PALAEOZOIC STROMATOPOROIDS AND THEIR SYMBIONTS: AN ATLAS OF IMAGES AND IDEAS FROM THE SILURIAN OF GOTLAND, SWEDEN

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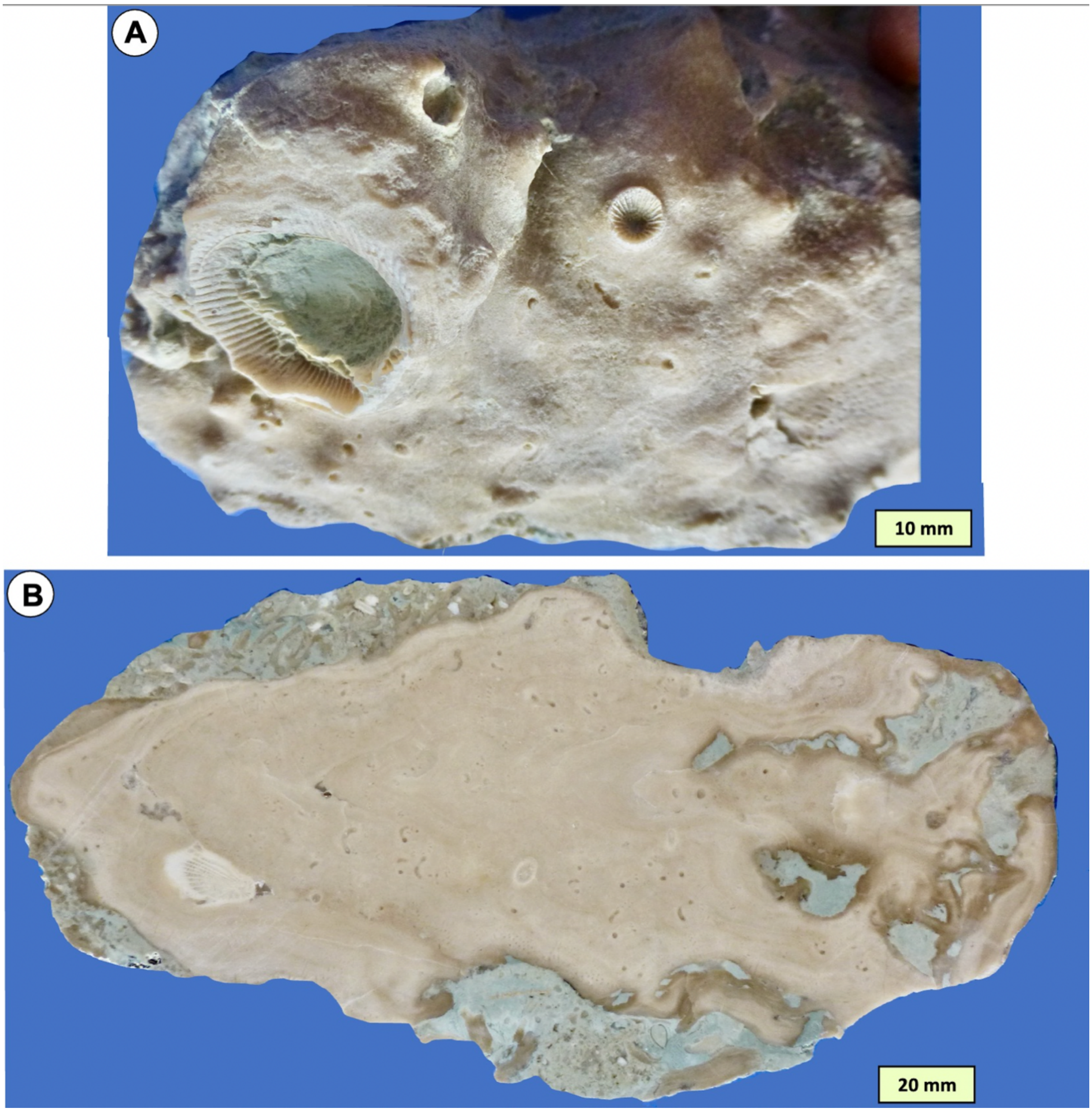

This document is a compendium of images intended as a palaeontological and sedimentological research tool

Front cover image (Fig. 1):
A) Surface view of stromatoporoid *"Stromatopora"* venukovi* with one large and two small rugose corals protruding from its surface; the corals are intergrown with the stromatoporoid. Below the big corals are small dark circles forming tiny craters on the stromatoporoid surface, that are the surface expression of spiral tubes visible in [B] which are also symbiotic with the stromatoporoid. At the surface the stromatoporoid formed a small mound around each spiral tube opening, indicating that the occupant of the tube protruded slightly from the stromatoporoid surface, so may have been using the stromatoporoid as a safe place to live. The same is presumably true for the corals, noting that corals are carnivorous animals in contrast to the presumed filter-feeding habit of stromatoporoid sponges. Note that in [A] the sample is presented upside down so the "face" can be seen.
B) Cut face of the reverse side of the sample shown in [A]; note that [A] displays only the left part of the sample. The stromatoporoid is cut obliquely (growth lines are faintly visible) making its growth form indistinct in detail, but overall is a domical form. The sample was collected in place and is illustrated the correct way up in [B], so we may presume that it was toppled onto its side and became entombed in that position, evidence that it may have lived in a relatively low energy environment and was affected by storms. On lower left the light-coloured ellipse is an oblique section through the interior of the large rugose coral shown in [A]. Many small intergrown spiral tubes of unknown nature occur in clusters through the stromatoporoid, visible as small darker wispy areas within the pink mass of stromatoporoid, and expressed as craters within mounds on the surface in [A]. However, not visible at this scale is that the entire stromatoporoid mass is indurated by yet another symbiont, a syringoporid tabulate. Later in this atlas is illustrated other specimens of this taxon in thin section, showing all these symbionts in detail.

Thus, this stromatoporoid specimen has: a) two taxa of rugose corals; b) one taxon of syringoporid tabulate; and c) at least one taxon of spiral tubes as symbionts within its structure, all living together while it was alive. Adhering to the side of the stromatoporoid is light-coloured sediment of a wackestone-packstone texture, containing debris of reef-associated fossils such as crinoids, brachiopods and stromatoporoid fragments, one of which is another stromatoporoid taxon.
Hemse Group, Ludlow, Silurian; sample collected in place, 1 m above the base of the Lower Biostrome, Kuppen 4, eastern Gotland, Sweden.
[*The genus name *"Stromatopora"* is in speech marks because the structure of this specimen aligns with the definition of a taxon called *Stromatopora venukovi* by Kei Mori in his 1970 monograph on stromatoporoids of Gotland; but since then the definition of *Stromatopora* was revised by Colin Stearn in 1993, so *S. venukovi* is not *Stromatopora*, but is a definite taxon and awaits formal identification.]

What does the "face" (Fig. 1A) mean to you?
This picture was accidental; I was trying to get a good photo angle on the sample to show the corals clearly, and only realised it was a face when I turned it around on the screen. But what a face! For me it expresses the tension that research is a serious business which occupies the mind and the emotions; and also the sense that geological materials are difficult to understand and might keep you awake at night.

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1. INTRODUCTION

1.1. Just what are stromatoporoids and why do they matter?

Stromatoporoids are the skeletal fossils of benthic organisms and are beautiful and intriguing fossils; they initiated as thin layers of calcium carbonate skeletal secretions on the ancient sea floor and accumulated layer-by-layer into sheets, domes, rounded bulbs, columns, branches, irregular masses, and could get very big, several metres across in some cases. In the appropriate circumstances they accumulated in enormous numbers to develop giant buildups on the shallow sea floors on which they lived. They seemed able to cope with a range of substrates and survived the effects of sedimentation; but they are rarely found in sandstones, and so seem to have been really limited to environments where the sediment was dominated by calcareous deposits (hence they form limestones).

For a long time stromatoporoids were thought allied to the Cnidaria (older name is coelenterates, the group of organisms that includes corals) and the older literature include cnidarian terms, such as coenosteum [no longer used] – a name for the entire fossil. However, in 1970 a landmark paper based on Caribbean material showed modern equivalents that are sponges; these were originally grouped together as Sclerosponges, but subsequent research showed that they are polyphyletic and thus the name of Sclerosponges is invalid and abandoned. Stromatoporoids are calcified sponges (actually formally called hypercalcified sponges because the skeleton comprises only calcium carbonate) and are the principal constructing organisms in the first major metazoan reef systems that dominated for about 100 million years in middle Palaeozoic shallow marine warm-water carbonate deposits around the world, between middle Ordovician and Late Devonian time (Wilson 1975, Chapter 4; Copper 2002). They almost totally died out, somewhat mysteriously, at the end of the Devonian Period, and thus almost completely disappeared from the rock record until the Triassic Period, when they bloomed again for some tens of millions of years. Nevertheless, their geological record is scarce in the most recent few tens of millions of years, yet there is a respectable suite of living examples that provide much insight into how the ancient ones may have lived. Stromatoporoids are the subject of detailed modern investigation in the 2015 volume of the Treatise on Invertebrate Palaeontology (Nestor 2015; Stearn 2015; Stock 2015; Webby 2015).

Stromatoporoids are important because their skeletal remains record events during their lives and permit a considerable insight into the nature and variations of the environments in which they lived. They are thus a valuable archive of palaeoenvironmental processes. Recent work documents key processes in their growth and diagenesis (Kershaw et al. 2018, 2021a,b) and reveals the following major points about Palaeozoic stromatoporoids:

Their growth is characterised by:

1. Relationship with substrate, both soft and consolidated substrates; stromatoporoids may be found on substrates bearing characteristics leading to the inference that they commonly grew on partly-lithified sediment, and are evidence of early sea-floor lithification in the times when they occur in the fossil record.

2. Growth history, including growth interruptions; stromatoporoids were commonly and repeatedly interrupted during growth, by such events as overturning and sedimentation, from which they commonly recovered; they thus record events of disturbance during their lives that give insight into the dynamic and fluctuating environments in which they lived.
3. Relationship between growth form and taxonomy; certain stromatoporoid taxa are limited to certain growth forms, and allow more detailed analysis of the relationship between their biology and the environments in which they lived.
4. Relationship with associated organisms, in particular symbionts; symbionts grew along with the stromatoporoids, and the interactions and comparisons between them provide valuable information to understand the lives of both the stromatoporoids and their associated organisms.

Their diagenesis is characterised by:

1. Consistently poor preservation in comparison with adjacent corals, brachiopods and bryozoans, but better preserved than adjacent molluscs. Molluscs are almost always recrystallised to low-magnesium calcite (LMC) from an original aragonite mineralogy, whereas corals are normally well-preserved due to their original LMC composition. Stromatoporoids may contain microdolomite rhombs, commonly interpreted to indicate they had originally high-magnesium calcite (HMC) skeletons that were altered to LMC during diagenesis. However, the relationship between dolomite rhombs and stromatoporoids is not fully consistent, so the nature of their original mineralogy remains unconfirmed.
2. Ubiquitous overprinting of the original skeleton by elongate club-shaped calcite crystals mostly orientated normal to the growth layers; this is fabric-retentive recrystallisation, through which all stromatoporoids are recrystallised to a greater or less extent, and the particular form of alteration that they display seems to be unique to stromatoporoids, but the controls on this are not understood
3. Evidence that they underwent alteration very early in diagenetic history, with clear indications that this began began just below the ancient seafloor, and possibly in the lower parts of specimens that had upper surfaces which were still alive on the seabed.

Stromatoporoids are quite variable in structure and largely fall into distinct consistent skeletal architectures that can be identified and given names. Their taxonomy uses these differences, but is a highly problematic taxonomy at all levels. There is an uncertain relationship between what have been called stromatoporoid species and actual biological species. In my opinion the best way to deal with this uncertainty is to regard each “species” as the lowest-level of taxonomic division achievable, but these may or may not be biological species; so I call them “lowest-level taxa” and I also do not try to combine them together into higher levels of families and orders because there is no evidence that these are biologically valid. I believe this is the most appropriate scientific approach to the understanding and application of their taxonomy, that strives to minimise assumptions about how the various taxa are defined and related. Nevertheless, a lot of very useful palaeobiological and palaeoecological information can be derived from the study of stromatoporoid taxonomy in combination with growth forms and sedimentary environments. There is extended discussion of this issue in a monograph on British Silurian stromatoporoids Kershaw et al. (2021b) that adopts the same approach to their taxonomy.

Some taxa included within the stromatoporoids lack what might be considered a key stromatoporoid structure: that is a combination of layers and holes, which is the origin of the term stromatoporoid (stroma = layer, poroid = holes). One of those non-consistent taxa is in this compendium; it is *Lophiostroma schmidti*, abbreviated to "Ls", and illustrated in many figures here; it's very nice, you'll like it. Ls has a solid skeleton of merged columns and lacks pores so the term stromatoporoid can be questionable, and indeed it is questioned as a valid stromatoporoid taxon in the 2015 volume of the Treatise on Invertebrate Palaeontology that deals with calcified sponges. However, in the images presented here I report for the first time some useful evidence that justifies the inclusion of Ls as a stromatoporoid, thus by inference a sponge, rather than it being any other kind of organism.

1.2. Rationale of this study

The recent studies cited earlier provide descriptions associated with the above summary features, but illustrated only part of the overall available image set. It is simply not possible to publish all images in peer-review literature, yet the published interpretations rely on the backdrop of a large number of specimens. Thus the purpose of this document is to present illustrations of that large number of samples, to show the full range of features, to thus provide an image toolbox to aid interpretation of data of stromatoporoid material in other deposits. Some new information is included here that has not been published elsewhere. Each image is described in a comprehensive caption. The images are of samples from the Silurian of Gotland, Sweden, which is one of the best places in the world to study stromatoporoids. The principles applied here can be used to examine stromatoporoids of all geological ages.

This is a non-peer-reviewed contribution to stromatoporoid science. The great value of non-peer review is that the author is free from the shackles of received opinion, and has power to express own views. However, as Spiderman once famously said, "with great power comes great responsibility", to ensure the errors are limited and views are fairly expressed. So, of course there can be other viewpoints on the material shown here; this work contains a lot of personal opinions that others may disagree with and is therefore presented as a discussion document. I aim for this atlas to be applied as a research tool for analysis of comparable material, so the information is intended to make you think about the processes rather than giving answers. Thus, I have broken away from strict scientific expression, opting instead for first person expression, to emphasise the personal approach to this study. However, please don't be lulled into a sense that this is scientifically less rigorous than peer-reviewed literature; each image in this presentation was carefully prepared. All the original rock samples illustrated here were collected and sectioned by me over many years, in many cases choosing specific orientations to show certain features. Some samples were repeatedly sectioned, and certain cases were prepared for thinner-than-normal sections to emphasise specific points. Each image has a caption that describes the content, and where appropriate discusses alternative interpretations; in many cases there are no clear answers, which makes this compendium all the more valuable because it encourages your inquisitive nature, thus to think carefully about the processes operating. There is a lot of information here that will hopefully have applications in other studies on stromatoporoids, and in my opinion a lot of the arguments also apply to corals, tabulates and heliolitids that occur in the same beds. Study of another hypercalcified sponge type, the chaetetids, may also benefit from the contents of this document.

You are thus encouraged to compare these images with your own material and consider the captions that in many cases offer alternative interpretations and unanswered questions; thus use this document to develop your own inspiration to interpret your material.

Updates: You can see from the front page and the filename that this is Version 01. However, fossils were living organisms and can grow, at least in numbers recorded (!); so there may be updated versions, which will be indicated in both the filename and front page. If you see any mistakes in this document, I would be most grateful if you could kindly email and tell me so I can correct them.

1.3. Big and small pictures; the format and approach of this atlas

Geologists try to see the "big picture", that is the general situation, the key trends, the large-scale overall understanding of the nature of the topic studied. The big picture is what we all strive for. However, it is an interesting and true observation that big pictures are made of lots of little pictures, which is another way to say that details matter. If the details contradict the general interpretation, then something is wrong. This atlas is about details; it encourages you to look at things carefully. It tries to go down to the deepest root of how stromatoporoids lived by looking at tiny features. Importantly, a principal outcome of my decades of detailed study is how the repeatability of small-scale features informs the big picture. From this came the realisation that stromatoporoids were capable of growing on substrates that are most reasonably interpreted as having been at least partially lithified when the stromatoporoids grew, with cascading implications for the general nature of the process of lithification and thus, potentially, the state of carbonate saturation of the oceans in the middle Palaeozoic. From Middle Ordovician through to end-Devonian, this can be observed and thus brings stromatoporoids into the fold as potential tools for studying ancient controls on ocean saturation and organisms' mineralisation, because they were abundant for such a long period of geological history. However, it is also clear that stromatoporoids commonly grew on unconsolidated sediment because of the common occurrence of well-preserved basal surfaces that could not have been cemented to the substrate. These organisms therefore had a flexible response to sea-floor conditions of substrate, which may have contributed to their successful development in the middle Palaeozoic Era. Therefore, in your search for the big picture, take account of the little pictures, they all have significance in one way or another.

1.4. Material presented in this document

I have selected case studies to show material and it is not exhaustive of the range of available samples, but is enough to show how much detail can be extracted from these fossils. The case studies are:

A) Marl below a thick biostrome, Hemse Group, middle Ludlow of Gotland.
B) The thick biostrome above that marl, Hemse Group, middle Ludlow of Gotland.

C) Some strange possible interactions between branching rugose and syringoporid corals without the presence of a stromatoporoid (weird) in another biostrome, Hemse Group, middle Ludlow of Gotland.
D) Some free-growing syringoporid corals not involved in intergrowths, Hemse Group, middle Ludlow of Gotland.
E) Some small complex stromatoporoids, Halla Fm, upper Wenlock, Gotland.
F) Additional information from the Upper Visby marls, lower Wenlock, Gotland.

1.5. Acknowledgments

Some samples in this document date back to my first PhD fieldwork on Gotland in August-September 1975, and their study is interwoven with the assistance and inspiration from others. Some of them have already passed to that great bioherm (or perhaps biostrome) in the sky; all helped the background this document in a diverse number of ways. I thank, in alphabetic order of surnames: Mike Bassett, Joan Bennett, Anne-Christine Da Silva, Al Fagerstrom, Christina Franzén, David Gowing, Li Guo, Susan Hak, Julian Harrigan, Emilia Jarochowska, Juwan Jeon, Lennart Jeppsson, Yue Li, Erik Karlkvist, Mike Keeling, Reginald Kershaw, Ruth Kershaw, Sven Laufeld, Ross McLean, Anders Martinsson, Axel Munnecke, Mari-Ann Mõtus, Björn Neumann, Arne Philip, Nicholas Palaus, Robert Riding, Olof Sandström, Carl Stock, Colin Stearn, Liza Timms, Barry Webby, Ron West, Graham Young. Also thanks to Kingston University, UK and the Nuffield Foundation for cathodoluminescence facility applied in a few of the images.

Although this document was inspired by the desire to spread knowledge of stromatoporoids for future studies, it is also a contribution to some UNESCO Projects:
IGCP591(2011-2016): The Early to Middle Palaeozoic Revolution;
IGCP596(2011-2015): Climate change and biodiversity patterns in the Mid-Palaeozoic (Early Devonian to Late Carboniferous);
IGCP700(2021-2026): Palaeozoic Carbonate Buildups in Southeast Asia.

1.6. Re-use of images

1.7. Some references

I will not burden you with extensive reading, but the information in these sources and in their reference lists contain the greater part of relevant literature.

Copper, P. 2002. Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages. Pp.181–238. *In* Kiessling, W., Flügel, E. & Golonka, J. (eds). *Phanerozoic Reef Patterns*, SEPM Special Publication No. 72.

Kershaw, S., Munnecke, A., Jarochowska, E. 2018. Understanding Palaeozoic stromatoporoid growth. *Earth Science Reviews*, **187**, 53–76.
Kershaw, S., Munnecke, A., Jarochowska, E., Young, G.A. 2021a. Palaeozoic stromatoporoid diagenesis: a synthesis. *Facies*, **67:20**, DOI: https://doi.org/10.1007/s10347-021-00628-x**.**
Kershaw, S., Da Silva, A-C., Sendino, C. 2021b. British Silurian stromatoporoids. Fauna, palaeobiology, and palaeogeographical significance. *Monograph of the Palaeontographical Society*, London: 1–92; pls 1–22. (Publ. No. 660, part of Vol. 175 for 2021.).
Mori, K. 1969. Stromatoporoids from the Silurian of Gotland, I. *Stockholm Contributions in Geology*, **19**, 1–100.
Mori, K. 1970. Stromatoporoids from the Silurian of Gotland, II. *Stockholm Contributions in Geology*, **22**, 1–152.
Nestor, H. 2015. Clathrodictyida: systematic descriptions. Pp. 755–768. *In* Selden, P.A. (Ed.). *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, liii +1223pp., 665 figs 42 tables.
Stearn, C.W. 2015. Stromatporellida, Stromatoporida, Syringostromatida, Amphiporida, and genera with uncertain affinities; systematic descriptions. Pp. 781–836. *In* Selden, P.A. (Ed.). *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vols 4–5. The University of Kansas Paleontological Institute, Lawrence, Kansas. liii+1223 pp., 665 figs, 42 tables.
Stock, C.W. 2015. Actinostromatida: systematic descriptions. Pp. 769–779. *In* Selden, P.A. (Ed.). *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vols 4–5. The University of Kansas Paleontological Institute, Lawrence, Kansas. liii+1223 pp., 665 figs, 42 tables.
Vinn, O., Wilson, M.A. 2021. Evolutionary history of colonial organisms as hosts and parasites. Pp99- In K. De Baets & J.W. Huntley (eds). *The Evolution and Fossil Record of Parasitism*, Topics in Geobiology 50, https://doi.org/10.1007/978-3-030-52233-9_4 . Springer.
Webby, B.D. 2015. Labechiida: systematic descriptions. Pp. 709–754. *In* Selden, P.A. (Ed.). *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vols 4–5. The University of Kansas Paleontological Institute, Lawrence, Kansas. liii+1223 pp., 665 figs, 42 tables.
Wilson, J.L. 1975. Carbonate Facies in Geologic History. Springer-Verlag, New York, Heidelberg, Berlin. 471 pp.

1.8. Abbreviations

Scattered through the captions and figures are abbreviations that are explained in the appropriate places, but are listed here in case you need them:

FRIC – Fabric-retentive irregular calcite (diagenetic alteration style of stromatoporoids)
CL – cathodoluminescence
PPL – plane-polarised light microscopy
XPL – cross-polarised light microscopy
VS* – Vertical section, that is: vertical in relation to the geometry of the stromatoporoid, and thus normal to the growth lines (in stromatoporoids another

word used is *longitudinal* instead of vertical; I prefer *vertical* because it is a shorter word!)
TS* – Transverse section, that is: transverse in relation to the geometry of the stromatoporoid, and thus parallel to the growth surface (in stromatoporoids another word used is *tangential* instead of transverse; I prefer *transverse* because it is a shorter word!)

*Because stromatoporoids are complexly curved fossils, a VS of the skeletal structure may include portions that are obliquely cut or even fully TS of the skeletal sructure, depending on the geometry of any particular sample; *vice versa* for TS sections that may include portions in VS.

Stromatoporoid taxa abbreviations: if you are bemused by taxonomic names and can't remember them, then help is at hand. I developed a short-form abbreviation for each taxon in this document; thankfully in this document there are only a few, they are:
Ll – *Labechia lepida*
Cm – *Clathrodictyon mohicanum*
Ls – *Lophiostroma schmidti*
Pc – *Petridiostroma convictum*
Ps – *Plectostroma scaniense*
Sb – *"Stromatopora" bekkeri*
Sv – *"Stromatopora" venukovi*
Sy – *Simplexodictyon yavorskyi*

2. FOSSILS ASSOCIATED WITH STROMATOPOROIDS

2.1. What is an associated fossil?

This section is included for clarification, so that the images in this compendium can be properly understood in relation to the fossils associated with stromatoporoids. Associated fossils are organisms that were alive approximately at the same time, although in palaeontology, the difficulty can be *proving* they were alive together, which is not always possible to demonstrate. Thus associated fossils include:

a) Organisms found in the same beds, close to each other, perhaps even touching, so at least they were subject to the same environmental constraints, whether or not they were alive at the same exact moment.
b) Skeletons of dead organisms (e.g. corals) that acted substrates upon which stromatoporoids encrusted, and conversely ones that encrusted dead stromatoporoids; in these cases the stromatoporoids were alive either after or before the associated fossil, respectively, but did not interact in a live-live relationship. Fossils found encrusting stromatoporoid surfaces are called epibionts. Stromatoporoids may be epibionts encrusting one another, so associated fossils may thus include other stromatoporoids of the same or different taxa.
c) Organisms that occur *within* the stromatoporoid structure *and* show interaction, so that the stromatoporoid and other organisms influenced each other while they were alive. There are some fossils found within stromatoporoids for which there is no evidence that they interacted, and these are post-mortem borings in stromatoporoid skeletons. Overall, these fossils are called endobionts.
d) Rarely, stromatoporoids show evidence of competition with other stromatoporoids and with tabulate and rugose corals; likely this is competition for space. Parasitism could be included here, although is a problematic area of interpretation. There are examples of interpreted competition affecting stromatoporoids in this document.

These categories impinge on the concept of symbiosis, considered next.

2.2. What is, and is not, a stromatoporoid symbiont?

Symbiosis has been given different meanings; an earlier idea is that the participants all benefit from the association; more modern ideas apply symbiosis more loosely to encompass all manner of relationships between participants, which thus might overlap with the four categories in the previous section. Also the nature of the relationship may play a part in terminology, with the rather simplistic traditional view that:

symbiosis = mutualism = mutual benefit
commensalism = one benefits but the other neither benefits nor loses
parasitism = one benefits while the other suffers.

This 3-fold grouping is somewhat outdated but the terms have value in modern research because they give some idea of success in the interacting participants. Also, in palaeontology it is not always possible to distinguish these 3 different cases, noting that we have only the mineralised skeletons and no soft parts to examine; thus determination of the type of relationship depends on interpretation, and it is common to find alternative interpretations. There is a very interesting discussion in a recent study by Vinn and Wilson (2021) which addresses the difficult issue of how to recognise whether a symbiont is a parasite or not.

As noted above, in palaeontology we also discriminate organisms that lived *within* others (endobionts) from organisms that lived *on* others (epibionts). Generally, for stromatoporoid study, epibionts grew after the host stromatoporoid had died, so there is a time gap between death of stromatoporoid and appearance of epibiont. There is evidence that some epibionts attached to the stromatoporoid while alive and then became embedded symbionts as the two grew together. Thus, many epibionts made use of the stromatoporoid as a place to settle and live to form a live-live relationship; others epibionts may have preferred to live on dead stromatoporoids, this not a live-live interaction because of the time difference of growth. Endobionts may also have appeared after stromatoporoid death, as in the case of bioeroding organisms that leave trace fossil borings in the margins of stromatoporoids. Conversely, stromatoporoids commonly encrusted the dead skeletons of other organisms, so this is also not a symbiosis, but it is interesting to note that some taxa of stromatoporoids are found more commonly encrusting other skeletons instead of sediment, so they showed a substrate preference, but because of the time gap between them symbiosis is probably not an appropriate term to describe this preference. In this atlas some of the stromatoporoid taxa show very obvious substrate preferences; and some live-live symbionts prominently occur between specific taxa implying but not proving a mutualistic biological relationship.

The broader definition of symbiosis stated above is probably a little too broad for the purposes of stromatoporoid study, so here symbionts are considered to be organisms that were alive at the same time, as far as it is possible to show that. However, their lives may not necessarily have precisely coincided, i.e. birth and death of each participant does not necessarily have to have been at the same time; they simply overlapped in parts of their lives. Such is clearly shown in stromatoporoid symbionts, and although cases of precise synchrony of life times can be found, they are uncommon; the normal case is to see symbionts and stromatoporoid hosts as having different life lengths. Symbionts are highly valuable in stromatoporoid study because they permit deeper insight into how these organisms lived and interacted; symbionts thus play a significant role in this compendium.

Below are 5 images showing what are considered symbionts and what are not, for the purposes of this study, illustrated by the relationship between the growth layering of the stromatoporoid adjacent to the symbiont.

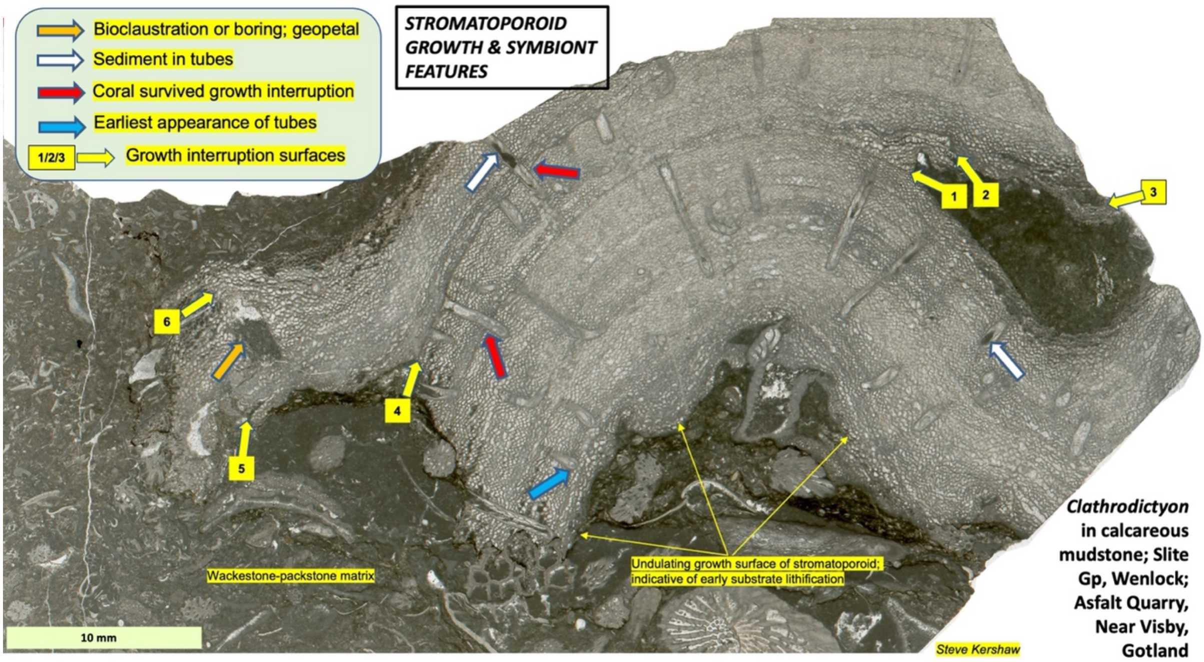

Fig. 2.1. VS whole thin section of a *Clathrodictyon* stromatoporoid containing evidence of the four aspects of stromatoporoid growth that are:

A) Growth on irregular substrate of packstone; the problem is how to explain the shape of this substrate feature, a simple option being to invoke early sea-floor lithification forming a solid surface over which the stromatoporoid grew. Irregular basal surfaces on stromatoporoids tightly fitting the substrate are very common and lead to the interpretation that the sea floor was commonly at least partially lithified to form a solid substrate for stromatoporoid growth. Perhaps the lithification occurred below the sediment surface, then currents stripped off the surface loose sediment to expose the lithified surface on which the stromatoroid encrusted; but the option is open that the lithification occurred on the sea floor directly. This has implications for the nature of the world oceans during the middle Palaeozoic time in relation to carbonate saturation and processes of lithification

B) Growth history of a stromatoporoid with several growth interruptions. The simplest interpretation is episodic sedimentation and recovery, but we cannot exclude the possibility that the stromatoporoid's own growth rate varied, and at a time when growth slowed, then sediment could settle. Note that many of the growth interruptions are evident at the stromatoporoid margin but cannot be traced into the interior; modern sponges are known to have ability to clear sediment and recover, so this option must be considered as an explanation for this specimen.

C) *Clathrodictyon* commonly has a low profile growth form; in this case growth interruption event #4 (a major event in the life of this particular specimen) is followed by continuing low profile growth, which may be evidence that it has a genetically low profile form, or it lived in a low-sedimentation-rate environment in this case that permitted low-profile development.

D) Intergrown corals started growing shortly after the stromatoporoid began. That fact is rather interesting; it implies that coral larvae were floating around in the water and chanced upon a friendly stromatoporoid surface on which they could settle and build a purposeful life. In this case the stromatoporoid had been growing for a short time before the corals found it. Other samples illustrated in this atlas show: a) the corals start right at the base of the stromatoporoid, indicating they began growth at the same time; b) the corals found the stromatoporoid at a later stage in its life, and allows the development of ideas that the event of a coral finding a stromatoporoid had a certain amount of luck involved, rather than being obligated to grow on the live stromatoporoid. It is also interesting that intergrown corals tend to be limited to only certain stromatoporoid taxa in an assemblage, and implies a real biological relationship (mutualism) rather than the coral simply using the stromatoporoid as a safe haven (commensalism); of course the corals may have just liked particular stromatoporoids, irrespective of whatever the stromatoporoids desired, so it could still be commensalism. Some corals were terminated at growth interruptions, others survived; perhaps the survivors had eaten a good lunch and protruded slightly higher on the surface of the stromatoporoid. Sediment in some of the coral tubes shows they were open after death and fine sediment trickled into the tubes. On left is a small cavity with geopetal; this may be a boring or a bioclaustration (symbiont organism lacking a shell and so no wall is visible); in this case there is no obvious way to prove whether or not it is a bioclaustration.

Slite Group, Lower Wenlock (Silurian); Asfalt Quarry, near Visby, Gotland. File: 1-HAK-121-AsfaltQ-Slite.

Fig. 2.2. Auloporid tabulate encrusted the upper surface of an unidentified stromatoporoid. The auloporid is not classed as symbiont because is an encruster on the presumed dead stromatoporoid surface. Yellow arrow shows a single rugose coral; it is not clear in this photo whether this coral is an encruster or is embedded as a symbiont – the sample needs to be sectioned to investigate this. Red arrow highlights a later compactional fracture during burial. Hemse group, Ludlow, Silurian; Kuppen, eastern Gotland. File: 2-KM7-Dec2019-Strom-EncrgAuloporid.

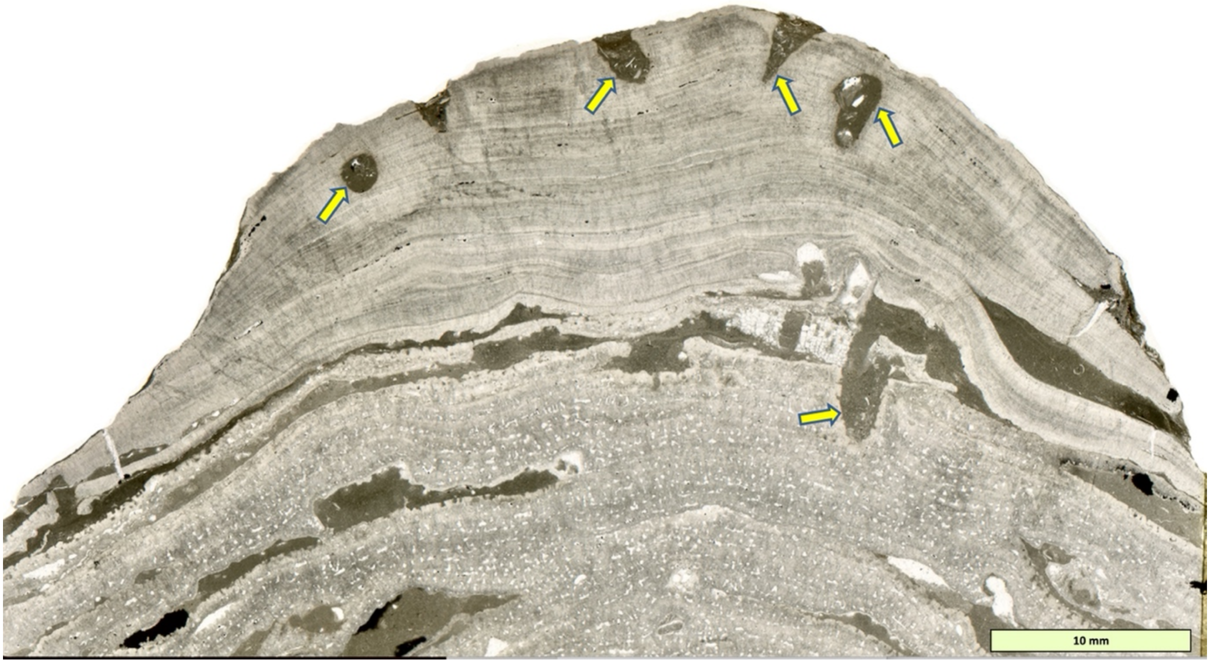

Fig. 2.3. Vertical thin section of two stromatoporoids; the lower one, with the porous-looking skeleton, is *Eostromatopora impexa*, one of my favourite stromatoporoids; the upper one, growing on the lower one, with the fine growth layering, is *Densastroma pexisum*, another one of my favourites [actually ALL stromatoporoids are my favourites]. Note the *Trypanites* borings (yellow arrows) that cut the stromatoporoid laminae and thus entered the stromatoporoids after they died. These are endobionts, but not symbiotic. Upper Visby Fm, Wenlock, Silurian; Ireviken 3, northwest Gotland. File: 3-I-10-SiDp-VS-B-WTS-Mod.

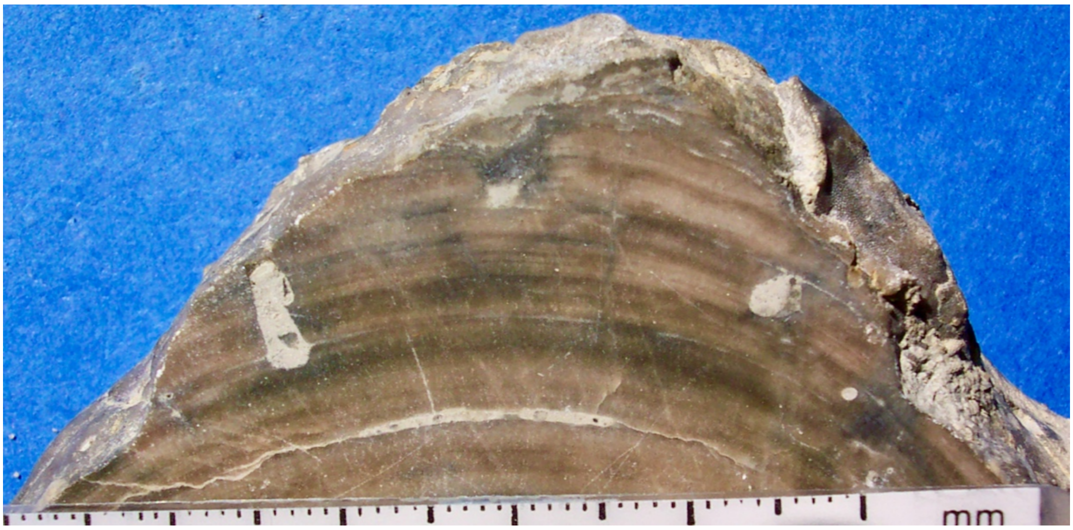

Fig. 2.4. Another nice example of *Densastroma pexisum*, with three endobiont boring *Trypanites* (with grey micrite fill) post-dating the stromatoporoid; the central boring has a geopetal fabric. These borings cleanly cut the stromatoporoid laminae, that show no reaction to the presence of the borers, so are interpreted as drilled after stromatoporoid death, so non-symbiotic. Upper Visby Fm, Wenlock, Silurian; Ireviken 3, northwest Gotland. File: 4-I-07-Dp-01-Mod.

Fig. 2.5. Rare case of what appears to be a *Trypanites* boring (yellow arrow) but the stromatoporoid (again *Densastroma pexisum*) shows a reaction to its presence by the down-bending of growth layering against the endobiont; this is good evidence the endobiont was growing in a live stromatoporoid. The endobiont has no mineralised wall, so this is a definite bioclaustration. There is

no information to allow interpretation of whether the endobiont is the same organism as the *Trypanites* borings in Figs 2.3 and 2.4. You might also note that this stromatoporoid sample has a growth history whereby the lower part was turned on its side and is presented in this picture in largely TS view; then it recovered and grew up again, and was affected by a growth interruption event that also terminated the bioclaustration; the stromatoporoid recovered and continued growing to the top with minor interruption events indicated by small sediment interdigitations in the edges. It is reasonable to suppose the stromatoporoid finally died from a large sediment influx from which it could not recover, perhaps during a storm. Upper Visby Fm, Wenlock, Silurian; Ireviken 3, northwest Gotland. File: 5-I-17A-1200-Mod.

2.3. Some features of stromatoporoid diagenesis

In order to understand the symbiont-stromatoporoid relationship fully, you need to know the basics of stromatoporoid diagenesis. The most visually impressive feature is the development of vertically-orientated (i.e. normal to the stromatoporoid growth lines, so orientation follows the growth lines) irregular, commonly club-shaped, crystals of diagenetic calcite that overprints the layered calcareous skeleton. Note that this feature was first described by Smosna (1984), then Rush and Chafetz (1990), and was subsequently cited and further illustrated by Kershaw et al. (2021a) who recognised this is fabric-retentive recrystallisation because the stromatoporoid skeleton can be seen overprinted by the alteration fabrics; it was named Fabric-Retentive Irregular Calcite (FRIC) by Kershaw et al. (2021a). FRIC can be seen in thin sections that are ground thin enough to see the shape of the overprinted crystals, but is normally barely visible in stromatoporoid thin sections made for taxonomy because they are much thicker (50-80 microns) than the normal 30 microns used in microscopy. For this atlas, numerous samples were deliberately ground thin to demonstrate the FRIC; if the thin section is ground down to around 20 microns or less, the stromatoporoid skeletal structure becomes almost invisible in plane polarised light (PPL) because of the recrystallisation, and FRIC can be seen well in thin PPL sections. However, FRIC shows its full glory in cross-polarised light (XPL) because of varying orientations of crystals in different positions of extinction.

The images below show examples of FRIC in two different stromatoporoid taxa that are closely physically associated; their FRIC has different details but in both cases it is clearly FRIC.

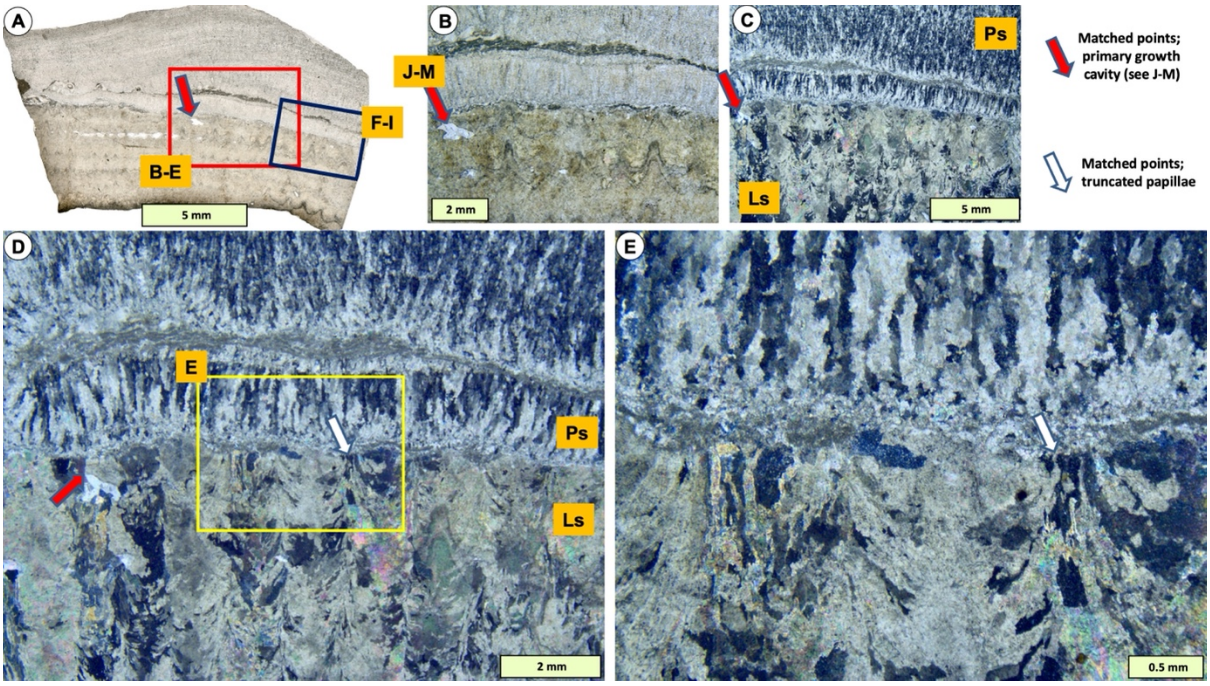

Fig. 2.6 [a set of 3 separate figures; this is the first of the three].
Fig. 2.6A-E. Diagenetic characters of stromatoporoids. **A)** Whole thin section scan in vertical section, comprising two stromatoporoid taxa: lower half is *Lophiostroma schmidti* (Ls in some photos), overgrown by *Plectostroma scaniense* (Ps in some photos). **B-C)** PPL [B] and XPL [C] emphasising fabric-retentive irregular calcite (FRIC) in XPL, that has a different structure in the two taxa. **D-E)** XPL enlargements emphasising differences of FRIC in Ls and Ps. White arrow shows the top surface of Ls is truncated, presumably by erosion, before Ps encrusted. In [A-E] a growth interruption, with a thin layer of micrite, is shown within the Ps; in [A-D] the red arrow points to a growth cavity, illustrated in detail in [J-M]; a line of growth cavities is seen in the white areas on left of sample in [A]. Hemse Group, Ludlow, Silurian; Kuppen 4, eastern Gotland. File: K4b1-i-ii-Ls-Ps-Pc-Rug-VS-01.

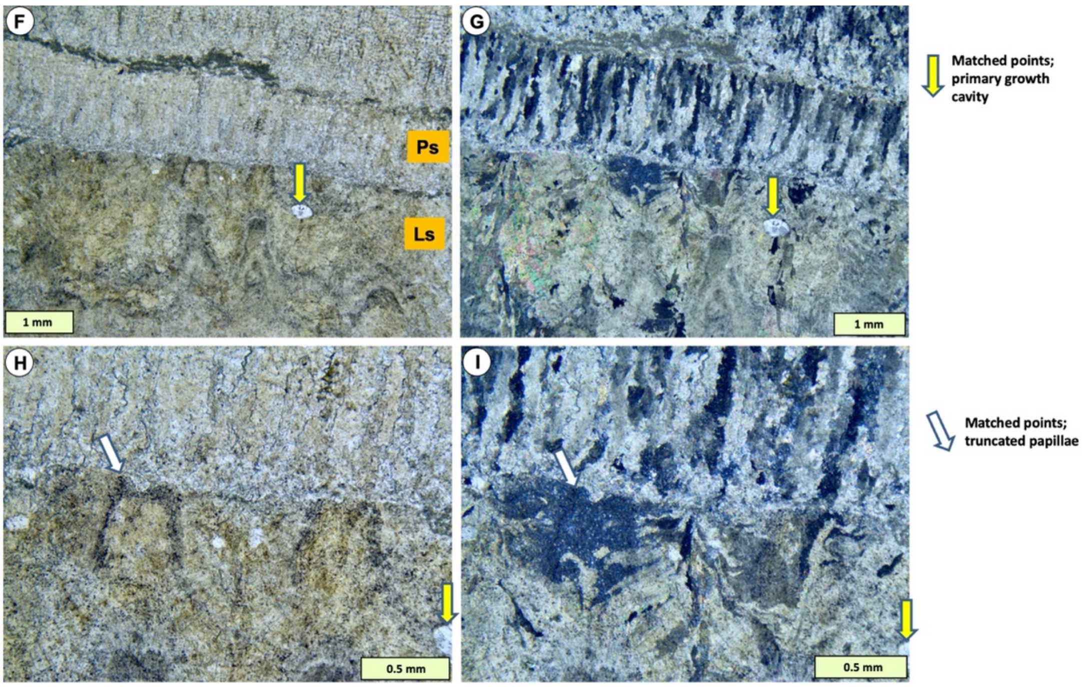

Fig. 2.6F-I. More PPL and XPL views in vertical section of Ls and Ps, showing the eroded top of Ls. Yellow arrow indicates a small growth cavity in Ls, filled with sparite; white arrow highlights the eroded top of Ls before Ps grew. Note the difference in FRIC between Ls and Ps, and how the FRIC does not cross the edge of each taxon (white arrow in[I]), which shows that the structure of the stromatoporoid

is somehow intimately associated with its diagenesis, although the reasons are currently obscure. File: K4b1-i-ii-Ls-Ps-Pc-Rug-VS-02.

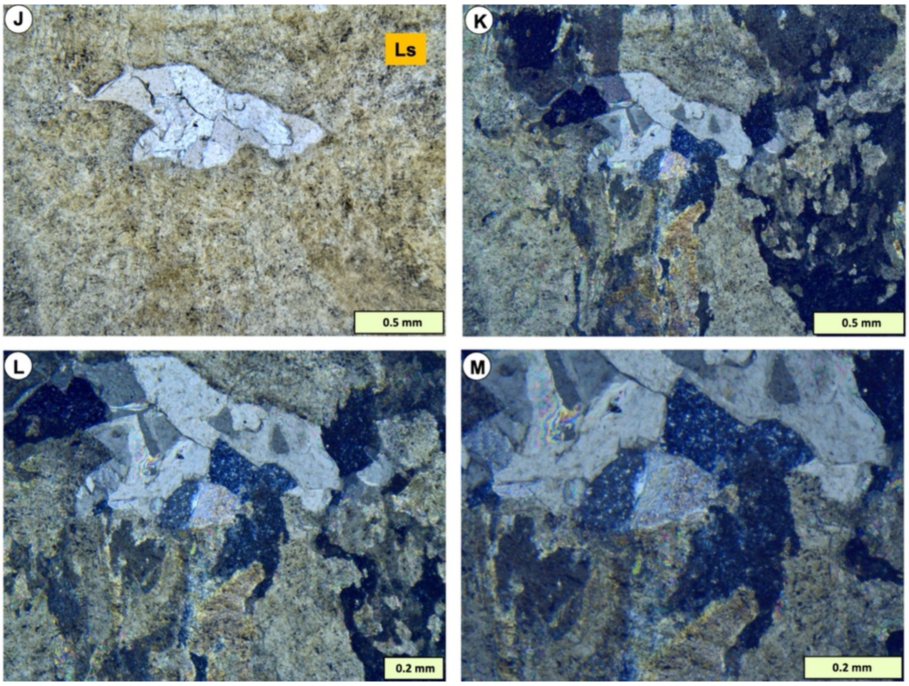

Fig. 2.6J-M. PPL [J] and XPL [K-M] of the growth cavity marked by red arrow in [D]. Critically this cavity has FRIC crystals passing into the cement fill directly from the stromatoporoid skeleton. This fabric, in other samples, was explored by Kershaw et al. (2021a) who interpreted it to indicate that the recrystallisation of the stromatoporoid occurred while the growth cavity was still open, and thus happened very early in diagenesis, perhaps when the stromatoporoid was just below the sea floor, possibly even when its growth surface (at the top of the specimen) was still alive. The features in these four photos has not been described before for Ls, but it has been shown in other stromatoporoids (Kershaw et al. 2021a); this is presented as evidence that Ls should be confirmed as an accepted stromatoporoid because its diagenetic behaviour is consistent with other stromatoporoids, noting that this style of fibrous FRIC seems to be unique to stromatoporoids. File: K4b1-i-ii-Ls-Ps-Pc-Rug-VS-03.

3. STROMATOPOROIDS AND THEIR SYMBIONTS FROM CALCAREOUS MUDSTONES BELOW STROMATOPOROID BIOSTROMES, HEMSE GROUP (LUDLOW, SILURIAN), AT KUPPEN, EASTERN GOTLAND, SWEDEN

3.1. Biostromal setting

These famous biostromes crop out across the eastern Gotland peninsula and may be the most stromatoporoid-rich deposits on Earth; they are examined in many papers by many authors (see reference list and references cited within). The images in this section include samples sectioned several times in parallel slices, and all these are included here, to show variation through a specimen.

