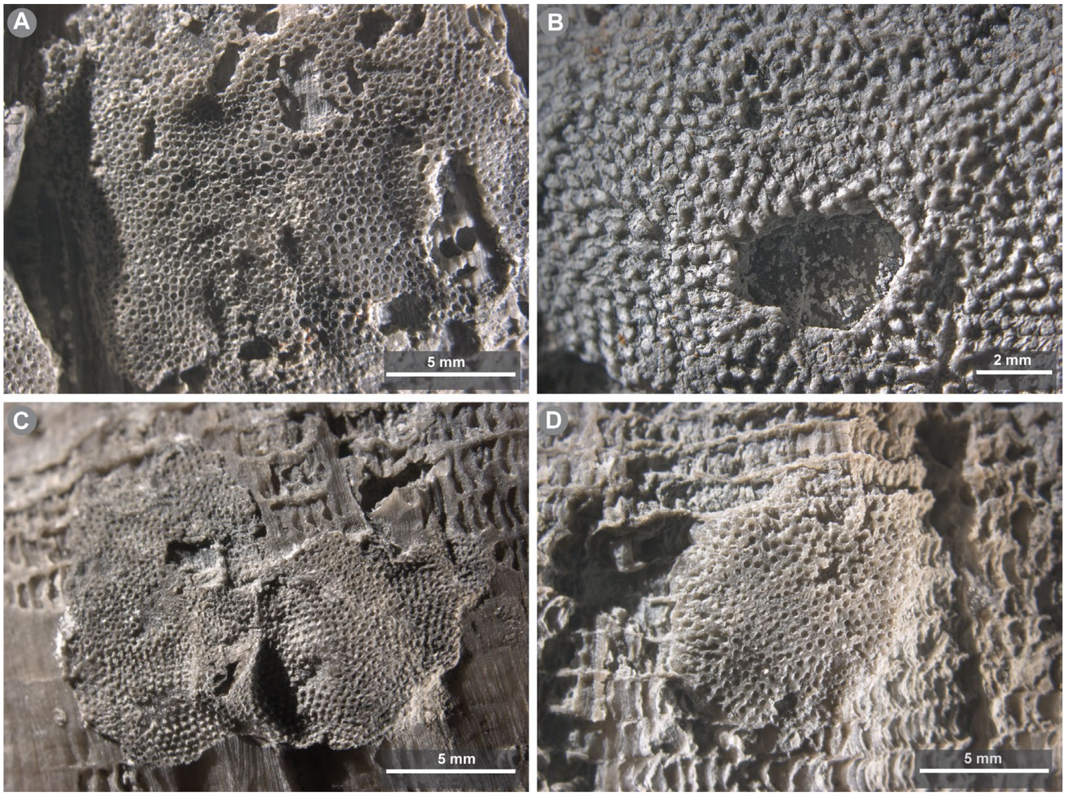

Fig. 11. Epibiontic bryozoans on ***Phaulactis angusta***; **A, B**: ***Fistulipora mutabilis*** growing on the epitheca of S6 (SMNH Cn71820); **C**: ***Ceramopora lindstroemi*** growing on the epitheca of T1; D: ***Ceramopora perforata*** growing on the exposed dissepiments of Y1 (SMNH Cn71829).

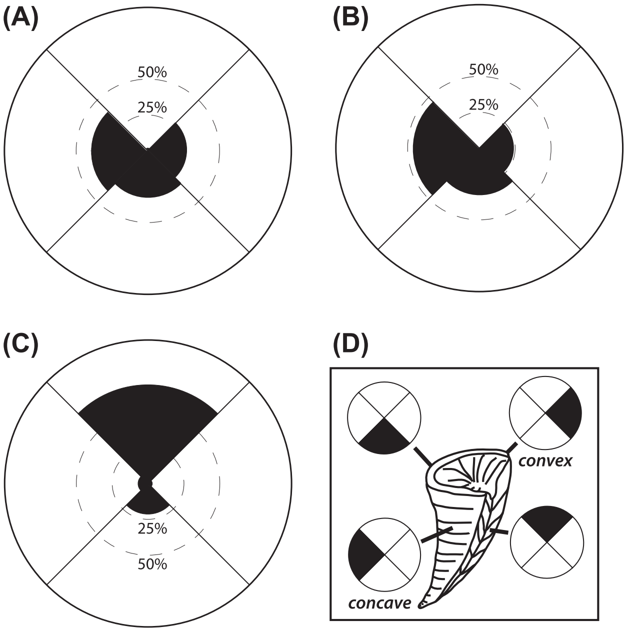

Fig. 12. Distribution of bryozoans and ***Trypanites*** borings on ***Phaulactis angusta***; black areas represent portion of total encrustation and borings in relation to the other sides; **A**: bryozoan encrustations on curved coralla; **B**: bryozoan encrustations on predominantly straight coralla; **C**: ***Trypanites*** borings on curved and predominantly straight coralla; **D**: attribution of sectors to the sides of the coralla.

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tween convex and concave sides was possible in 23 specimens, including those specimens with incipient curvature at their distal parts. Thereof, in 13 specimens, the concave and convex sides are abraded equally. Eight specimens are abraded more on the convex side, whereas in two specimens abrasion was stronger on the concave side. The epitheca of the most distal part of the corallites (last growth interval) is commonly very well preserved (for example, Fig. 5/1A, 2A, 3A).

There were no differences between localities in the way specimens were abraded.

Epibionts

Encrusting bryozoans occur on 24 specimens, for example, *Ceramopora perforata*, *Ceramopora lindstroemi*, and *Fistulipora mutabilis* (Fig. 11). The largest bryozoan colony was found on the surface of specimen F1 (not shown), where *Fistulipora mutabilis* covers an area of about 4 × 3 cm. Altogether, 182 epibiontic bryozoan colonies were recorded, some also growing on epibiontic stromatoporoids encrusting the corallites. The only specimens appearing to lack bryozoans are strongly abraded (F2, S1), embedded in limestone or partly overgrown by stromatoporoids (St1, R1). Bryozoans occur on all sides of the corallites, but are rarely observed on abraded parts (Fig. 11A, B). They are mostly located on the epitheca (Fig. 11A, C). In some cases it was observed that the epitheca was abraded in areas close to bryozoan epibionts (Fig. 11C, D).

On corallites with strong curvature 44 bryozoan colonies are attached on the concave side, 30 on the convex side, and 36 on the side opposite to the abraded side. On the abraded side only one single bryozoan colony was observed (Fig. 12A). On predominantly straight corallites 16 bryozoan colonies were counted on the side becoming convex in the latest growth stage. On the side that becomes concave in the latest growth stage, 32 bryozoan colonies were counted, whereas the side opposite to the abraded side is overgrown by 23 colonies (Fig. 12B).

Three of the 31 *Phaulactis* specimens examined are overgrown by stromatoporoids. Specimen F8 is covered by a stromatoporoid over the entire length of the corallite (Fig. 7/1A–C). One side of the corallite is strongly eroded (Fig. 7/1B–D). It is evident in transverse section (Fig. 7/1D) that there is less abrasion on those parts of the corallite covered by the epibiont. However, underneath the epibiont the corallite also lacks epitheca. It even seems that some sediment is trapped between the stromatoporoid and the corallite (Fig. 7/1C,D).

Borings

17 *Phaulactis* specimens exhibit a total of 120 borings assigned to the ichnogenus *Trypanites* (Mägdefrau 1932; Bromley 1972). The cylindrical borings have a diameter of 0.5–2 mm in diameter and up to 5 mm deep, generally directed perpendicular to the corallite surface (Fig. 6/1B,C). The depth of borings on the epitheca of un-abraded parts of the coralla is similar compared to the depth on eroded parts of the same corallites. Three specimens were not examined for the presence of borings because they are completely overgrown by stromatoporoids or embedded in limestone. Borings are most abundant on the abraded side of the corallites that exhibits a number of 83 borings (Fig. 12C). In most cases, they occur in areas where epitheca is not preserved. Twenty-five borings occur on the side opposite to the abraded side. On the convex and concave sides of the corallites borings are sparse, but are slightly more frequent on the concave compared to the convex side, showing a number of eight and four borings, respectively. On predominantly straight corals, one single boring was present, which was on the concave side. Some specimens (for example, F1 and S1) have multiple borings (21 and 20, respectively). In the specimen S1, borings are into the columella, which is exposed through abrasion (Fig. 6/1B,C).