Note that you will see repetition through the range of images because stromatoporoids commonly show a similar set of features that help to understand the pattern of their growth and their relationships with symbionts. Nevertheless, each sample is unique; all stromatoporoids are individual with their own growth history and life experiences recorded in their skeletons, showing the fluid state of the precise conditions in which they lived. Understanding the commonality and differences between similar samples allows us to develop patterns and identify departures from patterns.

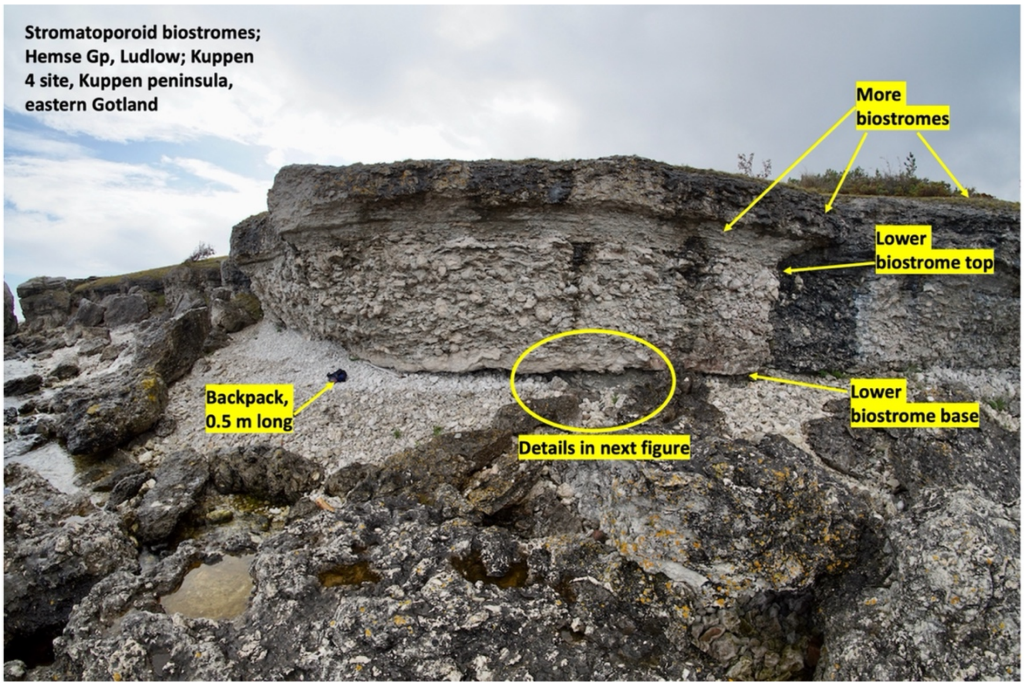

Fig. 3.1. View of stromatoporoid biostromes at Kuppen. This shows a small part of an extensive stacked biostrome system across eastern Gotland, containing tightly packed masses of stromatoporoids. There must be billions of them altogether, a truly extraordinary accumulation. This picture shows the best exposed location of Kuppen, where there is one thick biostrome, called informally the Lower Biostrome, overlain by more biostromes, a middle and upper biostrome, which are themselves further overlain by more biostromes that are less well defined on the surface outcrops. The Lower Biostrome was the subject of a focussed palaeobiological and taxonomic study (Kershaw 1990) which showed that one taxon, *Clathrodictyon mohicanum*, abbreviated to Cm, makes up ca. 40% of the sample of about 500 specimens. Cm figures importantly in the following images. Two other taxa, *Plectostroma scaniense*, abbreviated to Ps, and *"Stromatopora" bekkeri*, abbreviated to Sb, are also prominent. Altogether, 16 taxa of stromatoporoids are known from these biostromes. Hemse Group, Ludlow, Silurian; Kuppen 4, eastern Gotland, Sweden. File: K4Marl-Field01. [This site is my most favourite place in the world; I would like to be buried under the beach next to the backpack, so when the cliff collapses my remains will merge with the stromatoporoids, then I can roam the heavens with an understanding surpassing all I knew on Earth and hope to see the answers to the two most vexing questions about stromatoporoids: a) what was their original

mineralogy and how does this relate to their peculiar diagenetic fabric?; and b) how to resolve the currently-applied taxonomic system? (In my opinion that system is quite erroneous and obfuscates clear understanding of their biology)]

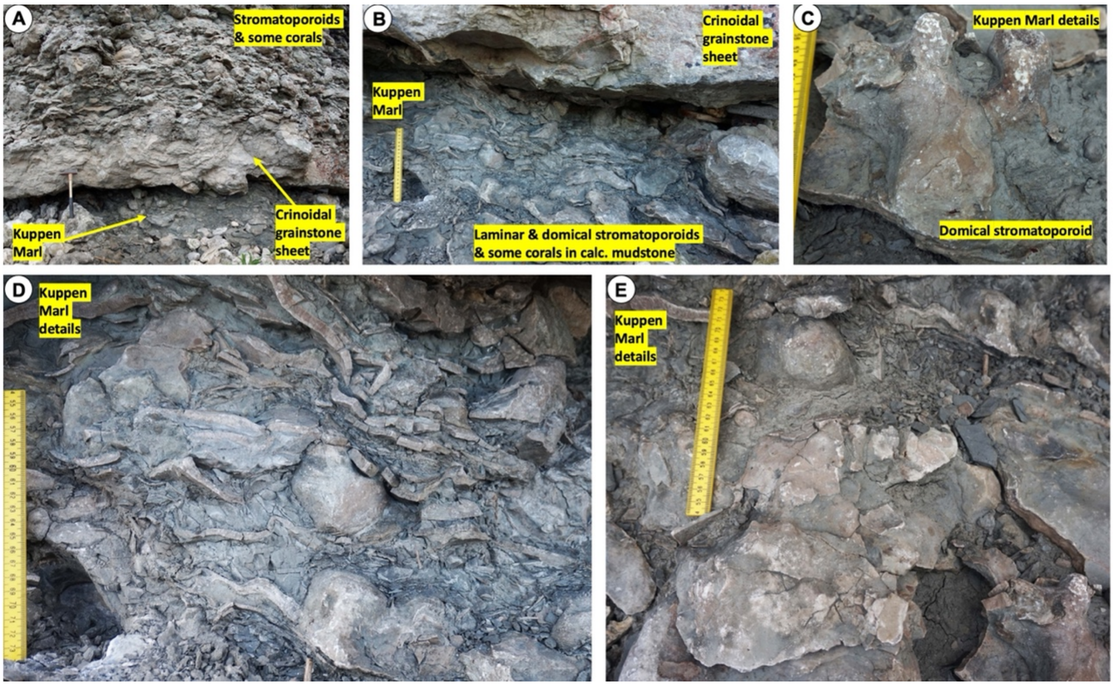

Fig. 3.2. Details of "Kuppen Marl" beneath Lower Biostrome at Kuppen, showing stromatoporoids in calcareous mudstone; visible are numerous laminar and domical stromatoporoids, that are different taxa. Hemse Group, Ludlow, Silurian; Kuppen 4, eastern Gotland, Sweden. File: K4Marl-Field02.

<u>3.2. The "Kuppen Marl", calcareous mudstone beneath the Lower Biostrome at Kuppen.</u>

This informally-named unit, here called Kuppen Marl for convenience, is a poorly exposed calcareous mudstone at beach level directly below the crinoidal grainstone that itself forms the basal unit of the Kuppen Lower Biostrome visible in Figs 3.1 and 3.2. Although the Kuppen Marl is briefly mentioned in prior publication (Kershaw et al. 2018) below is the first display of stromatoporoids from the Kuppen Marl. The Kuppen Marl is not always exposed, it depends on the storminess of the Baltic Sea and thus whether the beach debris is piled against the base of the cliff or not at the time you visit. It is most reliably exposed at Kuppen 4 locality (Fig. 3.2), and nearly all the samples displayed here come from the small exposure at the top of the Kuppen Marl from Kuppen 4. Some samples come from the Kuppen Marl beneath the biostrome at the much less accessible Kuppen 3 locality about 100 m southeast from Kuppen 4.

The images in this section demonstrate that the small sample of stromatoporoids in the Kuppen Marl includes six of the same taxa as found in the Lower Biostrome directly above it. These taxa are (with abbreviations): *Clathrodictyon mohicanum* (Cm), *Plectostroma scaniense* (Ps), *Petridiostroma convictum*, (Pc), *Lophiostroma schmidti* (Ls), *"Stromatopora" bekkeri* (Sb) and *"Stromatopora" venukovi* (Sv); the latter two are unresolved taxa so the published names are used here pending revision. There may be other taxa present in the Kuppen Marl, but need a bigger sample.

Furthermore, these six taxa have the same symbionts associated with the same stromatoporoid taxa as in the Lower Biostrome above. However, there are some differences; there are branching tabulates and rare finger-like stromatoporoids in the Kuppen Marl; although finger-like columns may be found in stromatoporoids in the Lower Biostrome they are more robust than the ones in the Kuppen Marl, thus an indication that Kuppen Marl stromatoporoids responded to lower energy conditions. Nevertheless, please note that the Lower Biostrome was also relatively lower energy, and not the higher energy interpretation that was made in earlier years. You can read the details of these features in papers cited; here you see illustration of the range of displayed characters of the stromatoporoids and their symbionts.

Study of the Kuppen Marl stromatoporoids is tremendously interesting regarding symbionts because the stromatoporoid-symbiont relationship in the Kuppen Marl is the same as in the overlying Lower Biostrome (that lacks the clay and is almost pure carbonate). This similarity is the best indication I have seen that the nature of the symbiotic relationships may be primarily biological rather than environmental; i.e. instead of the prior explanation that the symbionts used the stromatoporoids as a safe haven from storms, there is the additional complication that the participants interacted biologically. It is rather difficult to determine whether both environmental and biological drivers played a part in each example, or whether one or the other was the dominant control. Also the nature of any biological relationship is difficult to define.

The best example of symbiosis in the Kuppen Biostromes in general is the common stromatoporoid taxon *Petridiostroma convictum* (Pc) which is always accompanied by syringoporid tabulates that possess identical structure in all specimens and are likely to have been one taxon; in contrast almost no other stromatoporoids contain the syringoporids, despite the stromatoporoids being pressed cheek-by-jowl in these extraordinary limestone beds. Pc also commonly has branching rugose coral symbionts within it, and most of them are one taxon of coral that was called *Tryplasma flexuosum* by Kershaw (1987) based on identifications provided by a coral specialist at that time. That coral taxon is, however, now considered an unsafe identification, noting that the Ludlow rugose corals of Gotland in general require taxonomic revision, and it may instead be *Aphyllum* (Ross McLean, personal communication, December 2021). Nevertheless, this coral is clearly recognisable as a distinct taxon, so there is certainly a repeated presence of it in Pc, which may be due to a biological relationship. However, it remains possible that the corals are commensal (i.e., the coral benefits but the stromatoporoid neither gains nor benefits), but preferred this particular stromatoporoid taxon. It is rather curious that although Pc always contains syringoporids, it doesn’t always have rugose corals. In samples where all three fossils co-occur, they are distinctive and extraordinarily beautiful in thin section.

Amazingly, and tantalizingly, in the Middle Biostrome at Kuppen, I found three samples of the rugose coral and syringoporids growing amongst each other in a patch, yet no stromatoporoid was involved. In these samples, the relationship between the syringoporids and rugose coral looks very similar to their arrangement as symbionts in Pc, leading to the remarkable prospect that the corals themselves were interacting biologically, regardless of the stromatoporoid; but with only three small samples (that are illustrated in this atlas), this remains an avenue for further study to confirm or deny a possible biological relationship.

Another example is the stromatoporoid taxon "*Stromatopora" venukovi* (Sv) which not only has syringoporids, but also has spiral tubes and rugose corals; yet spiral tubes don't occur in *Petridiostroma convictum* (Pc), so there must have been something special between spiral tubes and Sv. Not all specimens of Sv have symbionts, but where they occur you can get four fossils for the price of one!

The figures in this section are all from the Kuppen Marl.

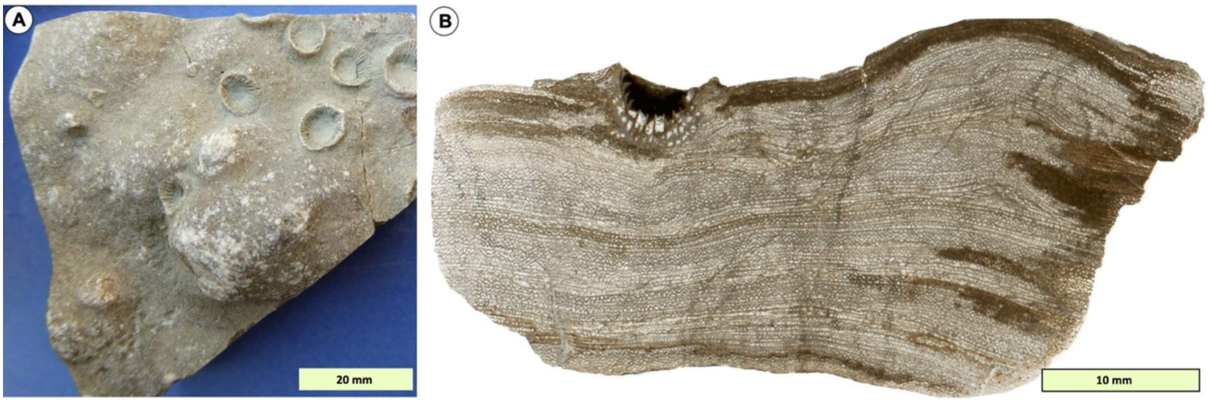

Fig. 3.3. Upper surface [A] and vertical thin section [B] views of *Clathrodictyon mohicanum* (Cm) with unidentified symbiotic rugose coral. [A] shows the rugosans are clustered in the right part of the sample, characteristic of branched corals emanating from a single corallite deep within the sample; thus the vertical section in [B] cuts through a single corallite that is orientated obliquely, so the section cuts the margins of the branching cluster. The dark areas on right and top of the Cm are zones where the stromatoporoid skeleton is partially silicified. File: 1-K4Mud01-Cm-Rugs-Silic.

Fig. 3.4. Vertical section of *Clathrodictyon mohicanum* (Cm) with unidentified symbiotic rugose corals. The origin of left coral is likely out of the plane of section but clearly it started near the base of the stromatoporoid, indicating the coral larvae discovered the stromatoporoid early in its history. The right coral, however, shows it grew horizontally at 90 degrees to the plane of section, and thus may have attached during a growth interruption event; but no growth interruption is evidence in the stromatoporoid at that level, so the coral's presence may be explained by invasive activity of the coral on the living surface of the stromatoporoid at that location. However, if this is true, then the stromatoporoid was not particularly affected, but grew easily around the coral, closing around the coral; such may indicate the flexibility and recoverability of the stromatoporoid to disturbance. Thus this could be a commensal relationship. The coral passed out of the plane of section, so we will never know whether the coral's calyx was protruding above the stromatoporoid surface and thus survived or not. However the left coral seems to have been open at the stromatoporoid surface, so we may surmise they died at the same time, quite possibly due to a sufficiently large sediment depositional event that overwhelmed the sediment-clearing mechanisms of both coral and sponge. File: K4Mud04-Cm-Rugs.

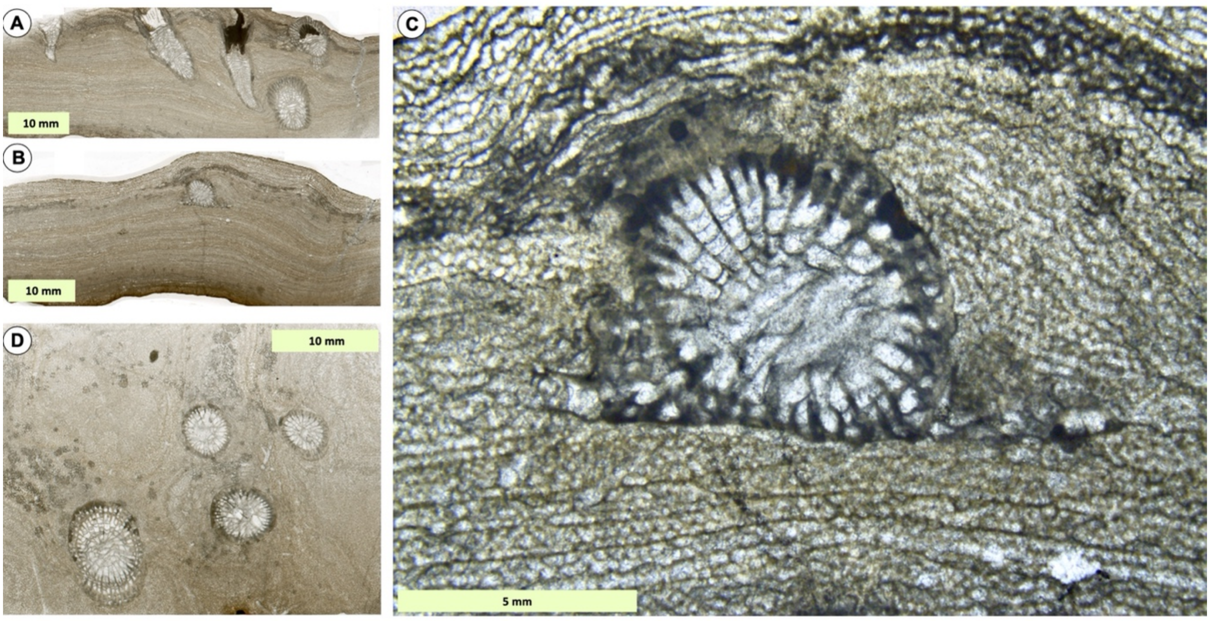

Fig. 3.5. A-C) Vertical sections and transverse section **[D]** of *Clathrodictyon mohicanum* (Cm) with unidentified symbiotic rugose corals, showing similar features to Fig. 3.4. In [C] the coral base is minutely irregular and irregularity extends off to the right edge of the picture at the same level; this may be micro-pressure solution within the stromatoporoid, obfuscating clear view of the nature of contact between the stromatoporoid and coral. File: K4Mud07-Cm-Rugs.

Fig. 3.6. Vertical section of *Clathrodictyon mohicanum* (Cm) with unidentified symbiotic rugose corals, showing similar features to Figs 3.4. & 3.5. However there is a weak indication of growth interruption coinciding with the base of the right rugose coral. This stromatoporoid specimen also has three small tubes [left] that the Cm reacted to, indicating live symbiotic growth, although the nature of these tubes is not known. Note that all three tubes have geopetal infills that are upside down to the growth orientation of the stromatoporoid, evidence that the stromatoporoid was turned over, possibly after death. Note that the growth form of Cm is known as low profile, laminar to low domical form from previous studies, thus subject to easy overturning by storm action; no previous studies have shown Cm to be an encrusting form, so it is presumed to have lived unattached on the substrate. File: K4Mud09-Cm-Rugs.

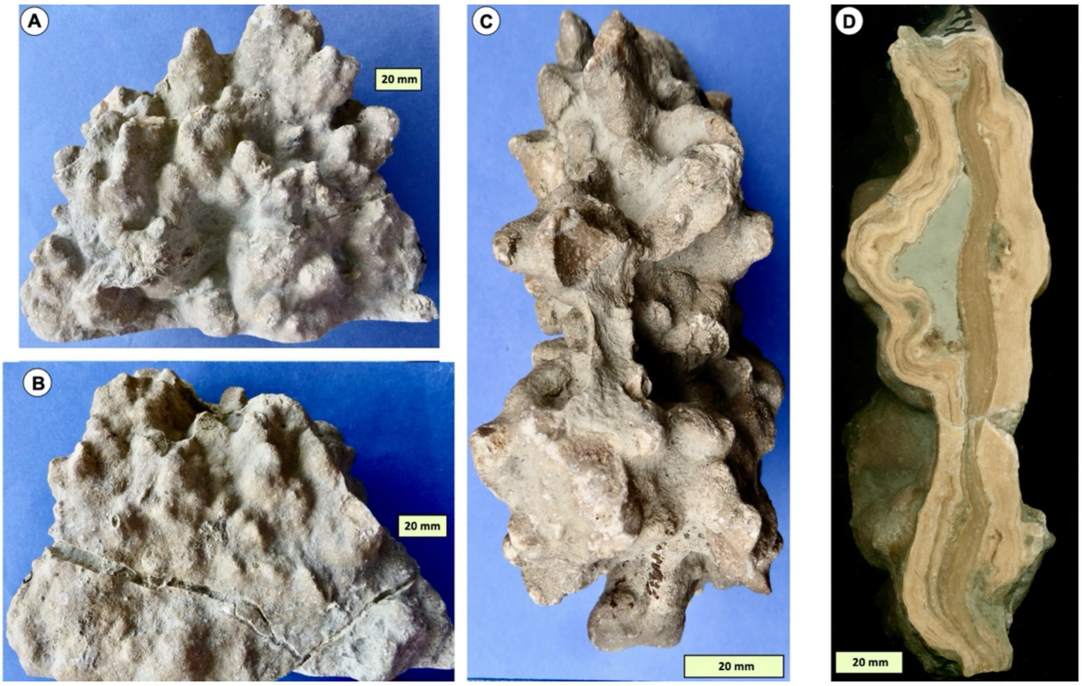

Fig. 3.7. [a set of 3 separate figures]. A-D) A remarkable example of an alveolitid tabulate with abundant growth protrusions, encrusted onto a laminar stromatoporoid of taxon *Clathrodictyon mohicanum* (Cm). **A-B)** Side views of exterior of the alveolitid with copious growth protrusions that are not all vertically orientate; rather they somewhat "fan out" so that some are oblique to the top edge of the sample. **C)** Top view looking down on the sample so both sides illustrated in [A] and [B] can be seen; the protrusions are thus orientated upwards towards you. **D)** View of the bottom of the sample, cut flat to reveal its interior, so that the original base is not seen; in fact that base was not preserved in the original sample, The laminar Cm is the darker brown stripe in the centre of the specimen, and the cream-coloured outer bands are the alveolitid. The grey patch is fine-grained carbonate sediment (micrite). Thin section views are shown in [E] and [F], where more is revealed. File: K4Mud12-Cm-Alveo-01.

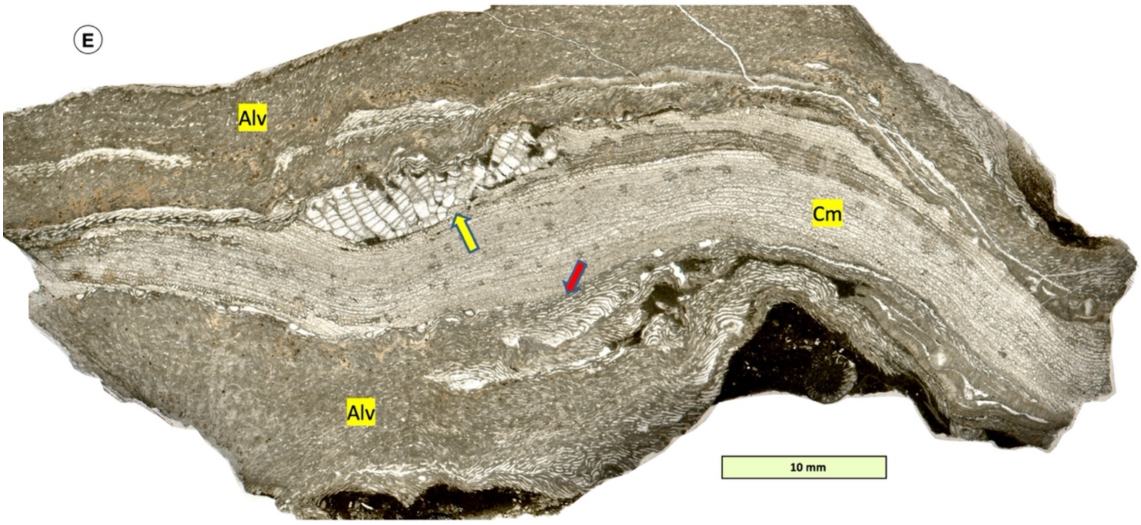

Fig. 3.7E. Thin section of the lower part of the sample illustrated in Fig. 3.7D. Cm commonly forms a laminar growth shape and in this case the base of the specimen is shown by the red arrow and its top by the yellow arrow, which is encrusted by a favositid tabulate. However, the alveolitid encrusts both the base and top of the Cm, and Figs 3.7A-B indicate an upward growth, so the view in this photo is

parallel to the sea bed; therefore the Cm must have been orientated as a vertical plate on the sea floor and was encased by alveolitid growth. This sequence can be explained if the Cm grew as a laminar form, unattached on the sea bed as is typical of that taxon, and was then hit by a storm and broke up, with pieces thrown about and this piece became stuck vertically in the mud; then the storm ended and all went quiet, and stayed quiet for a long time, to allow the alveolitid to encrust and encase it. If this is true then it means the Kuppen Marl environment was not necessarily low energy all the time, but was affected by occasional storms; the same is true for the overlying Lower Biostrome, the difference being that the Lower Biostrome lacks clay. Overall the environment of both the Kuppen Marl and the Lower Biostrome may have been similar, of low energy, and the difference is there was episodic influx of clay at the time of the Kuppen Marl. This discussion is not published anywhere else, and adds to the well-established recognition that stromatoporoids were capable of tolerating clay-bearing sediment substrates. File: K4Mud12-Cm-Alveo-02.

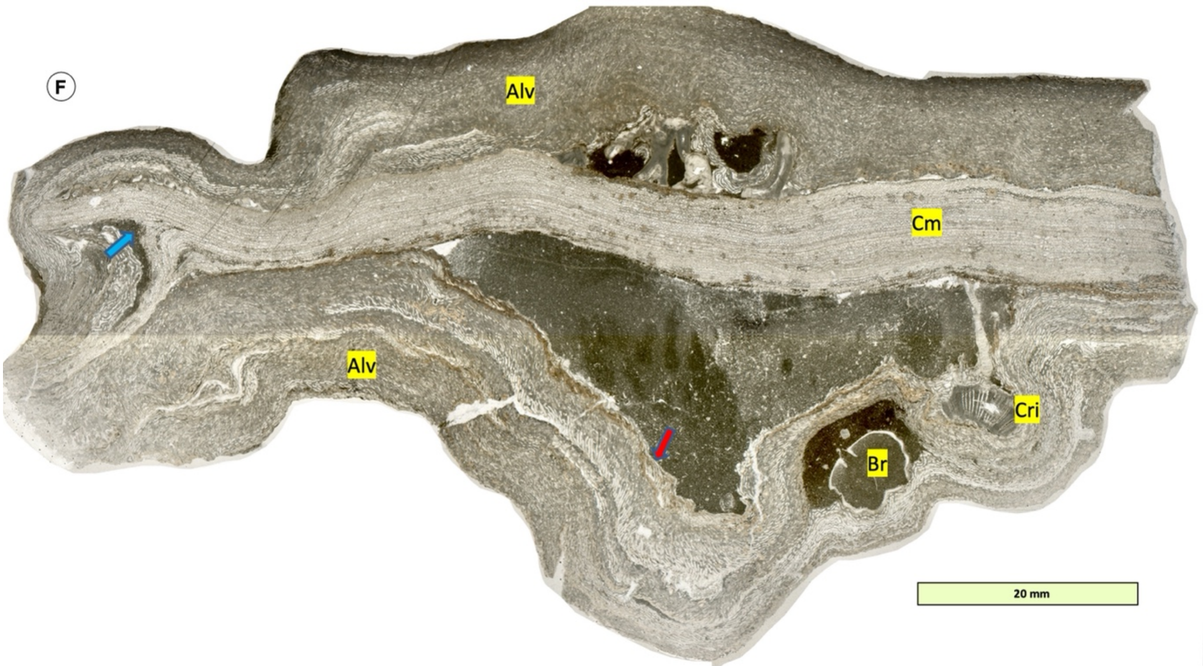

Fig. 3.7F. Thin section of the upper part of the sample illustrated in Fig. 3.7D, the caption to Fig. 3.7E applies here. Note the crinoid holdfast encrusting the Cm, upper centre of the photo (not labelled) and also lower right (Cri). Blue arrow highlights a growth interruption event affecting the margin of Cm while it was alive. Presence of a brachiopod (Br) in micrite correlates with a growth interruption surface in the alveolitid. Red arrow highlights that the alveolitid is not in complete contact with the Cm, so there is a large area below the Cm that is occupied by micrite, and the base of the alveolitid is very irregular; also there is indication that the micrite has a geopetal character. How can this geometry of components be explained? Options depend on whether the large area of micrite was present before the alveolitid grew or came in later to fill a primary cavity; but if there was a primary cavity, then why did it occur, noting that the alveolitid is in contact with the Cm elsewhere? It seems easier to imagine that the large area of micrite was there before the alveolitid grew and was thus partially lithified and eroded, presenting an irregular substrate that the alveolitid simply encrusted. The apparent geopetal character of the micrite might be explained if there was dissolution of sediment and infilling with calcite; this is known elsewhere in the Kuppen biostromes. So, we have a workable hypothesis that completely explains this sample, but that doesn't mean it is correct; can you think of alternatives, and how would you investigate it further? File: K4Mud12-Cm-Alveo-03.

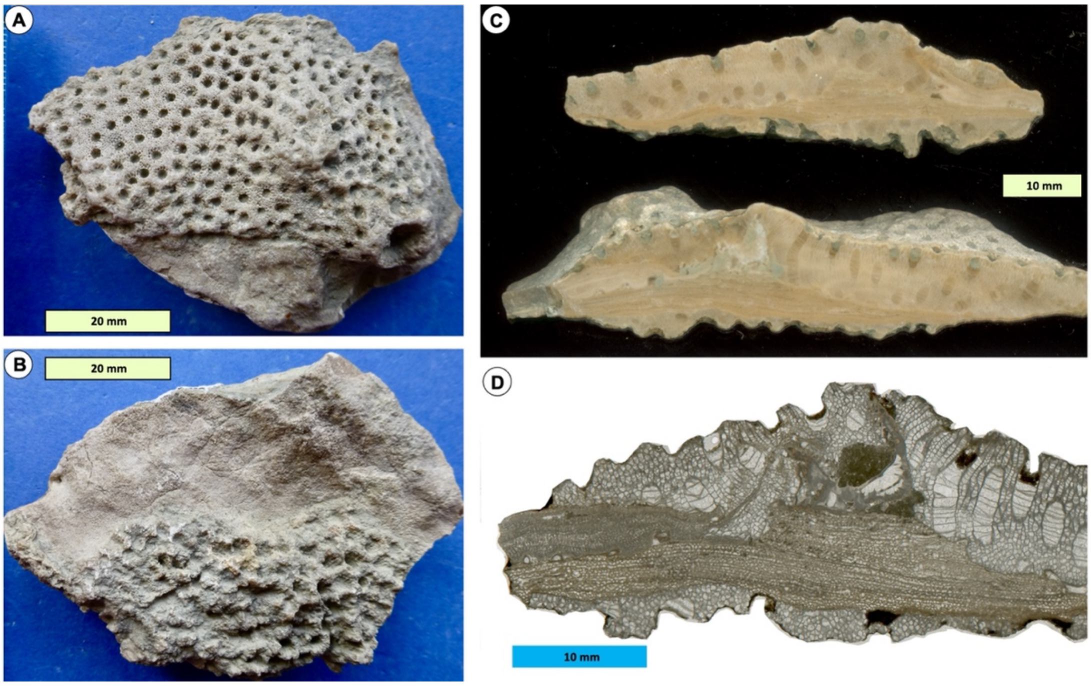

Fig. 3.8. Heliolitid encrusting both base and top of stromatoporoid *Clathrodictyon mohicanum* (Cm). **A)** top view; **B)** basal view; **C)** side views of hand specimen after cutting; **D)** whole thin section in VS. this is not a symbiotic relationship, but shows the eroded nature of the Cm sample, another indication that high energy affected the Kuppen Marl, despite its clay-rich, low-energy facies appearance. The fact that the heliolitid encrusted both the top and base of the Cm is an indication of overturning during the history of this specimen, consistent with other samples in this suite from the Kuppen Marl. File: 8-K4Mud16-Cm-Heliolitid.

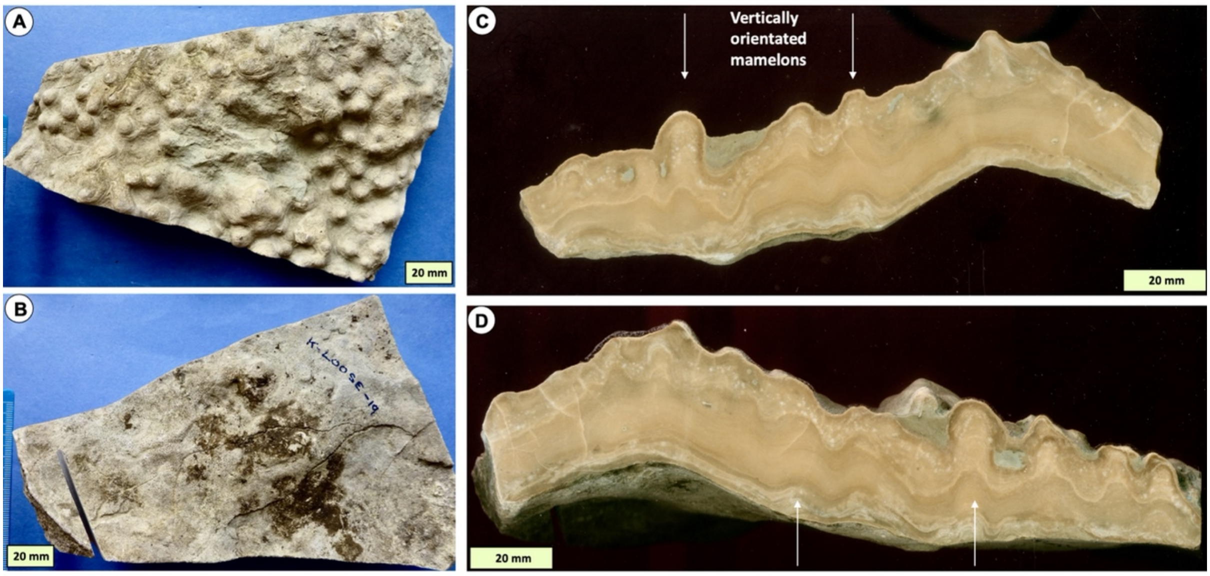

Fig. 3.9. Part of a laminar stromatoporoid *Clathrodictyon mohicanum* (Cm, which is normally laminar to low domical in the Hemse Group biostromes). **A)** Top view; **B)** basal view; **C-D)** side views. This specimen has columnar outgrowths that are orientated vertically despite the slightly changing slope of the stromatoporoid that must have followed the undulating shape of its substrate. The columns are thus geotropic, and is another example of geotropism in this taxon, in addition to the several samples recorded in previous work for the Lower Biostrome (Kershaw 1990). Geotropism in stromatoporoids is a potential indicator of a phototropic response in stromatoporoids, which is a fascinating idea that has been around for a long time, but lacks any evidence in the skeletal structure of stromatoporoids,

except perhaps the geotropic form of columnar outgrowths. In the Lower Biostrome most samples of Cm do not have this columnar structure, the laminae are just gently curved, following the shape of the substrate. So it is very peculiar to find a few specimens with prominent geotropic columns, and might indicate growth in shaded areas of the biostrome surface. The Kuppen Marl, with its higher clay content, may have been in more turbid water, with reduced light levels; but if that is true then why do the other specimens of Cm in this study lack the geotropic columns? It is a mystery that requires a focused study to try to work out the causes of the geotropic columns. File: 9-KLoose19-K4Mud-Cm-Mamelons.

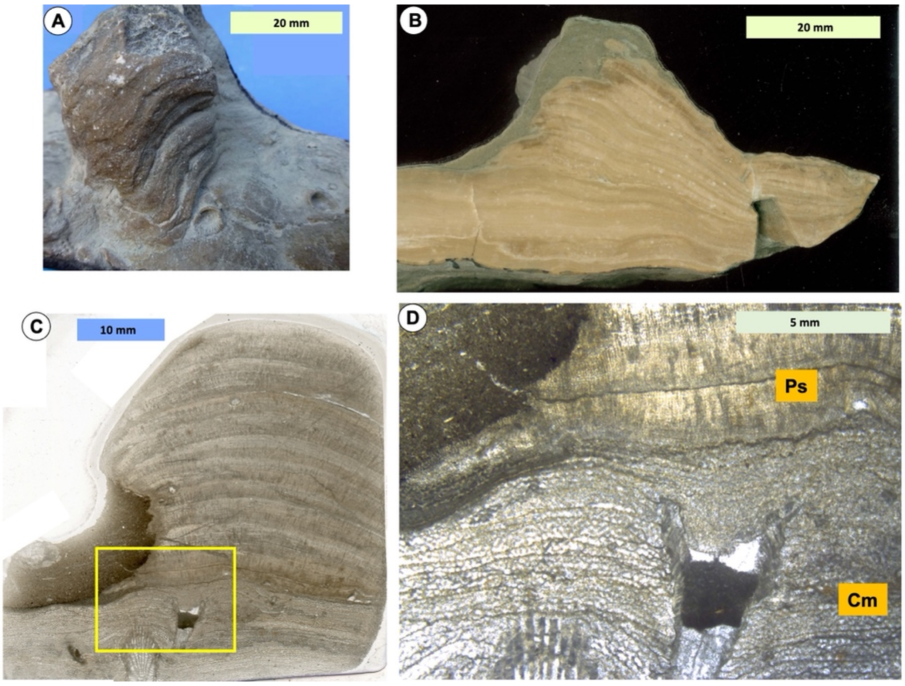

Fig. 3.10. *Clathrodictyon mohicanum* (Cm) encrusted by *Plectostroma scaniense* (Ps). Cm has two rugose coral symbionts, and the right hand one looks like it was killed by sedimentation [D], and then its top overgrown by more Cm growth before the Cm was finally terminated. Does this mean that Cm was able to deal with a sedimentation event, while the rugose coral was not? I guess we will have to go back to the Silurian in a time machine to try to see it happening. The overgrowing Ps also shows an interesting margin, that terminates with an undulating line of interdigitation with sediment, but only on the left side; the right side is a smooth margin of overlapping laminae. Was the interdigitated margin *caused* by episodic sedimentation, or did the margin naturally grow like that, then sediment came later? If it was caused by sedimentation, why does the right side show smooth overlapping laminae? Another mystery. File: 10-KM12-Cm-Ps.

VIEW 1

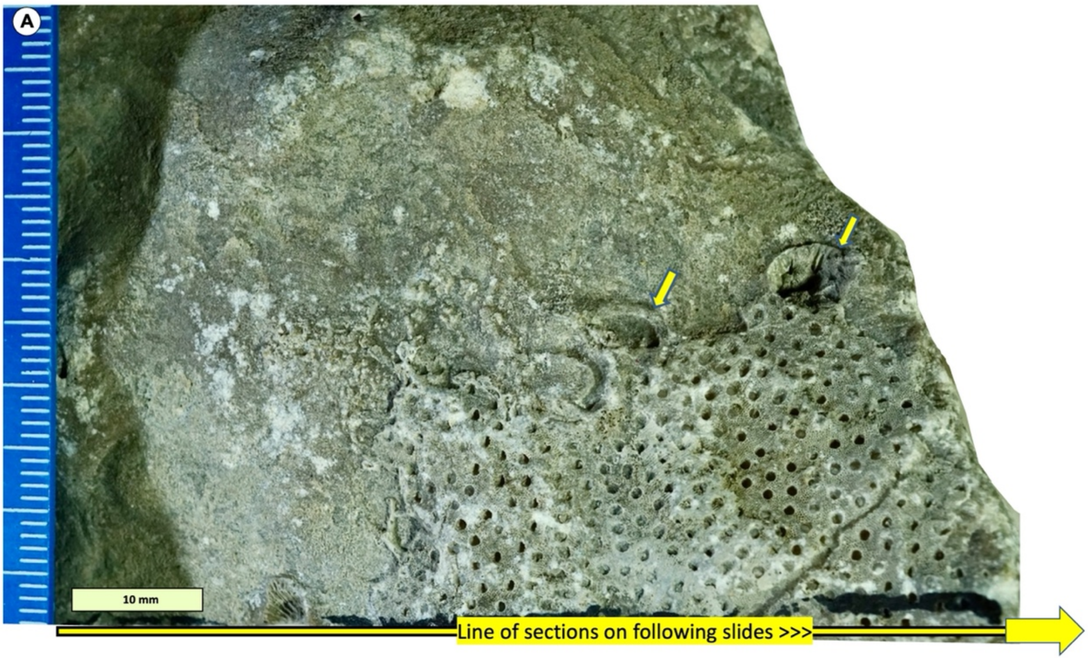

Fig. 3.11 [a set of 12 figures using several thin sections and divided into 5 subsets, each called a "View" and numbered top left in each figure].
Fig. 3.11-View1. Top view of a laminar form of *Clathrodictyon mohicanum* (Cm) with two symbiotic rugose corals (yellow arrows), and an encrusting heliolitid, which is of course not a symbiont because it came later, and grew partly over the rugose corals.
File: 11-KM14-Cm-HeliolitidEncr-01.

VIEW 2

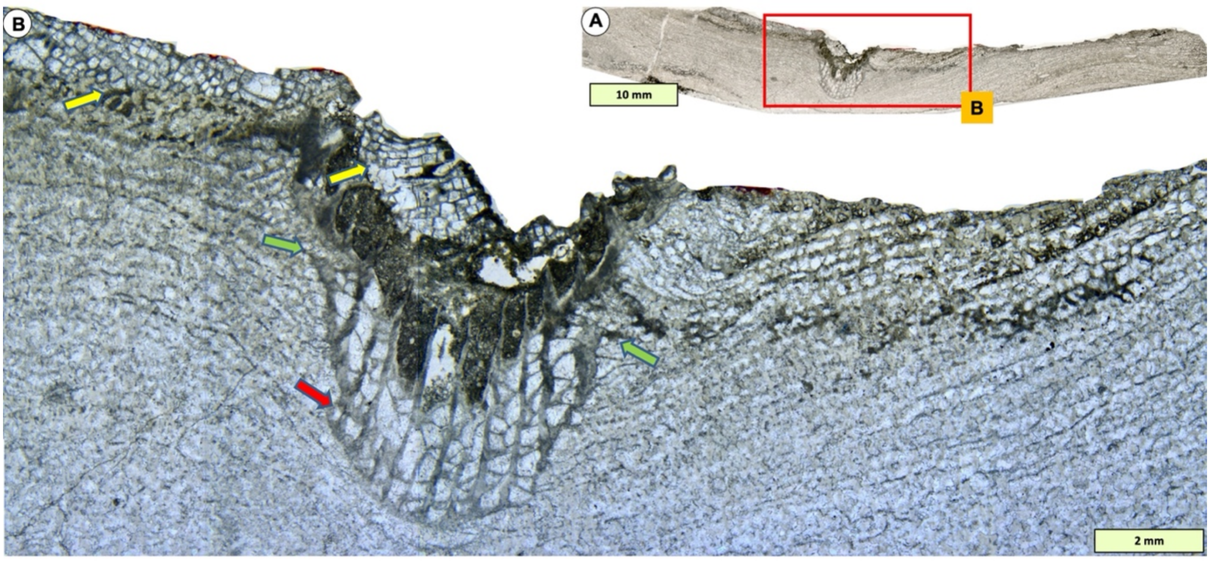

Fig. 3.11-View2A-B. Vertical section. This interesting sample shows the lower part of the rugose coral is bordered by downbending laminae of *Clathrodictyon mohicanum* (Cm), but above the level of the green arrows the Cm laminae bend upwards to meet the coral. This change may be interpreted to indicate a relative increase in coral growth rate. Later, a thin layer of micritic sediment (dark, yellow arrows) in many places between the top of the Cm and the base of the encrusting heliolitid (partly overgrowing the rugosan), shows the heliolitid developed after death of Cm and rugosan. File: 12-KM14-Cm-HeliolitidEncr-02.

VIEW 2

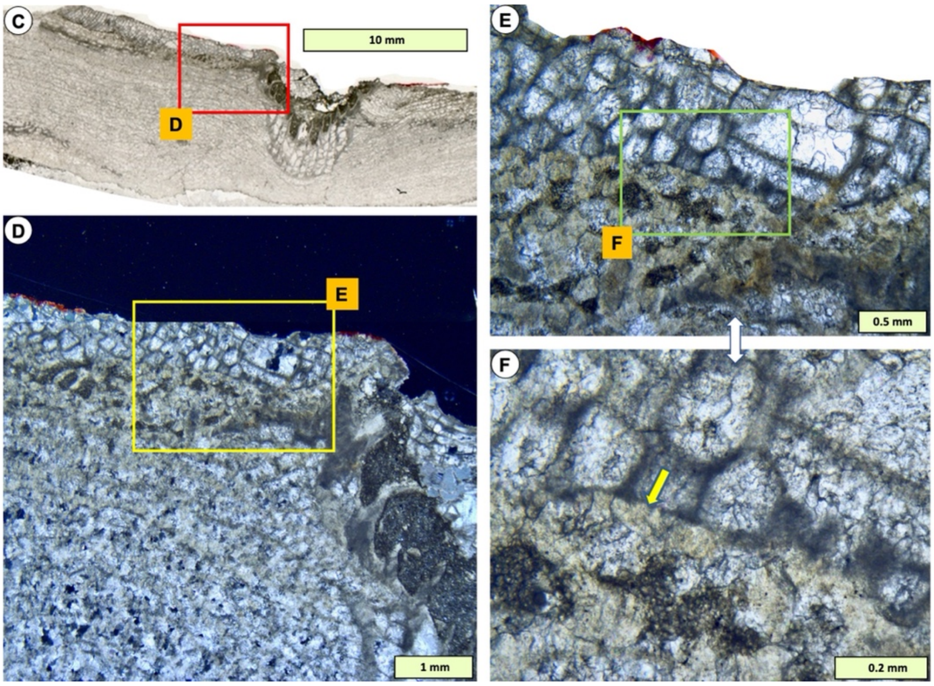

Fig. 3.11-View2C-F. Vertical section. Continuing from the previous figure, these photos show that not all the heliolitid was on micrite, some of it was directly on the stromatoporoid surface. In [F] there seems to be no wall to the basal coenenchymal tube, which may be evidence of the stromatoporoid surface lacking soft tissue and thus dead when the heliolitid encrusted. File: 13-KM14-Cm-HeliolitidEncr-03.

VIEW 2

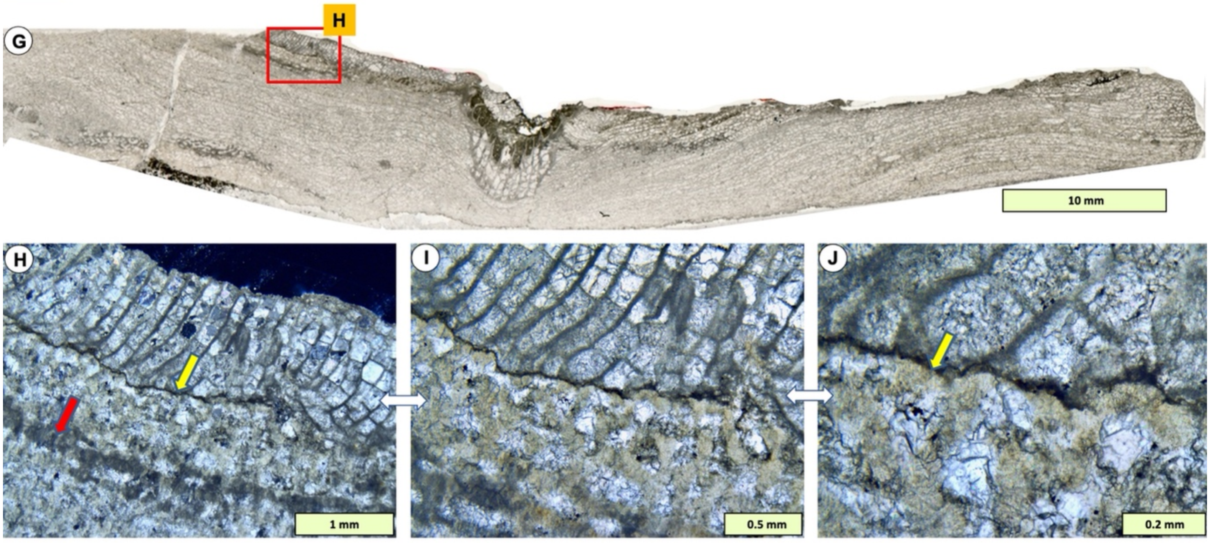

Fig. 3.11-View2G-J. Vertical section. This part of the sample shows the contact between the stromatoporoid and heliolitid is very irregular, with a very fine dark line between the two, interpreted here as a pressure solution line (stylolite, yellow arrow). Red arrow shows a thin layer of micritic sediment as a growth interruption layer, that the stromatoporoid recovered from. File: 14-KM14-Cm-HeliolitidEncr-04.

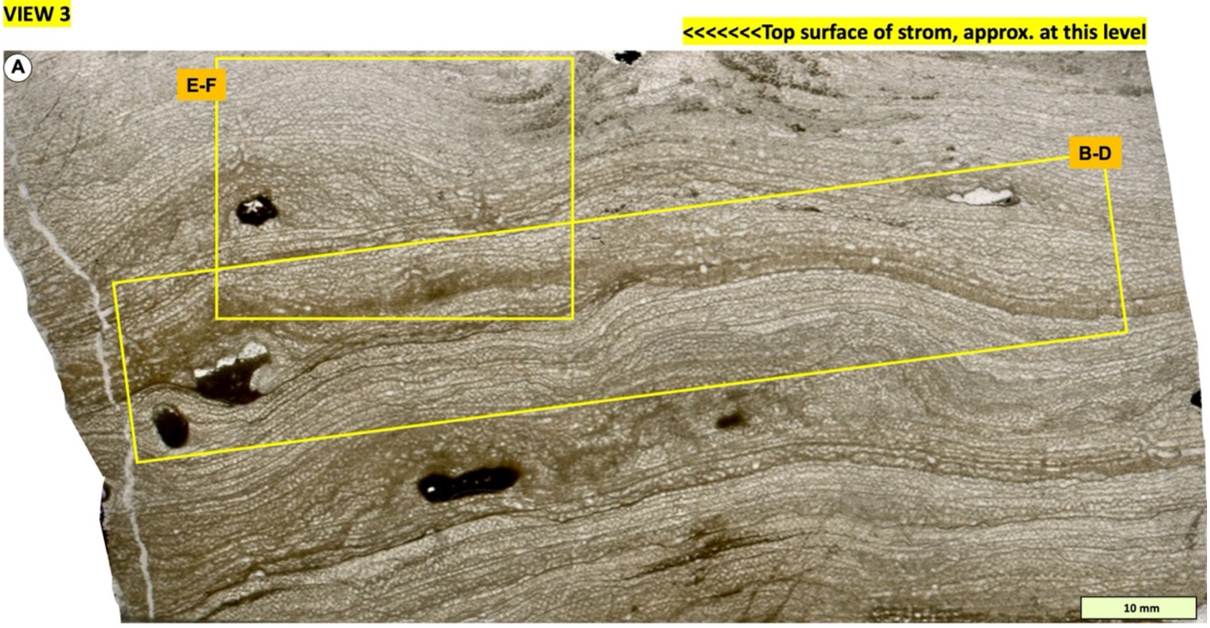

Fig. 3.11-View3A. *Clathrodictyon mohicanum* vertical whole thin section below the surface illustrated in Views 1 & 2. Note undulating layering and growth interruption surfaces indicated by dark lines. The several cavities show associated disturbance of stromatoporoid laminae, which may indicate these were bioclaustrations; whatever, they were open to the surface because of geopetal sediment infills. File: 15-KM14-Cm-HeliolitidEncr-05.

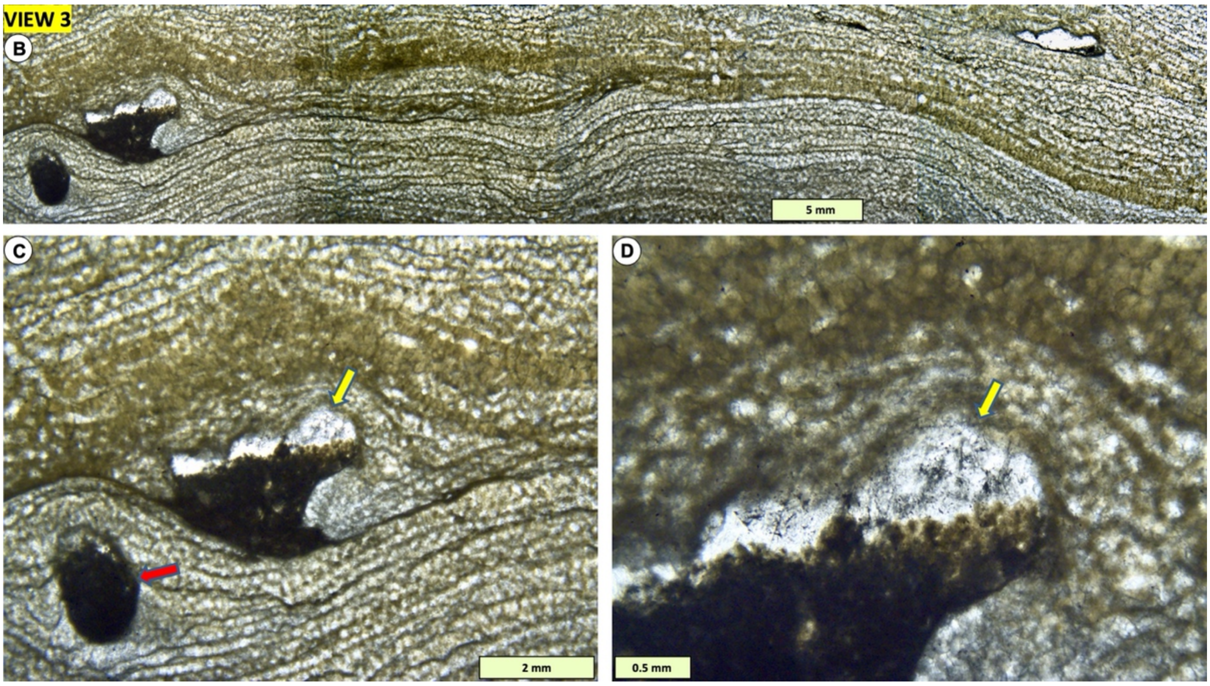

Fig. 3.11-View3B-D. Details of one geopetal cavity showing disturbance of stromatoporoid laminae around the edge of the cavity; its curved shape is good evidence of a bioclaustration, although not clear what it is. File: 16-KM14-Cm-HeliolitidEncr-06.

VIEW 3

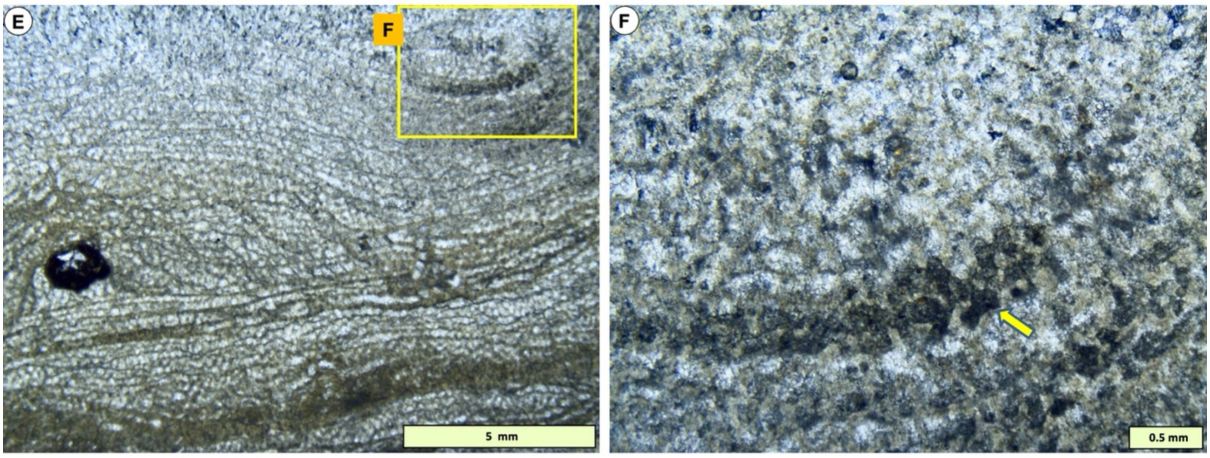

Fig. 3.11-View3E-F. Vertical section enlargement of box in [A] showing details of sediment deposition within the structure of the *Clathrodictyon mohicanum* (Cm) stromatoporoid (yellow arrow); the sediment layer extends only a short distance along the growth layers, possibly because the stromatoporoid sponge was able to clean itself of sediment, allowing accumulation in a small area, that died, but recovered by continued growth of surviving parts. File: 17-KM14-Cm-HeliolitidEncr-07.

VIEW 4

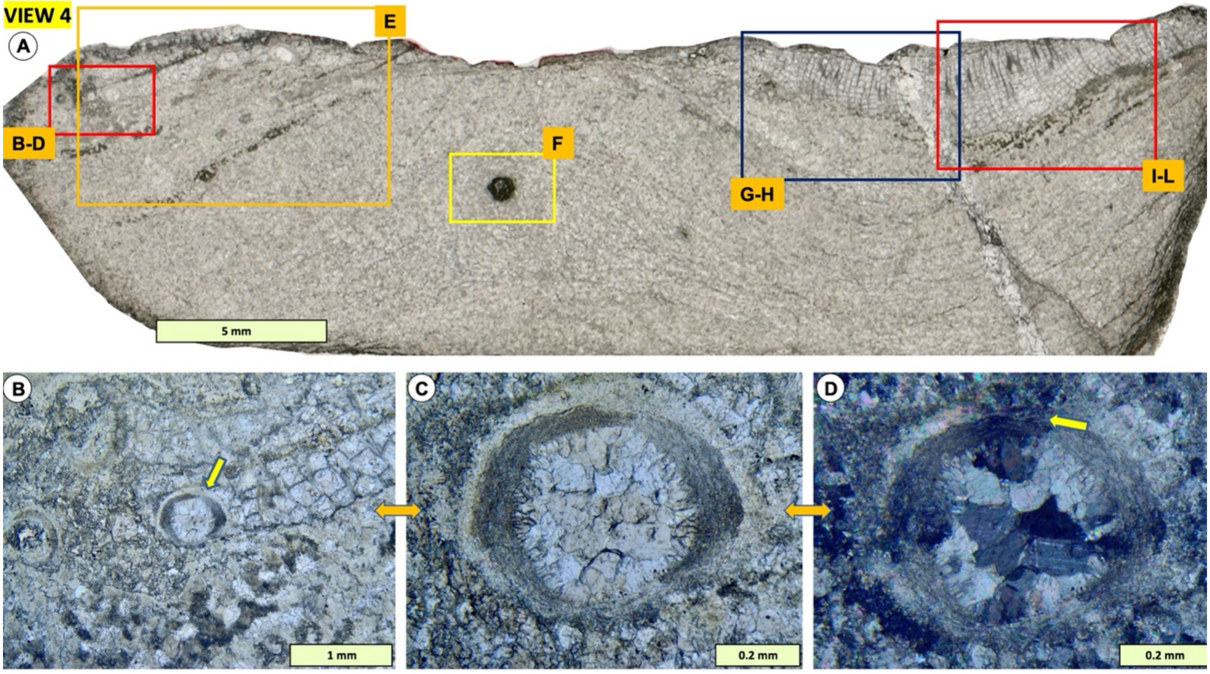

Fig. 3.11-View4A-D. Vertical section of another thin section of the same sample of *Clathrodictyon mohicanum* in above photos in Fig. 3.11.
A) whole thin section view showing location of other pictures. **B-D)** Auloporid encruster on the stromatoporoid surface, which in XPL [D] shows partial alteration of the coral tube wall, so that its extinction is in continuation with the cement infilling the tube. This is rather similar to the ability of stromatoporoids to recrystallise to include syntaxial continuation of cement in growth cavities, and may be evidence of early diagenetic change in the auloporid. File: 18-KM14-Cm-HeliolitidEncr-08.

VIEW 4

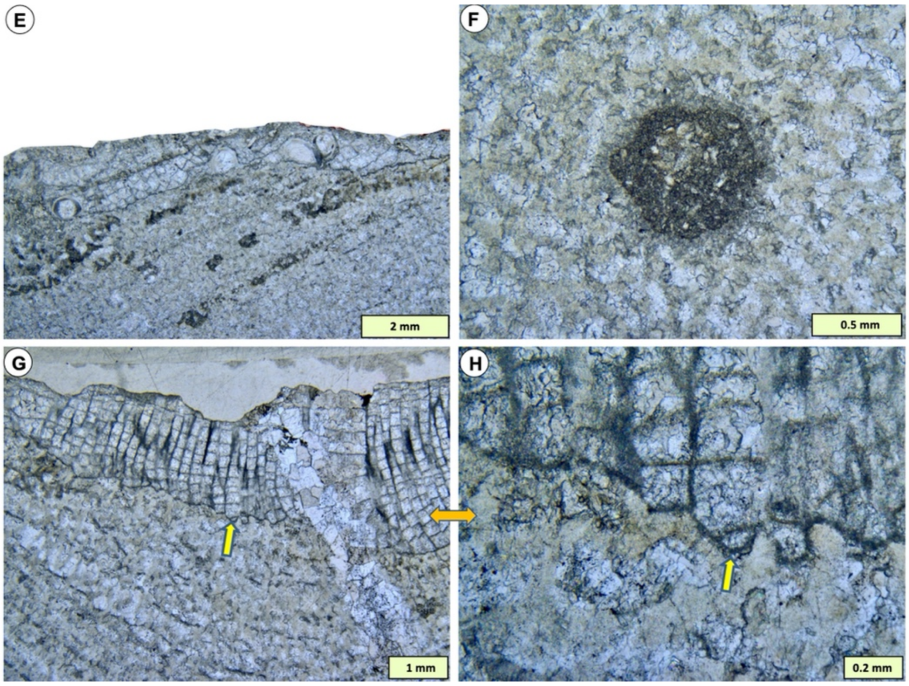

Fig. 3.11-View4E-H. Enlargements showing more details. **E)** upper surface of Cm encrusted by auloporid and heliolitid; **F)** detail of micrite-filled cavity that looks like a boring cut in TS. **G-H)** Irregular contact between the Cm and the heliolitid that encrusted it. Yellow arrows show matched points. The irregular contact with the dark line of matrix along the irregular line is likely to indicate pressure solution at the contact between the Cm stromatoporoid and the encrusting heliolitid. File: 19-KM14-Cm-HeliolitidEncr-09.

VIEW 4

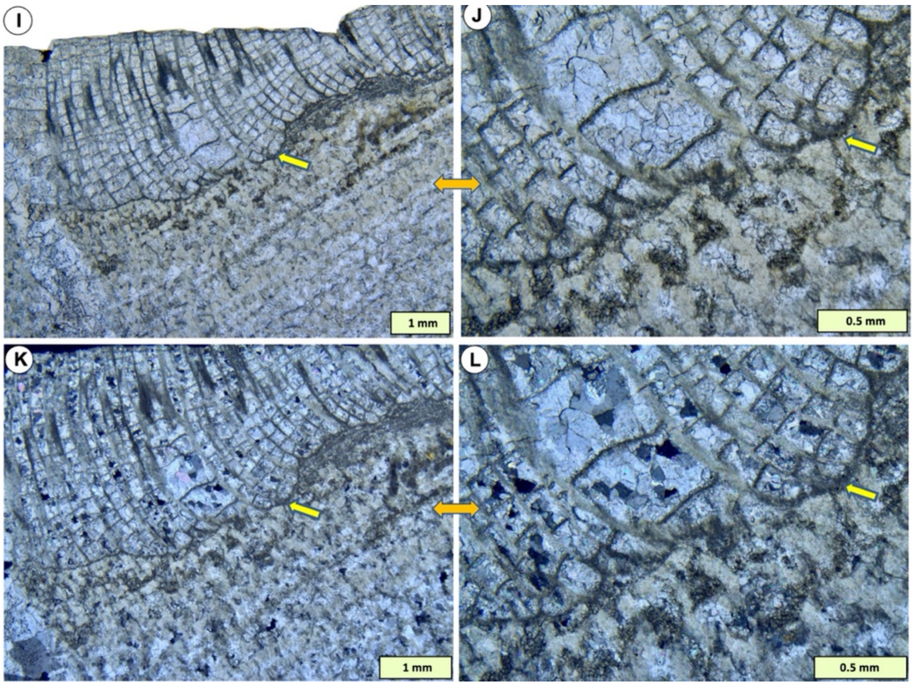

Fig. 3.11-View4I-L. Enlargements in PPL [I, J] and XPL [K, L] of nature of contact between stromatoporoid Cm and encrusting heliolitid. Yellow arrows show matched points. Sediment lies between the two fossils indicating a time gap between death of stromatoporoid and growth of heliolitid, but this has been modified by pressure solution. File: 20-KM14-Cm-HeliolitidEncr-10.

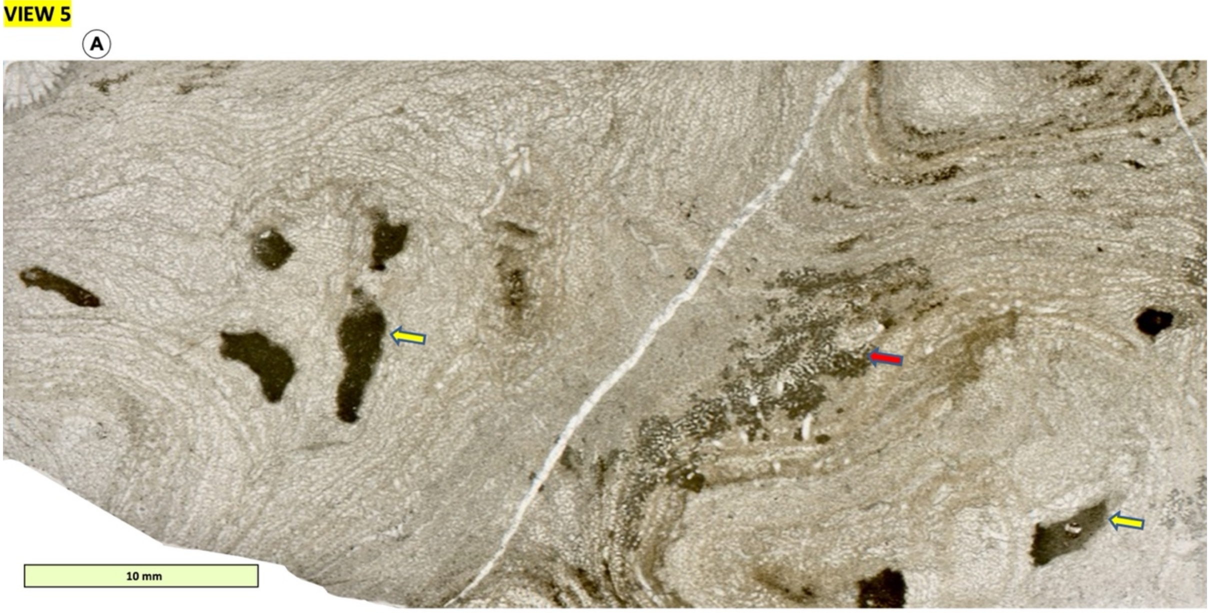

Fig. 3.11-View5A. TS view of whole thin section of Cm; the dark areas (yellow arrows) are sediment-filled cavities displayed in TS; it is not clear whether these are sediment deposits on interruption surfaces that are partly shown in a flat TS view, or represent infills of endobionts. Red arrow shows an area of sediment infiltration in the stromatoporoid structure detailed in next figure. File: 21-KM14-Cm-HeliolitidEncr-11.

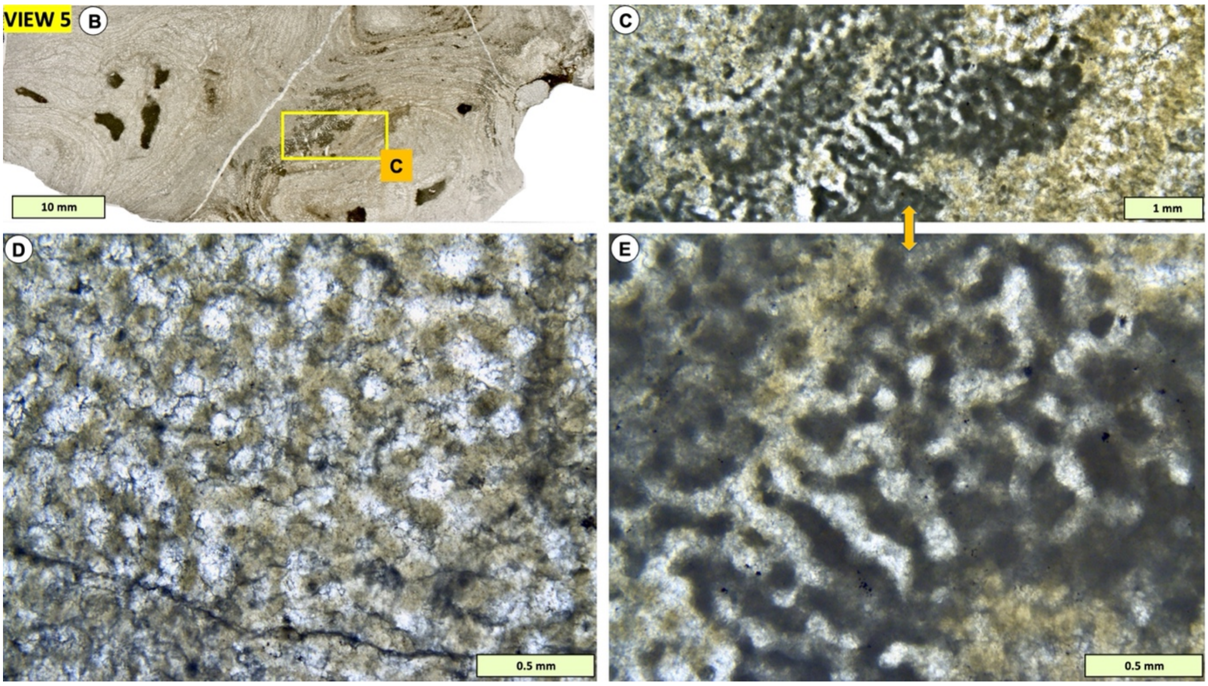

Fig. 3.11-View5B-E. Enlargements of TS view of Cm showing its structure in TS and the infill of the skeletal galleries with sediment after death, but before cement growth in the gallery spaces; this is evidence that the galleries were left open for long enough after death of the stromatoporoid to allow sediment to accumulate. File: 22-KM14-Cm-HeliolitidEncr-12.

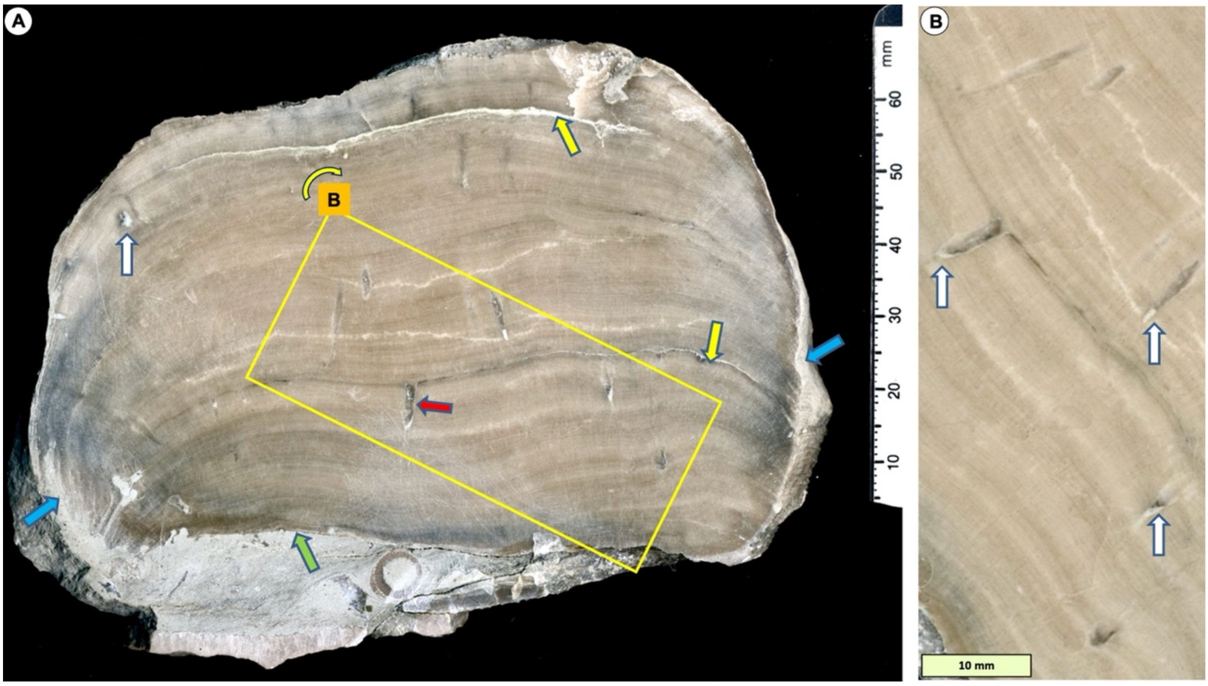

Fig. 3.12. Vertical section through "*Stromatopora" bekkeri*" (Sb).
A) Green arrow: base of Sb is directly on the sediment substrate, indicating an ability to grow on the sediment; however, we have to be careful because in another plane of section there may be some debris present that allowed the Sb to initiate, advising us that stromatoporoids are 3-dimensional so drawing conclusions needs more information. **Blue arrow** on left shows a finely interdigitated margin with sediment that may have been caused by periodic small sedimentation events, possibly due to current transport of unconsolidated sediment across the sea floor; yet **blue arrow** on right emphasises there is no interdigitation here; whether this is due to directional currents is a tantalising possibility in stromatoporoids that has not really been investigated. **Red arrow** points to an endobiont associated with a growth interruption surface (**lower yellow arrow**), and it may be a boring into the temporarily partly-killed stromatoporoid surface. **Upper yellow arrow** shows another growth interruption surface. **White arrow** shows another endobiont, possibly a boring that has a geopetal infill orientated to the left. **B)** Enlargement of yellow box in [A] highlighting the endobionts; look carefully and you can see geopetal infills of light-coloured sediment in the tubes, that are consistent in orientation with the one in [A] (white arrow); these consistent geopetals show this specimen was disturbed on the substrate, but why do these geopetals occur in endobionts that seem to be at different levels within the Sb? Maybe they all extend to the stromatoporoid's uppermost surface, not visible in this plane of section. (Isn't it amazing that such a large amount of potentially useful palaeoenvironmental information can be derived from such an apparently unremarkable specimen?!) File: 23-K4Mud-2017-01-Sb.

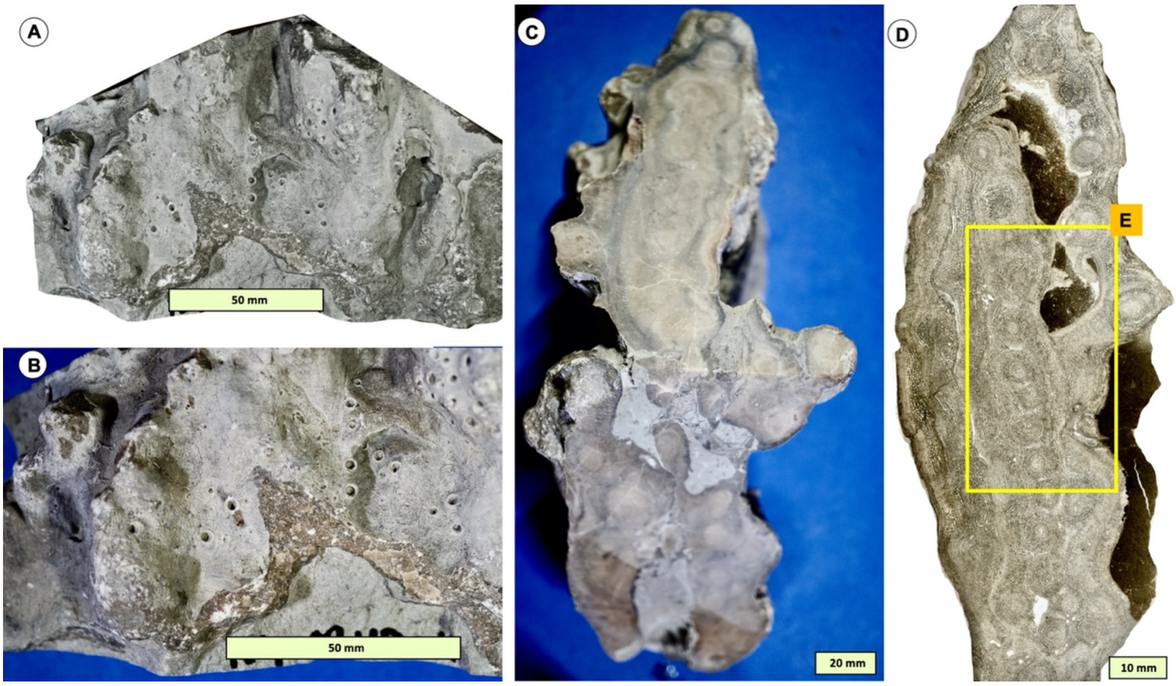

Fig. 3.13A-D. *“Stromatopora” bekkeri* with symbiotic rugose corals. **A, B)** opposite side views of the narrow multicolumnar specimen viewed from the top in [C]. In [A] & [B], the corals are visible as small dark spots**. C)** top cross section and **D)** whole thin section views cut tangentially to reveal the multicolumnar nature of the specimen, composed of merged columns of stromatoporoid skeleton. See [E] for enlargement of box in [D]. File: 24-K4Mud11-Sb-Columns-01.

Fig. 3.13E. Enlargement of box in Fig. 3.13D, showing skeletal structure of *“Stromatopora” bekkeri* with a symbiotic rugose coral (lower left) that is open to the side surface of the specimen, here orientated so the side is at the bottom of the photo. The multicolumnar structure of the stromatoporoid can be appreciated by the mixture and arrangement of vertical and transverse sections through the skeleton. File: 25-K4Mud11-Sb-Columns-02.

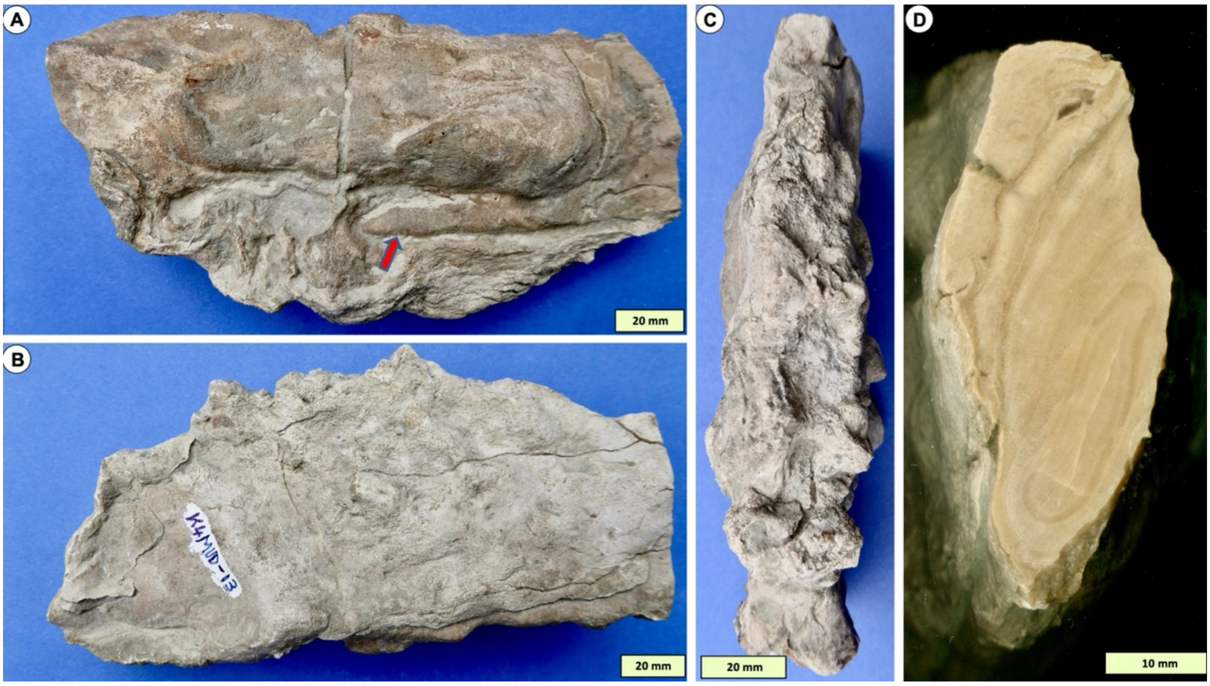

Fig. 3.14. A-B) Part of a sample of *"Stromatopora" bekkeri* lying on its side for these photos, so that it grew to the left as erect columns (red arrow in [A]), but then fell over and continued growth to cover the columns [B]. C) Edge view and D) cut end view (thus parallel to the sediment surface). File: 26-K4Mud13-FingerStrom-Sb.

Fig. 3.15. Part of a sample of *"Stromatopora" bekkeri* that grew as erect columns, seen from the side in [A-B], the edge in [C] and in TS cross-cut parallel to the sea floor in [D]. File: 27-K4Mud15-FingerStrom-Sb.

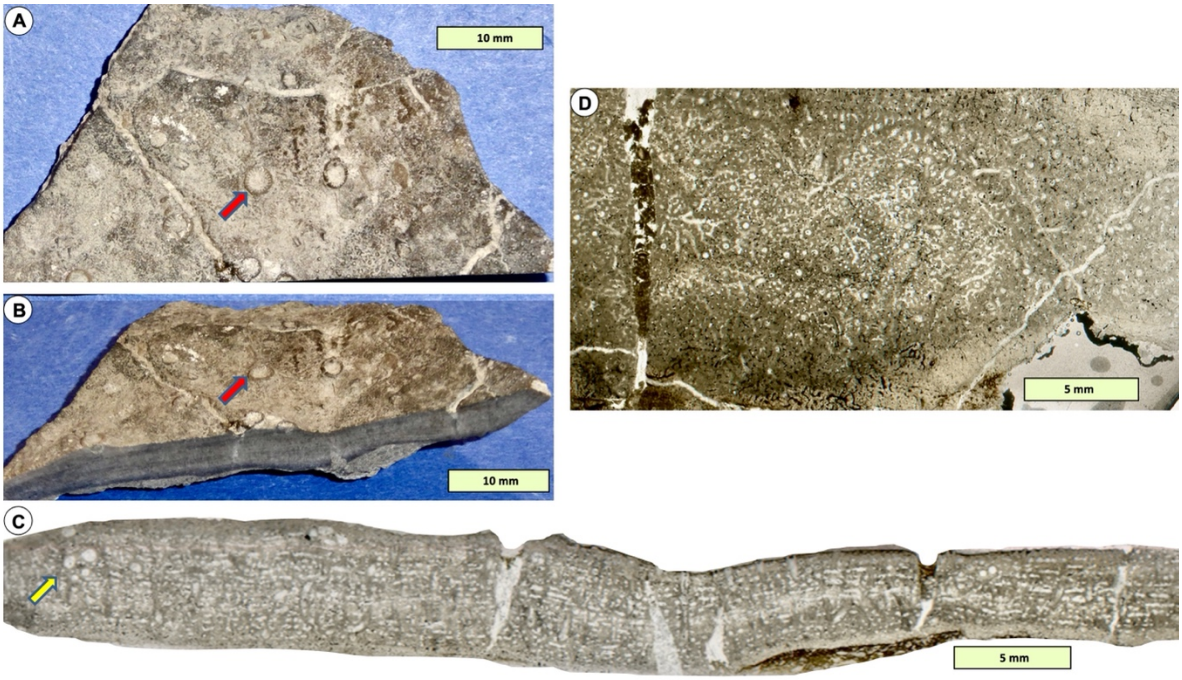

Fig. 3.16. Laminar form of *"Stromatopora" venukovi*, showing intergrown symbiotic rugose corals, syringoporid tabulates and spiral tubes (yellow arrow in [C]) [C] shows four wedge-shaped fractures, but this plane of section does not pass through any corals. File: 29-KLoose42-Sv.

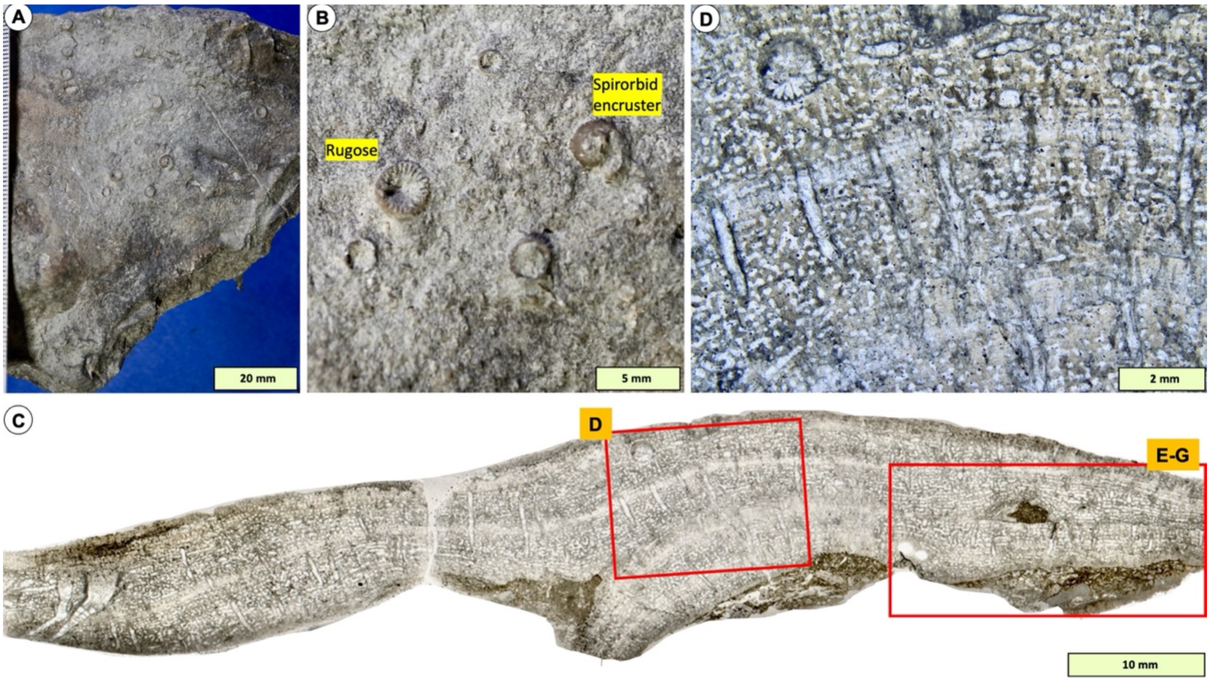

Fig. 3.17A-D. Laminar form of *"Stromatopora" venukovi*, showing intergrown symbiotic rugose corals, syringoporid tabulates and a surface encruster (spirorbid). File: 30-KLoose44-Sv-Rugs-Cauno-Tubes-01.

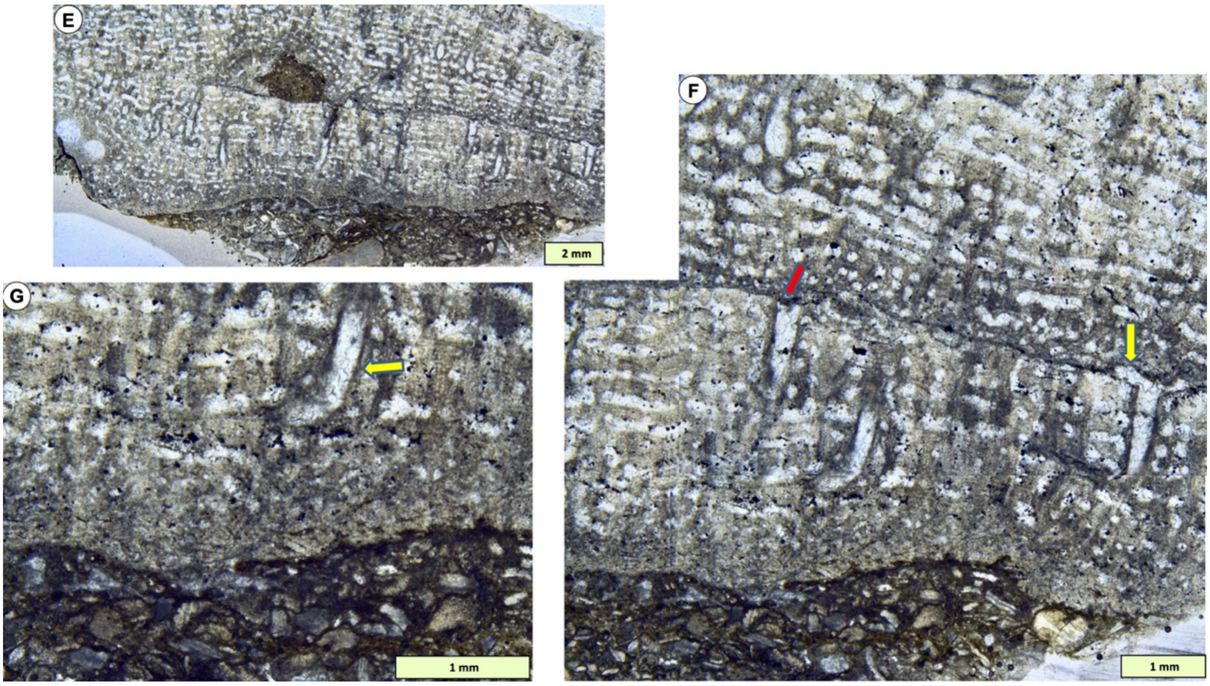

Fig. 3.17E-G. Laminar form of *"Stromatopora" venukovi* (Sv), showing intergrown symbiotic syringoporid tabulate tubes. Note the basal part of the Sv lacks the syringoporid tubes, evidence that the tabulate larvae did not immediately find the Sv on the sea floor. In [F], red arrow shows termination of a syringoporid tube at a growth interruption surface; yellow arrow shows part of the cross-tubes present in syringoporids. The growth interruption surface in the right-hand part of this sample in [F] shows modification of the interruption surface by pressure solution. In [G], yellow arrow shows the earliest tube in this specimen. In [F] and [G], sediment below the Sv is bioclastic packstone made of mostly crinoid fragments with dark micrite, probably containing some clay. File: 31-KLoose44-Sv-Rugs-Cauno-Tubes-02.

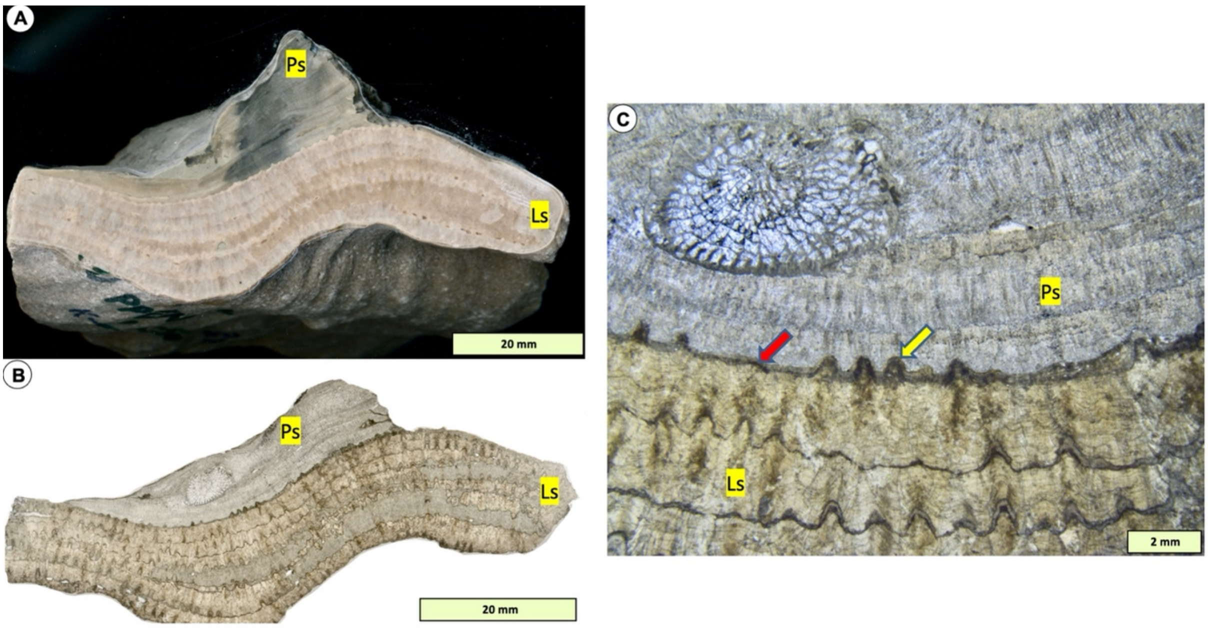

Fig. 3.18. *Lophiostroma schmidti* (Ls) encrusted by *Plectostroma scaniense* (Ps).
A) Hand specimen scan in VS; **B)** Whole thin section in VS; **C)** Enlargement of centre-left part of B, showing the Ls has papillae (yellow arrow) that are not present across all the surface (red arrow) of the Ls; this is not common and raises the question about why. If it is caused by erosion then all the papillae would be expected to have been removed, so this variation may be a growth characteristic of

the Ls, yet why it happens is a mystery. It is interesting that Ls in the sample set of this study, Ls is found either alone, or as part of an encrusting stack, but Ls is always the lowest in the stack. Furthermore, the base of Ls specimens is in almost all cases exposed and shows growth ridges, altogether indicating an ability to grow on unconsolidated substrates that are easily removed by modern weathering. In contrast, Ps is in almost all cases found encrusting other stromatoporoids, indicative of a different behaviour towards the substrate in these two taxa. You will be able to consider these points in the subsequent figures. File: 32-KLoose23-K4Mud-Ls-Ps.

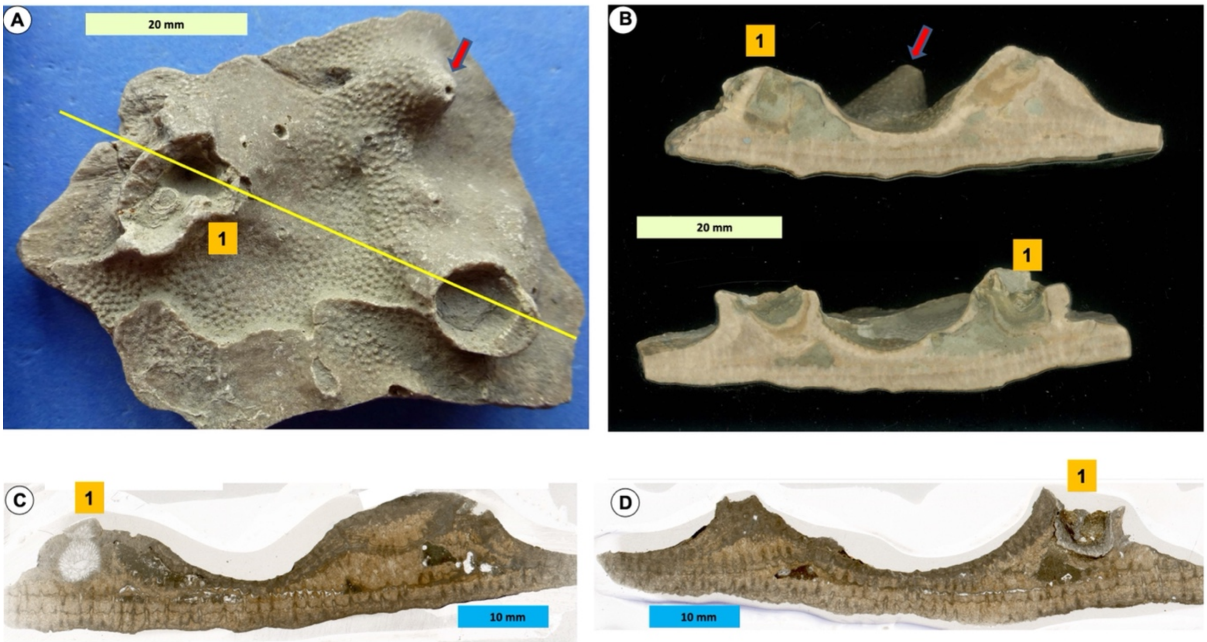

Fig. 3.19A-D. Small sample of *Lophiostroma schmidti* with embedded rugose coral symbionts plus a small chimney (red arrow) of an unknown tube. **A)** top view; **B)** side views of cut line in [A]; **C-D)** whole thin section views from approximately along the cut line in [A]. The number 1 identifies the same point in each image. File: 33-KM07-Ls-Chimneys-Rugosa01.

Fig. 3.19E. Enlargements of [C-D] in the previous figure. Growth interruption surfaces in this sample are shown by presence of patches of sediment at two different levels within the sample. The lower interruption surface shows evidence of primary cavity formation in the white areas, yet other parts of the same level show no primary cavity; the reasons for this variation are not known. File: 34-KM07-Ls-Chimneys-Rugosa02.

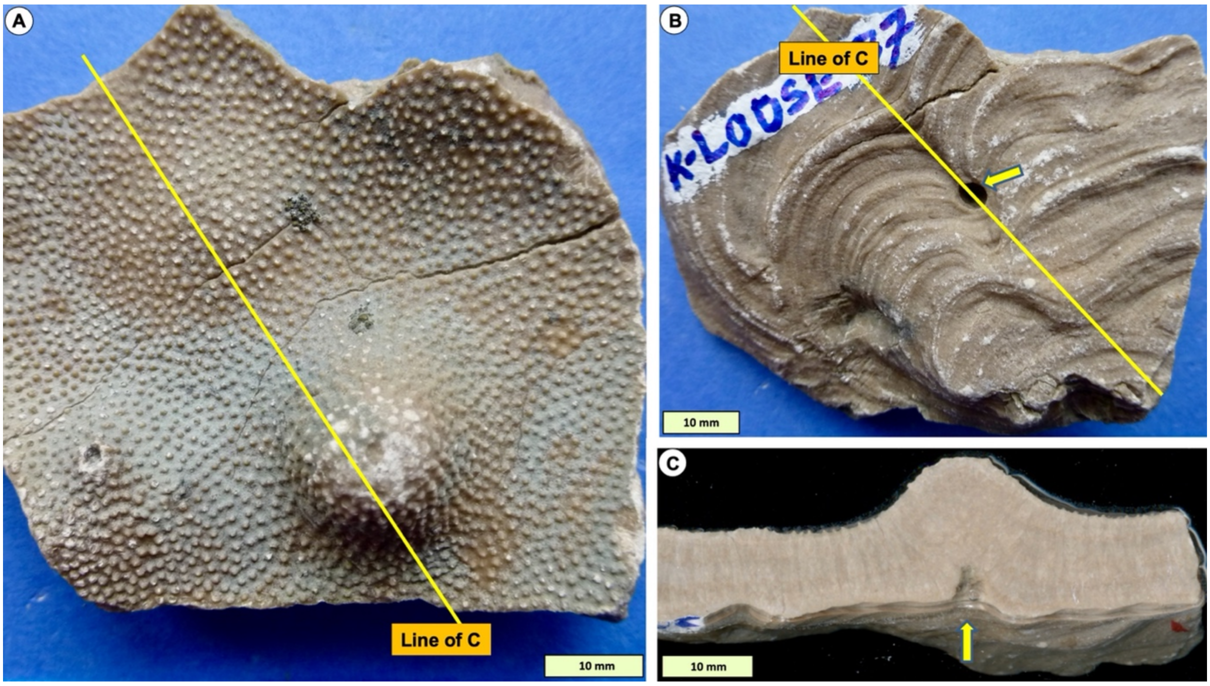

Fig. 3.20. Small sample of *Lophiostroma schmidti* (Ls) with unusual feature in the base [B] that expresses itself on the top surface [A], and shown as a small cavity [C, yellow arrow]. The basal ridges [B] indicate growth directly on the unconsolidated sediment surface, and the unusual basal cavity shape implies an object existed on the substrate that the Ls grew over. However, why that object led to a prominent updoming of the entire thickness of the Ls is not consistent with simple growth over an uneven substrate; more likely the cavity represents presence of another organism, but the nature of this is not known. Altogether a mysterious phenomenon that is begging for more detailed study. File: 34a-KLoose37-Ls.

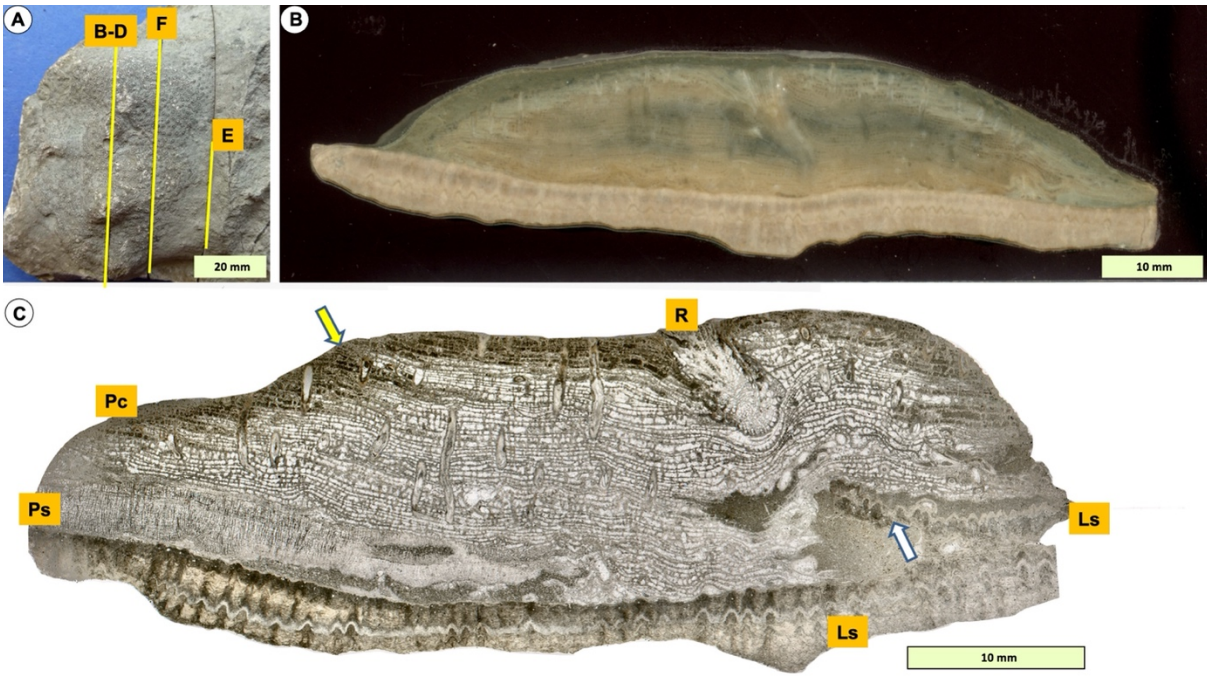

Fig. 3.21 [5 separate figures]
Fig. 3.21A-C. Three stromatoporoid taxa, from bottom to top they are: *Lophiostroma schmidti* (Ls), *Plectostroma scaniense* (Ps) and *Petridiostroma convictum* (Pc), an encrusting stack, and including growth interruptions and two forms of symbionts, rugose coral (R) and syringoporid tabulates in the Pc, all packed into a small specimen! **A)** top view of hand specimen, showing lines of cuts in figs 3.21B-F; **B)** VS of one of the cut views along B-D in [A]; **C)** VS of whole thin section showing overall nature of the encrusting stack. Ls is at the base, as it always is, encrusted by Ps covering left-hand half of the Ls, followed by Pc in which syringoporid tabulates appear close to the base. The rugose coral (R) has its origin out of this plane of section, so it cannot be determined, but presumably started growing shortly after the prominent upper growth interruption surface in the Pc. White arrow shows further growth of Ls after the lower growth interruption on the right side, followed by the middle of the three growth interruptions visible in this section. The entire upper surface of the Pc is indurated with micrite a few mm down from the surface, evidence that the gallery spaces were left empty for sufficiently long enough to allow sediment accumulation at an early stage after death of the Pc. File: 35-K4Mud10-LS-Ps-Pc-01.