Discussion

*Mode of life of **P. angusta**, and palaeoecological implications*

Most of the *P. angusta* coralla are straight. In the absence of any visible attachment scars, even on specimens with the apex preserved, we suggest that *P. angusta* had a liberosessile mode of life, with individuals usually well supported by sediment. Vertical growth of a corallum without attachment is possible if the corallum is supported in an upright position, with the sedimentation rate matching the growth rate, or the corallum sinking into the sediment at the same rate as the growth rate (cf. Neuman 1988; Sorauf 2001). Vertical growth is indicated by the horizontal orientation of the calices and growth ridges that are mostly developed perpendicular to the growth axis.

Almost all coralla show changes in their growth direction, in many of them this occurred only during the terminal period of growth (Fig. 9). There are indications that curvature in *P. angusta* is a result of disturbance of a usually straight growth position of the corallites. Continuous sinking of the corallum into the soft sediment due to increased weight probably resulted in uniform curvature (for example, S3; Fig. 5/1). Sudden events such as storms may have resulted in abrupt changes in growth direction, as shown in S9, which exhibits a sharp bend (geniculation) of the corallum (Fig. 7/2). Hubbard (1970) named instability of the substrate, unfavourable initial attachment and oblique growth away from sediment surface as likely causes for geniculation. Scolecoid growth as in T2 and S8 indicates a repetition of such events (Fig. 5/5; Fig. 6/2). A change in growth direction, which often occurred together with a markedly decrease in diameter was observed during the last growth interval of many coralla (Fig. 9). This feature suggests that although *P. angusta* was able to redirect their growth axes, many of the corals finally died after a toppling event.

Phaulactis is one of the genera noted as being exceptional among rugose corals in its apparently ability to tolerate toppling onto its side. Toppling, unlike in most other rugose corals, does not necessarily appear to result in death, but often in drastic reorientation of the growth vector (*cf.* Scrutton 1998; Neuman 1988). This ability is also known from other rugose coral species. The Devonian rugose coral *Heliophyllum halli* (Milne-Edwards and Haime 1850) was also able to react effectively to toppling and “other causes of burial” by forming an angle of curvature close to 90°, what resulted in highly variable growth forms (Sorauf 2001).

Constriction and expansion of the corallite may be caused by the polyp reacting to changes in ecological conditions (Berkowski 2012). A sudden decrease in calyx diameter may be the result of a reduction in the size of the polyp, which may have been caused by environmental stresses or increased sedimenta-

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tion rate (Hubbard 1970; Elias 1982; Neuman 1988; Scrutton 1998). A decrease in diameter due to a lack of food sources is also considered (Berkowski 2012).

The ability of individual species to redirect their growth vector may be affected by calyx geometry and size, as well as the number of septa (Sorauf 2001). Evidence from experiments on sediment rejection in Scleractinia by Hubbard & Pocock (1972) indicated that calices with flat bottoms and steep convex walls are disadvantageous for polyp expansion, whereas ornamentation of septa proved beneficial. The flat calyx and steep convex walls of *P. angusta* may therefore be inadequate to protect the polyp from heavy sediment input. Sorauf (2001) referred to observations on modern Scleractinia by Marshall & Orr (1931) and Yonge (1940) and listed a large calicular diameter as well as a large number of septa, which is related to the number of polypal tentacles. These observations may also apply for *P. angusta*, which has a comparably large diameter (max. 7.7 cm in S6) and number of septa (max. 98 in Y2).