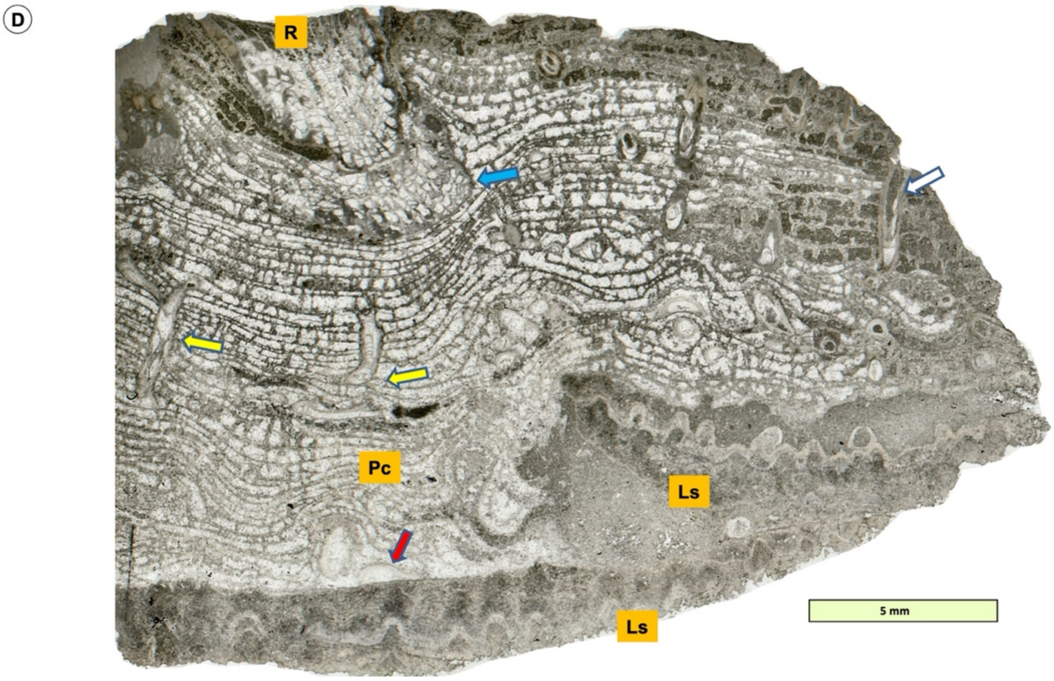

Fig. 3.21D. A parallel VS thin section to Fig. 3.21C showing the same features, but allows recognition of encrusting auloporids on the Ls surface (red arrow) indicating a time gap before the Pc grew. Yellow arrows in Pc show early syringoporid tubes. Blue arrow shows Pc laminae abutting the outer wall of the rugose coral. While arrow shows detail of micrite infiltration into the Pc gallery space and also into the open tube of a rugose, demonstrating that the latter was open to the surface at that level as the structure developed. File: 36-K4Mud10-LS-Ps-Pc-02.

Fig. 3.21E. A parallel VS thin section to Fig. 3.21C showing the same features as the left side. Note the Ls surface lacks papillae, and is slightly irregular so may have been eroded before micrite deposition (centre) and Ps encrustation (left and right). Ps may have been terminated by growth interruption with sediment (red arrow) but that surface was cleaned before the Pc grew. Yet this assumes that the Ps was killed by sedimentation, but what if it was able to clear itself? Here we might have a situation where the Ps was overrun by the Pc, while the Ps was still alive (unfriendly), which could indicate a higher competitive ability of Pc; this is conjecture but we will see more of this in later figures. In this picture can also see that the syringoporid tubes started growing after only a few laminae of Pc had accreted, evidence that the syringoporids found this specimen early. White arrow

shows micrite infiltration into a syringoporid tube, evidence that the tube was open to the Pc surface, but note there is a very minor growth interruption (sediment) just above the white arrow, so the sediment in the syringoporid tube may have come from that event, not necessarily from the final stromatoporoid upper surface. File: 37-K4Mud10-LS-Ps-Pc-03.

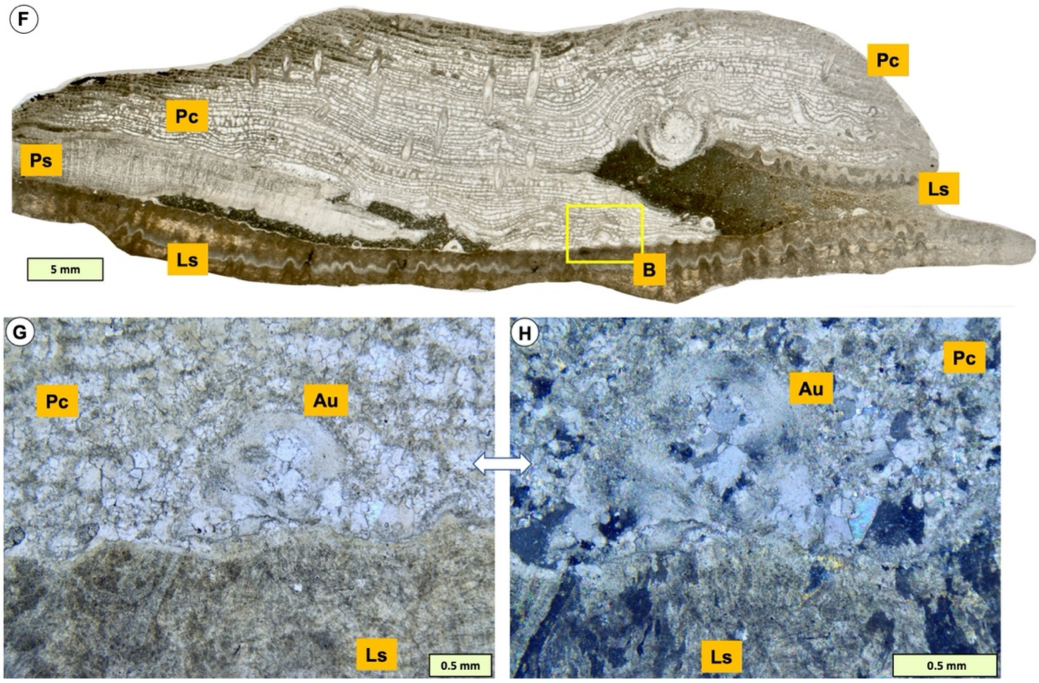

Fig. 3.21F-H. Another section showing similar features to the previous figures, but indicates more detail of the encrusting auloporid on the Ls. Auloporid shows a partially altered tube as seen in a previous figure. File: 38-K4Mud10-LS-Ps-Pc-04.

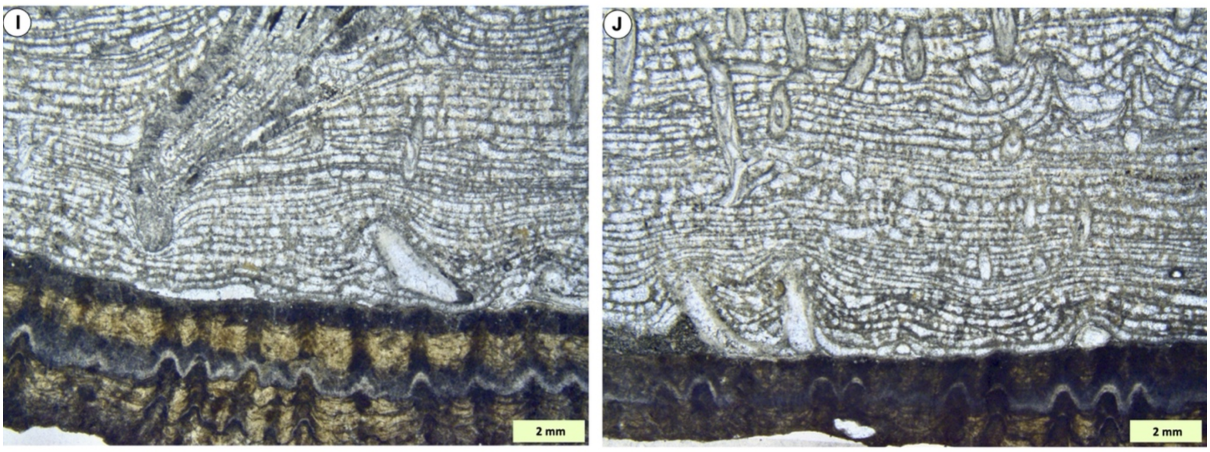

Fig. 3.21I-J. More details of the early growth of the Pc in this sample, and reveals auloporid tubes that grew up from the top surface of Ls but the Pc laminae curved up and over the auloporids, evidence that the Pc outgrew the auloporids and smothered them. A short time later, syringoporids found the stromatoporoid, but in their case they were not overgrown by the stromatoporoid but kept pace with it

as the sample developed. The rugose coral also clearly started at a very early stage in the Pc growth. File: 39-K4Mud10-LS-Ps-Pc-05.

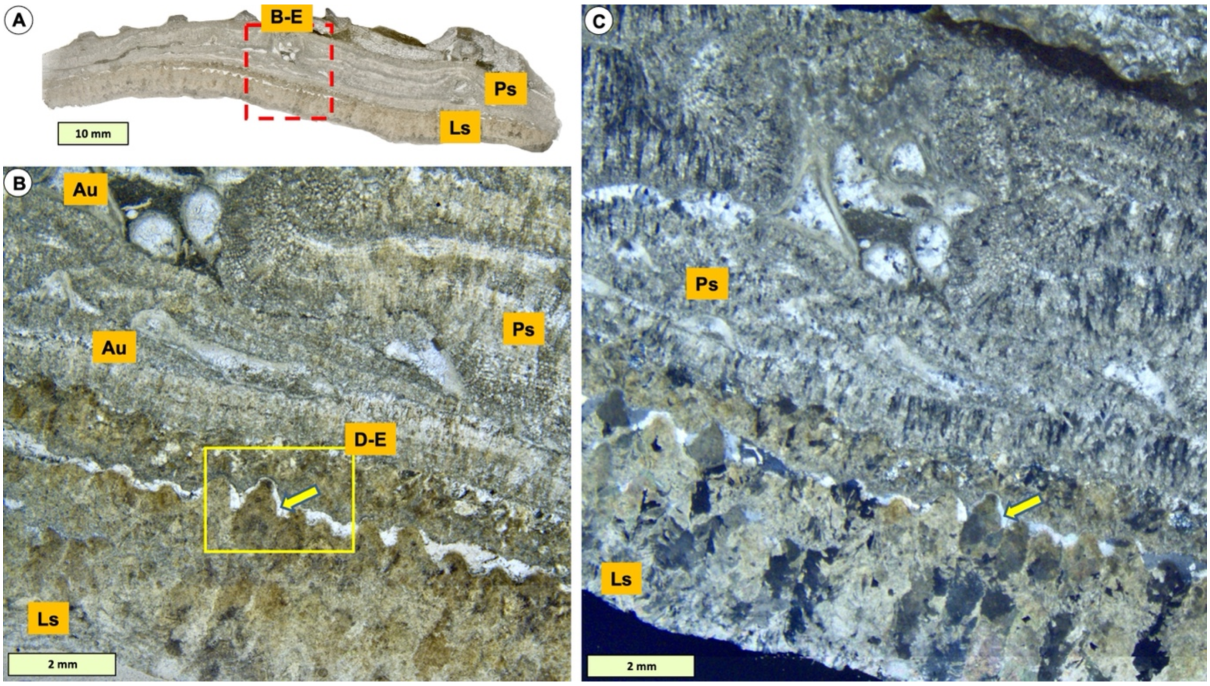

Fig. 3.22 [8 separate figures]

Fig. 3.22A-C. A) Whole thin section view of *Lophiostroma schmidti* (Ls) encrusted by *Plectostroma scaniense* (Ps); **B-C)** PPL [A] and XPL [B] views of box in A showing primary growth cavities in Ls, and auloporid tabulates encrusting growth interruption layers within Ps. The XPL view in [C] also demonstrates the difference of the diagenetic styles between Ls and Ps of the fabric-retentive irregular calcite (FRIC). Yellow arrow in [B] and [C] show matched points, and are enlarged in [D] and [E]. File: 40-KLoose47-i-Ls-Ps-01.

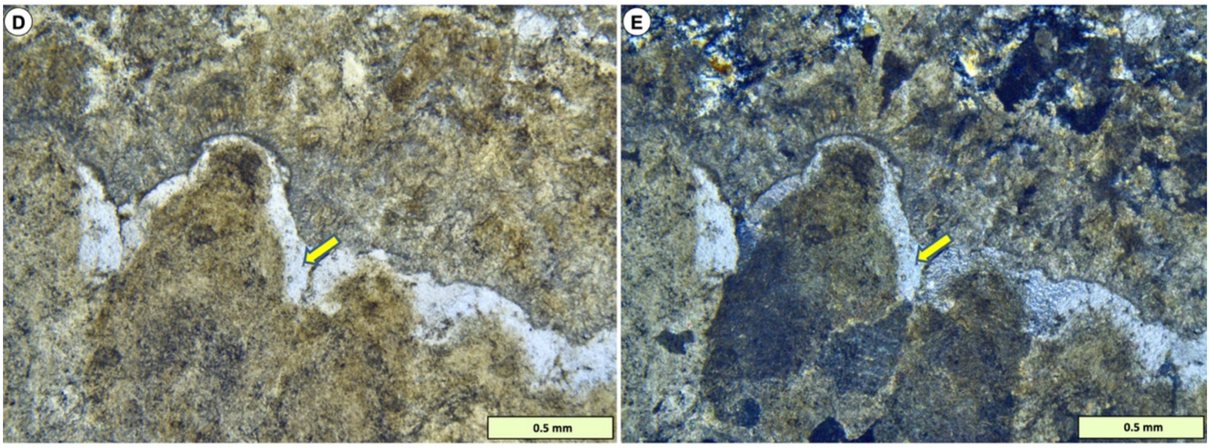

Fig. 3.22D-E. Enlargements of box in [B] highlighting sparite cement in primary growth cavity along a growth interruption surface in the Ls. Yellow arrows show matched points, that also match the same points in Fig. 3.22B-C. Reasons for formation of primary cavities within the Ls are not known, but these pictures show that the sparite in the cavity is not in optical continuity with the FRIC of the Ls, evidence that the cavity was filled with cement before the diagenesis of the stromatoporoids. This contrasts the cement infills in Fig. 2.6J-M where the cement **is** in optical continuity with the skeleton (that indicates the cavity was open when diagenesis occurred so the cement simply passes into the cavity). This contrast in diagenetic cements in a similar situation within one taxon is known elsewhere in stromatoporoids (Kershaw et al. 2021a), and demonstrates variability in timing of cement formation in relation to recrystallisation within stromatoporoids. File: 41-KLoose47-i-Ls-Ps-02.

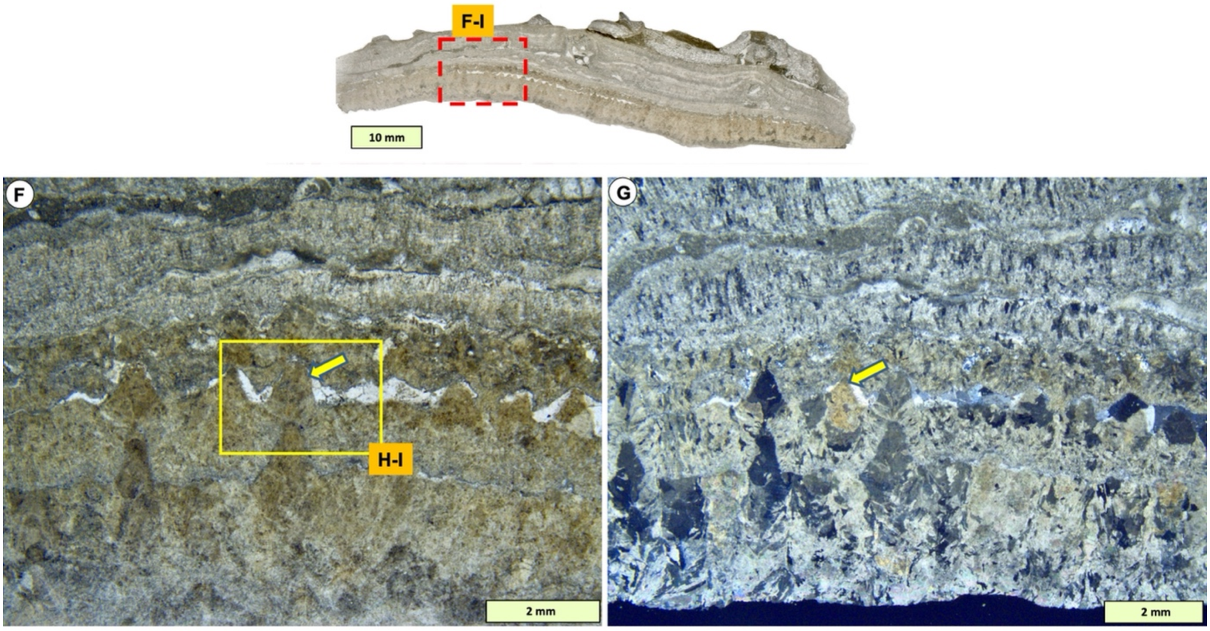

Fig. 3.22F-G. Another detail of primary cavity cement fill in Ls, continuing from the previous two figures. Note again then contrast in FRIC between Ls (lower stromatoporoid) and Ps (upper stromatoporoid). File: 42-KLoose47-i-Ls-Ps-03.

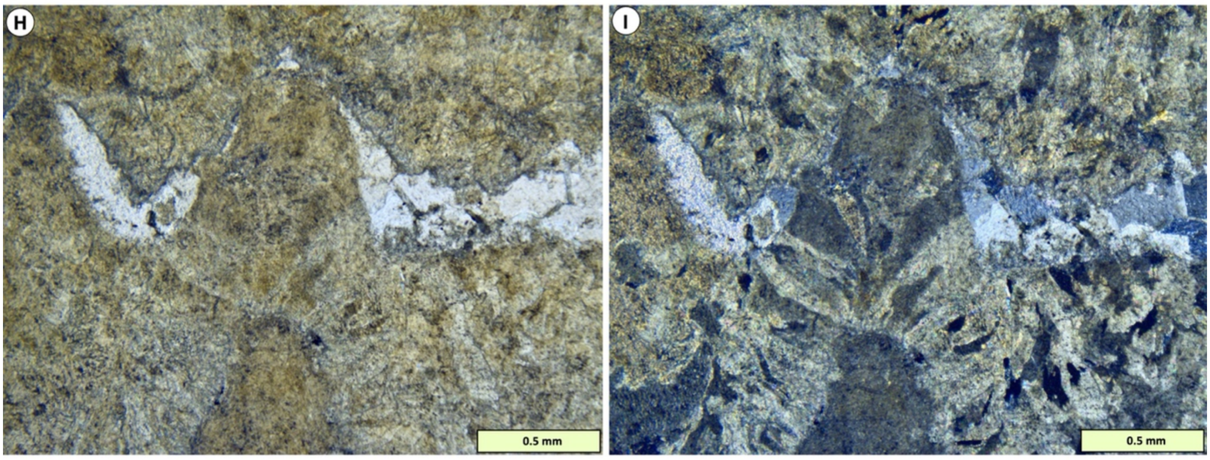

Fig. 3.22H-I. Enlargement of box in Fig. 3.22F, showing more images of details of FRIC, shown in Fig. 3.22D-E. This emphasises that the primary cavity was filled with cement before the stromatoporoid diagenesis occurred, because the cement in the cavity does not continue in optical continuity from the recrystallised stromatoporoid calcite. File: 43-KLoose47-i-Ls-Ps-04.

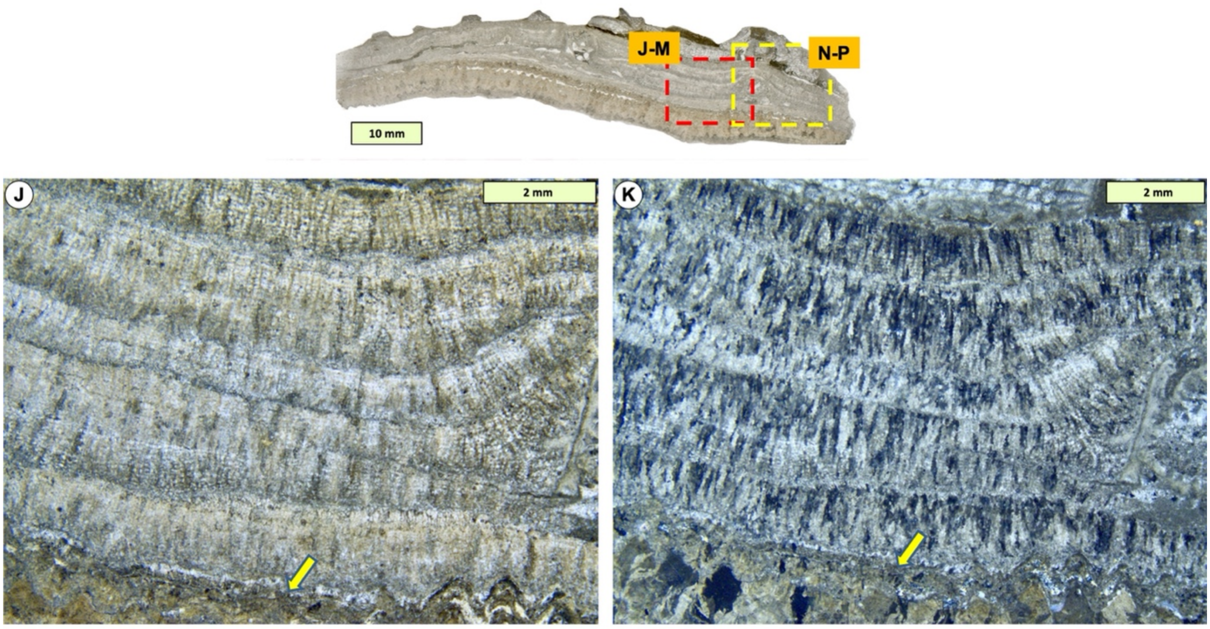

Fig. 3.22J-K. PPL [J] and XPL [K] views of Ls (bottom of photo) and Ps (most of photo) showing contrast in recrystallisation fabric between the two taxa. Yellow arrows show matched points. At the position of the yellow arrow, the Ls lacks papillae, whereas on the right side of the picture papillae are present. There is the possibility that the papillae were partly eroded, but then we would wonder why not all of the papillae are eroded, so the reason for the flat surface in the region of the yellow arrow is not known. The overlying Ps shows prominent growth layers emphasised in XPL [K] by the non-continuation of FRIC across layer boundaries. These lines between sections of skeleton are growth interruption events, that may have been caused by episodic sedimentation, but because sediment is lacking in these views, that cannot be confirmed; it would be necessary to trace the growth lines out to the specimen margins to look for sedimentation interfingering with skeleton; however, in this sample

the margins are not shown so the potential cause of the interruption surfaces cannot be investigated. Nevertheless, the layers vary in thickness which may be evidence that the growth layers are not annual banding, for instance. This sample demonstrates the difficulty of understanding the cause of banding in stromatoporoids. Note the auloporid tabulate (right edge) within the Ps, shown in more detail below. File: 44-KLoose47-i-Ls-Ps-05.

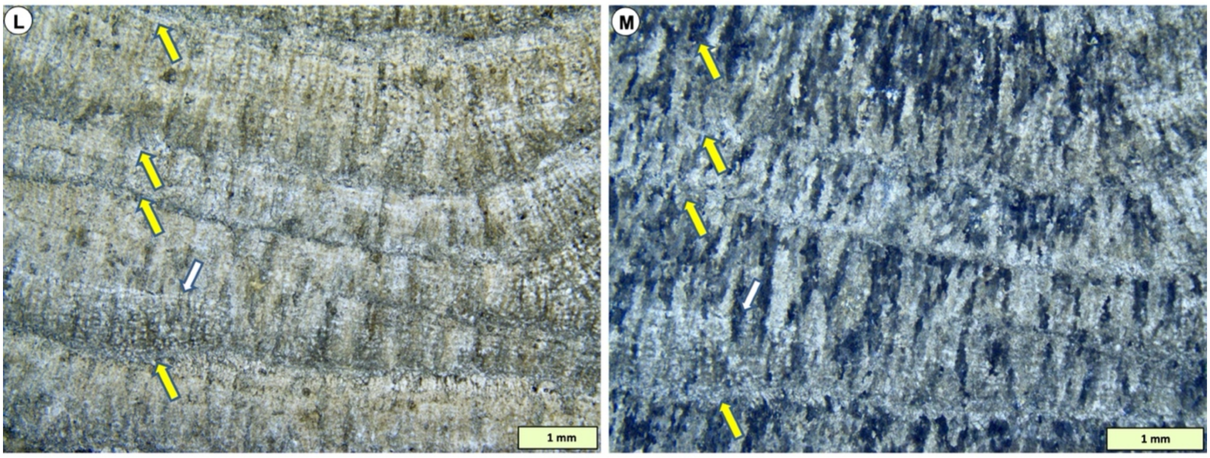

Fig. 3.22L-M. Enlarged views of growth banding in Fig. 3.22J-K in PPL [L] and XPL [M]. Yellow arrows show event boundaries; white arrow shows a detail of the FRIC. File: 45-KLoose47-i-Ls-Ps-06.

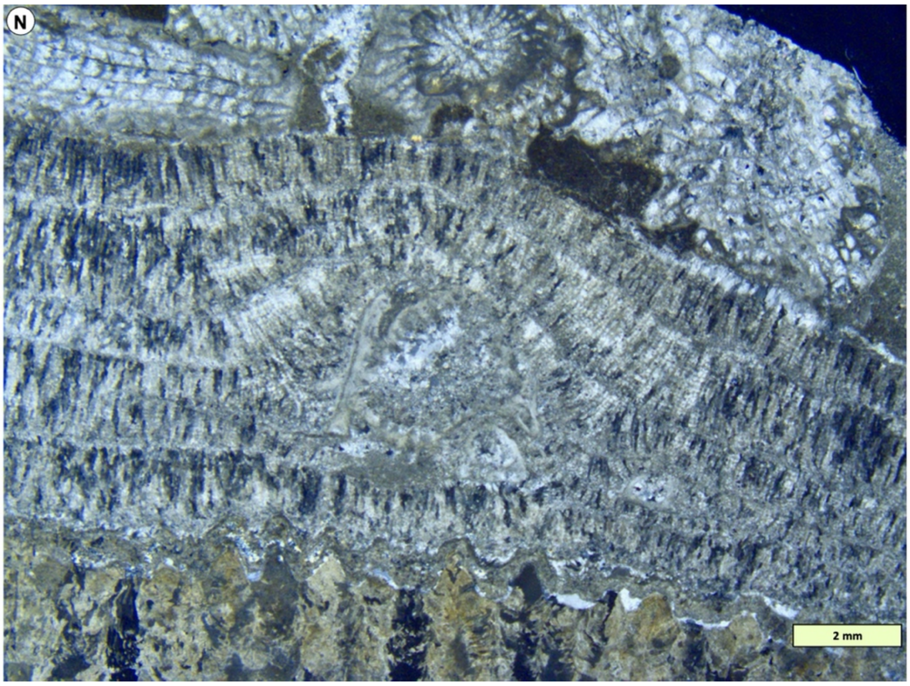

Fig. 3.22N. XPL view of Ls (lower) and Ps (centre) showing encrusting auloporid within the Ps at the level of the first growth line, which is evidence that this is a growth interruption surface; it is presumed the auloporid lived as the Ps grew. Note also encrusting rugose corals on Ps (top). Growth banding in the Ps is disturbed by the presence of the auloporid. File: 46-KLoose47-i-Ls-Ps-07.

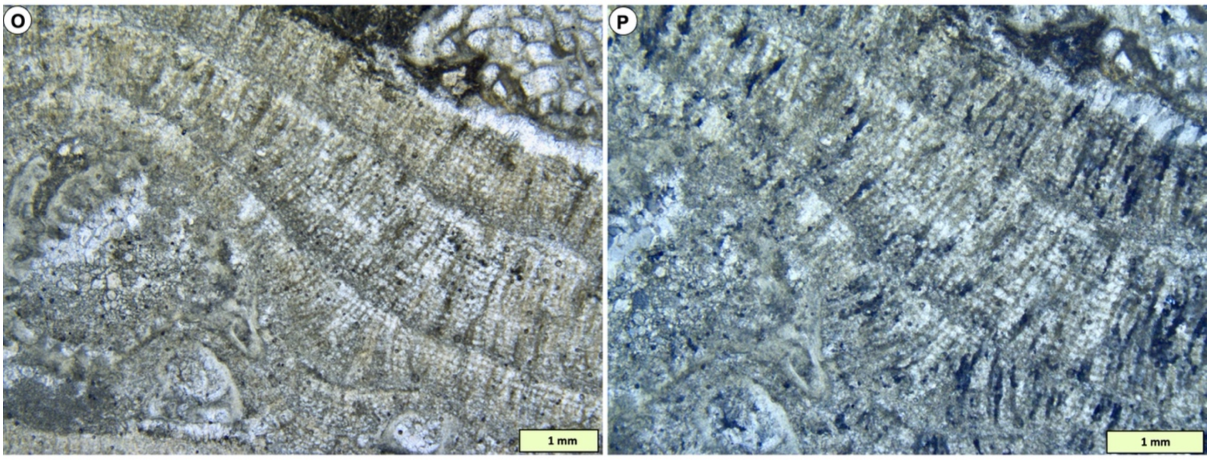

Fig. 3.22O-P. More views of the auloporid, growth interruption surfaces and FRIC in this sample; see Figs. 3.22A-N for the context. File: 47-KLoose47-i-Ls-Ps-08.

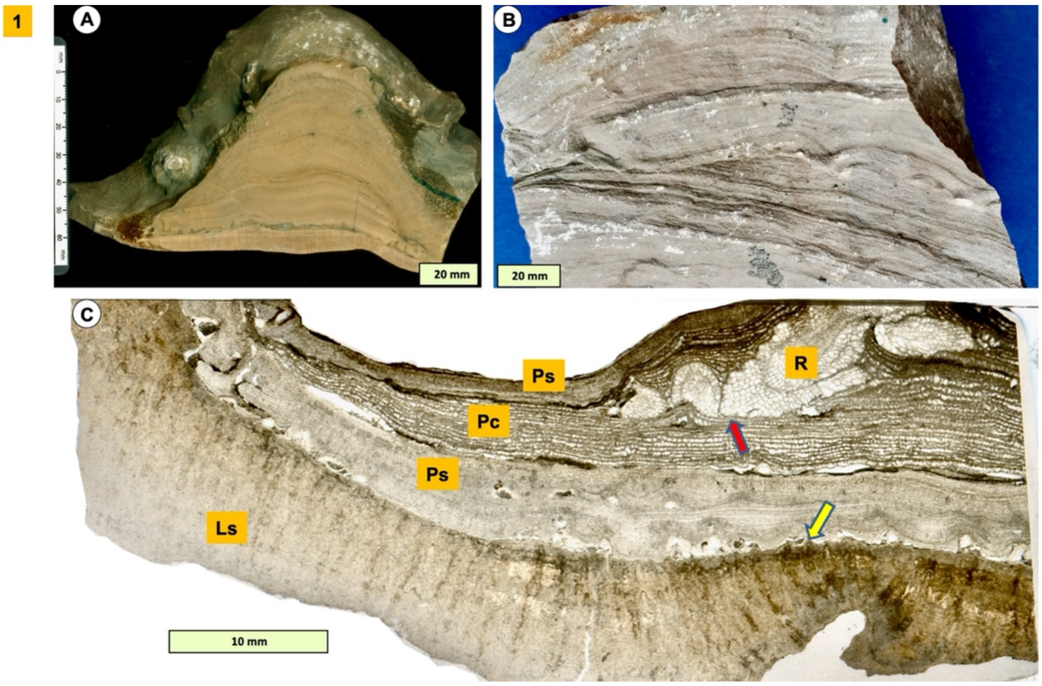

Fig. 3.23. [8 separate figures]
Fig. 3.23-View1A-C. A) VS of hand specimen. *Lophiostroma schmidti* (Ls) is the thin layer at the bottom; the remainder is comprised of *Plectostroma scaniense* (Ps) and *Petriostroma convictum* (Pc). **B)** basal view of hand specimen showing part of basal ridges on Ls (the sample is only a small part of what was originally a much bigger sample). This undulating ridged surface that has no sediment adhering to it is evidence of growth on an unconsolidated sediment, possibly forming growth cavities. **C)** Whole thin section, VS, showing stacked encrusting stromatoporoids, from base: Ls, Ps, Pc with encrusting rugosa, and finally a thin Ps. Yellow arrow points at auloporid encruster on Ls upper surface before Ps growth, indicating a time gap between Ls and Ps; red arrow highlights rugose encrustation on a Pc interruption surface, but Pc recovered and grew up the side of the rugose and

possibly encased it. Note that the corallite calyces are not shown in this section and may have paced the Pc growth to maintain an open connection to the seawater at the stromatoporoid surface. This sample shows the nature of beginning of the rugose, taking advantage of a growth interruption event in the stromatoporoid to establish the coral growth, and the ability of stromatoporoids to address the presence of an encrusting taxon by growing up around it, a situation commonly seen in stromatoporoids. Note this view shows there are no syringoporid tabulates in this plane of section, so presumably the syringoporid larvae did not find the stromatoporoid during this sequence of growth. Finally, note the peculiar notch in the base of Ls around which its growth laminations curve; there must have been something present there, but we don't know whether this was just a fragment of shell or another item. File: 48-KLoose54-Ls-Pc-Ps-Sample1-01.

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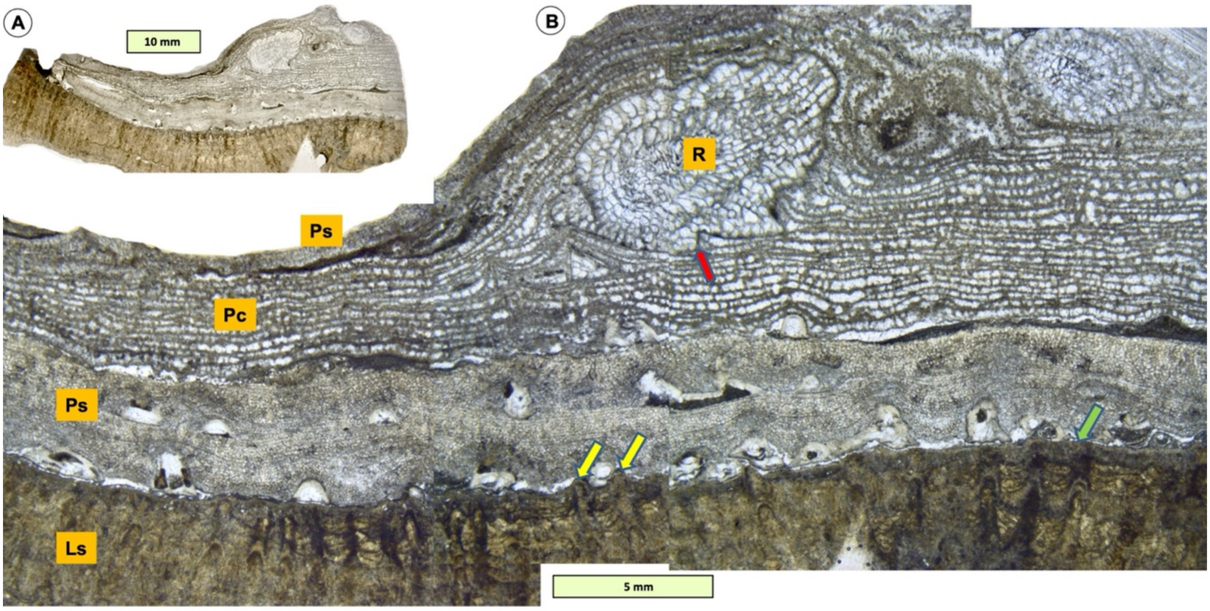


Fig. 3.23-View2A-B. Another VS parallel to Fig. 3.23-View1C showing the same sequence and features. Note detail of relationship between Pc and rugose, with close growth of the Pc laminae around the rugose. Between the two rugose corallites, the Pc is seen in TS, showing how the stromatoporoid grew over and around the coral. As in the previous figure, no syringoporids occur in the Pc. The clear triangular area in centre left of the Ls is thin section damage. File: 49-KLoose54-Ls-Pc-Ps-Sample1-02.

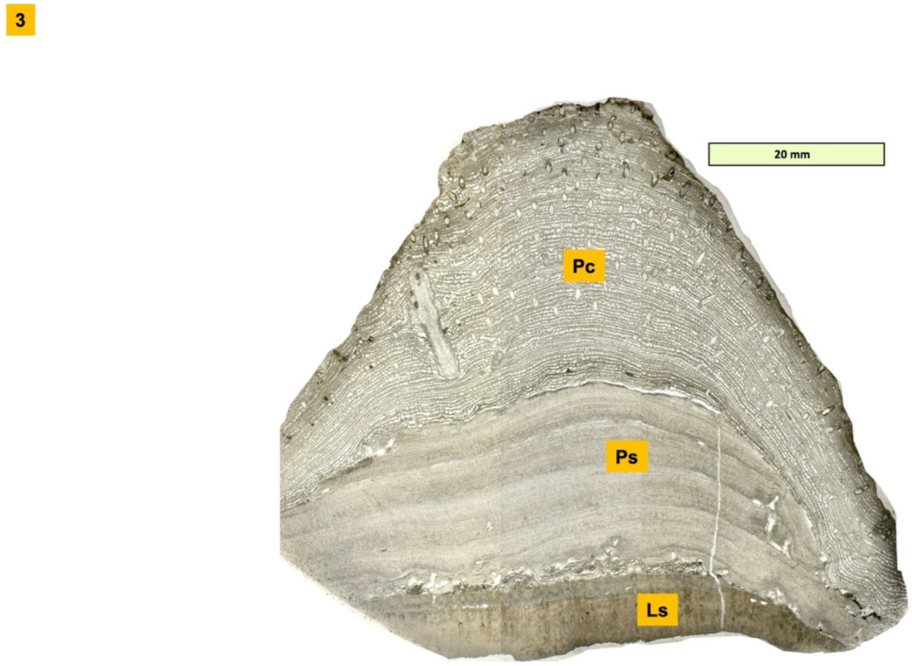


Fig. 3.23-View3-Overview. A different thin section from the same sample as previous two figures, showing a similar sequence, showing that the lower part of the Pc also lacks syringoporids, but higher up they are abundant. Compare this with the previous two figures that show no syringoporids, noting that those two figures are also in the early part of the Pc growth. This sequence of figures demonstrates that the appearance of syringoporids in Pc occurs at different levels in different specimens, and adds to the evidence that the syringoporids found the Pc specimens on the sea floor by chance; hence the stromatoporoid was fine without the syringoporids, but could not prevent them from indurating its structure, yet the syringoporids had no detrimental effect on the Pc growth. Don't you think this is amazing?! File: 50-KLoose54-Ls-Pc-Ps-Sample1-03.

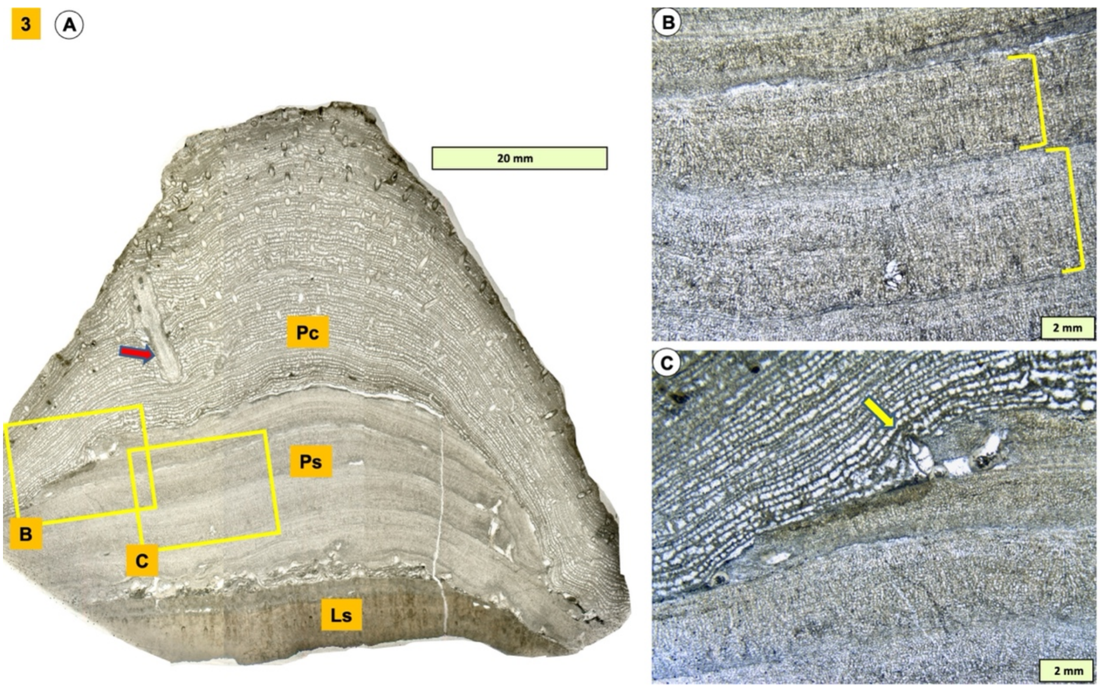


Fig. 3.23-View3A-C. The enlargement in [B] shows fairly regular growth interruptions in the Ps that are not recognisable on the right side of [A] as related to sediment deposition, so the cause of the

interruptions cannot be linked clearly to sedimentation, and may have been an orbital forcing feature. In [C] the lower part of Pc encrusted an apparently eroded Ps upper surface (yellow arrow); also the lower part of Pc does not contain symbiotic syringoporids, as in Figs. 3.23-Views1&2.
File: 51-KLoose54-Ls-Pc-Ps-Sample1-04.

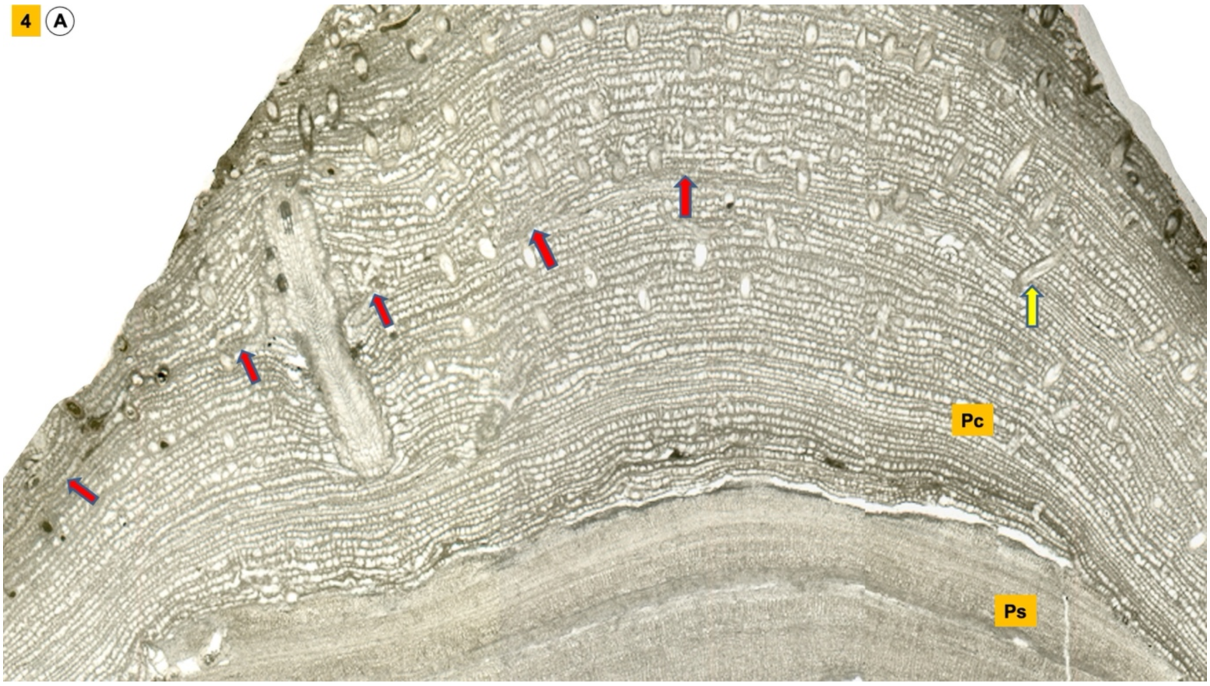


Fig. 3.23-View4A. Following on from previous figures, the Pc shows syringoporids began growing across the same lamina of Pc, implying settlement of syringoporid larvae across the whole stromatoporoid surface at the same time. Red arrows point out a growth interruption event that does not affect the rugose coral, but causes minor disruption to the syringoporid tubes, some of which do not pass through the interruption, but some prominently do so (yellow arrow). File: 52-KLoose54-Ls-Pc-Ps-Sample1-05.

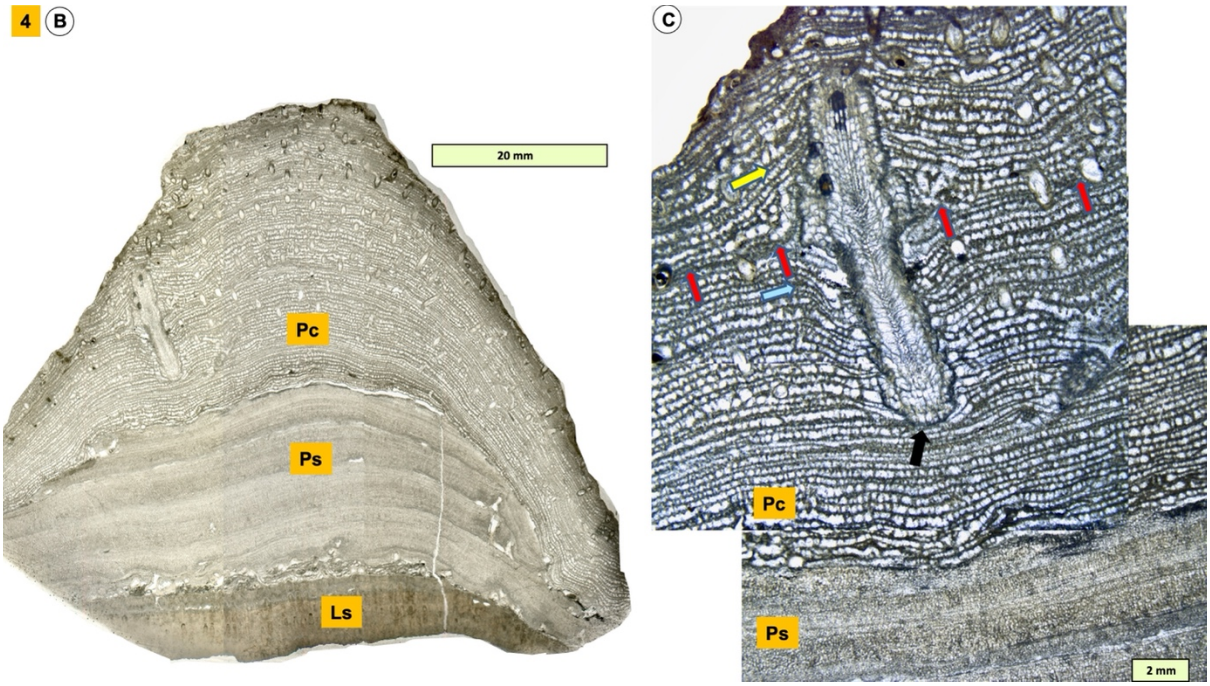


Fig. 3.23-View4B-C. Continuing from the previous figure, this shows more details of the relationship between the rugose and the Pc. Black arrow: seems to show the origin of the rugose on one level in the Pc, yet seems not to be associated with any growth interruption event in the Pc. Perhaps the rugose just began growing on the live stromatoporoid surface. Light blue arrow: Below the growth interruption event pointed out by red arrows, the Pc laminae bend down to the rugose likely indicating that Pc grew faster than the coral, and maybe the coral was struggling. Yellow arrow: above the growth interruption event the Pc laminae bend up to meet the coral, evidence that either the coral accelerated growth rate or the stromatoporoid slowed down. File: 53-KLoose54-Ls-Pc-Ps-Sample1-06.

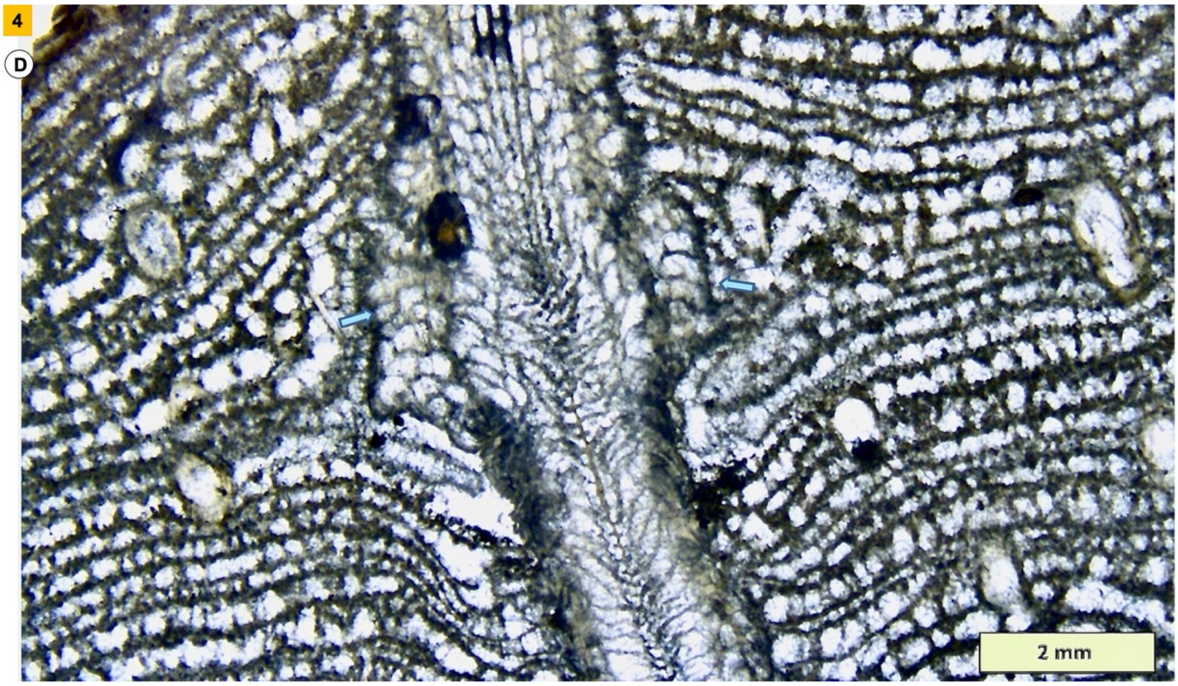
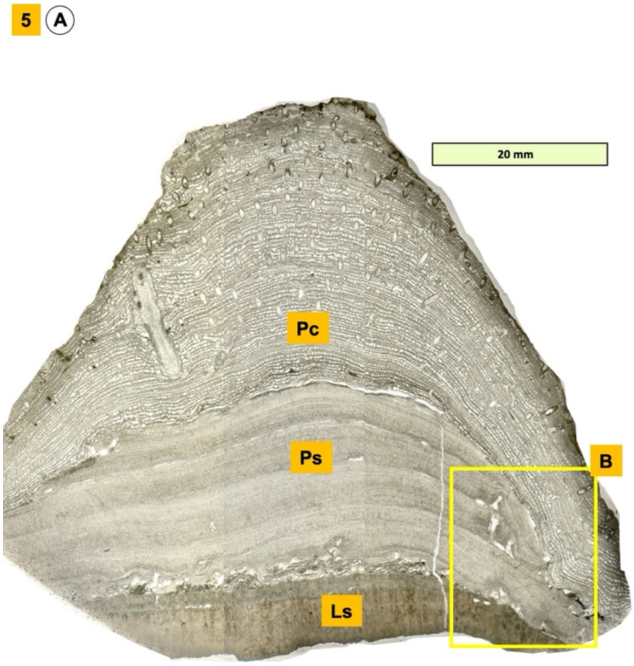


Fig. 3.23-View4D. Detail of central part of rugose coral from previous figure, showing the development of thickening of the rugose wall structure (light blue arrows) directly above the growth interruption surface. File: 54-KLoose54-Ls-Pc-Ps-Sample1-07.