Two specimens document a "recovery" phase after tilting (Y4 and Y5; Fig. 4/5). Both started growth as independent coralla but experienced a disturbance that appears to have tilted them towards each other. Continuing growth after the disturbance event, the coralla actually fused following reorientation of both corals. In contrast, in specimen Y5 a marked change in growth direction, accompanied by a decrease in corallum diameter in the last growth interval, occurred following the disturbance event (Fig. 4/5). The following sequence of events appears probable: a disturbance event affected specimen Y4, it toppled and died. Later, specimen Y5 fell on top of specimen Y4. Subsequently, specimen Y5 reoriented its growth vector, but also died shortly thereafter. Probably, the two specimens did not live contemporaneously, but toppled over during two different events, because it is unlikely that specimen Y4 toppled, while the more exposed specimen Y5 with similar diameter remained unaffected.

Flattening of one side of the corallites, already mentioned by Jeppsson (1997b, p. 489), differs between individual coralla. Flattening is a result of post-mortem damage, as indicated by an almost complete absence of epitheca on the abraded side of the corallites. Instead, flattening appears to be caused by physical abrasion. The following scenario therefore seems probable: The corals, most of them still alive, were toppled and remained lying on one side in a stable position. The most stable depositional position for solitary rugose corals with curvature is the plane of curvature and bilateral plane of symmetry lying horizontal (Elias et al. 1988, their Fig. 12). The convex side of the coralla may have faced into the current, because this represents the hydrodynamically most stable position. It seems that the concave side of the corallites is less prone to abrasion than the convex side. Corals without curvature may have been abraded more uniformly because they have an unstable position after tilting, and can be rolled easily on the sea floor. Abrasion probably already affected upright oriented corals during life, as indicated by higher amount of erosion in the more proximal part of the corallites. The latter aspect is an indicator that the corals grew superstratal. Mechanical abrasion was probably produced by smaller bioclasts, which were moved by water energy.

Borings are most abundant on the abraded side of the corallites (Fig. 12C). The same depth of borings on the epitheca of un-abraded parts of the coralla and on eroded parts of the same corallites suggests that the borings were produced after death of the corals and after abrasion of the corallites. The greater number of the borings on the abraded sides compared to un-abraded parts of the same coralla is an indicator – in addition to the abrasion of these parts – for the coralla coming to rest on the sediment in this apparently highly stable post-mortem position, resting on a lateral side rather than the convex or concave side.

The distribution of bryozoans in a seemingly random fashion across all sides of the coralla except the abraded parts may be an indication that epibionts inhabited the corals mostly while the polyps were alive and in growth position, and certainly before abrasion took place.

In specimen F8, a straight corallum without curvature, the stromatoporoid had grown on the side of the corallum facing into the sediment when collected (Fig. 7/1). The stromatoporoid-bearing side lacks the epitheca which therefore must have been abraded prior to growth of the stromatoporoid (Fig. 7/1C,D). After overgrowth by the stromatoporoid, the corallum was overturned by some process prior to burial.

Comparison with Carboniferous caninioid corals from north-west Ireland

The *Phaulactis* layer shows similarities to the occurrence of large solitary rugose corals from the Carboniferous (late Viséan) limestone-shale sequences of northwest Ireland (Hubbard 1966, 1970). Similarities can be observed not only in the external morphology of the corals but also in their occurrence and sedimentological settings. The coral-rich bedding plane is traceable along the cliff and corals mainly comprise caninioids, for example, *Syphonophyllia samsonensis* (Salée 1913). Straight and geniculate forms cover limestone beds, e.g., at the famous sites Serpent Rock and Streedagh Point located at the Sligo coast. Coral density within the planes is variable. They show a high variability in their growth forms from straight, uniformly curved to complexly geniculated (Dixon 1970; Hubbard 1970). Penecontemporaneous abrasion usually affected the upward facing sector of the corallum (Dixon 1970; Hubbard 1970). The caninioid-dominated bedding planes of north-west Ireland are interpreted to represent condensed composite death assemblages (winnowed death assemblages) with coralla of different generations (Hubbard 1970). Several aspects such as the occurrence in a coral-dominated layer, variation in growth form with reorientation of the growth axis and abrasion of the upward facing part of the corallum, were also observed in the Silurian rugose coral *P. angusta*. During their lifetimes, both species probably formed "coral meadows" in the sense of Aretz (2010), each representing the dominant species in this habitat.

Duration of the deposition of the ***Phaulactis*** *layer*

The Ireviken Event was an extinction event at the Llandovery/Wenlock boundary interval associated with a major positive carbon isotope excursion (Munnecke et al. 2003). Mostly trilobites and conodonts were affected, with a loss of 50% and 80% of all species, respectively. In contrast, shallow-water faunas and reefs were barely affected. The ultimate causes of this event are still debated (Munnecke et al. 2010). The occurrence of *P. angusta* in the lowermost part of the Upper Visby Formation, i.e., at the onset of the δ^{13}C excursion, reflects a substitution of faunal constituents within the coral community that seems to relate to the Ireviken Event (Jeppsson 1987, 1997b). For the interpretation of the *Phaulactis* layer, the duration of its formation is very im-

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portant. Was it just a single event, e.g. deposited during a major storm or tsunami? Or does it represent a longer time period? And if so, how long?

Compared to the depositional environment of the underlying Lower Visby Formation, which was deposited below storm wave base (Samtleben et al. 1996), the water depth during the formation of the *Phaulactis* layer was lower, and deposition took place between fair weather and storm wave base. Unfortunately, no detailed sedimentological study has been carried out in this interval so far. However, it is evident that the *Phaulactis* layer does not represent a single event such as a storm layer (Fig. 2B). Most of the sediments surrounding the corals in the *Phaulactis* layer are micritic limestones and marls similar to overlying sediments of the Upper Visby Formation (Fig. 2); however, in some localities, thin (few cm) grainstone layers are observed documenting phases/events of enhanced water energy (Mitchel 1990).

The fact that most specimens of *Phaulactis* are abraded on the upper side, sometimes down to the columella, clearly documents phases of erosion. During these erosion phases, the lower parts of the calyces where washed out, eventually the corals tilted and most of them died shortly thereafter. If the time of non-deposition was long enough the calyces were subject to abrasion. This interplay of sedimentation and erosion phases results in a highly condensed interval. This is confirmed by the fact that the δ^{13}C values measured from brachiopod shells show an increase of ca. 1.5‰ within just a few dm of sediment (Fig. 1; Munnecke et al. 2003), which is a lot compared to the 2‰ increase in the overlying 10 m of sediment, and indicates overall condensed sedimentation during the deposition of the *Phaulactis* layer (cp. discussion in Cramer et al. 2015). In Nyrevsudde, which represents the most offshore section exposing the *Phaulactis* layer (Fig. 3), the layer is at least 1.6 m thick and shows a δ^{13}C increase of about 0.5‰ per metre (Munnecke et al. 2003). Assuming a more or less constant increase of the δ^{13}C values during the increasing limb of the Ireviken excursion, this indicates a high degree of condensation of the thin *Phaulactis* layer in the northeastern sections and less condensation in the deeper water settings towards the southwest. However, even in the deeper water setting in Nyrevsudde, the increase of the δ^{13}C values per meter of sediment is still about 2.5 times higher compared to the overlying part of the Upper Visby Formation (Munnecke et al. 2003) indicating that even here the depositional rates were comparatively low.

The palaeoenvironmental change represented by the *Phaulactis* layer resulted in an almost monospecific coral fauna. The scattered distribution of *P. angusta* coralla within the *Phaulactis* layer (Fig. 1B) indicates that not all corals within the *Phaulactis* layer grew contemporaneously. This aspect is most notable at the most distal (i.e., offshore) location Nyrevsudde 1, where the *Phaulactis* layer shows thickness of more than 1.6 m (Plate IIc in Munnecke et al. 2003). Obviously, the *Phaulactis* layer was formed during a highly dynamic period with rapid changes between phases of sediment accumulation and erosion. During this time, palaeoenvironmental conditions were suitable for *P. angusta* over a wide area (at least several hundreds of km^2). Speculating on a potential cause for the absence of other rugose coral species, the large size of *P. angusta* might give a clue. If the growth lines (Fig. 4) represent annual cycles, the growth rate of *P. angusta* was approximately two centimetres per year. The rapid growth rate and large size of coralla may have helped *P. angusta* survive short pulses of rapid sedimentation. Good preservation of, e.g. brachiopods in the Lower as well as in the Upper Visby Formation indicate sedimentation pulses embedding small fossils rather that continuous sedimentation which would led to disintegration of shells while exposed on the sea floor. Confirmation of this hypothesis requires additional research on the sedimentology of the *Phaulactis* layer and on the ontogeny of *P. angusta*.