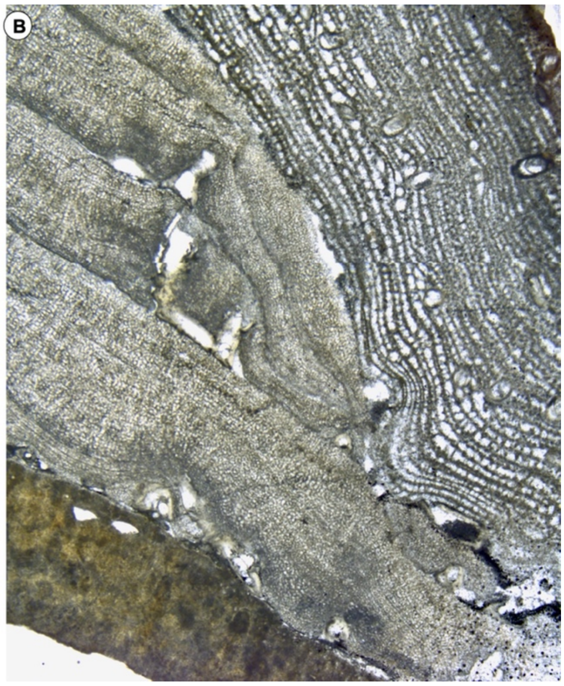


Fig. 3.23-View5A-B. Following from previous figures, this shows detail of the right margin of the Ps, where the growth banding shows decrease of growth of the central band of Ps growth, so the upper 2 bands grew down to meet the surface of the lower band; the second band became highly restricted here. There is no obvious reason why this sequence should have occurred, but the white areas in the Ps in this area may be related. These white areas are cement-filled but not obvious at this magnification is that auloporid corals are present as encrusters here; their location may have been detrimental to the Ps growth in this portion of the stromatoporoid, and is a potential example of parasitism. However, how to recognise parasitism in this case? Maybe the corals were simply blocking the stromatoporoid growth at this point, rather than deliberately taking resources from the stromatoporoid. Such discrimination is a big problem in stromatoporoids that needs further investigation to fully characterise the relationship. File: 55-KLoose54-Ls-Pc-Ps-Sample1-08.

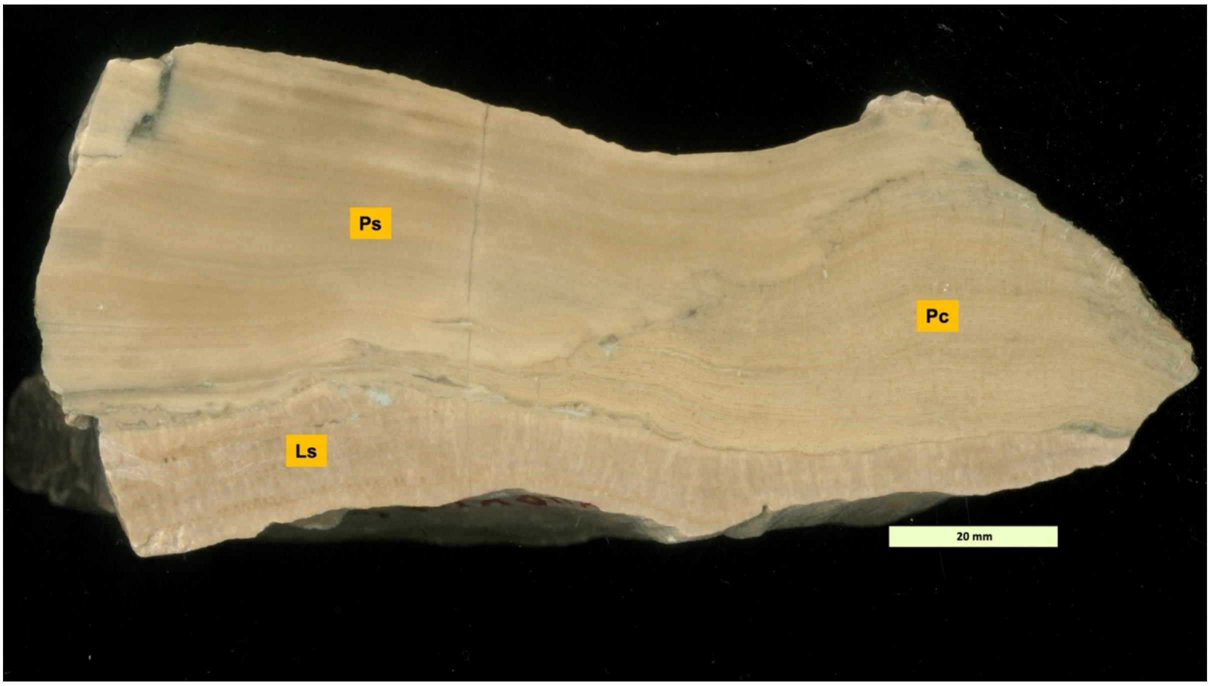


Fig. 3.24. [6 separate figures].

Fig. 3.24-HandSpecimen. Vertical section through part of sample showing stacked encrustations of stromatoporoids. At the base is the laminar plate of *Lophiostroma schmidti* (Ls) that in almost all cases where it is part of encrusting stacks is found only at the base of stacked encrustations in the Kuppen Marl (and in the overlying Lower Biostrome). Ls is also commonly found alone, presuming it died and was buried in sediment before encrusting stromatoporoids could make use of it. In this case, auloporids (not clear on this photo), then *Petridiostroma convictum* (Pc) built on top of the Ls and then *Plectostroma scaniense* (Ps) arrived; you will see in the subsequent photos that the Ps and Pc seem to be competing for space, adding another aspect to the complex biology evident in these associations. File: 56-KLoose54-Ls-Pc-Ps-Sample2-01.

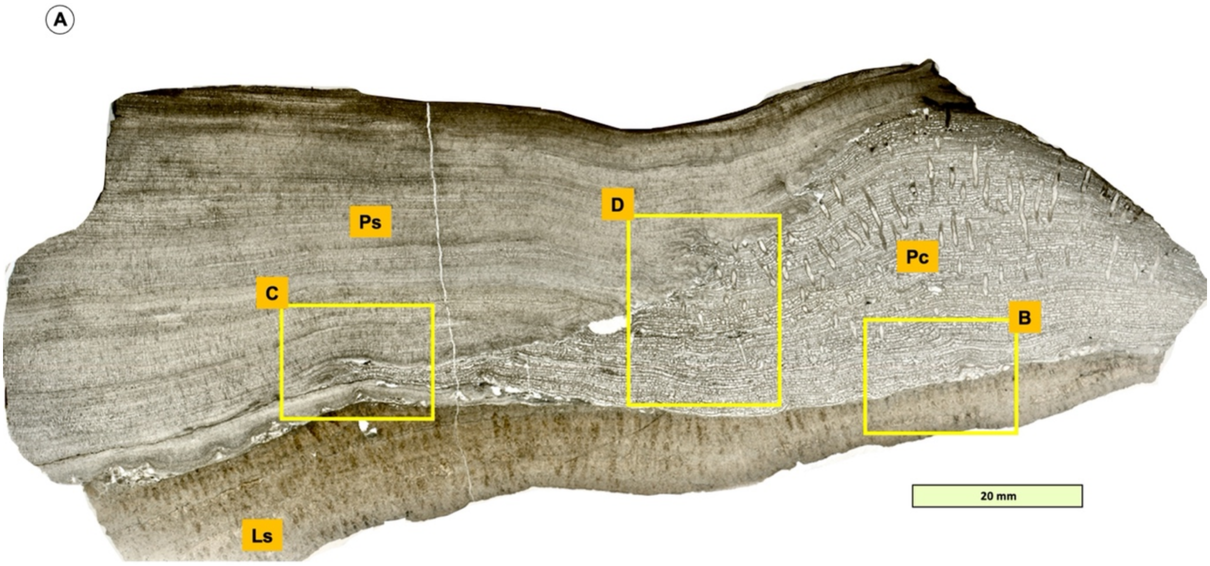


Fig. 3.24A. Whole thin section in VS of hand specimen in previous figure, showing overall sequence of this sample and locations of enlargements in subsequent figures. Note that *Lophiostroma schmidti* (Ls) has encrusting auloporids on its top surface. *Petridiostroma convictum* (Pc) shows abundant syringoporid symbionts in the upper ¾ of its thickness, but the lower ¼ has none, indicative that the syringoporid larvae did not discover the Pc until the Pc had been growing for some time. The syringoporids occur in only the Pc, not either Ls or Ps, emphasising a biological relationship between Pc and syringoporids. The Ps and Pc are tightly in contact, and subsequent figures show they may have been competing for space. File: 57-KLoose54-Ls-Pc-Ps-Sample2-02.

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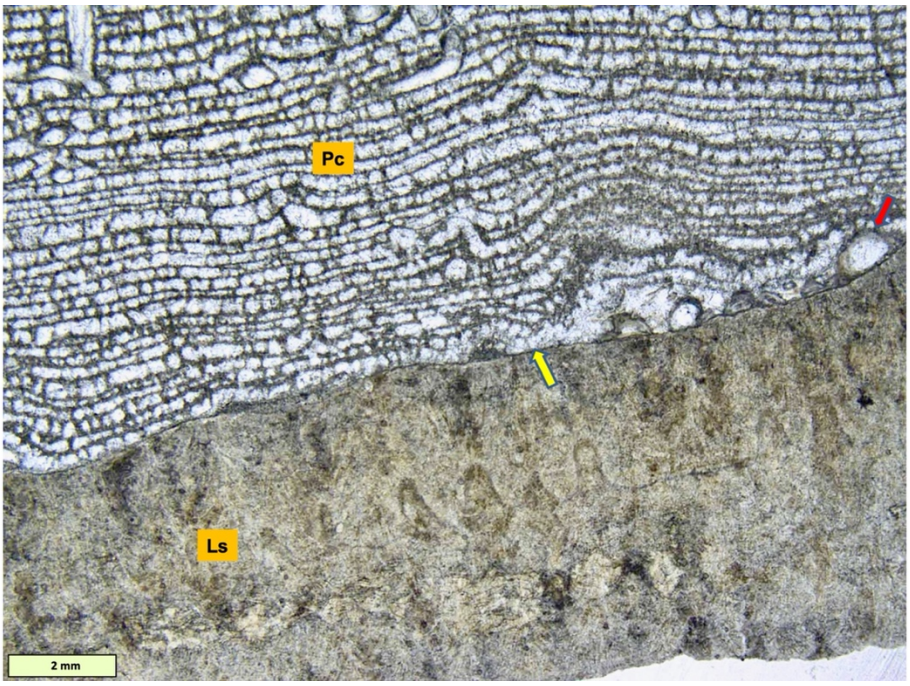

Fig. 3.24B. VS enlargement of Ls and Pc. Note the smooth upper surface (yellow arrow) of Ls, which may indicate it was eroded prior to encrustation by auloporids (red arrow) and by Pc. Note the syringoporids are not present in the early part of the Pc growth but notice the small tube-like structures just below and below right of the “Ps” label on the photo; these look like syringoporid tubes, but: 1) are isolated in the specimen; 2) have small upward inflections of Pc laminae directly above and 3) merge with the stromatoporoid structure rather than being discrete tubes; 4) they are inconsistent with the usual case that syringoporids normally appear right across the Pc sample at one level. Such features are not always easy to resolve as to whether they are actually another organims or are part of the stromatoporoid structure; in this case these are VS through astrorhizae (canals carrying excurrent water tubes in sponges). If you are brave enough to delve deeply into stromatoporoid taxonomy you will find in taxonomic descriptions of Pc that it has rare astrorhizae; this is stated by Mori (1970, p. 88 and Plate II, figs 3-6) cited in the reference list. You can be sure they are astrorhizae and not syringoporids because those two tubes merge into the gallery space of the stromatoporoid, and are thus part of the stromatoporoid structure. There are more astrorhizae above-right of the “Ps” label at the top of the picture. File: 59-KLoose54-Ls-Pc-Ps-Sample2-04.

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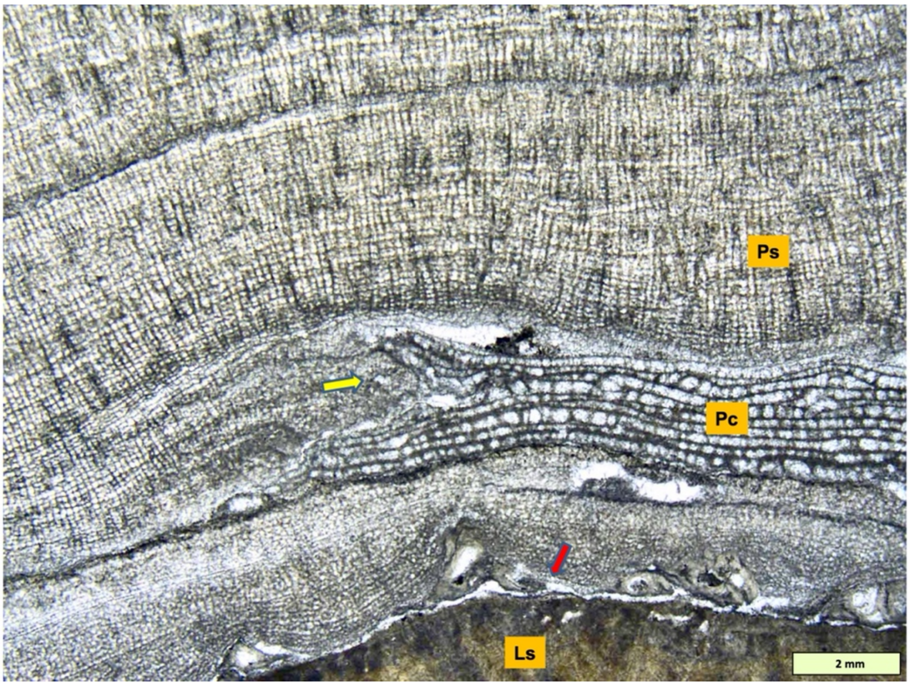

Fig. 3.24C. Details of relationships between stromatoporoids in this sample. Red arrow area shows encrusting auloporids on top surface of Ls. Yellow arrow seems to show competition between Ps and Pc, which is unusual. File: 60-KLoose54-Ls-Pc-Ps-Sample2-05.

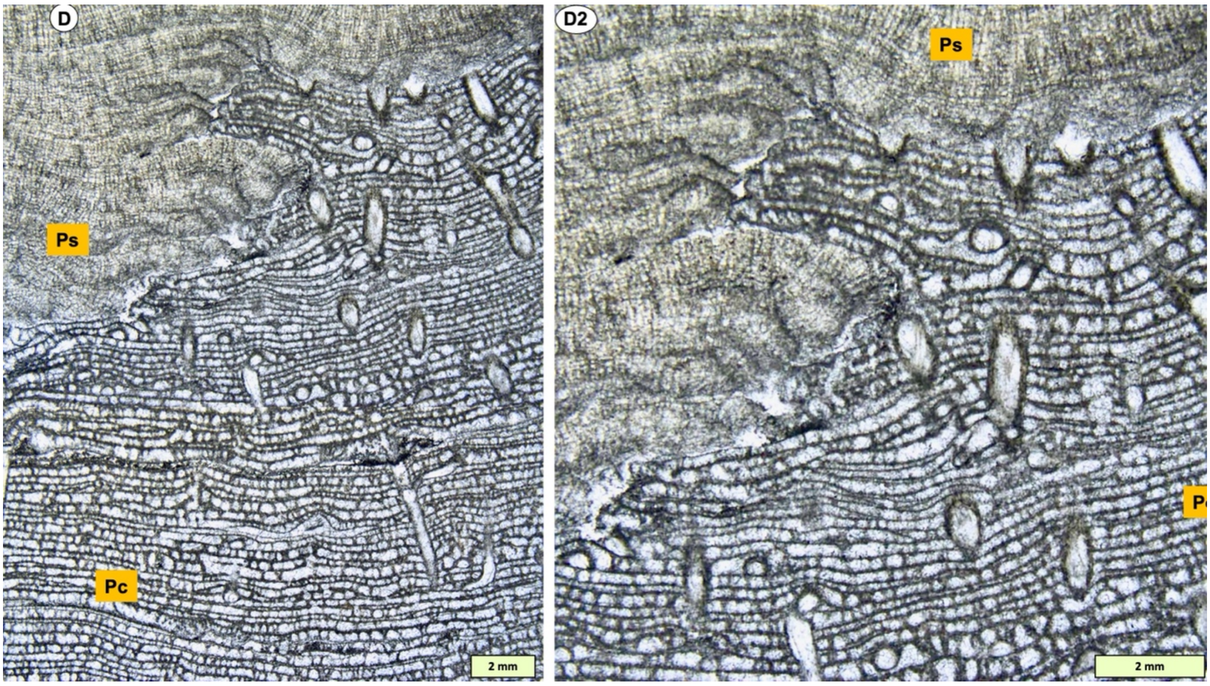

Fig. 3.24D. More details of interaction between Pc and Ps that are tightly intergrown with no sediment present; thus it is most reasonable to interpret this relationship as competition between the two stromatoporoid taxa. It seems that Ps was the winner, bravo! Note the syringoporids in Pc stop abruptly at the contact with Ps, and do not pass into the Ps; this adds to the view that there was a biologically faithful relationship between Pc and syringoporids. File: 61-KLoose54-Ls-Pc-Ps-Sample2-06.

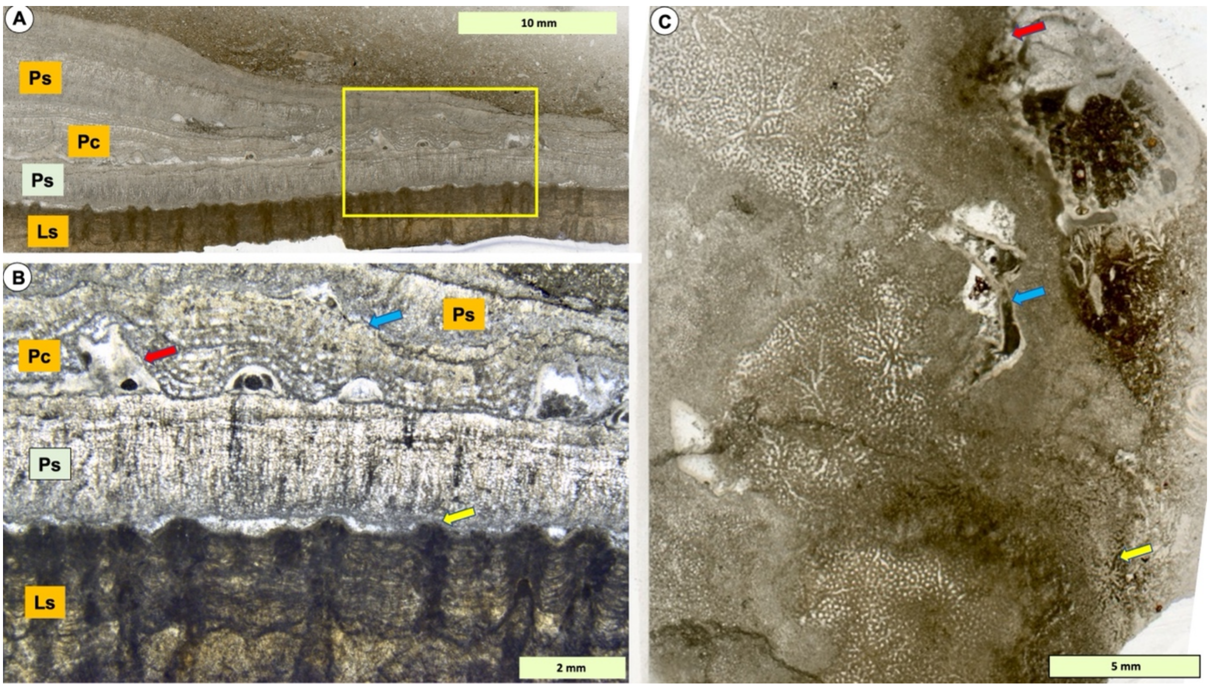

Fig. 3.25. Another specimen of stacked encrustations of Ls, Ps and Pc, showing details of encrusting relationships. **A)** whole thin section in VS. **B)** Enlargement of box in [A]. Yellow arrow shows papillae of Ls and a small primary cavity below the overlying Ps. Red arrow shows auloporids encrusting the top surface of the Ps, indicating it was dead before the auloporids grew. Just above the red arrow is evidence, somewhat indistinct, of a very thin growth of Pc, that barely got going before Ps came again. Blue arrow shows a somewhat indistinct irregular boundary in the sample and seems to be within the Ps. Such indistinct structures are not rare in stromatoporoids and may interfere with a clear understanding of the meaning of the structure. **C)** TS through the Ps portion of the sample, showing very nice astrorhizae that are common in this taxon (in contrast to rare astrorhizae in Pc as mentioned in previous figure caption). Yellow arrow shows contact with enclosing sediment. Blue arrow shows auloporids, with sediment in one tube; note that this is not likely encrusting the Ps but is a fortuitous TS through an auloporid that is slightly older than the Ps, which is simply surrounding the auloporid tube. Red arrow shows adpressed relationship with a rugose coral in TS; it seems the two are simply grown up against each other. File: 62-KM04-Ls-Ps-Pc.

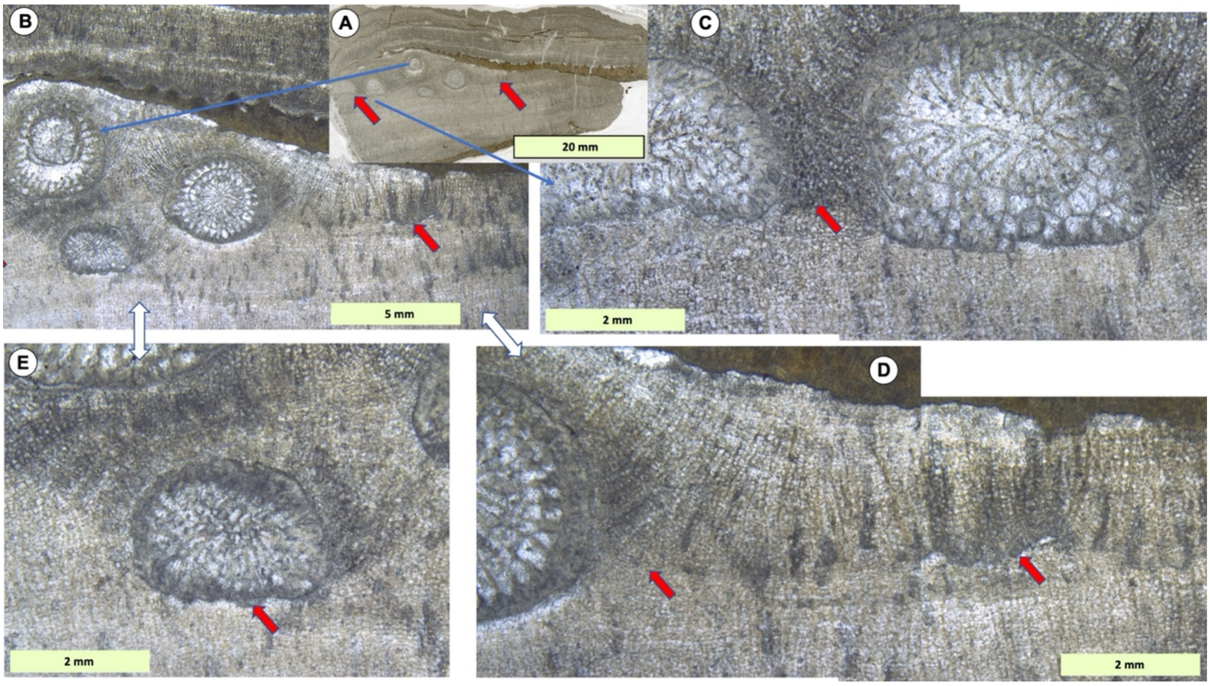

Fig. 3.26. VS through *Plectostroma scaniense* (Ps) with associated rugose corals. **A) whole thin section; B)** detail of central part of section; note the unusual case of *Lophiostroma schmidti* (Ls) encrusting the Ps, and there is another Ps on top of the Ls. In the lower Ps, whether the corals were actively symbiotic intergrowths in the Ps is a matter of debate; the corals are cut in TS and seem to be using the Ps as a substrate. However, the relationship is made difficult to analyse by the narrow irregular lines running horizontally through parts of the sample **[C, D, E**]; these are pressure solution lines (stylolites) that are common in stromatoporoids. Note that stylolites are normally associated with accumulation of clay along the pressure line, because clay is almost always present as a minor component in limestones. But this is a pressure line running within a stromatoporoid skeleton, that is made of pure calcium carbonate, so in this case there is no dark line of residual clay. File: 63-KM11-Ls-Ps-Rugs.

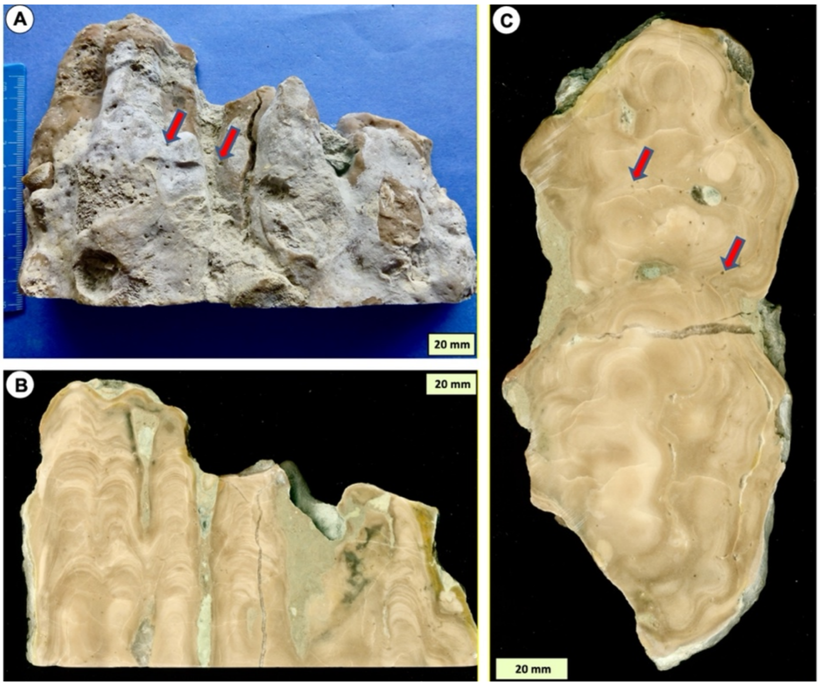

Fig. 3.27A-C. *Plectostroma scaniense* (Ps) showing its creative abilities as a growth form; here the entire sample is composed of merged columns. In **A)** the side view surface is dotted with small dark spots (red arrows) that are the exits of intergrown tubes present in the sample. **B)** is a VS showing the beautiful merged columns. **C)** is a TS showing the amalgamation of the columns with dark spots of intergrown tubes highlighted by red arrows. Next figure shows details of the intergrown tubes. File: 64-KLoose31-Ps-Columns-SpiralTubes-01.

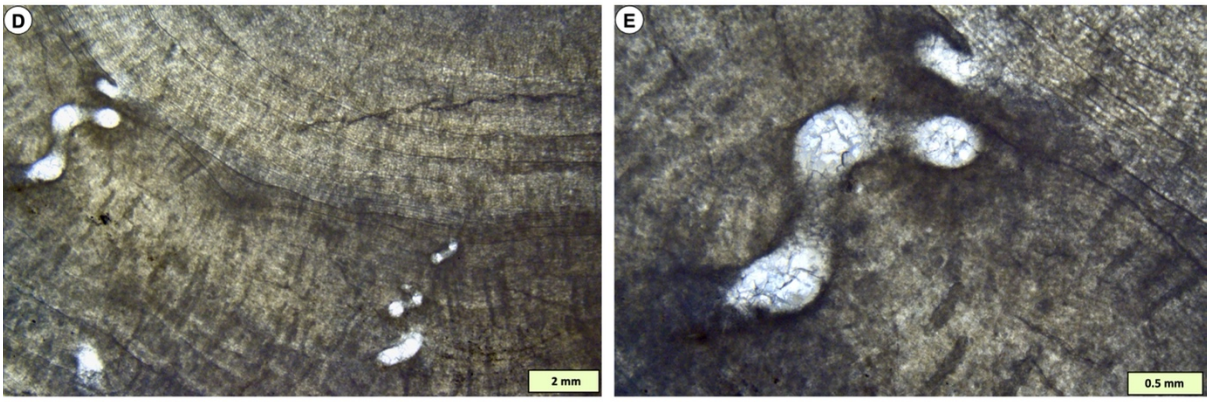

Fig. 3.27D-E. Enlargement of thin section from previous figure sample showing spiral tubes intergrown within the Ps. It is rather interesting that in other figures of Ps in this document such spiral tubes seem to be uncommon. But this sample shows that Ps can also harbour symbionts. In [E] the wall structure of the symbiont is unclear; it seems that there *is* a wall but it is not entirely clear, and this could be a bioclaustration; perhaps we could call it a “biofrustration”; it could be resolved by making a thinner section of this specimen. File: 65-KLoose31-Ps-Columns-SpiralTubes-02.

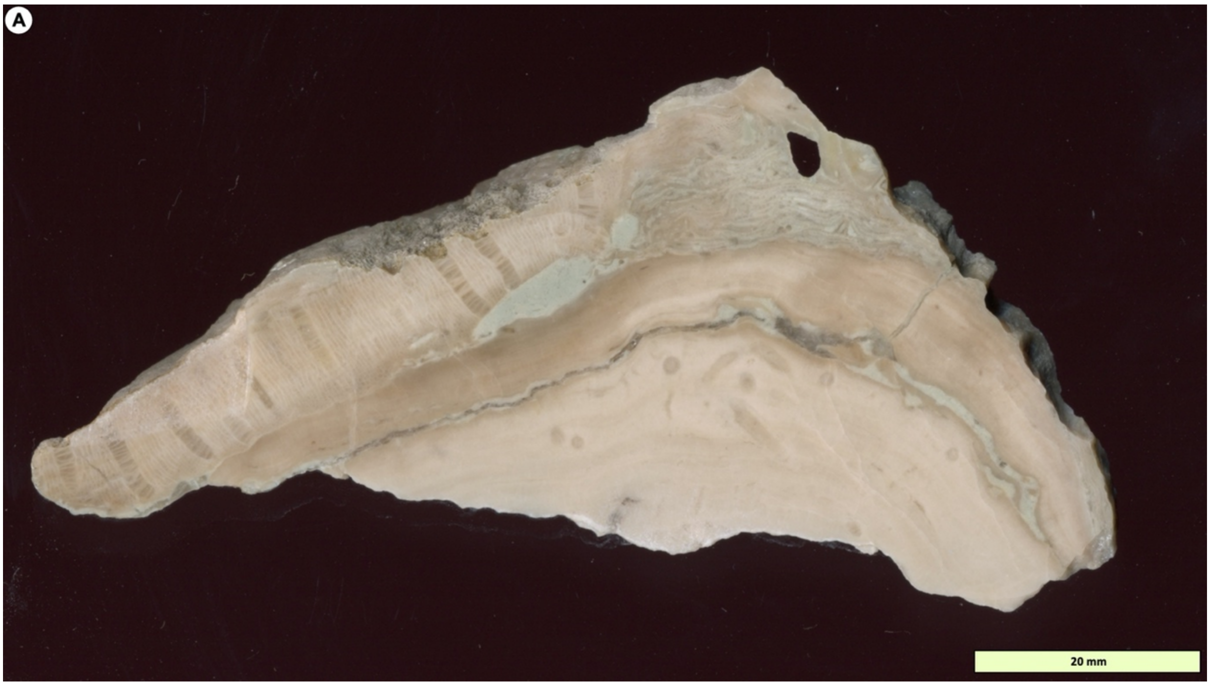

Fig. 3.28A. VS of hand specimen of stacked encrustations of three stromatoporoids and a heliolitid tabulate. The two lower stromatoporoids, separated by a growth interruption with sediment, are *Plectostroma scaniense* (Ps); the upper stromatoporoid is *Simplexodictyon yavorskyi* (Sy) that looks a bit like Pc, but has a much bigger laminae and pillar structure and has an overall different construction. The black blob near the top of the sample is a hole because the sample was very thin at this point. File: 66-KLoose26-K4MUD-Ps-Helio-01.

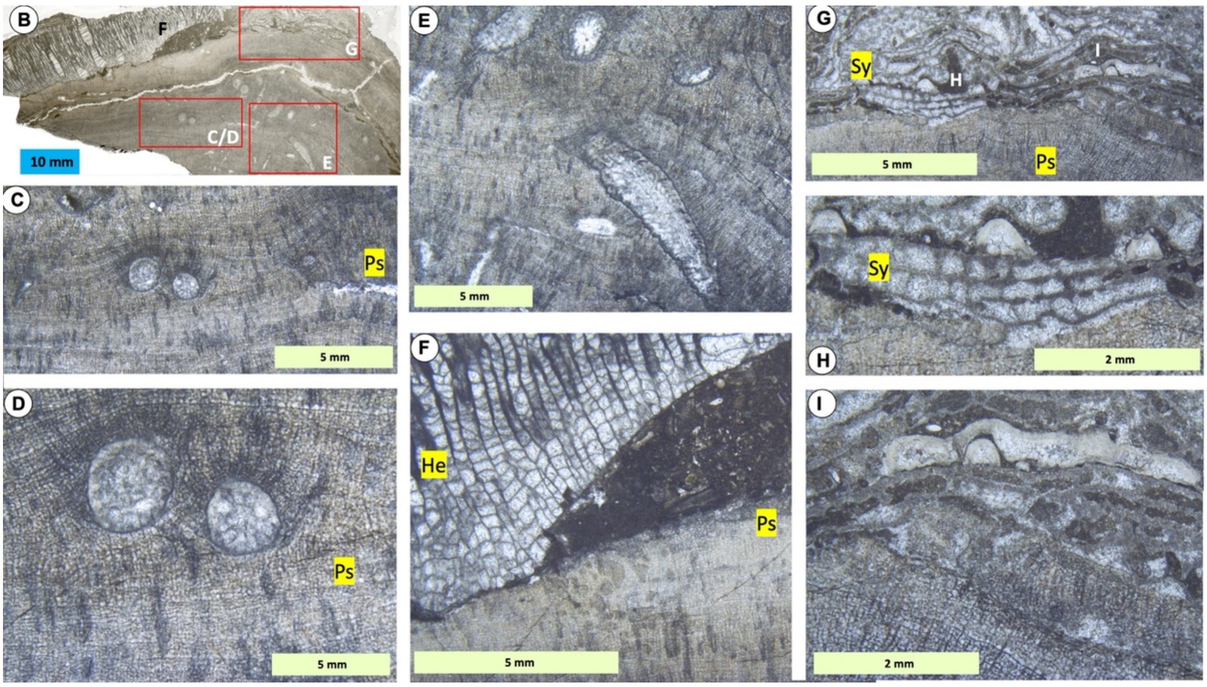

Fig. 3.28B-I. B) Whole thin section VS, in which you can see that the lower Ps has intergrown corals, but the upper Ps lacks them. **C-D)** Enlargement of box in B of Ps with two corals; the Ps skeleton reacted to their presence, growing around and encasing the coral tubes. However, in this plane of section it is not possible to determine whether the coral calyces are open to the surface or not. **E)** more examples of intergrown rugosa**. F)** the Ps was quite likely buried by sediment influx but then much was removed, and so the heliolitid could grow on a mixture of Ps skeletal surface and sediment;

certainly there is a growth interruption at the top of the Ps. **G-I)** details of contact between Ps and encrusting Sy together with auloporids in the Sy indicating growth interruption at an early stage of development of the Sy. Note that Fig. 3.28A shows the heliolitid overgrew the top of the Sy so Sy was relatively short-lived. File: 67-KLoose26-K4MUD-Ps-Helio-02.

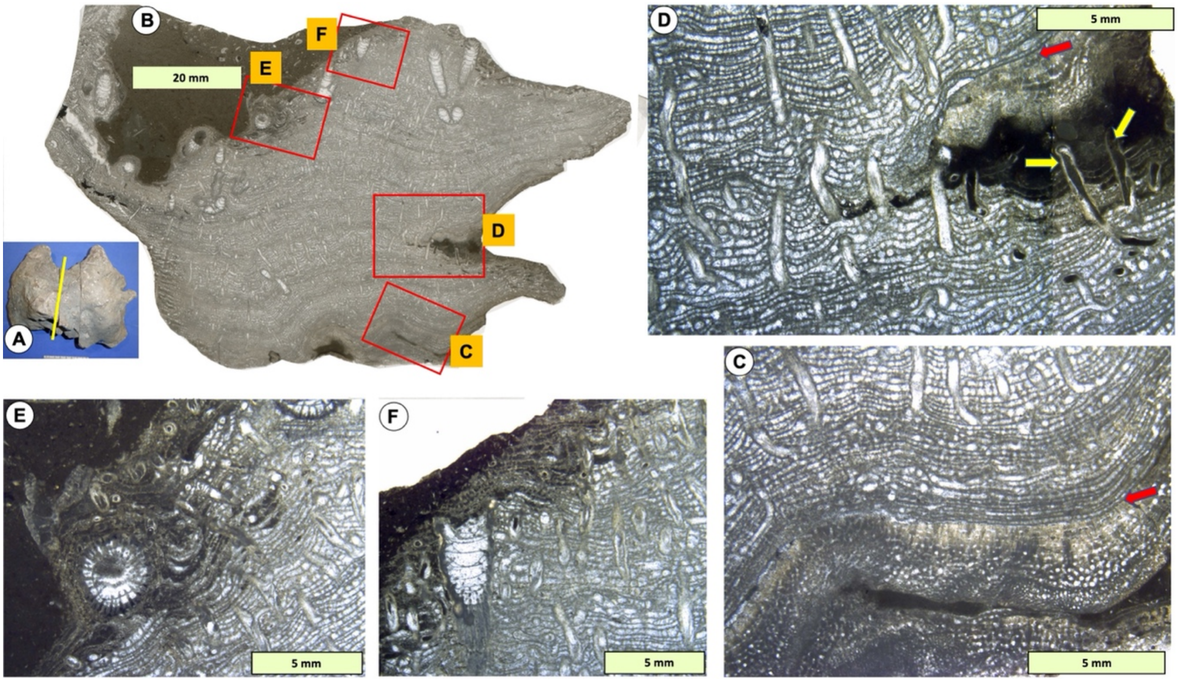

Fig. 3.29. *Petridiostroma convictum* (Pc), with small area of *"Stromatopora" venukovi* (Sv) at the base. **A)** Sample, top view, showing line of cut of B-F. **B)** whole thin section VS showing buildup of this specimen in relation to sedimentation. It is essentially a low domical form that is modified by sedimentation events into a more irregular overall shape, but the internal growth lines demonstrate its low-profile tendency. **C)** basal part showing Sv in lower half, lacking any syringoporids; note that some specimens of Sv contain abundant symbionts, but this one does not. In fact prior work (Mori 1970) showed that Pc in almost all cases had symbiotic syringoporids, but Sv contained them much less commonly; perhaps the syringoporids were more selective of Pc or alternatively required the right combination of circumstances to infest Sv; a topic for more investigation. Top surface of Sv here (red arrow) is encrusted by Pc, which is commonly found encrusting other fossils. The lower part of the Pc lacks syringoporids, a feature of many samples displayed in this document, and indicates the syringoporids found the Pc by chance rather than being obligate. **D)** Growth interruption in Pc, with some syringoporids indurated with fine sediment (yellow arrows); these syringoporid tubes protruded above the Pc surface, a common feature, indicating separation of the living tissue in the syringoporid tube tops from the stromatoporoid surface. Look carefully above the yellow arrows: there is sediment and a small growth of Sv again, but that gets quickly overrun by Pc; we might theorise that Pc grew faster than Sv. **E-F, compare with B)** There are two small rugose tubes in the lower left of the Pc, otherwise the corals are in the upper part of the stromatop. It seems that rugose corals mostly associated with this sample of Pc at a later stage in its life, showing a quite different growth relationship compared to the syringoporids. Does this mean that the population of rugosans in this setting was less abundant, or that the rugosans didn't feel the need for settling on stromatoporoids as much as the syringoporids did? Or can it be that the stromatoporoid actively discouraged the rugosans from settling on it, but in some cases did not succeed? Are there any other possible interpretations of the relationship between the corals and Pc? File: 68-K4Mud-2017-08-Pc-Sv-Rugs.

3.3. Summary of the Kuppen Marl stromatoporoids and their symbionts.

The sample of Kuppen Marl stromatoporoids assembled for this study contains a total of 48 specimens; their numbers and features are summarised as follows:

Lophiostroma schmidti (Ls):
11 individuals
Growth form: laminar
Substrate: 10 were on sediment, 1 encrusted another stromatoporoid (Ps)

Petridiostroma convictum (Pc):
4 individuals
Growth form: laminar to domical*
Substrate: all on other stromatoporoids, none on sediment

Plectostroma scaniense (Ps):
12 individuals
Growth form: laminar to domical to columnar*
Substrate: all on other stromatoporods, none on sediment

“Stromatopora” bekkeri (Sb):
5 individuals
Substrate: one on sediment but other 4 have incomplete basal portions.

Clathrodictyon mohicanum (Cm):
11 individuals
Growth form: laminar
Substrate: all on sediment

“Stromatopora” venukovi (Sv):
4 individuals
Growth form: laminar to domical*
Substrate: all on sediment

Simplexodictyon yavorskyi (Sy):
1 individual
Growth form: domical
Substrate: another stromatoporoid.

*Prior work shows these taxa begin as a laminar form and develop into a domical form if they large enough; so laminar forms are small early stages of the growth.

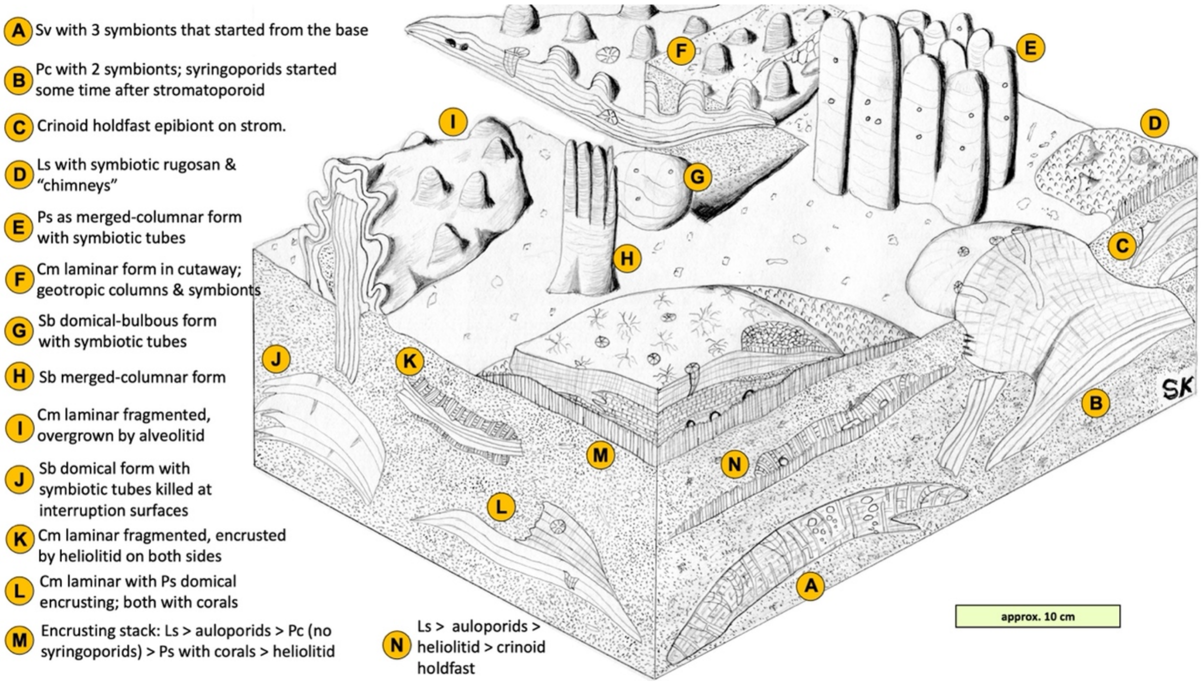

Fig. 3.30 – Reconstructions of the stromatoporoids at Kuppen. Ls = *Lophiostroma schmidti*; Pc = *Petridiostroma convictum*; Ps = *Plectostroma scaniense*; Cm = *Clathrodictyon mohicanum*; Sb = *"Stromatopora" bekkeri*; Sv = *"Stromatopora" venukovi*.

Fig. 3.30A. A reconstruction of the stromatoporoid assemblage during Kuppen Marl times. The items illustrated are inspired by images in the photo figures. Please note the scale is a little flexible because of space issues on a page; items in the forefront are shown enlarged to reveal their details.

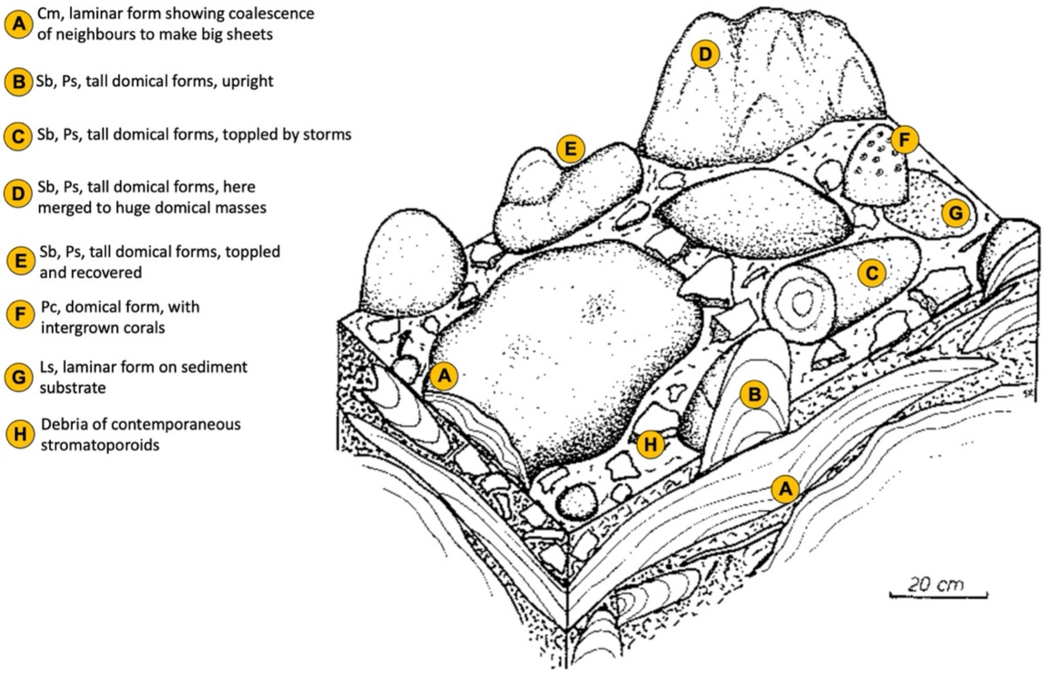

Fig. 3.30B. Reconstruction of the overlying Lower Biostrome. Diagram from Kershaw (1990. Stromatoporoid palaeobiology and taphonomy in a Silurian biostrome on Gotland, Sweden. *Palaeontology*, **33**, 681-705), acknowledgment to The Palaeontological Association. Annotations added to compare with Fig. 3.30A (note the difference in scale).

The three most abundant taxa in the Kuppen Marl (Ls, Pc, Cm) are also abundant in the overlying Lower Biostrome; noting that only 48 samples will have some bias in regard to overall taxa distribution, but the stromatoporoid suite of the Kuppen Marl is essentially no different from the Lower Biostrome that overlies it, and indicates that the assemblages are fundamentally the same. Furthermore, the distribution of symbionts in the Kuppen Marl stromatoporoids is in the same taxa as in the Lower biostrome, so relationships between organisms between this marly facies and the purer limestone facies are not really any different. However, note that the Kuppen Marl is in the same location and setting as the Lower Biostrome and these are strongly contrasting the deeper water marly facies such as the Hemse Marl to the WSW of the Kuppen area. In the Hemse Marl, stromatoporoids are smaller, different taxa and have very rare symbionts intergrown. A compilation of stromatoporoids in the Silurian of UK (Kershaw et al. 2021b), close to the developing Caledonian suture zone, shows that in the Midland Platform region of England, there are NO recorded cases of intergrown corals in stromatoporoids, part of the interpretation that those stromatoporoids grew towards the margins of their ability to survive a changing environment, despite the presence of small reefs there. Although intergrown in stromatoporoids are essentially a reefal-facies phenomenon, it seems the conditions had to be very good before such symbioses developed. The giant carbonate platform that occupied the Baltic region on stable continental crust, during a period of raised sea level provided the regional conditions for luxurious reef growth and enabled symbionts to develop.

4. STROMATOPOROIDS AND THEIR SYMBIONTS FROM THE "LOWER BIOSTROME", HEMSE GROUP (LUDLOW, SILURIAN), AT KUPPEN, EASTERN GOTLAND, SWEDEN

In the introduction to Section 3 is illustrated the stromatoporoid biostromes at Kuppen, so please look at Figs 3.1 and 3.2 for a visual overview of this setting, and reconstruction in Fig. 3.30B. This informally-named unit is the subject of a large-scale palaeoecological study of stromatoporoids published in several papers since 1981 (see citations), including a published focused study on stromatoporoid-coral intergrowths (Kershaw 1987). Thus a detailed description of this site and its stromatoporoid assemblage is not repeated here but if you want to know all the detailed background, please see the reference list and references therein. Basically, this biostrome is built almost completely by stromatoporoids, with very few corals, and no algae (nobody knows why there are no algae, this is very peculiar). Yet it formed in shallow marine conditions and was subject to repeated erosion, forming a stack of biostromes with overlapping rocky shoreline features. The biostrome environment was relatively low energy, interspersed with episodic storms; it may have been a back-barrier setting, like a lagoon, but the palaeophysiography of the outcrops has not yet led to confirmation of the setting. The stromatoporoid assemblage is dominated by *Clathrodictyon mohicanum* (Cm) that makes up ca. 40% of all stromatoporoids sampled [about 500 specimens]; also common are *Plectostroma scaniense* (Ps), *"Stromatopora" bekkeri* (Sb), *Lophiostroma schmidti*

(Ls) and *Petridiostroma convictum* (Pc), all of which are illustrated in the previous section for the Kuppen Marl. Thus the stromatoporoid assemblage of the Kuppen Marl simply continued up to build the giant megacity-style biostromes above.

The information provided below augments the general story outlined in the previous paragraph by display of images, with particular focus on the range of symbionts in stromatoporoids in the Lower Biostrome in order to further develop understanding of the lives of these organisms all those millions of years ago.

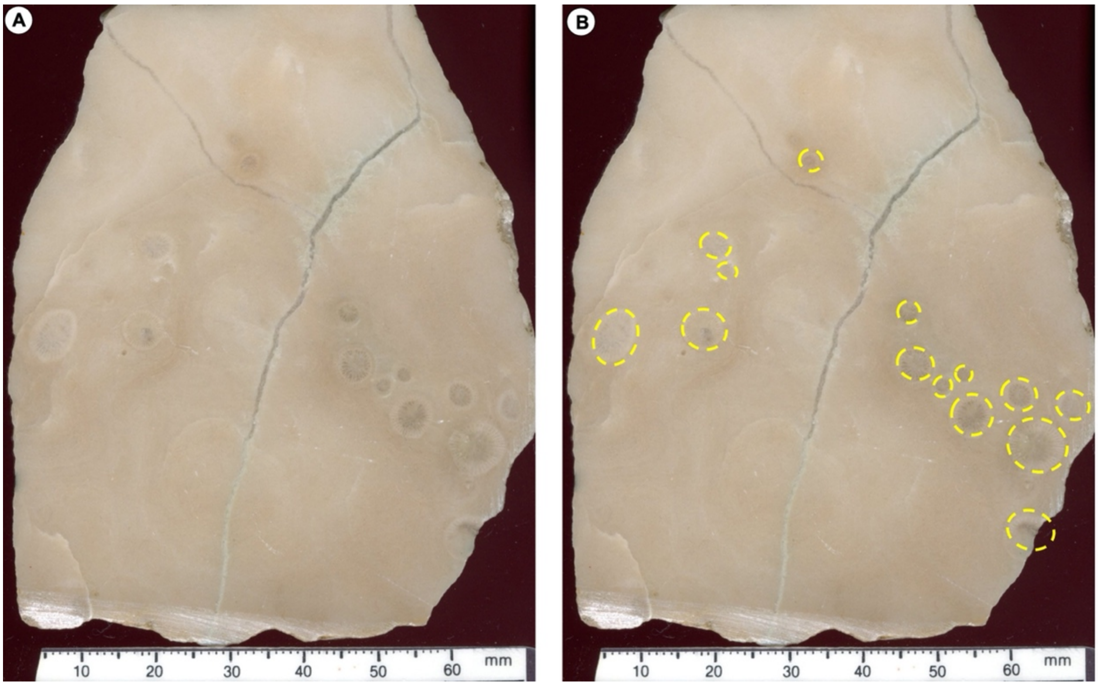

Fig. 4.1. TS through an unidentified stromatoporoid showing TS of rugose coral symbionts. **A)** the raw image. **B)** raw image with yellow ellipses indicating location of rugose corals. Note they are clustered because they are branching, so the corals underwent their own branching process while growing as symbionts in the stromatoporoid. There remains some uncertainty regarding the extent to which the rugose corals were biologically interacting with the stromatoporoids, in contrast to the syringoporid tabulates that are found in some taxa, which are shown in the Kuppen Marl photos above to have been much more tightly associated. File: 4.1-KLoose64-TSsampleStromAndRugosans-02.

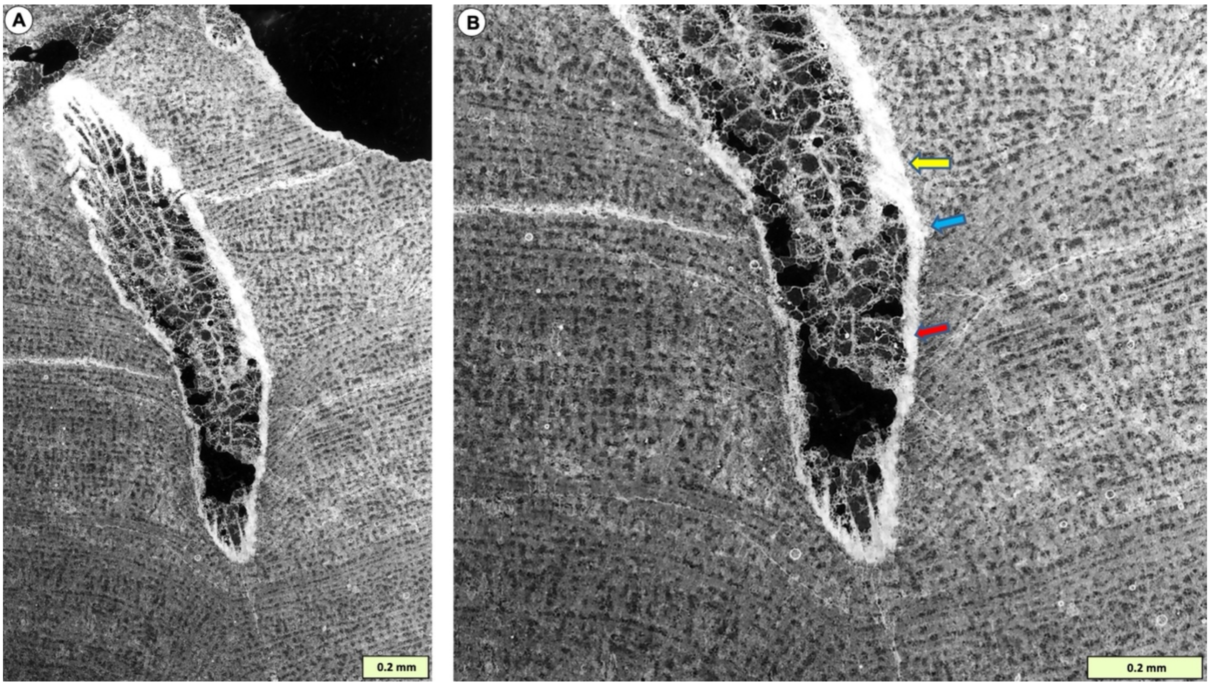

Fig. 4.2. VS of a negative image of thin section of *"Stromatopora" bekkeri* (Sb), with intergrown rugose coral. The origin and termination levels of the coral is unknown because it passes out of the plane of section bottom and top. Note the variation in relationship between the rugose coral tube and the adjacent stromatoporoid laminae. Red arrow shows laminae bend down to the coral, on both sides of the coral at that level; this may indicate the coral was growing slower than the stromatoporoid, or perhaps the coral had some discouraging influence on the stromatoporoid close to the coral, forcing the stromatoporoid to avoid the coral. However, at the level of the blue arrow, the downbending of stromatoporoid laminae becomes less, and by the level of the yellow arrow, the stromatoporoid laminae are bending up to meet the coral; nevertheless on the opposite side of the coral at the level of the yellow arrow, the stromatoporoid laminae are still downbending to the coral. So, overall, it is not clear why the stromatoporoid laminae have this trend of change of bending arrangement, but it is clear that the coral was having minimal, perhaps no, adverse effect on the stromatoporoid, which seemed to be able to grow quite happily alongside the coral. [This picture is from my 1979 PhD thesis]. File: 4.2-i-Sb-Rugs-KershawFig5.35-1.3mmW.

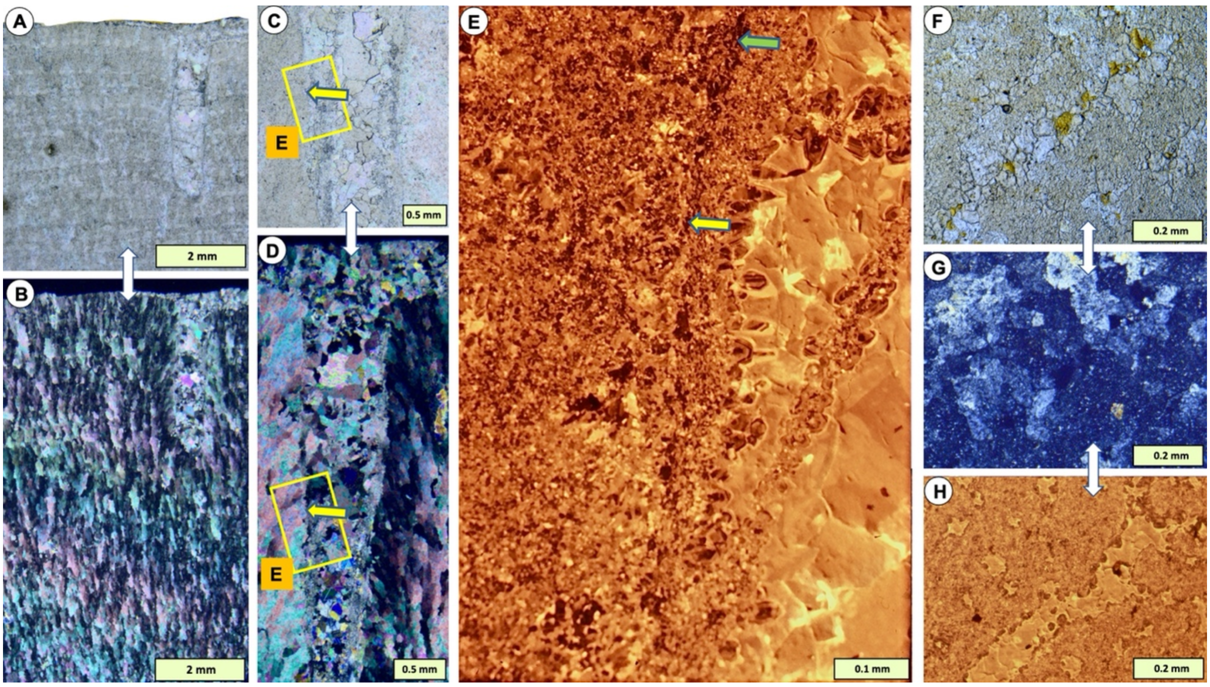

Fig. 4.2. Another sample of *"Stromatopora" bekkeri* (Sb) using a very thin section (about 25 microns, noting the excessively strong 3rd order birefringence in XPL view in B&D), and cathodoluminescence (CL) in [E,H]. **A-B)** VS of Sb in PPL and XPL; there is a rugose coral tube on right side. **C-D)** Enlargement of part of the coral tube showing its sparite fill; yellow box is enlarged in [E]; yellow arrows mark matched points. **E)** CL image from yellow box in [C-D], yellow arrow matches the same point in [C-D]; here the yellow arrow tip identifies the contact point between the outer edge of the rugose coral and the stromatoporoid skeleton that reveals a speckled appearance in CL. Green arrow marks another point of the outer edge of the coral. The CL image thus allows the edge of the coral to be precisely located, yet the coral skeletal structure does not look much different from the stromatoporoid structure here; the coral is partially recrystallised, uncommon for rugose corals, but demonstration that the original low-magnesium calcite of corals is not immune from alteration. Within the coral cavity is cement zoning of dark>bright>dull cements consistent with gradual burial into anoxic diagenetic environments. In the stromatoporoid, some areas of larger crystals in the CL image reveal where the galleries are located, in contrast to the skeletal material in the finer speckled areas. **F-H)** three matched-area photos of PPL, XPL and CL show the issues of studying stromatoporoids in thinner-than-normal thin sections. In PPL the stromatoporoid laminae are shown as indistinct finer-grained areas, the gallery cement is larger sparite; the brown-yellow patches are burn marks from the CL electron beam. In XPL [G] the stromatoporoid structure is not at all visible, as in [B] and [D], which is why I think that the use of microstructures in stromatoporoid taxonomy is worthless, because they are diagenetically over printed! The CL picture [H] shows the laminae, speckled areas, while gallery cement shows the same sequence of dark>bright>dull luminescent cement, matching the sequence in the coral cavity in [E]. File: 4.2-ii-4a6-8.50-Sb-Cauno-CL.

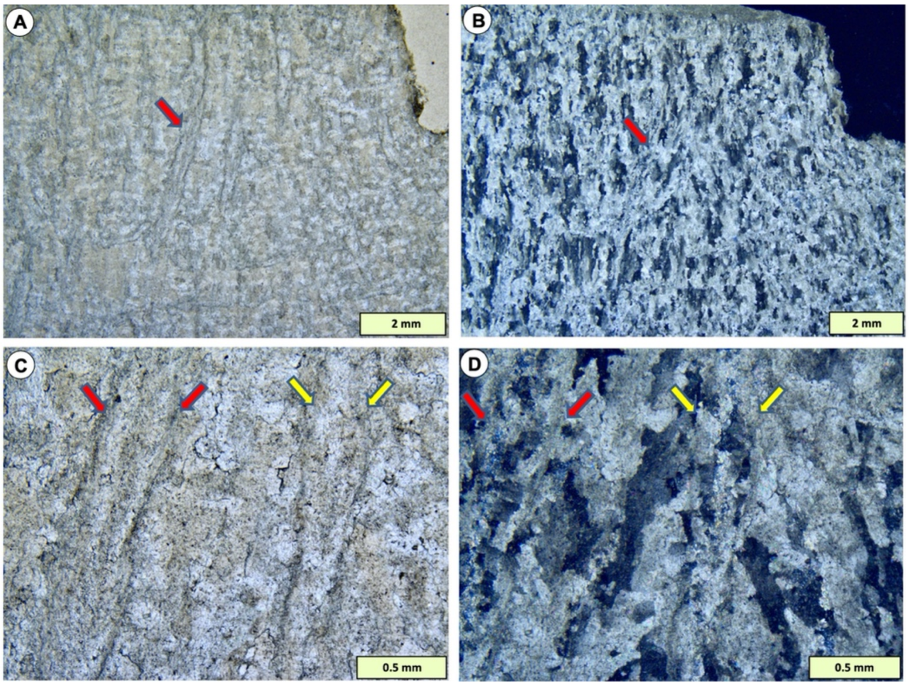

Fig. 4.3A-D. VS views of thinner-than-normal thin sections of *"Stromatopora" venukovi* (Sv) to illustrate more details of the character of syringoporid tabulates. **A-B)** PPL and XPL views showing syringoporid tubes intergrown with stromatoporoid skeleton; red arrow marks a matched point. Note in the XPL image the coral tube is almost invisible because of partial alteration along with the stromatoporoid. **C-D)** Enlargement of the central area of [A-B], with red and yellow arrows marking the outer edges of the left and right syringoporid tubes respectively, and these arrows also mark matched points between [C] and [D]. These photos emphasise the point that syringoporids are not so well-preserved in these specimens, and this is actually characteristic of intergrown syringoporids in stromatoporoids. File: 4.3-2c1-5.39-Sv-Cauno-01.

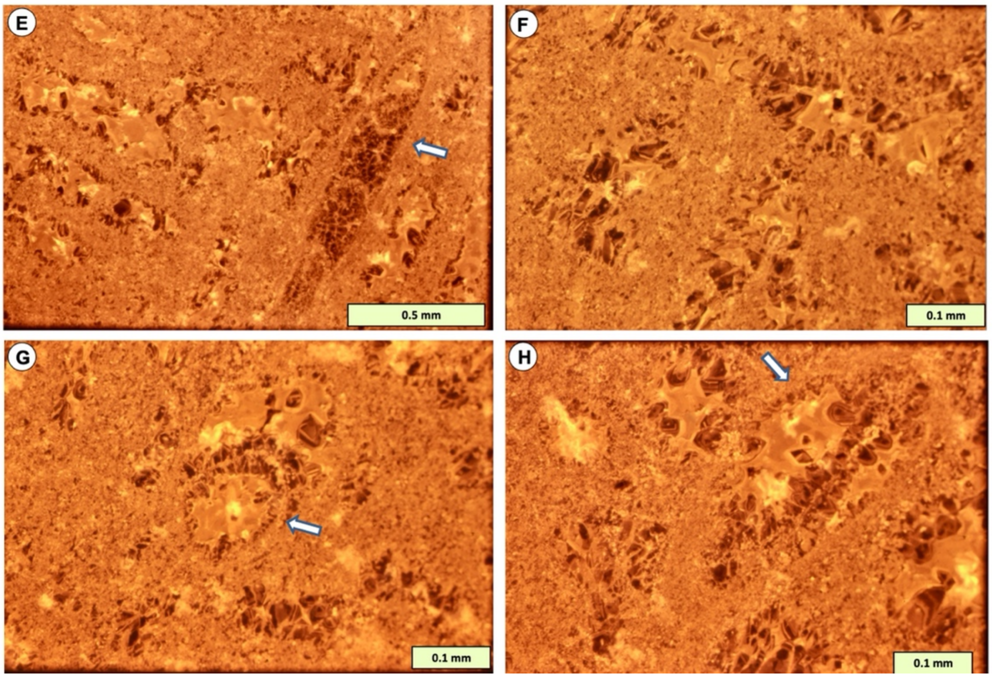

Fig. 4.4E-H. CL images from the same specimen as in Fig. 4.4A-D but not matched to normal-light images. These four photos show the speckled appearance of stromatoporoid skeletal structure, the sparite of gallery spaces and the similar speckled appearance of syringoporid tubes (white arrows) in [E – in VS], [G – TS] and [H – oblique]; [F] does not contain syringoporids. These pictures corroborate the normal-light views that indicate syringoporids are not well-preserved in these materials. File: 4.4-2c1-5.39-Sv-Cauno-02.

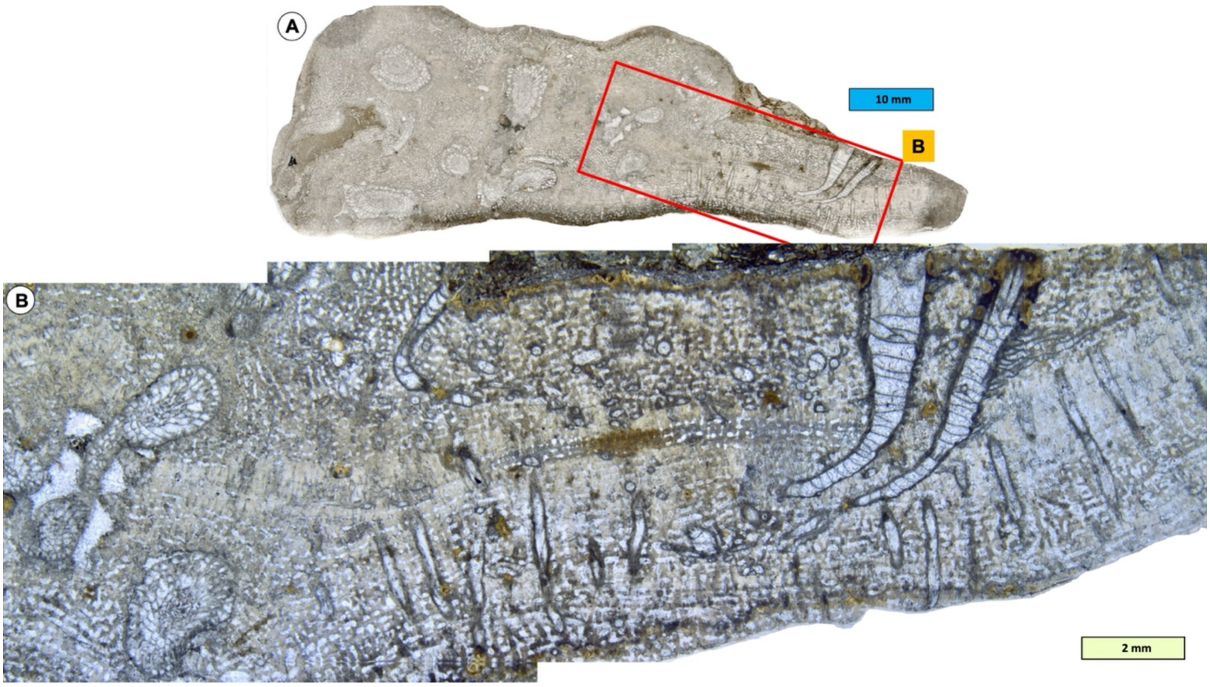

Fig. 4.5A-B. A) whole thin section in VS of *"Stromatopora" venukovi* (Sv) with rugose coral symbionts clearly visible. **B)** Enlargement of red box in [A] showing three symbionts are present in this sample: rugose corals, syringoporid tabulates and some rather indistinct spiral tubes, seen in more detail in the next 3 figures. File: 4.5-KLoose41-Sv-Rugs-Cauno-Tubes-01.

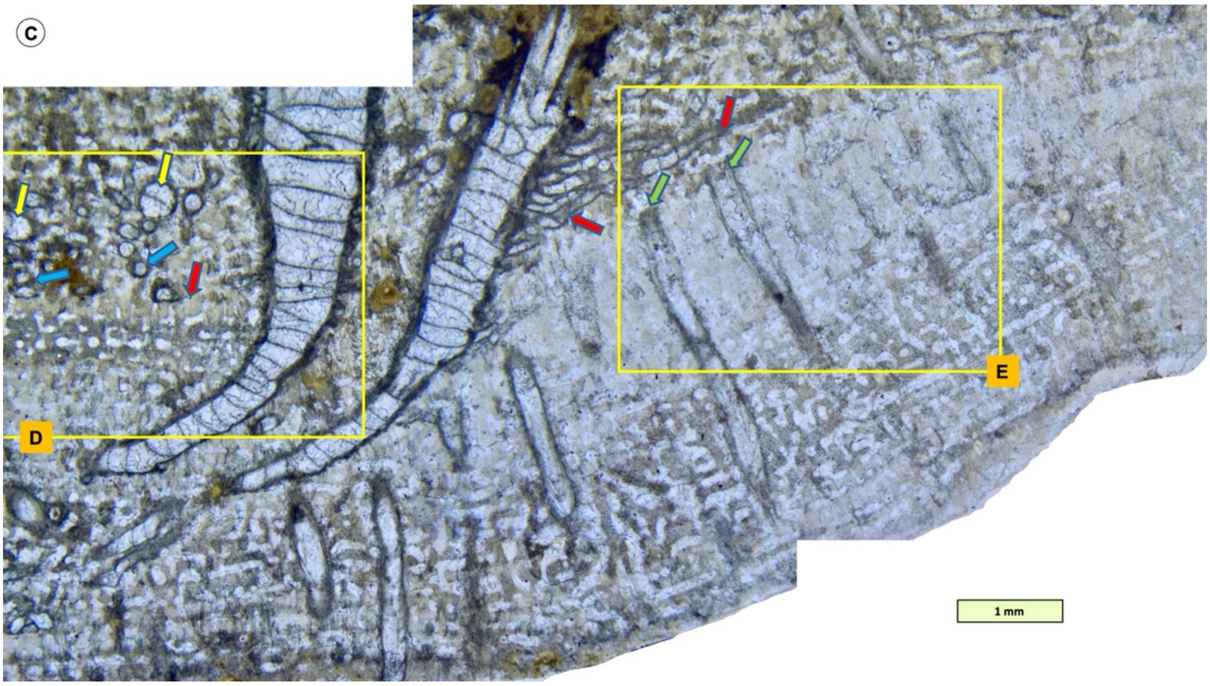

Fig. 4.5C. Enlargement of right-hand part of Fig. 4.5B revealing the three intergrown organisms, see [D] and [E] for details, where the arrow colours are explained. Note the syringoporid tubes inhabit the stromatoporoid from near its base. File: 4.6-KLoose41-Sv-Rugs-Cauno-Tubes-02.

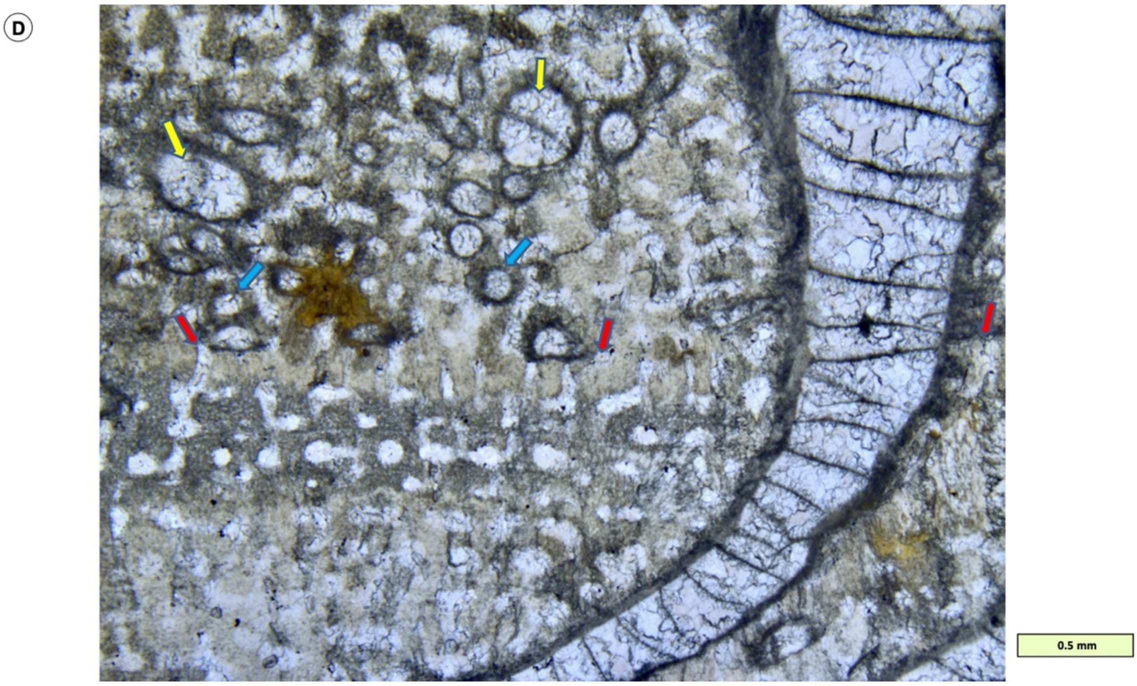

Fig. 4.5D. Spiral tubes and syringoporid tubes in the Sv structure. Red arrows show the origin level of the spiral tube (note the flattened bases of the tubes, encrusted onto the stromatoporoid skeleton); blue arrow points to a prominent part of the tubes, that occur as a series of ellipses vertically through this part of the specimen. However, the situation is complicated by two much larger ellipses (yellow arrows) that are cross sections through syringoporid tubes in this part of the structure that are actually passing within the spiral of the spiral tubes. Nearby to the right is a rugose coral tube. This picture therefore shows the close proximity of the symbionts to each other within the stromatoporoid, and we may wonder what interactions existed between the symbionts; maybe they had nice conversations, or hated each other, being trapped so close together. File: 4.7-KLoose41-Sv-Rugs-Cauno-Tubes-03.

E

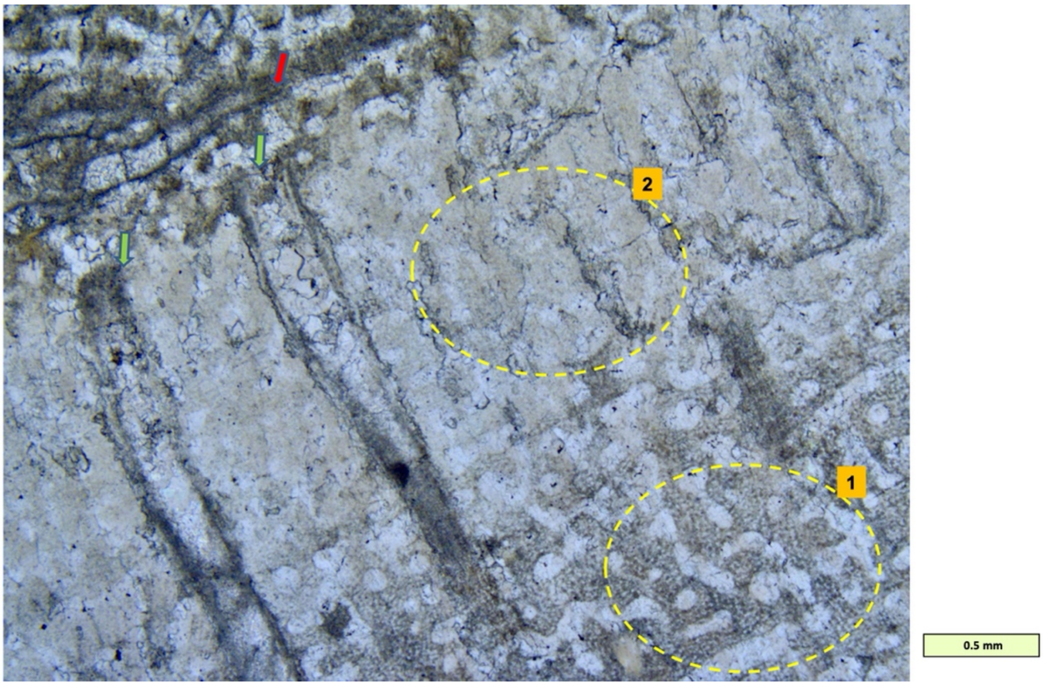

Fig. 4.5E. Enlargement of part of Sv with two syringoporid stubes on left. Green arrows show termination of these two syringoporid tubes at a growth interruption surface. Red arrow shows an unknown cellular-looking structure that is a very thin extension of a feature visible in Fig. 4.5C, that is adpressed to the rugose coral; it is not clear whether this is part of the coral or not, and may represent another fossil. The two dashed ellipses labelled 1 & 2 in this photo highlight the differences in preservation of the stromatoporoid structure in different layers of its structure only 2 mm apart. Area 1 shows an apparently well-preserved "cellular" appearance, while Area 2 lacks this definition and the skeleton is almost indiscernible against the overprinting calcite. This thin section is the same thickness across its area, so the difference between Areas 1 & 2 are due to diagenesis, emphasising the complexity of diagenetic change in stromatoporoids that can cause considerable problems in taxonomic identification. File: 4.8-KLoose41-Sv-Rugs-Cauno-Tubes-04.

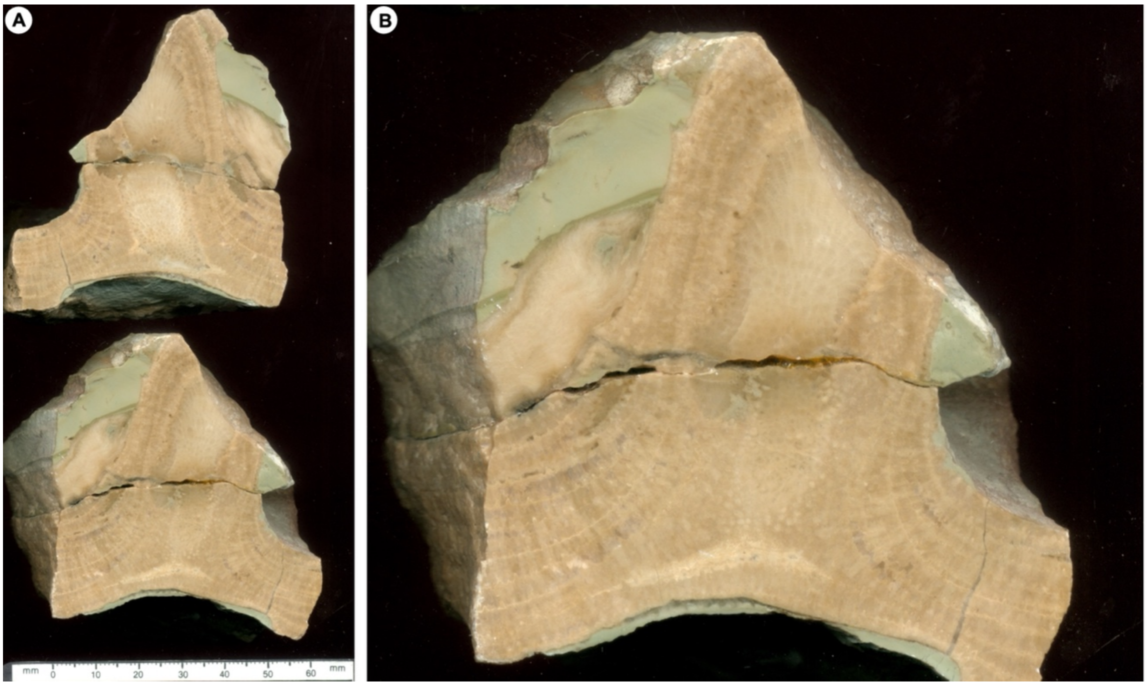

Fig. 4.6. *Lophiostroma schmidti* (Ls) and associated columnar tabulate (*Laceripora*). These pictures show the Ls began as a flat plate, which is its growth form, it does not occur in any form other than laminar growth if it grew alone. The origin of the coral is not known in this sample because it is outside the plane of section. The coral may have grown on a dead part of the Ls, or may originate outside the

Ls but may be presumed to have crossed into the growth area of the Ls. Whichever is the case, the Ls responded to the coral's presence and encased it forming a column; this arrangement is very unusual for Ls. A second stromatoporoid encrusted the Ls surface on the left side in [B]. File: 4.9-Kuppen2-LS-02.

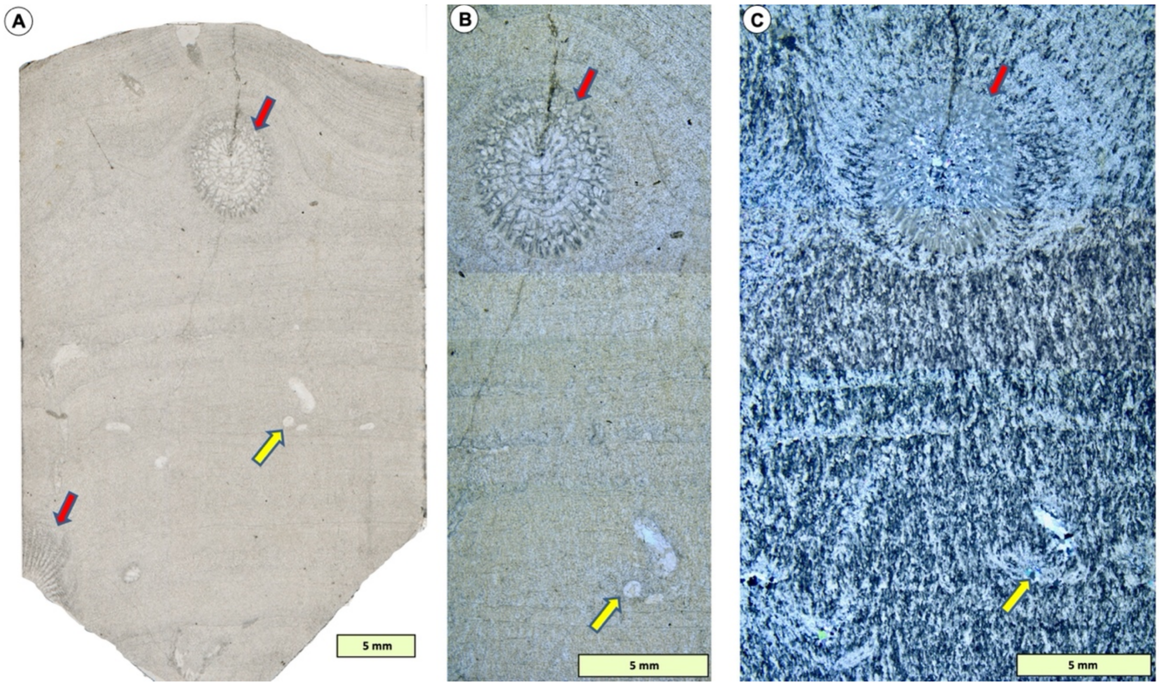

Fig. 4.7. A) VS whole thin section of *Plectostroma scaniense* (Ps) with two intergrown rugose corals (red arrows) and a spiral tube (yellow arrow). **B-C)** PPL and XPL enlargements of [A]. Red and yellow arrows are matched points, also matched in [A]. [C] shows the display of FRIC and the effect of the upper rugose coral on the orientation of skeletal elements, causing a splaying effect as the stromatoporoid skeleton wraps around the coral, also visible to a lesser extent around the spiral tube. Growth laminations demonstrate their effect on the FRIC. The diagonal zones are alteration along the fracture line visible in PPL [B]. File: 4.10-3c6-2.03-Ps-Rug-Tubes-VS.

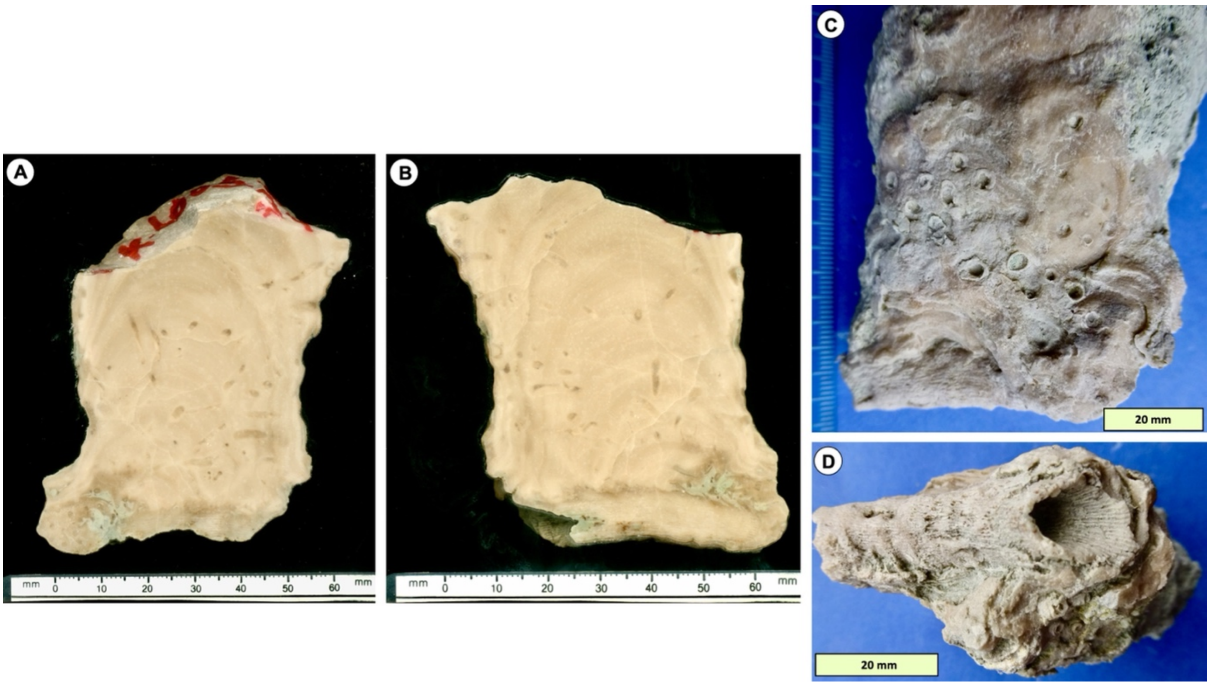

Fig. 4.8A-D. Partly broken hand specimen of Ps showing intergrown corals on the cut surface [A-B] and outer surface [C]. Also this stromatoporoid grew on a rugose coral as a substrate [D]. File: 4.11-KLoose39-Ps-Rugs-Tubes-01.

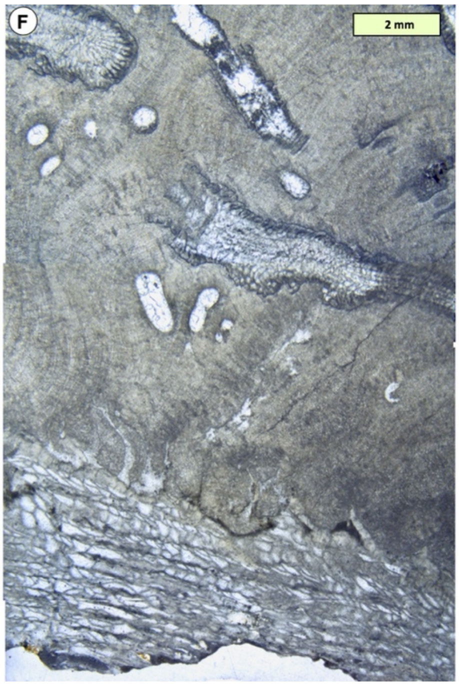

Fig. 4.8E-F. Whole thin section VS of sample of Ps in Fig. 4.8A-D, showing presence of rugose corals and spiral tubes, with growth attitude of the symbionts to the left. There are geopetals in open tubes in the upper part of [E] indicating the sample fell over and tubes infilled while it was in an oblique position. Note that the symbionts in upper part splay out up, left and right implying that growth was upwards in the orientation of the photo; but the lower symbionts in [F] and [G] contradict that interpretation because they are clearly expanding to the left. This conundrum could be resolved if the symbionts always grew approximately normal to the growth layering, which means in this case they grew sideways. However, other samples illustrated in this document show rugose corals oblique to the growth layers (e.g. Fig. 3.28 also in Ps), so this sample is not fully understandable. File: 4.12-KLoose39-Ps-Rugs-Tubes-02.

Fig. 4.8G. Enlargement of spiral tube in Fig. 4.8E (red box) showing it lacks a wall and is therefore a bioclaustration. File: 4.13-KLoose39-Ps-Rugs-Tubes-03.

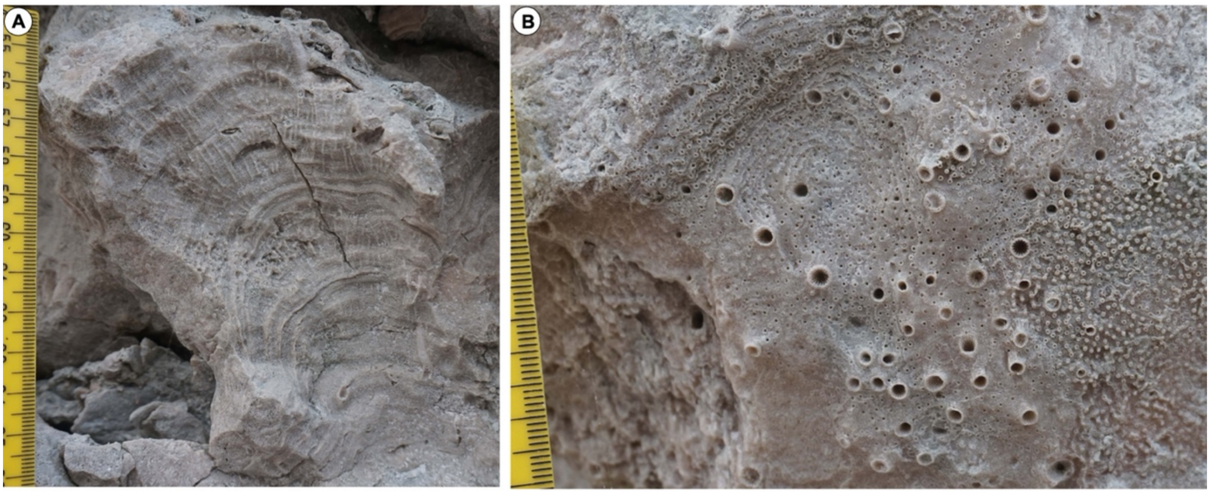

Fig. 4.9. Field views of *Petridiostroma convictum* (Pc) in the Lower Biostrome at Kuppen. **A)** shows symbiotic rugosans that occur on what appears to be the vertical edge surface of the Pc (more on this in later photos). **B)** surface view showing a plan view of both rugosans and syringoporids protruding from the stromatoporoid surface, evidence that the corals kept their soft tissues above the level of the stromatoporoid surface, possibly to avoid competition. File: 4.14-KuppenBiostromes-StromCoral-Field.

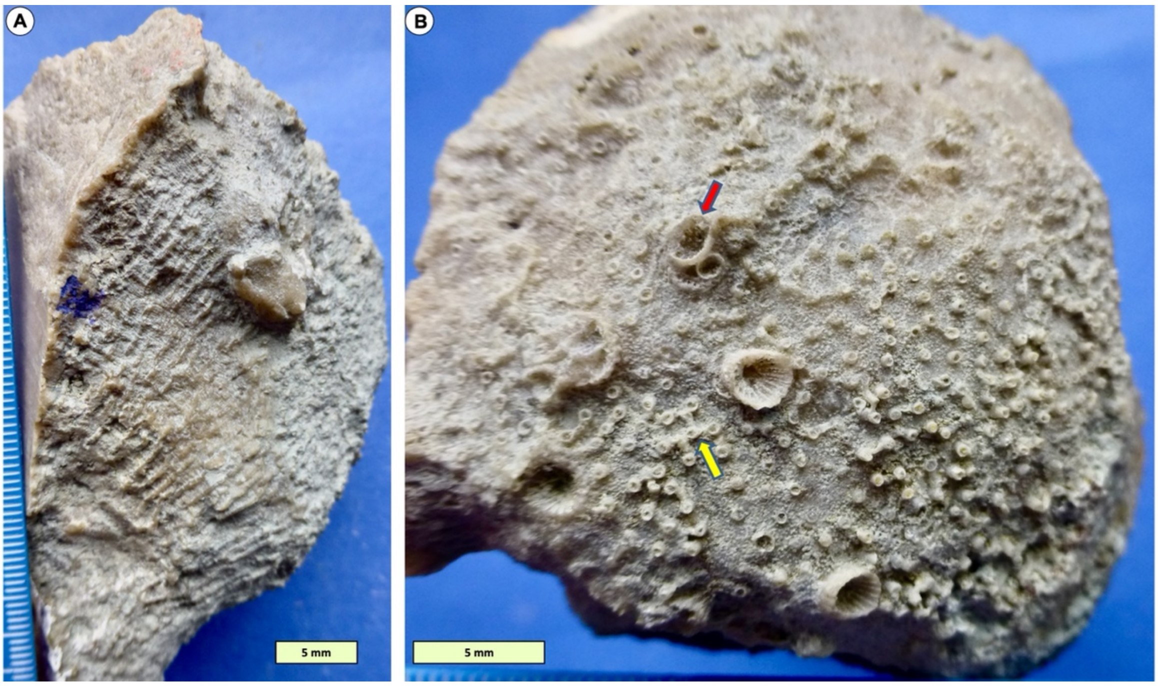

Fig. 4.10. A) surface side view of Pc showing the syringoporids grew on the outside of the edge of the stromatoporoid. **B)** rugose coral branching (red arrow) and syringoporid with cross partition tubes (yellow arrow) joining vertical tubes across the stromatoporoid surface. File: 4.15-KLoose-Pc-02-CoralsSurface.

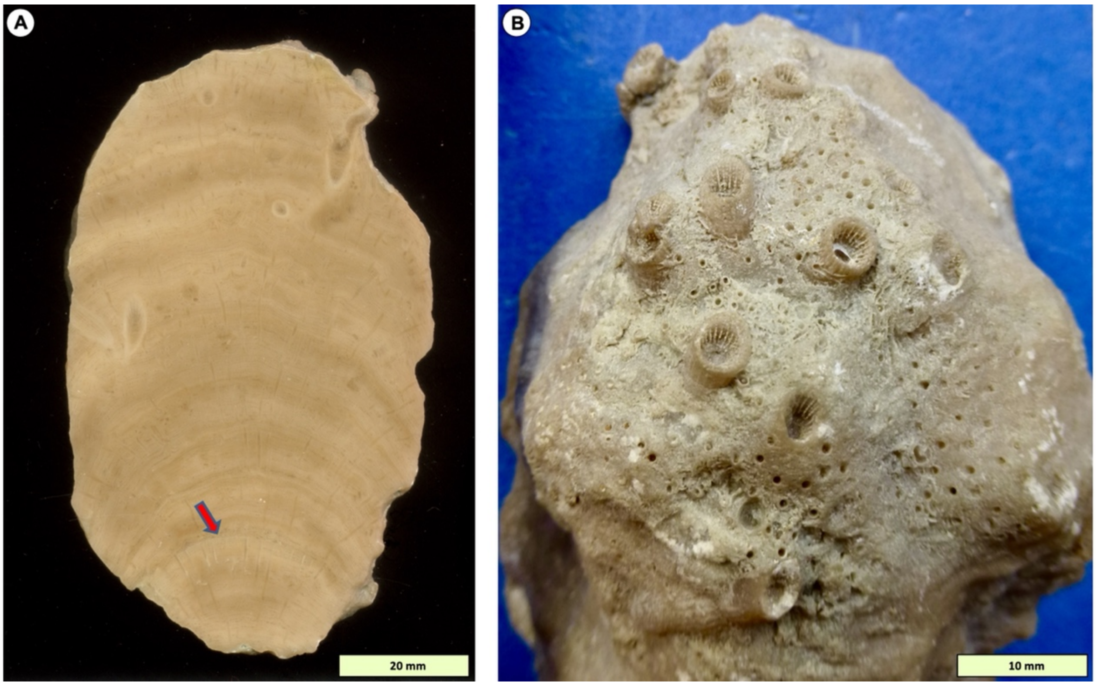

Fig. 4.11. A) Vertical section through partly broken bulbous form of Pc, with a growth interruption event in its early life (red arrow). Note that rugose corals are not present until the upper part of the stromatoporoid, in common with many other cases of this association in Pc. **B)** Surface view of the reverse side of the sample in [A], showing protruding rugose corals and abundant syringoporid symbionts. The rugose corals protrude several mm from the stromatoporoid surface; it is not clear whether the rugose corals had any mutual biological relationship with the stromatoporoid that hosted it. File: 4.16-Pc-Rugs-Cauno-VS01.

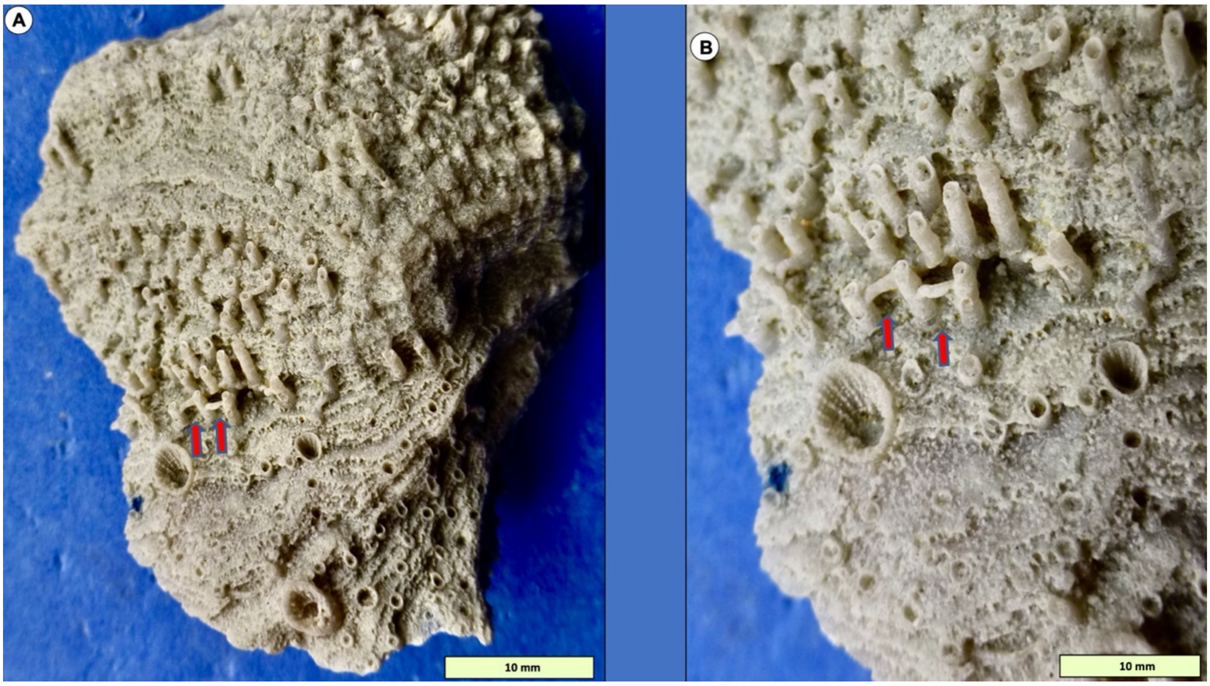

Fig. 4.12. Surface view of Pc with abundant syringoporids and some rugose corals. The syringoporids protrude more prominently from this surface than in other specimens observed in this study; note cross tubes (red arrows) between corallites above the stromatoporoid; cross tubes are a characteristic of syringoporid tabulates and are present in free-growing syringoporids as well as in symbiosis with stromatoporoids. Cross tubes are also seen in the parts of the syringoporids inside stromatoporoids (see other figures) and indicate that the symbiotic relationship between the syringoporids and Pc did

not cause disruption of the growth habit of syringoporids. File: 4.17-Kuppen4-7-Pc-Rugs-Cauno-Surface.