Implications for sea-level development

So far, no sequence stratigraphic investigation has been carried out for the Visby to Högklint formations on Gotland, and the sea-level development is a matter of debate (see, e.g. discussion in Loydell 2008; Cramer & Munnecke 2008; Munnecke et al. 2010). For example, based on increased δ^{18}O values in conodonts, Lehnert et al. (2010) argue for a "Sheinwoodian glaciation", and consequently for a sea-level drop during the deposition of the Upper Visby Formation. In contrast, Calner et al. (2004, p. 117) provisionally attributed the Lower Visby Formation to a TST (transgressive systems tract) whereas the prograding Upper Visby Formation is interpreted as HST (highstand systems tract). Consequently, the *Phaulactis* layer would represent the time of maximum flooding (mfs; also called "maximum starvation interval"; Brett 1995), and thus should represent an interval characterised by condensed sedimentation with sediments enriched in resistant calcitic and phosphatic skeletons such as echinoderm plates and/or conodonts (e.g. Brett 1995; Schlager 2005). Such deposits usually develop under low water energy, and therefore the strong mechanical abrasion observed on the *Phaulactis* specimens contradicts a mfs, but Brett (1995) reports evidence for physical erosion as well as chemical dissolution also from such intervals of maximum starvation. However, at maximum marine flooding, sedimentation rates in offshore areas should be at a minimum (Brett 1995), and therefore the fact that the *Phaulactis* layer thickens in offshore direction (Munnecke et al. 2003) argues against a mfs.

Alternatively, the *Phaulactis* layer may represent an interval of falling sea level, or earliest transgression. This interpretation is supported by the fact that the late Llandovery in Laurentia is characterised by a major unconformity, called the "Late Llandovery Unconformity" after Murphy et al. (1979), which according to Cramer et al. (2006, p. 335) correlates with the onset of the Ireviken excursion. In addition, also the other two major Silurian positive δ^{13}C excursions (Mulde and Lau excursions), which are very similar to the Ireviken excursion (Munnecke et al. 2003), show the onset of the δ^{13}C excursion during falling stage systems tracts (FSSTs). On Gotland, this is recorded in the Gannarve Member (Mulde excursion; Samtleben et al. 2000), and in När Formation of the uppermost Hemse Group (Lau excursion; Samtleben et al. 2000; Eriksson & Calner 2008). Also in Poland the onsets of the Mulde and Lau excursions correspond to FSSTs (Kozłowski & Munnecke 2010; Jarochowska & Munnecke in press; Jarochowska et al. in press).

In summary, the sea-level history of the *Phaulactis* layer is not fully understood so far and requires a detailed sedimentological investigation.

Conclusions

- *P. angusta* had a liberosessile mode of life in their mature growth stages. The corals grew in an upright position part-

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ly embedded in a soft substrate, and are not preserved in life position.

- The growth form of P. angusta is controlled by sedimentological and ecological processes. A straight corallum is generated in times of undisturbed quiet water conditions. Curvature of the coralla is a response to sudden or continuous sinking into the sediment, caused by the increasing weight of the coral, or by increased water energy, followed by redirection of the growth vector.
- Flattening of one side of the corallites is a result of post mortem abrasion, indicating exposure to currents.
- Encrustation of the coralla by bryozoans occurred mostly during lifetime of the corals, whereas stromatoporoid overgrowth occurred mainly after tilting of the corallites and after death of the polyps. Borings into the coralla were produced post mortem.
- The Phaulactis layer represents a condensed interval characterised by repeated phases of sedimentation (and coral growth) and erosion, and does not represent a single sedimentological event. This condensed interval either represents a maximum flooding interval, or a falling stage systems tract.

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