Fig. 4.13. VS of Pc sample with both syringoporids and a mass of branching rugosans. The origin point of the rugosan is not visible in this plane of section, but the syringoporids began growth about 30 mm above the basal point of the sample, evidence that the syringoporids did not encounter the Pc until it was well-established, as has been seen in other specimens earlier. A drawing of this sample was illustrated in Kershaw (1987). File: 4.18-Pc-Rugs-cauno-Kershaw1987-Mod.

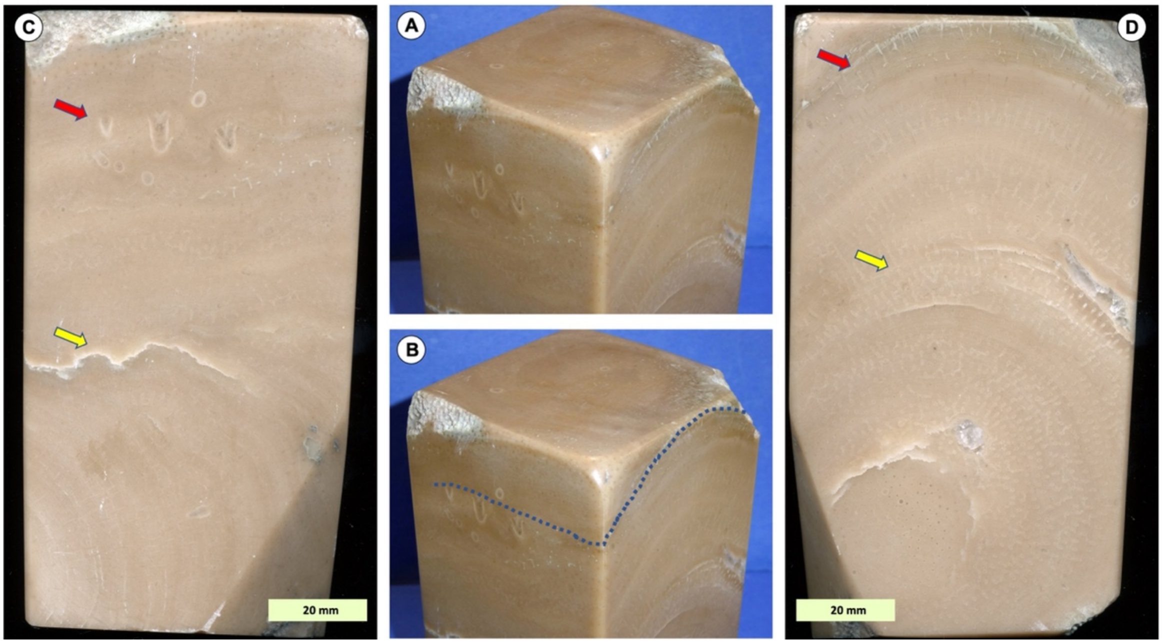

Fig. 4.14. 3D view of a block of Pc with syringoporid symbionts. **A-B)** dome-shaped growth of the Pc is seen the cut faces of this block. **C)** On this face, the Pc growth layers show a prominent change in growth direction at about the level of the yellow arrow (note the sample is cracked here). There is a growth interruption event at the level of the red arrow. **D)** There are two interruption surfaces visible here at the yellow and red arrows; in both cases the syringoporid tubes are infilled with light-coloured micrite at the top of the layer directly below each interruption surface. File: 4.19-KLooseCUBE-Pc-Cauno.

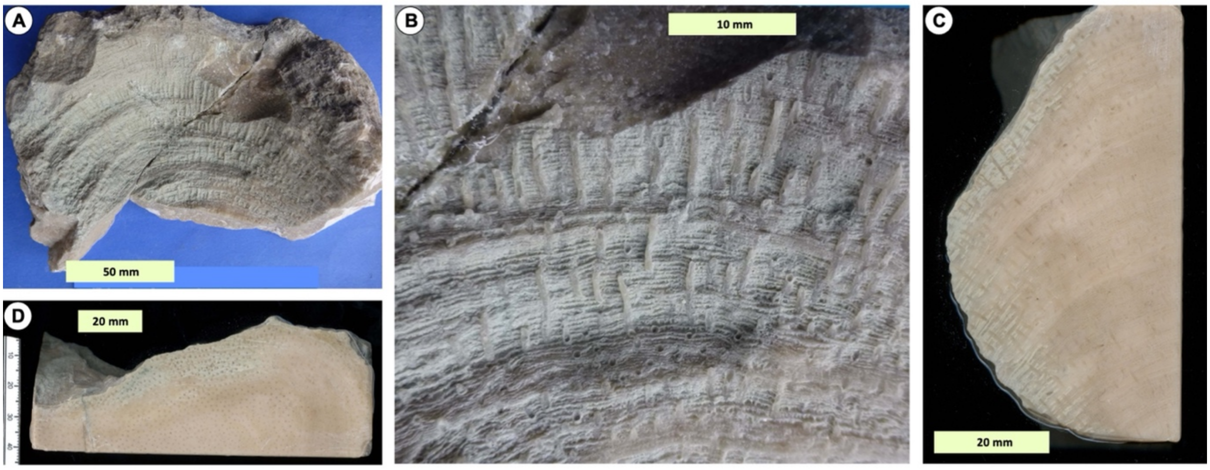

Fig. 4.15. A) Piece of a domical Pc indurated with symbiotic syringoporids; **B)** enlargement of central part of [A] showing the syringoporid tubes are present on the outer vertical surface of the Pc, demonstrating that the intergrowth extends all the way through the stromatoporoid. **C-D)** vertical and transverse cuts, respectively, through the Pc structure. Note in both [C] and [D] that gallery space in the outer margin is indurated with micrite, showing that the stromatoporoid gallery space is not filled with sparite until at least some time has elapsed after death of the stromatoporoid. File: 4.20-Kuppen4-28-Pc-Cauno.

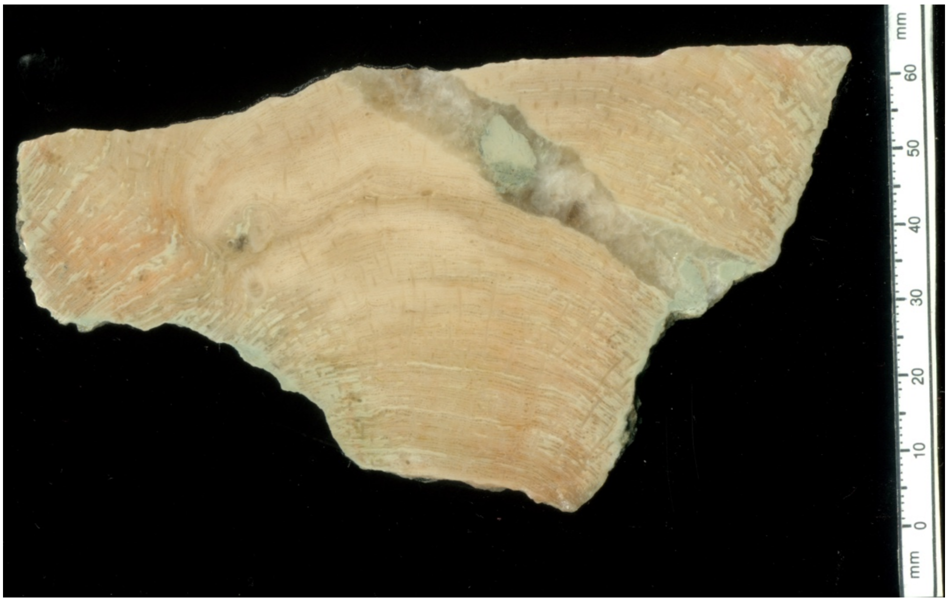

Fig. 4.16. VS through sample of Pc with symbiotic syringoporids. Note this is similar to Fig. 4.15C because the outer edges are indurated with micrite, passing into the gallery space. Note this sample is fractured and the fracture filled with broken pieces of stromatoporoid, sediment and cement, and is a later feature. File: 4.21-Kuppen4-6-Pc.

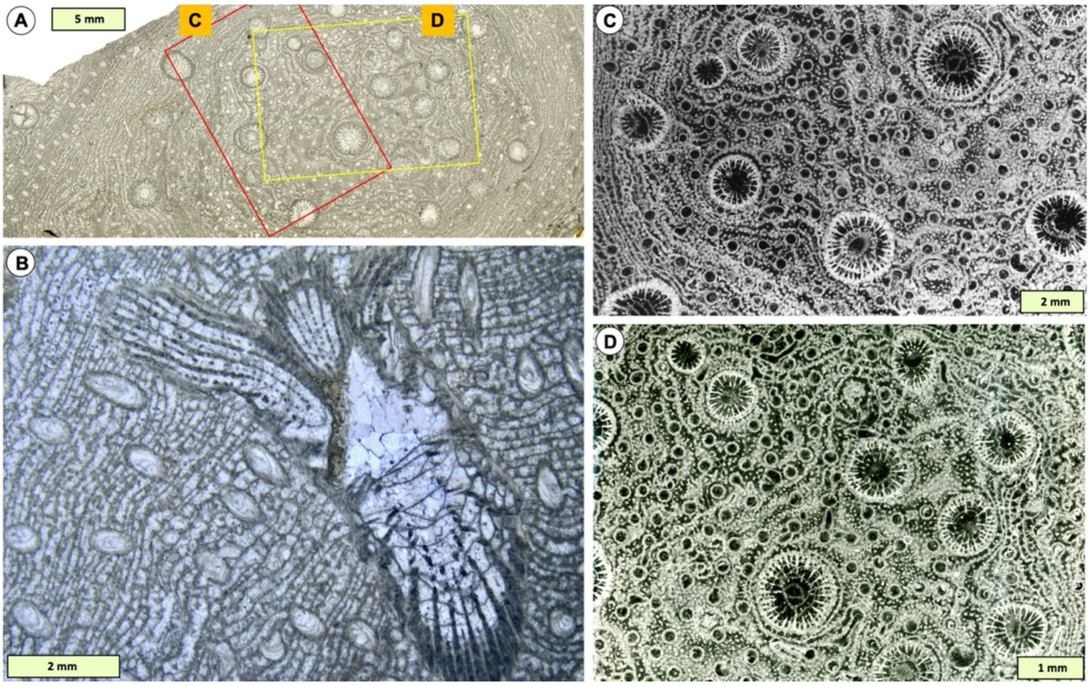

Fig. 4.17. A) TS whole thin section view of Pc with both syringoporid and branching rugosan symbionts; this is from a domical sample so the centre of the view is in full TS, passing to oblique outwards. The rugose coral branches into 4 at each branch point; this is best seen on the very left side of [A] where a corallite is just in the process of splitting into 4; also seen in the cluster of rugose corallites centre-left, in the TS portion of the view. **B)** is a different specimen of the same structure, chosen because it has a more VS area, and illustrates the branching of rugose corallites into 4. **C-D)** Negative photos to highlight the stromatoporoid and symbiont structures more visually, and shows in [C] the cross-tubes in syringoporids; [D] upper right has a cluster of rugose corallites in a pattern of 4, these branched a short distance below in this sample. Part of the TS was illustrated in Kershaw (1987) and Kershaw et al. (2018) File: 4.22-G172-Pc-Rugs-Cauno.

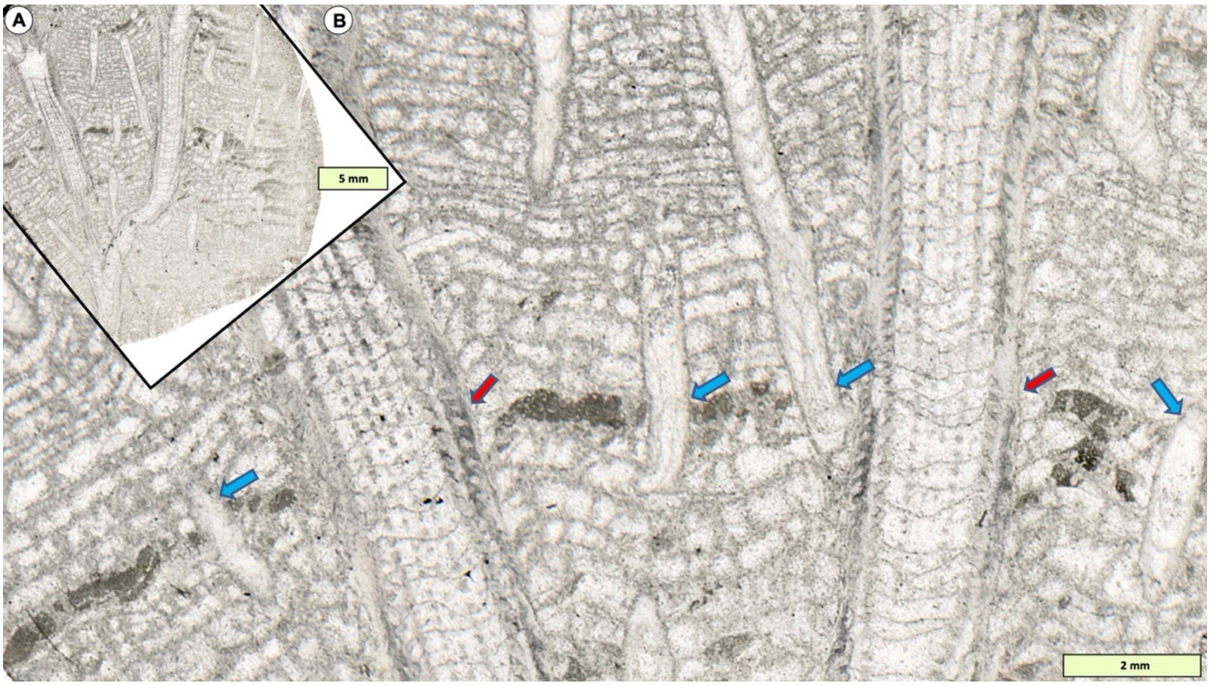

Fig. 4.18. A) VS whole thin section of Pc with rugosans and syringoporids. **B)** shows a prominent growth interruption event, dark zone of sediment-filled structure. However, all the coral tubes of both rugose (red arrows) and syringoporids (blue arrows) survived the interruption, and the stromatoporoid recovered. Another picture of this thin section was illustrated in Kershaw (1987). File: 4.23-4b7-3.52-Pc-Rugs-Cauno-VS.

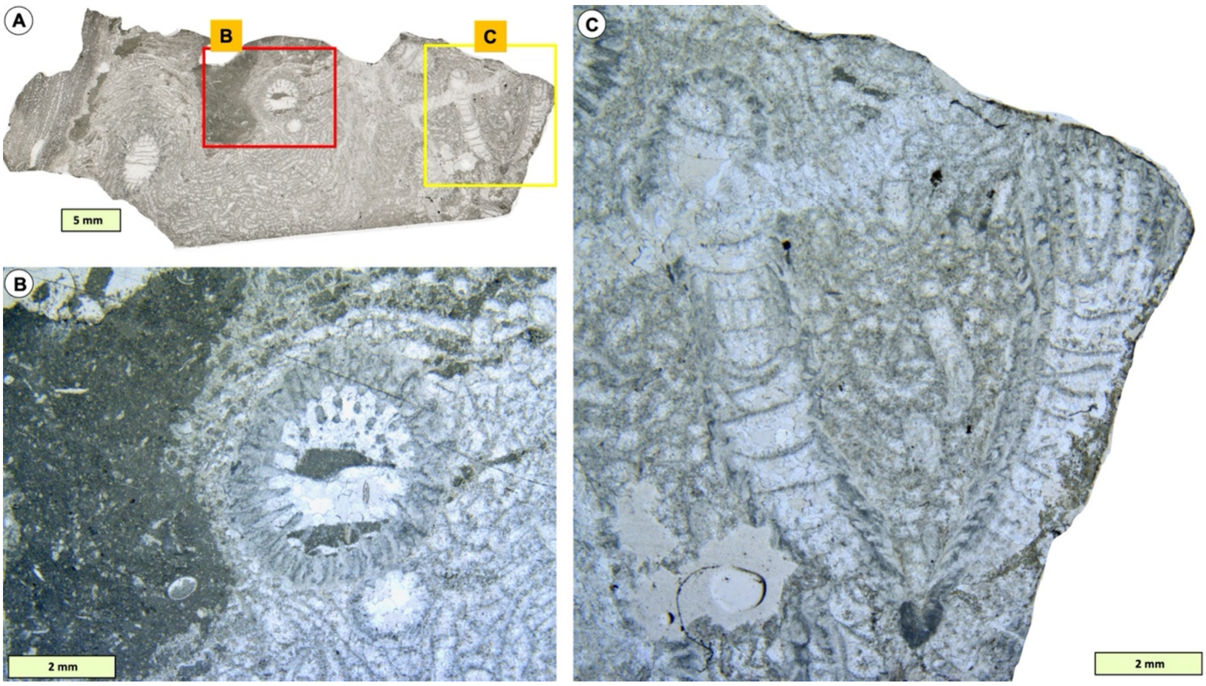

Fig. 4.19. A) VS of whole thin section of Pc containing rugose corals and syringoporid symbionts. The coral in **B** has geopetals and the outer gallery space of the Pc has sediment infiltration. **C)** shows a vertical section through a branched rugosan. File: 4.24-4c7-0.39-01-Pc-Rugs-Cauno.

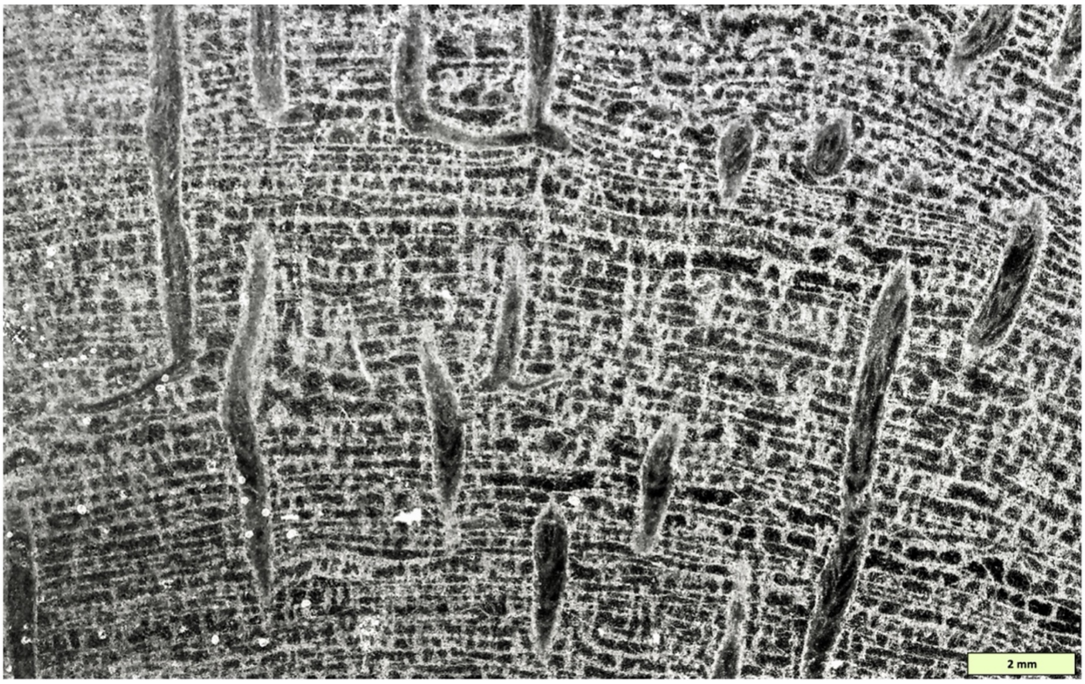

Fig. 4.20. VS negative photo of detail of Pc with syringoporid symbionts. Note the variation in laminae spacing that may be interpreted as seasonal banding, surmised to indicate summer (wider spaced laminae in faster growth) and winter (closer spaced laminae in slower growth) periods, but there is really no firm basis for this interpretation; there may be other reasons why the stromatoporoid growth rate changed, noting that it is necessary to trace these bands to the margins of the specimen in order to gather more information about, for example, growth interruption events that may have affected the growth rate. Figured in my PhD thesis from 1979. File: 4.25-Kershaw1979Fig5.34a-Pc-Cauno.

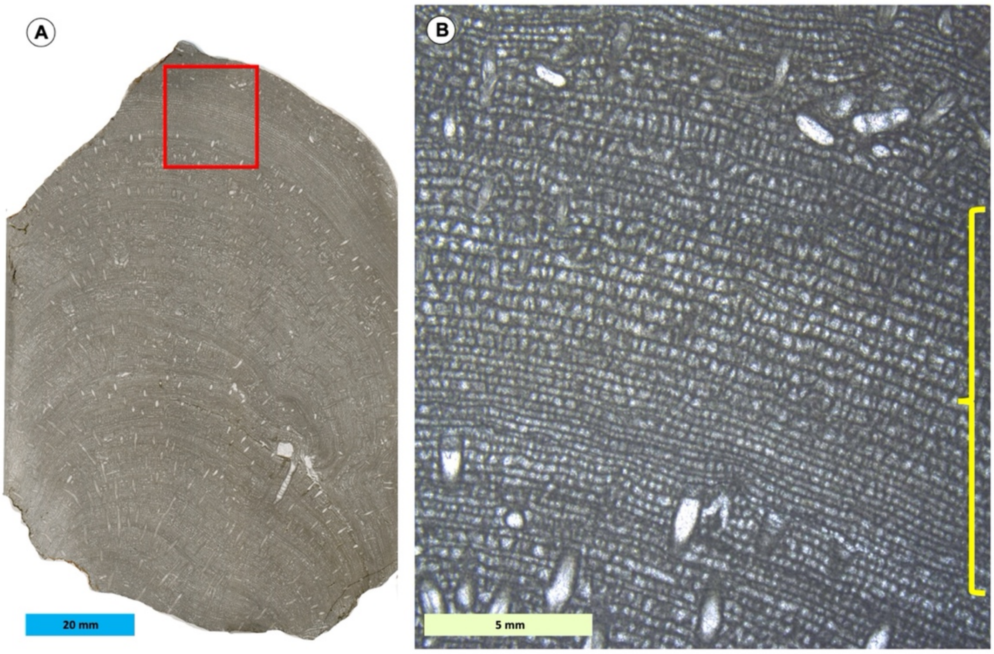

Fig. 4.21. A) VS whole thin section view through Pc with symbiotic syringoporids. **B)** Enlargement of red box in [A] showing that the central part of the box (yellow bracket) lacks syringoporids, while the upper and lower parts contain syringoporids. This is very unusual because it means that some cause made the corals disappear, yet the stromatoporoid carried on growing, then the corals came back! The area bereft of syringoporids also shows variation in spacing of laminae, and thus imply growth rate variations within it. We can really only guess as to the cause of the disappearance of the syringoporids and also their reappearance. What do you think? File: 4.26-KLoose32-Pc-Cauno-01.

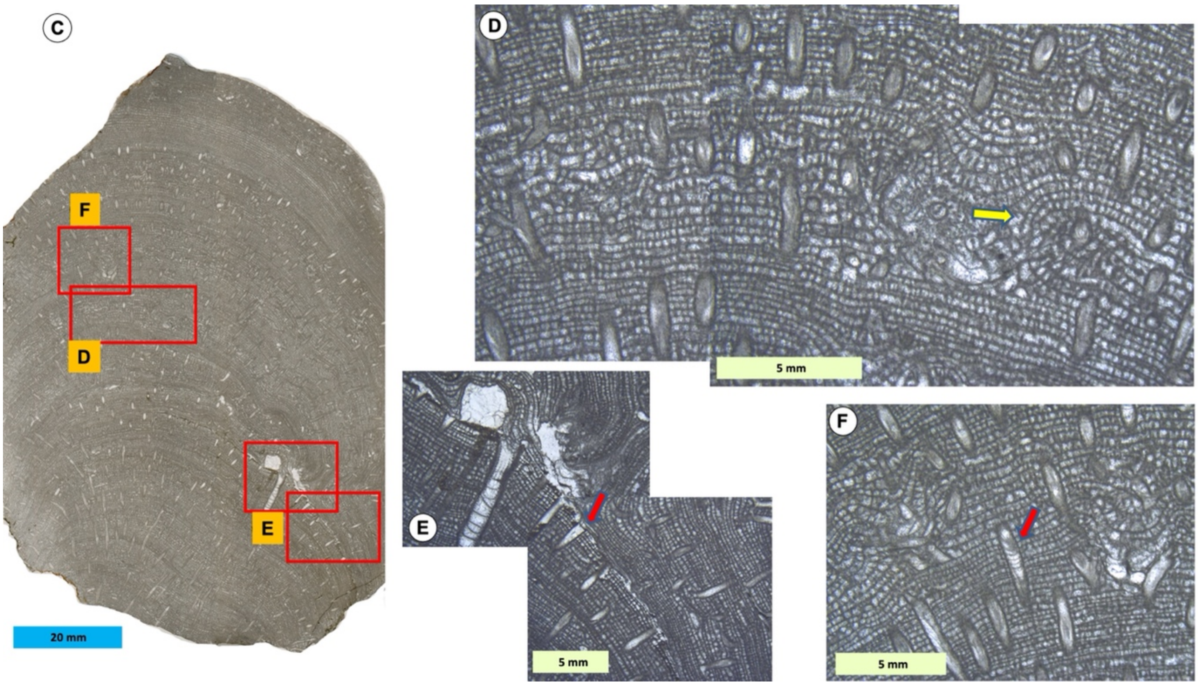

Fig. 4.21C-F. C) shows the locations of [D-F]. **D)** Central zone shows disruption of the Pc growth (yellow arrow) where a portion of the skeleton shows a sharp edge to some laminae laterally, and the succeeding growth wrapped vertically around the blunt end of the affected part of the Pc. To the left of the arrow is another sharp edge of laminae, the space infilled by more chaotic growth. This feature is ucommon. A potential explanation is that the stromatoporoid was involved in a physical impact that broke part of its surface, and subsequent growth filled in that irregular space. **E)** Growth interruption surface where rugose and syringoporid corallites are abruptly terminated and some micrite infiltrated into the calyces forming geopetals. This may have been caused by a sedimentation event, from which the stromatoporoid recovered (self-clearing mechanisms are common and effective in modern sponges) and regrew across its own dead surface; the corals reappear after a few laminae have been formed and may indicate that the corals were killed and then new coral larvae discovered the stromatoporoid once more. This is an interesting contrast from earlier photos and [F] below, that showed the corallites survived a presumably minor growth event that killed that part of the stromatoporoid, but where recovery of the stromatoporoid also occurred by lateral growth from neighbouring areas of the Pc skeleton. **F)** Apparent growth interruption event that a syringoporid corallite survived (red arrow). File: 4.27-KLoose32-Pc-Cauno-02.

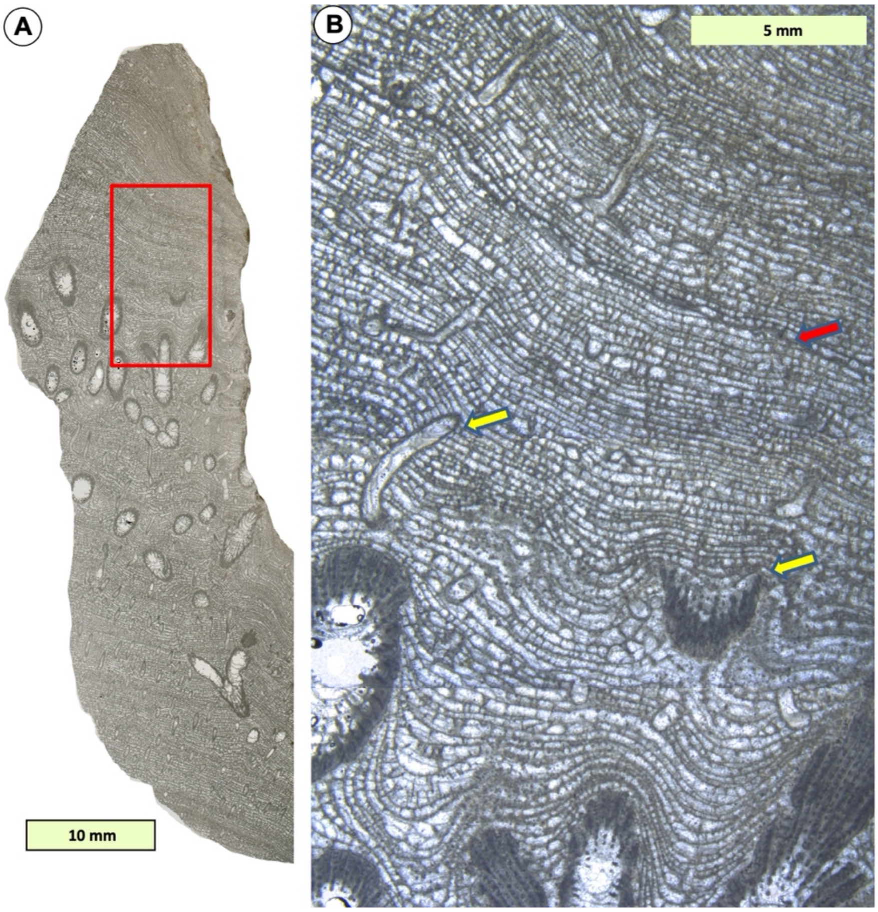

Fig. 4.22. A) VS whole thin section showing Pc with syringoporids and rugosans; it seems the rugosans appeared and then disappeared, bearing in mind that they may have passed out of the plane of section in the upper part and may not have necessarily stopped growing. **B)** However, this shows something unusual: a rugose coral (right yellow arrow) that apparently did not survive an interruption even, while a syringoporid tube (left yellow arrow) did. There is another apparent growth interruption event at the level of the red arrow. Note that throughout this section of the Pc, there are few syringoporids, in contrast to other specimens illustrated in this document that shows abundant syringoporids. I am sure you can think of lots of alternative reasons to explain this peculiar and unusual behaviour. File: 4.28-KLoose63-Pconvictum.

Fig. 4.23A1. VS through a Pc with some rugosans and with abundant syringoporids. The specimen was cracked, presumably by compaction and the gap filled with cement. Note the growth layering annotated in next photo. File: 4.29-Kuppen4-3-Pc-01.

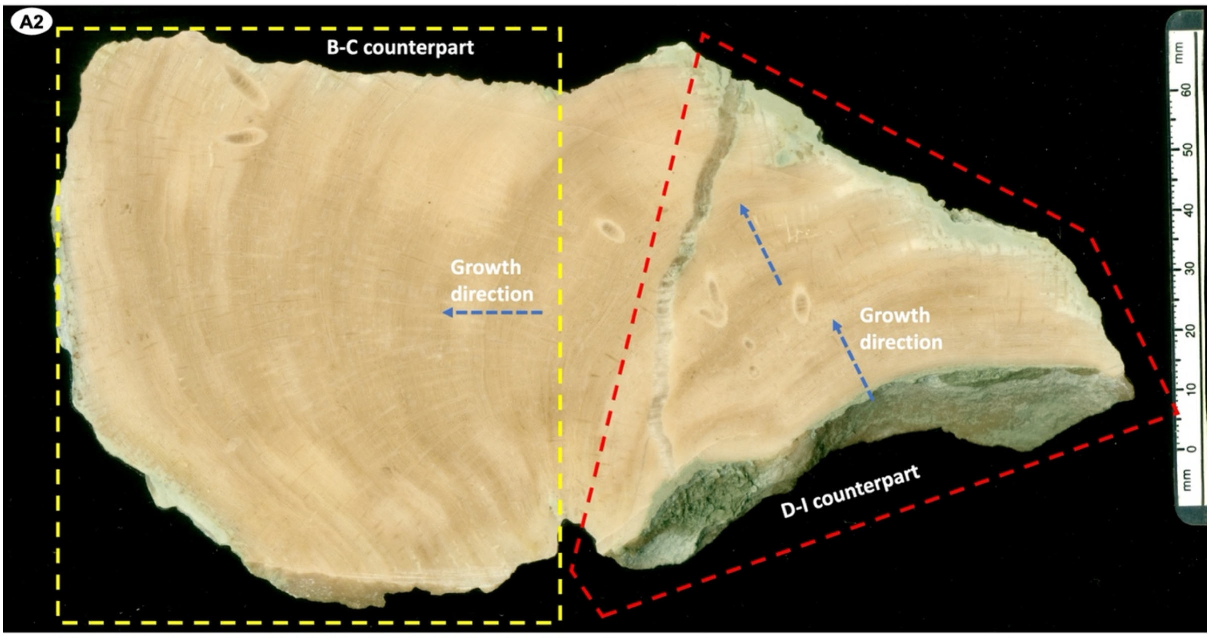

Fig. 4.23A2. Same as A1 but with labels. The change in growth direction of this stromatoporoid is evidence that it was moved during life and left in another position, from which it continued to grow. We presume that stromatoporoids grew upwards, so this sample is displayed on its side, having been moved again. In the upper right part the edge shows a green infilling of micrite that infiltrated the outer part of the stromatoporoid before it became cemented. File: 4.30-Kuppen4-3-Pc-02.

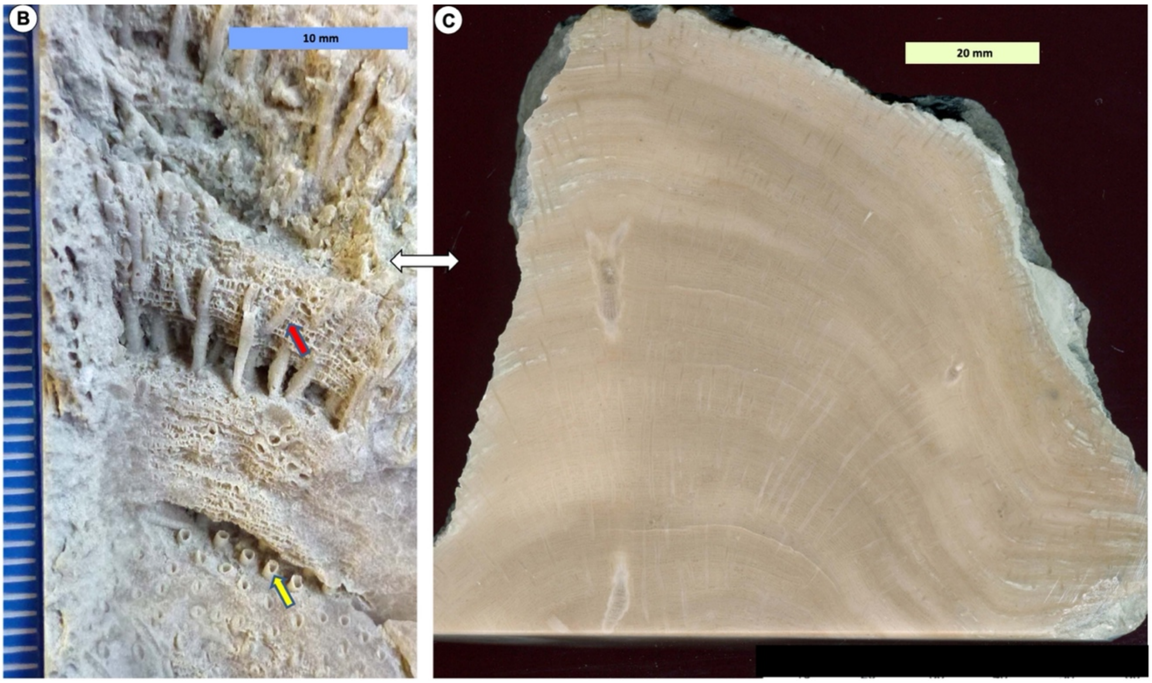

Fig. 4.23B-C. VS through counterpart of area in yellow dashed box in Fig. 4.23A2. the side view of this specimen shows the syringoporids at the edge of the sample, indicating the syringoporids (red arrow) fully indurate the stromatoporoid structure. Yellow arrow shows syringoporid calices protruding above the stromatoporoid surface. File: 4.31-Kuppen4-3-Pc-03.

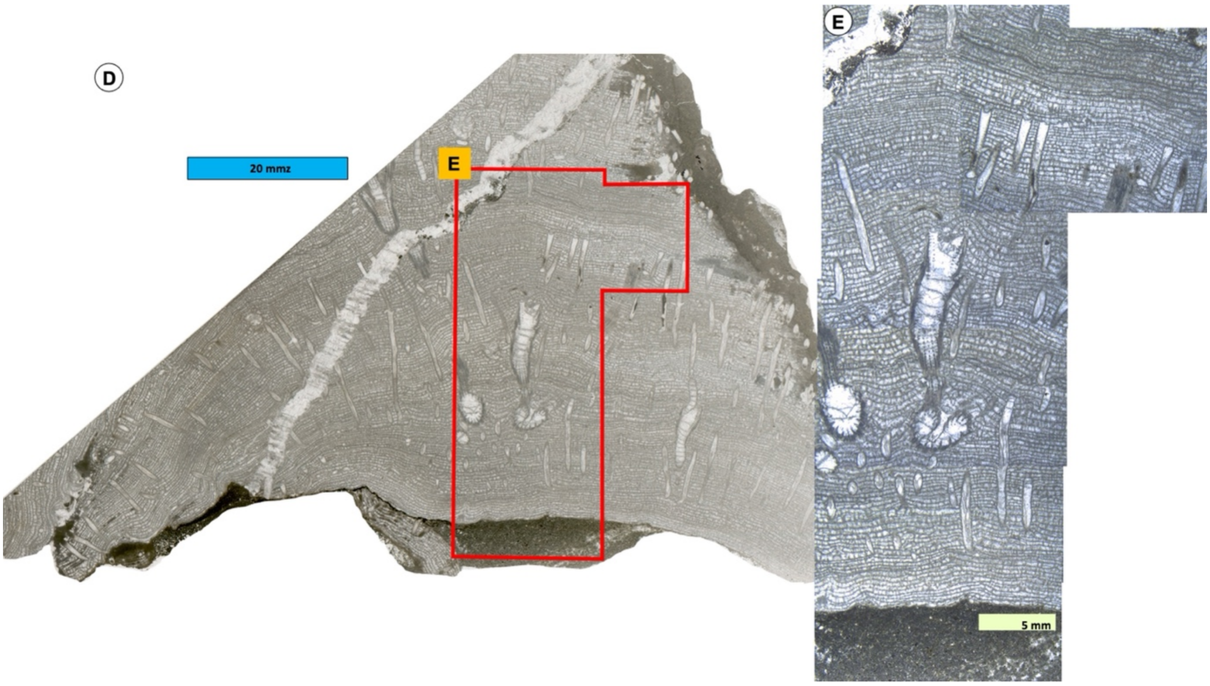

Fig. 4.23D-E. D) VS through counterpart of area in red dashed box in Fig. 4.23A2. Note the position of the fracture to correlate with Fig. 4.23A2. Note micrite infiltration on right side. **E)** Enlargement of red box showing some branching rugosans and also growth interruption events that killed syringoporids near the top of the red box area. This stromatoporoid seems to have grown on a sediment surface, seen at the bottom of the box. File: 4.32-Kuppen4-3-Pc-04.

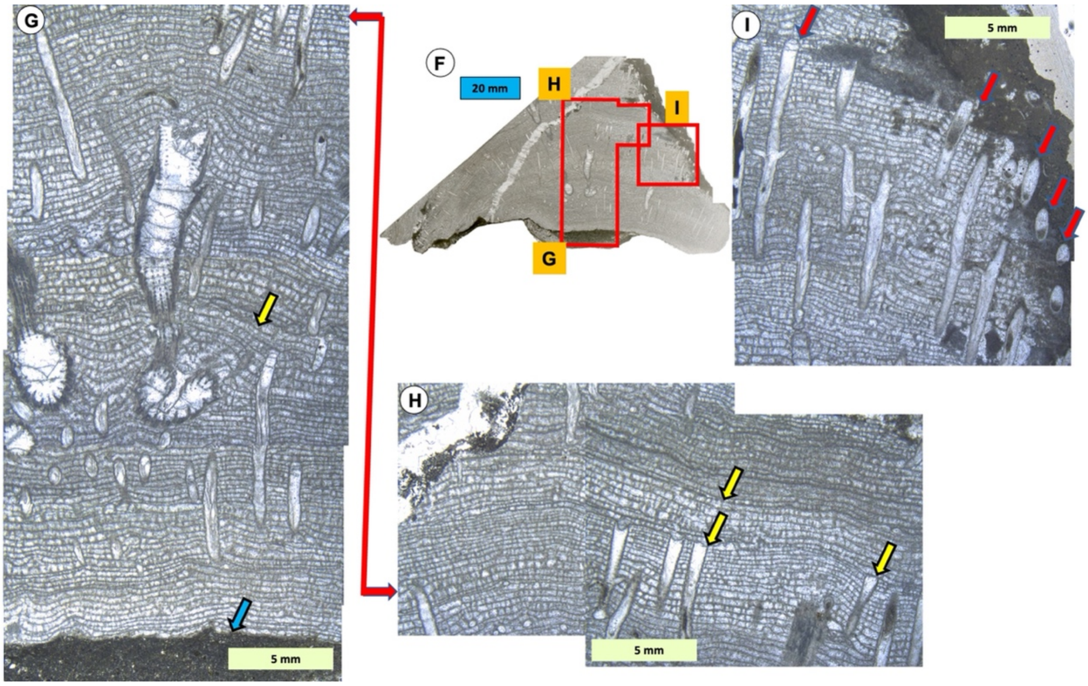

Fig. 4.23F-I. More details of views from previous figure. Yellow arrows show growth interruption events; Blue arrow emphasises stromatoporoid base on sediment; red arrows show protruding syringoporids at sample margin, that is covered by sediment (dark material). File: 4.33-Kuppen4-3-Pc-05.

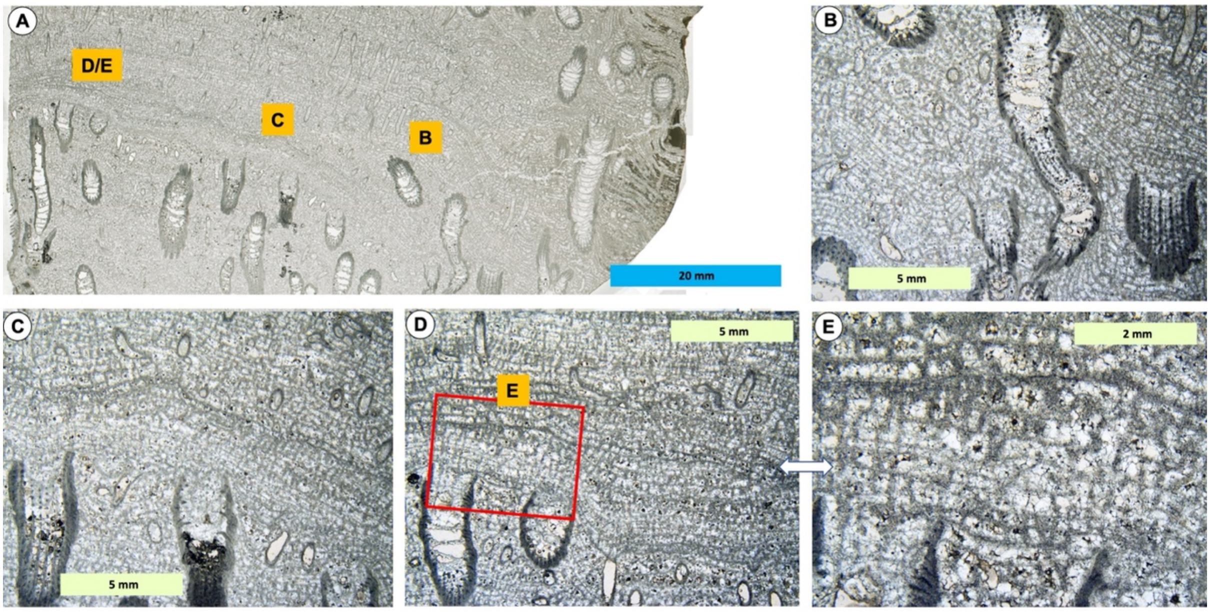

Fig. 4.24. A) VS whole thin section of Pc with rugosans and syringoporids. There is a prominent interruption surface across the top of the rugosans in the left half of the view. **B)** Enlargement from [A] shows a prominent rugose corallite that passes unscathed through the growth interruption level, while the other rugose corals along that line are all terminated, shown in details in **C-E**; also notice that the syringoporids disappear from the Pc for a few laminae above that interruption level. However there is no obvious disturbance of the stromatoporoid at that level. Isn't that crazy? How could you explain this sample? File: 4.34-PC-CoralErlangen01.

[Backstory to this sample; in Erlangen in 2016, I glanced into the waste rock bin in the cutting room and there was this interesting-looking sample that was immediately recognisable as a stromatoporoid with rugose corallites, so I grabbed it and just for fun made a thin section; this is that section!!!! It came from the Hemse Group biostromes, a loose beach pebble, so its horizon and locality are unknown; but I am very grateful to the unknown person who discarded this most interesting sample].

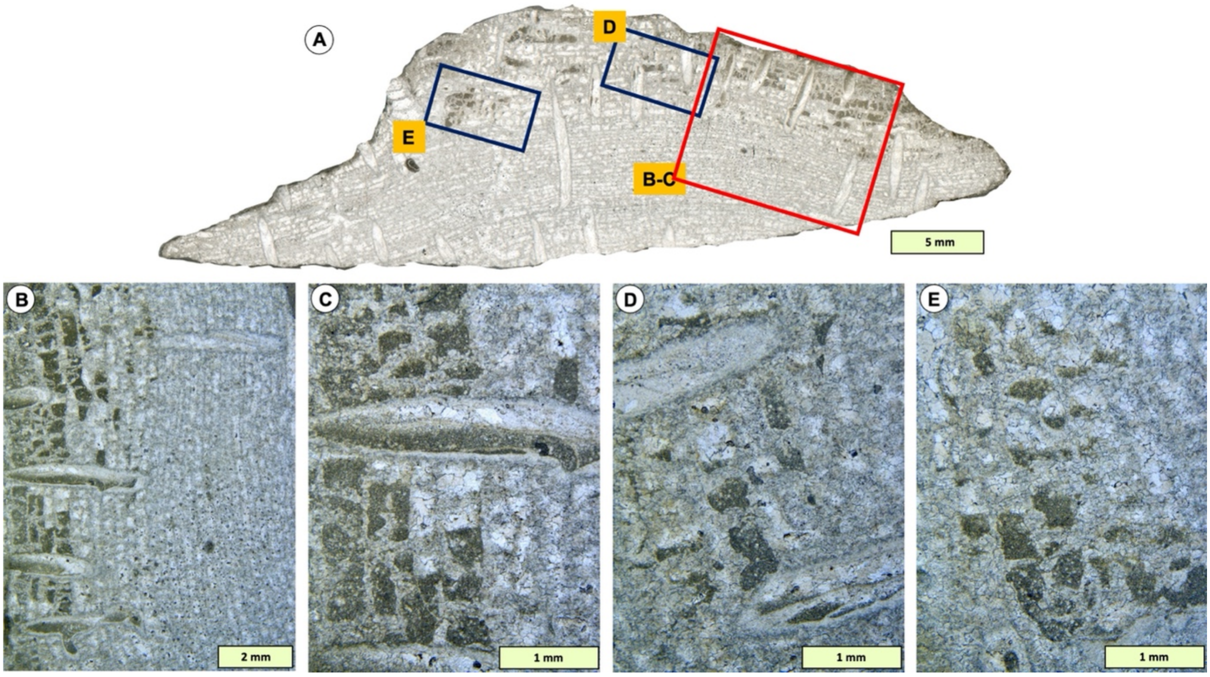

Fig. 4.25. A) Piece of a Pc sample from the outer part of a stromatoporoid, with geopetals in both the gallery space and the coral tubes; **B-E)** displayed at 90 degrees to [A], the geopetals are in correct orientation thus they are all sideways to the stromatoporoid structure, so this is evidence of a storm event that disrupted the stromatoporoid and deposited it out of position, then the sediment trickled into the spaces. File: 4.35-3b5-2.16-Pc-Cauno-VS-GeopetalRotated.

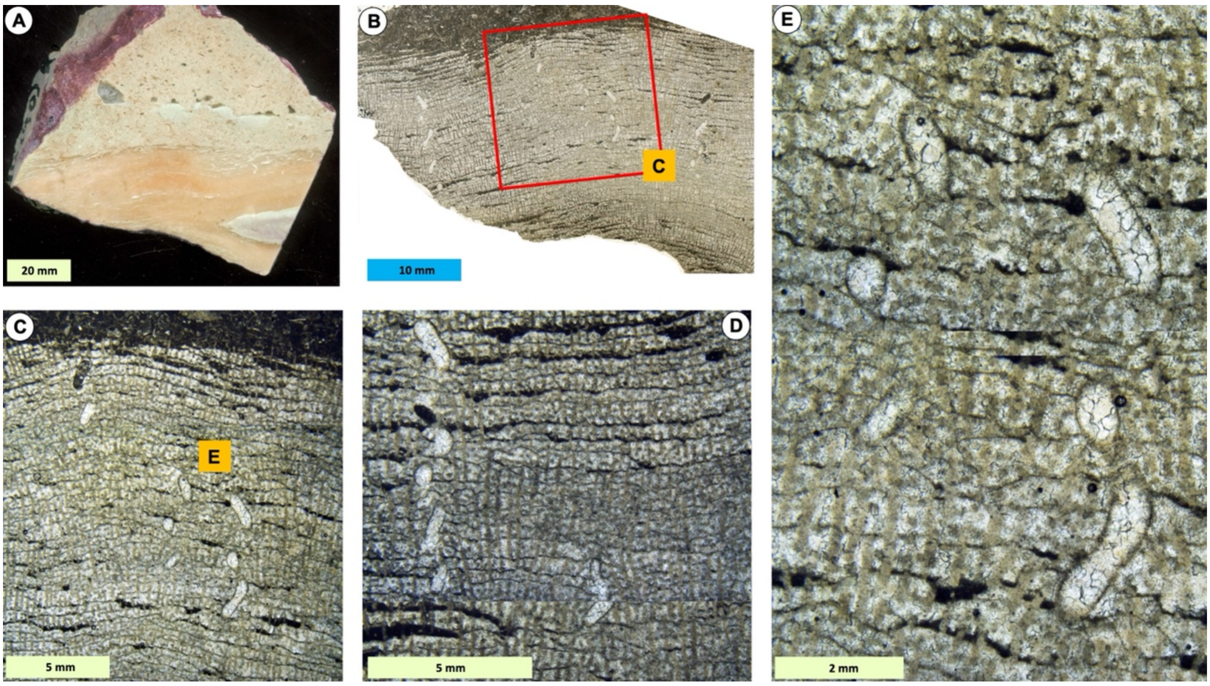

Fig. 4.26. A) VS through sample of *Labechia lepida* (Ll) and wackestone sediment. **B-E)** Sections through areas showing spiral tubes symbiotic with the Ll. Note numerous small interruption events marked by sediment accumulation, yet the spiral tubes survived these to the final event at the top of the stromatoporoid. In the upper part of [A] you can see a line of small geopetals in cavities in the sediment; evidence of early lithification, dissolution and infilling prior to final burial. File: 4.36-KLoose27-G190-Ll-SpiralTubes.

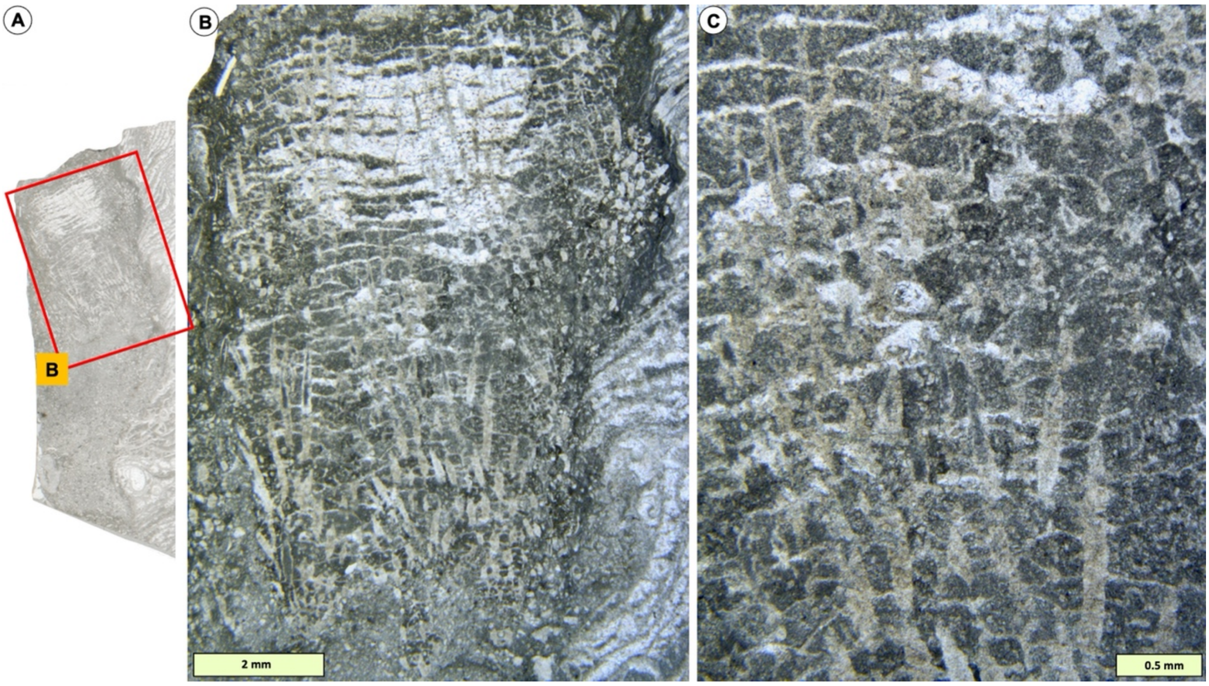

Fig. 4.27A-C. Fragment of *Labechia lepida* showing induration of the gallery space with sediment; the presumed history is that the stromatoporoid was broken up by storm action and transported then deposited. The infilled gallery space indicates the gallery space remained uncemented in the early stage of post-mortem development. This must indicate that in life the stromtoporoid had a low density, so was quite light and presumably easy to move and break up. File: 4.37-3c9-3.74-Pc-cauno-Ll.

5. THE "MIDDLE BIOSTROME", THE MIDDLE OF THREE BIOSTROMES IN THE CLIFF SECTION AT KUPPEN 3 SITE.

This informally-named unit is a minor biostrome formed on the eroded top of the Lower Biostrome. Its stromatoporoid suite is unstudied but likely to have the same composition as the Lower Biostrome. In this section of the atlas are illustrated three unusual samples from the Middle Biostrome, of syringoporid tabulate colonies intermixed with branching rugose corals, in the absence of stromatoporoids. In contrast, in the Lower Biostrome, the two corals are common as symbionts in the stromatoporoid *Petridiostroma convictum*, and the interactions have been considered as interactions between stromatoporoid and coral. However, the presence of the two corals in close association, in the absence of stromatoporoids, carries the implication that the corals had some kind of biological interaction. Unfortunately, only three samples cannot be conclusive, but is a fascinating potential avenue for investigation.

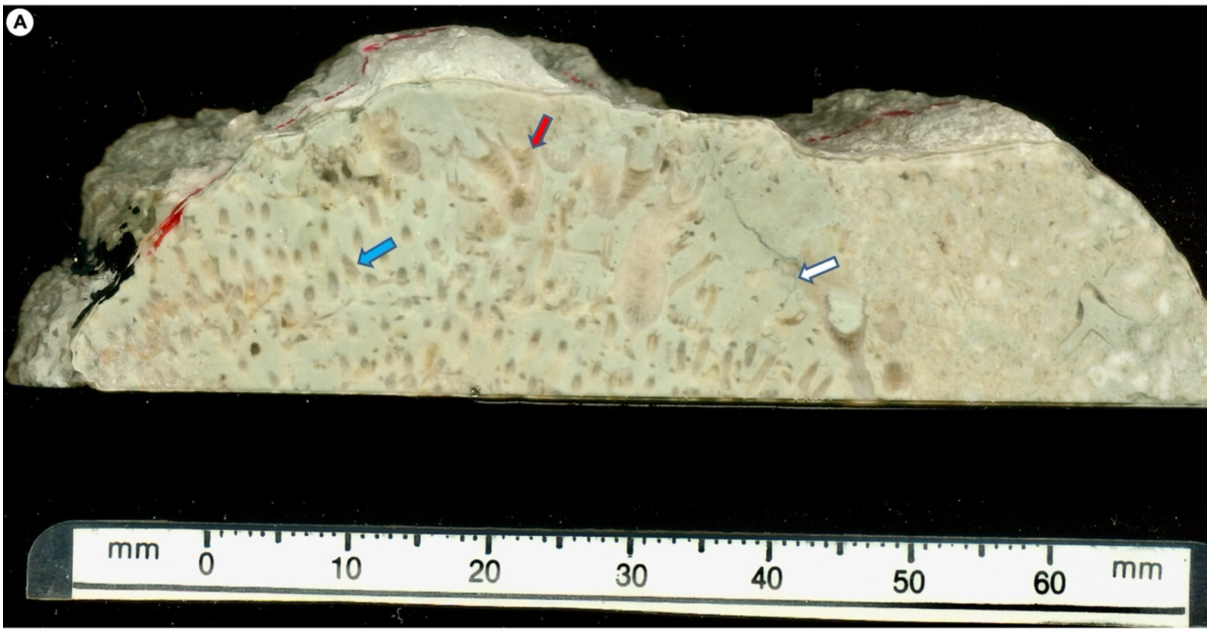

Fig. 5.1A. TS cut section of sample showing rugose corals (red arrow) and syringoporids (blue arrow), forming a discrete patch with sediment infilling and prominent margin against bioclastic packstone (white arrow). File: 5.1-Kuppen-MB04-05-06-TwoCoralAssn-NoStrom-01.

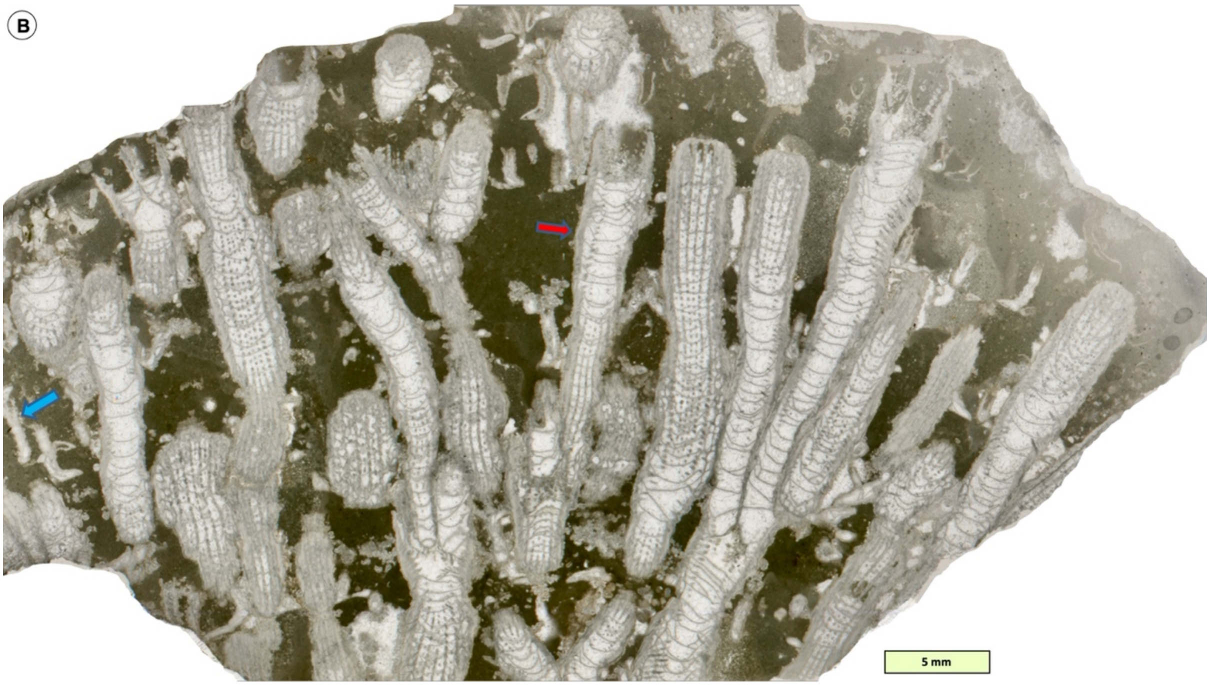

Fig. 5.1B. VS thin section showing both rugose (red arrow) and syringoporid (blue arrow) corals with no stromatoporoid. File: 5.2-Kuppen-MB04-05-06-TwoCoralAssn-NoStrom-02.

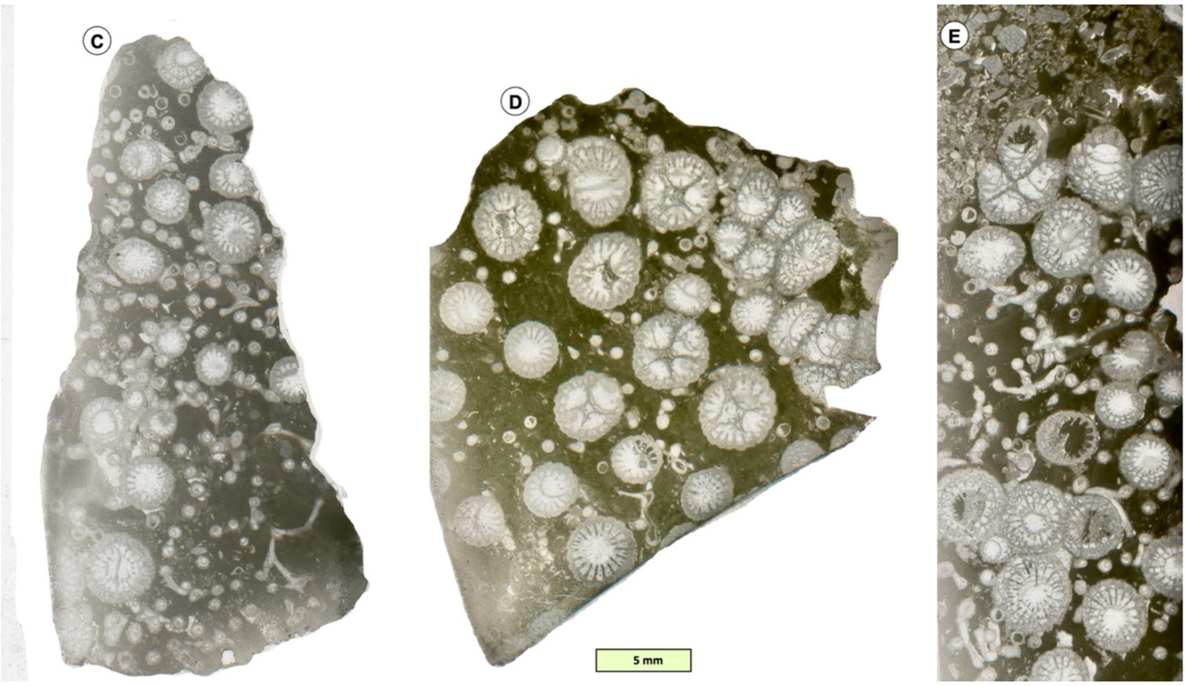

Fig. 5.1C-E. 3 TS thin sections showing both rugose and syringoporid corals with no stromatoporoid. File: 5.3-Kuppen-MB04-05-06-TwoCoralAssn-NoStrom-03.

6. BIG STROMATOPOROID COLLECTED LOOSE ON TOP OF CLIFF AT KUPPEN

This sample sat in my garden for 30 years, and then, because nobody wanted it (can't understand why), I photographed, then broke it up and made thin sections, revealing three intergrown symbionts in some sections! This sample turned out to be beautiful in thin section.

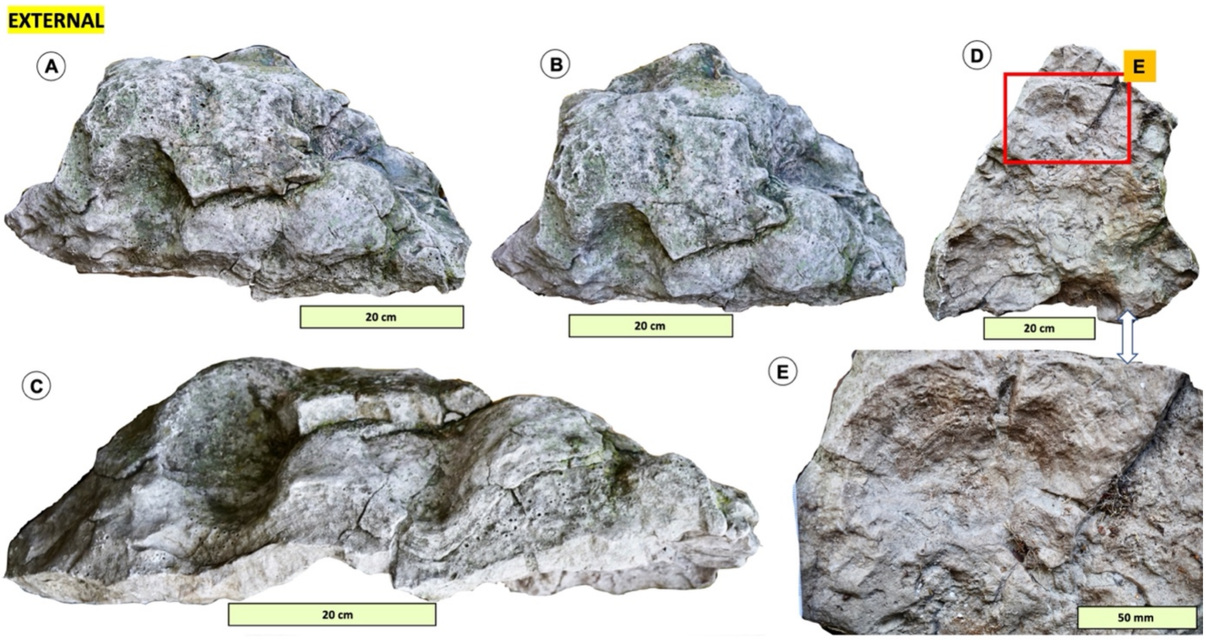

Fig. 6.1. "Hand" specimen of big stromatoporoid (it weighed at least 20 kg). **A-B)** Oblique top views showing domical form; **C)** Side view of low domical form, with clear lamination along broken margins; **D-E)** Basal view showing several centres with basal ridges indicating this is a merged form from several smaller individuals that coalesced to form the large fossil; coalescence is common in big, low profile stromatoporoids and was offered by Kershaw (1990) as an explanation of how such stromatoporoids became so dominant in the Palaeozoic.. File: KBS01-Sv-Rugs-Cauno-Tubes-01.

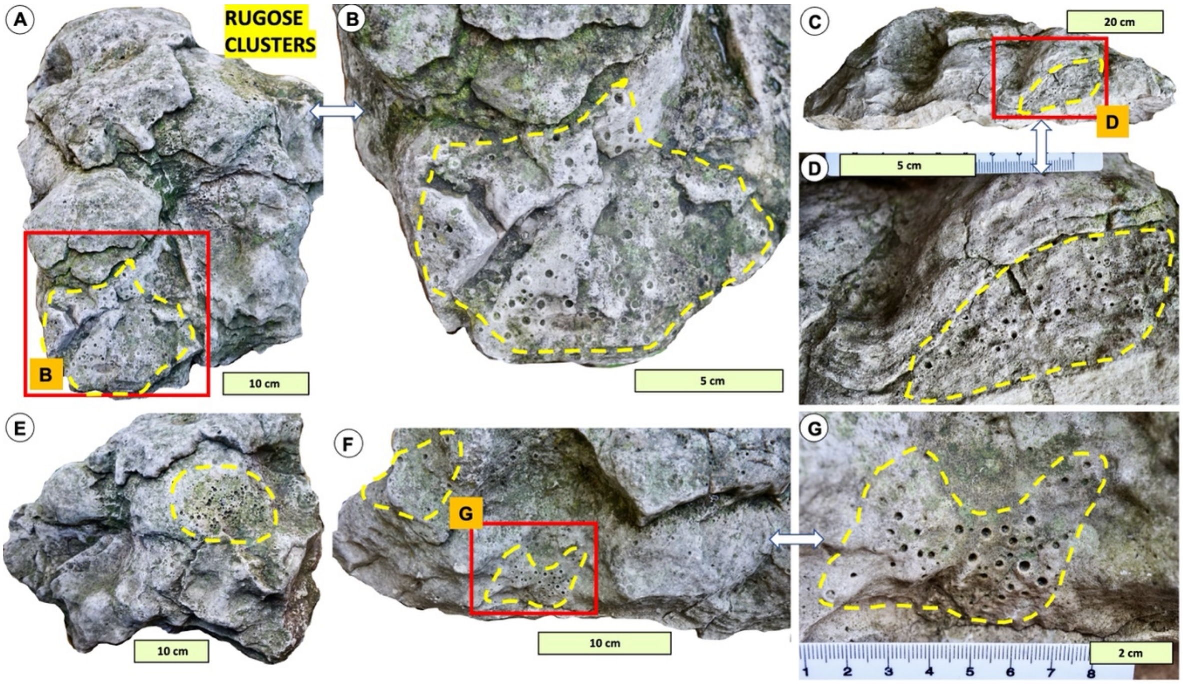

Fig. 6.2. Views of different parts of the upper and sides of the stromatoporoid with dashed yellow lines outlining areas of rugose coral calices on the surface. These indicate places where rugose corals developed branching colonies within the stromatoporoid; thus the rugose corals were not evenly distributed in the stromatoporoid mass, in contrast to syringoporids. File: KBS01-Sv-Rugs-Cauno-Tubes-02.

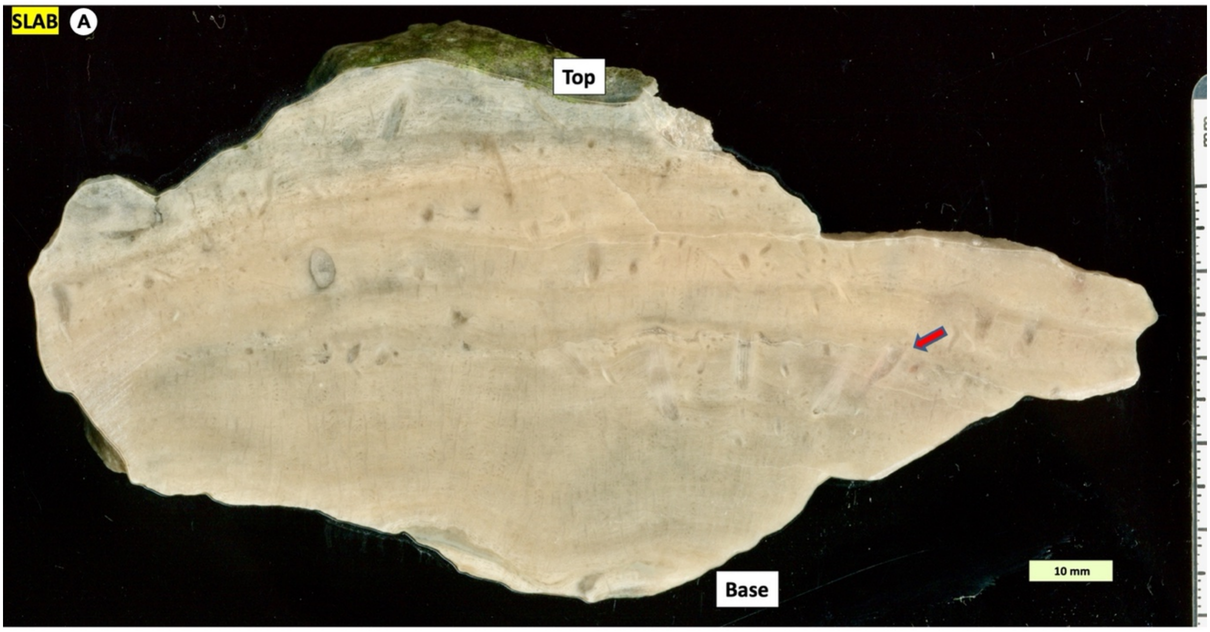

Fig. 6.3. VS slab showing rugose corals and a growth interruption surface (red arrow) at which some corals terminate. File: KBS01-Sv-Rugs-Cauno-Tubes-03.

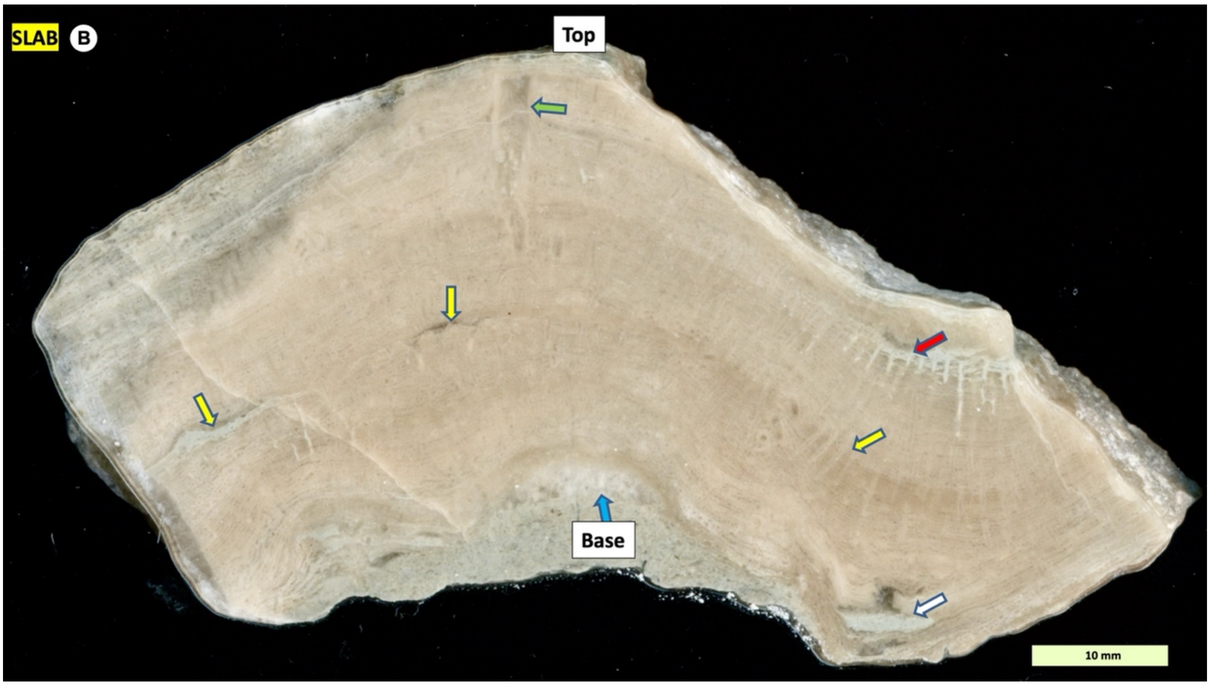

Fig. 6.4. VS slab showing irregular basal surface on sediment and sparite; not clear what the sparite represents, whether it is a recrystallised fossil or is a cement-filled cavity. White arrow shows sediment in a dip in the stromatoporoid surface, thus a growth interruption. Yellow arrows show second growth interruption, but right yellow arrow shows syringoporids pass through the interruption. Red arrow marks a third interruption where syringoporids terminate at an interruption surface and the coral tubes infilled with micrite. Green arrow marks a rugose coral in the upper part of the stromatoporoid. File: KBS01-Sv-Rugs-Cauno-Tubes-04.

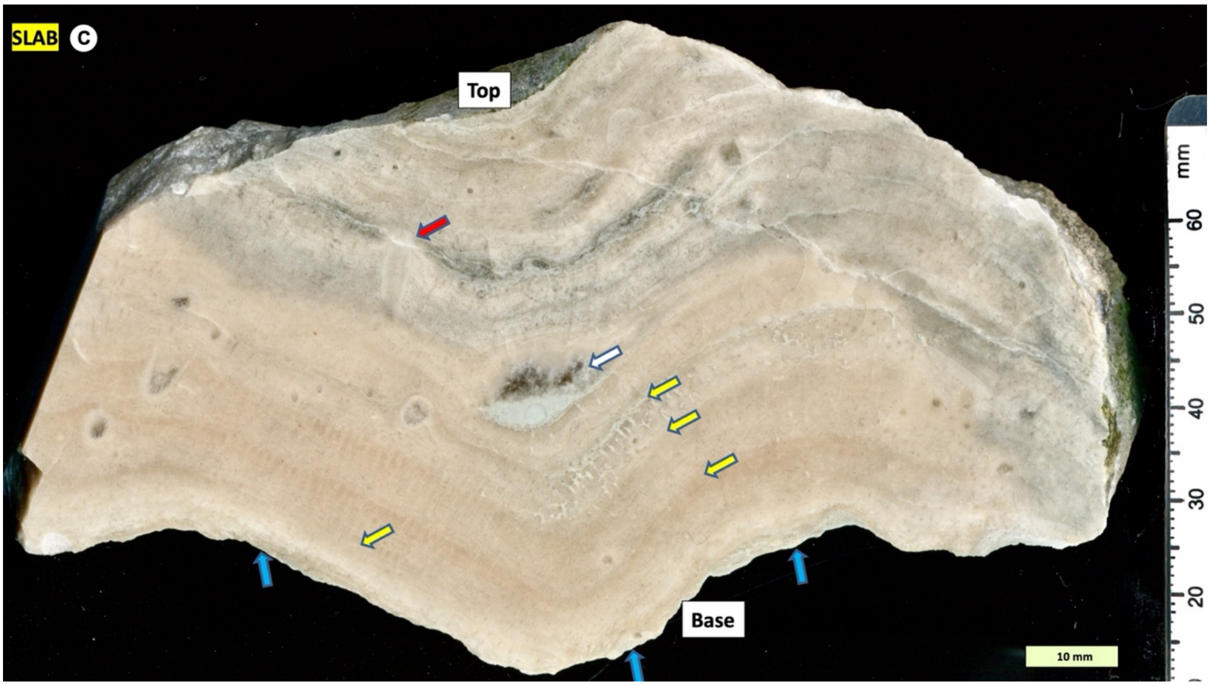

Fig. 6.5. VS slab. Blue arrows show the undulating base that was presumably in contact with sediment upon which it grew (see Fig. 6.4 where some sediment is preserved). Yellow arrows show numerous growth interruptions; white arrow points out a geopetal cavity. Red arrow shows an upper interruption surface that seems to also be a pressure solution line. Some rugose corals are seen on the left, as part of a cluster. File: KBS01-Sv-Rugs-Cauno-Tubes-05.

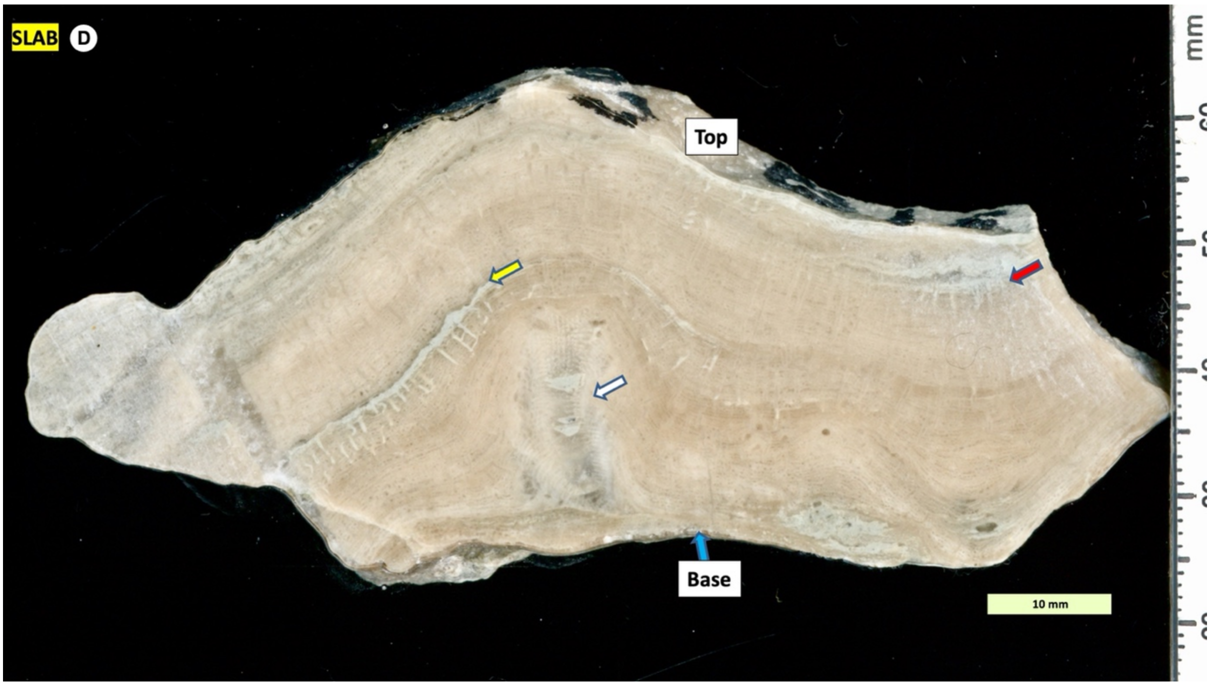

Fig. 6.6. VS slab showing early growth of rugose coral with reaction by stromatoporoid laminae upbending. Yellow and red arrows mark growth interruptions with sedimentation in coral tubes. File: KBS01-Sv-Rugs-Cauno-Tubes-06.

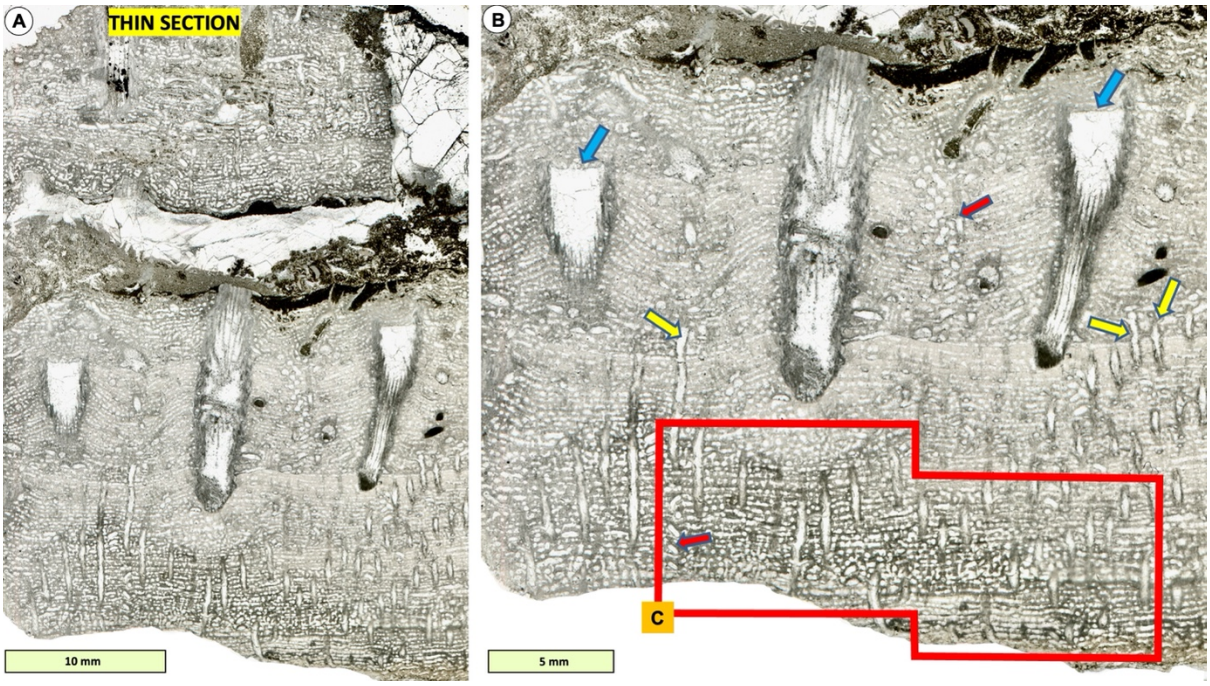

Fig. 6.7A-B. VS whole thin section including the base of the strom and revealing it as *"Stromatopora" venukovi* (Sv). Yellow arrows: syringoporids; blue arrows: rugose corals, in this case with growth interruption affecting two of the corals but not the central one. Note that the syringoporoids become much rarer in the upper part of the section, which may indicate the stromatoporoid could overgrow the syringoporids; this situation is also visible in Fig. 4.5 in the Kuppen Marl. Red arrow: spiral tubes. File: KBS01-Sv-Rugs-Cauno-Tubes-07.

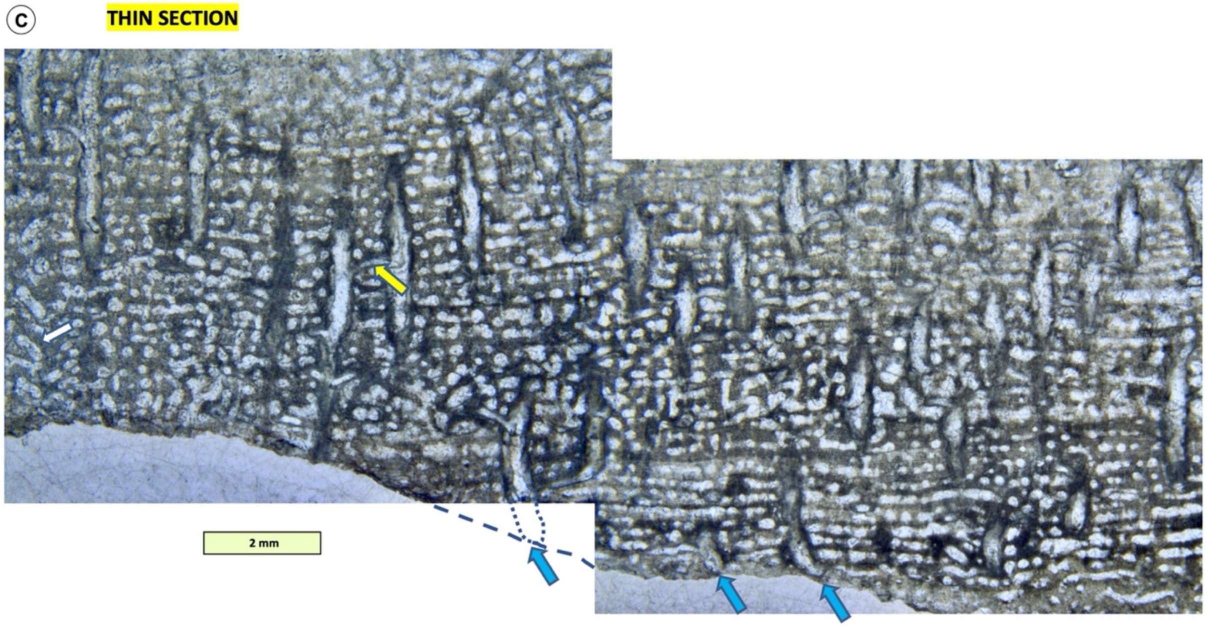

Fig. 6.7C. VS enlargement of basal portion showing syringoporids appear at the absolute base of the stromatoporoid, so the syringoporid larvae discovered the Sv at the same time that it formed. Yellow arrow shows cross tube between two syringoporid tubes. White arrow (left edge) shows the edge of a spiral tube. KBS01-Sv-Rugs-Cauno-Tubes-08.

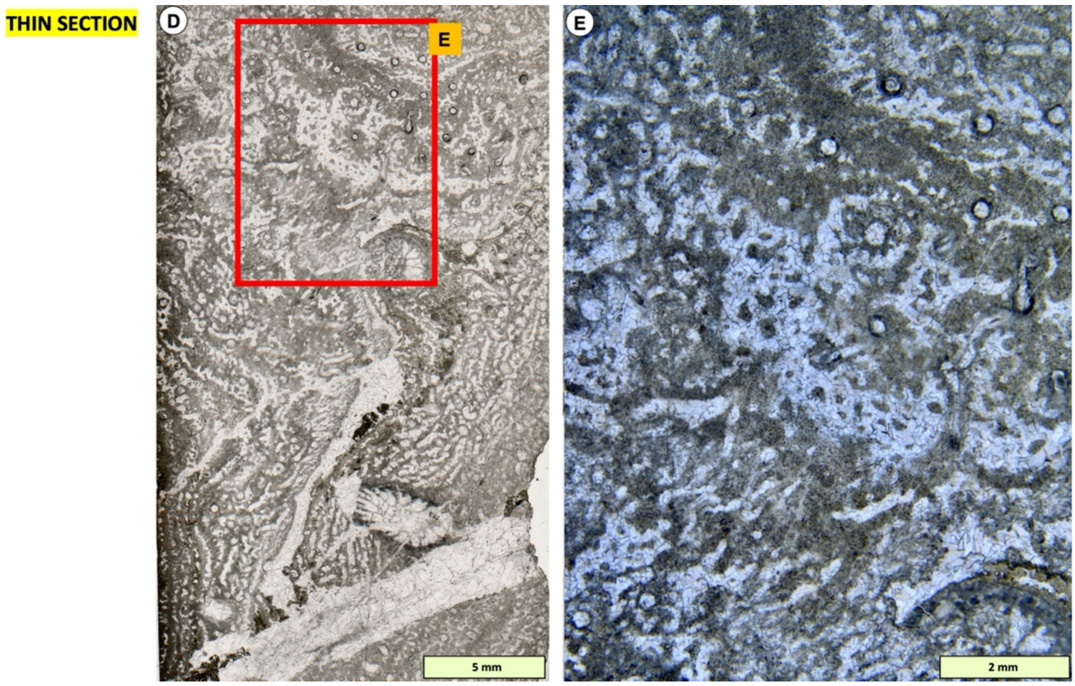

Fig. 6.7D-E. TS showing astrorhizae and distribution of syringoporids; also part of a rugose corallite lower right corner. File: KBS01-Sv-Rugs-Cauno-Tubes-09.

7. SYRINGOPORIDS AS SEPARATE ORGANISMS, NOT IN ASSOCIATION WITH STROMATOPOROIDS, IN HEMSE GROUP LIMESTONES, EASTERN GOTLAND

These samples are from Grogarns site, a few km north of Kuppen, in fine-grained fossiliferous limestones, stratigraphically a few metres below the Hemse Group biostromes. At Grogarns, a rich benthic fauna is present, including corals, but no stromatoporoids, for unknown reasons. In this section, syringoporids are illustrated; they have thicker wall structure than syringoporids found as symbionts in stromatoporoids. It is a matter of debate as to whether the intergrown syringoporids are taxonomically distinct or were modified in response to presence within stromatoporoids. However, the existence of free syringoporids in the Middle Biostrome, described earlier, that had the same structure as those in the stromatoporoid symbionts, may indicate the syringoporids inside stromatoporoids are different taxa from those at Grogarns.

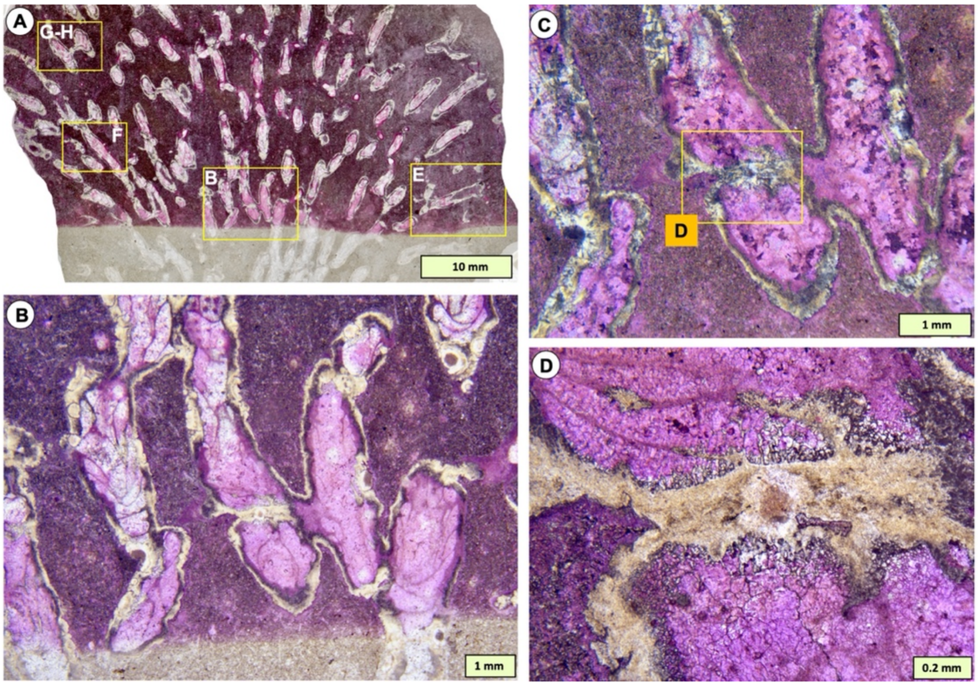

Fig. 7.1A-D. Syringoporid whole thin section, stained with Alizarin Red S and potassium ferricyanide (ARS-KFeCN). Unstained areas (brown) are silicified, showing silicification of only the corallite walls and tabulae. Note cross-tubes. File: Grogarns-D3-Syringoporid-01.

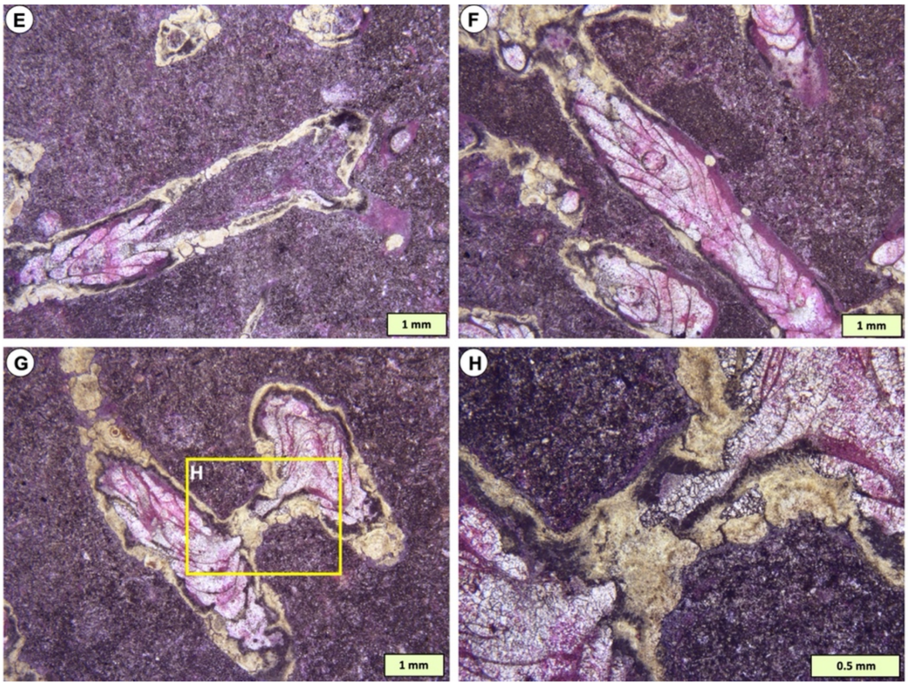

Fig. 7.1E-H. Details of the syringoporid, emphasising silicification of the walls but not cement infills or sediment. The presumption may be that there was organic matter in the walls creating an acid microenvironment for silica precipitation. Presumably this happened at and early diagenetic stage. Hemse Group, Ludlow (Silurian); Grogarns, eastern Gotland, Sweden. File: Grogarns-D3-Syringoporid-02.

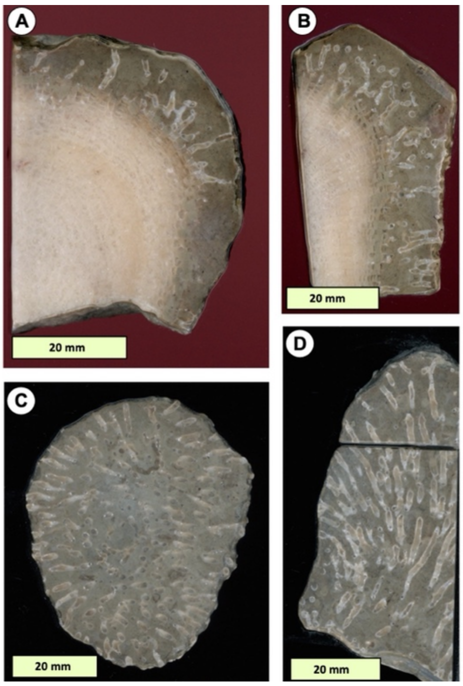

Fig. 7.2. A-B) Syringoporid encrusting a favositid; **C-D)** Free-growing syringoporid. Hemse Group, Ludlow (Silurian); Grogarns, eastern Gotland, Sweden. File: Grogarns-SyringoOnFav.

8. STROMATOPOROIDS FROM UPPERMOST HALLA FM (WENLOCK), AT GOTHEMSHAMMAR, EASTERN GOTLAND

Here are displayed a few specimens of unusual small stromatoporoids that are complex and detailed. This preliminary sample is part of an ongoing study and the stromatoporoids are not yet identified. These small specimens each show a complex individual history and demonstrate the rapid changes in environment that stromatoporoids are capable of recording. Intergrown symbiotic corals are present in only the stromatoporoids and may be possibly explained by a biological relationship, but the detailed nature of that relationship requires a more comprehensive study.

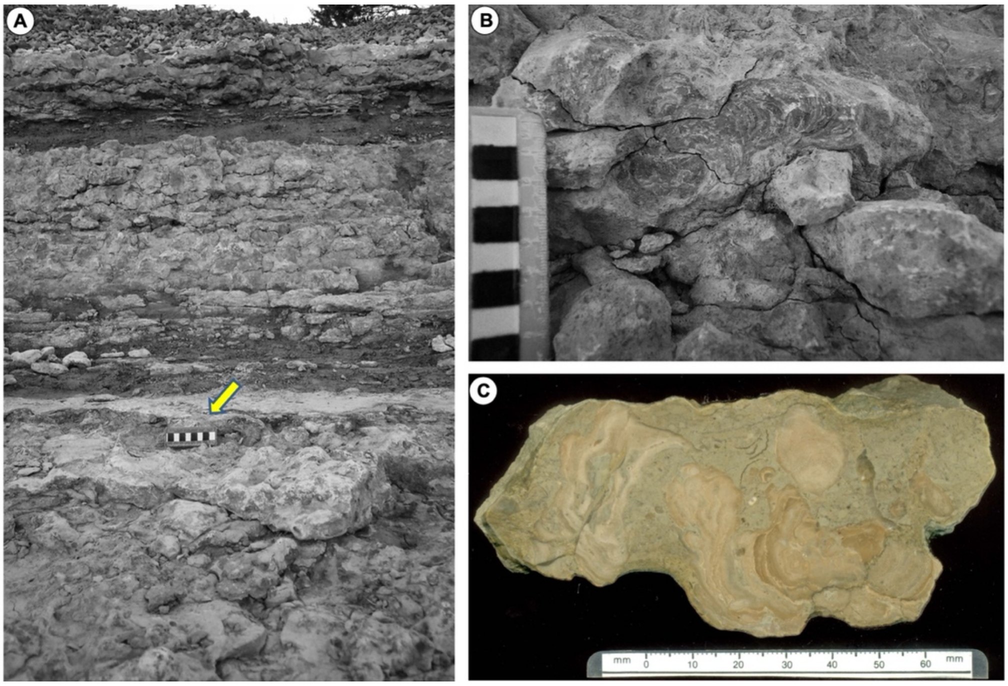

Fig. 8.1. A) Outcrop photo at Gothemshammar. Yellow arrow marks a hardground surface; directly below this level is the sampling level. **B)** Outcrop close-up showing stromatoporoids (dark areas) in lighter-textured matrix. **C)** VS of slab containing several small stromatoporoids in different orientations. File: GothemshammarStrom-01.

Fig. 8.2. A) VS whole thin section containing three small domical stromatoporoids that grew on a bioclast (ovoidal object lower centre right) that itself has a sequence of encrustation, beginning with a coral and contains some stromatoporoid growth. Above the ovoidal clast, the first stromatoporoid started on a rugose coral clast and has a spiral tube (red arrow) in its later growth; this stromatoporoid was terminated at an interruption surface followed by encrustation of the second stromatoporoid. The entire sample was overturned and the third stromatoporoid grew over the basal part of the first one; the sample was then reinverted back to its original orientation to give the final view. Thus the sample developed in a low energy setting periodically subject to high energy events. **B)** Enlargement showing details of growth relationships and the spiral tube. File: GothemshammarStrom-02.

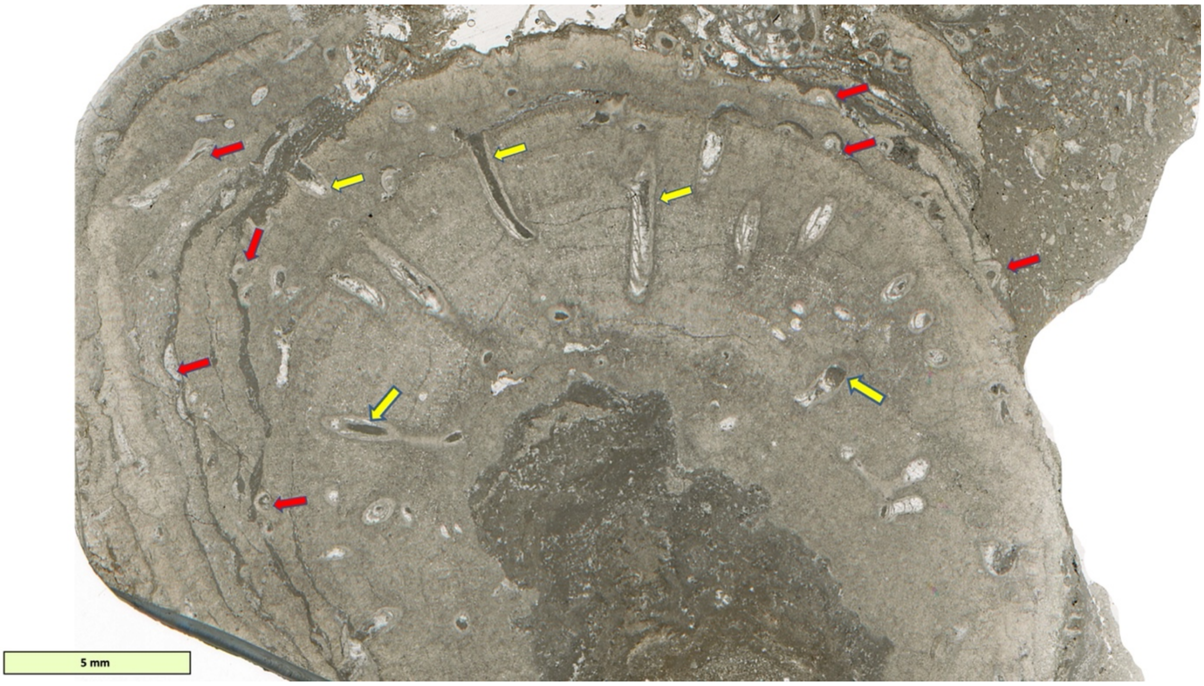

Fig. 8.3. Oblique VS through small rounded domical stromatoporoid; its oblique section can be appreciated by the large central micritic area with highly curved shape, that can really only be explained as an oblique section. However, the tightly curved shape allows full VS sections in the areas of the yellow and red arrows. Yellow arrows show abundant syringoporid tabulate tubes into which sediment trickled before continued growth. Note several interruption surfaces encrusted by

auloporids (red arrows). This specimen demonstrates the rapid changes in development of this sample. File: GothemshammarStrom-03.

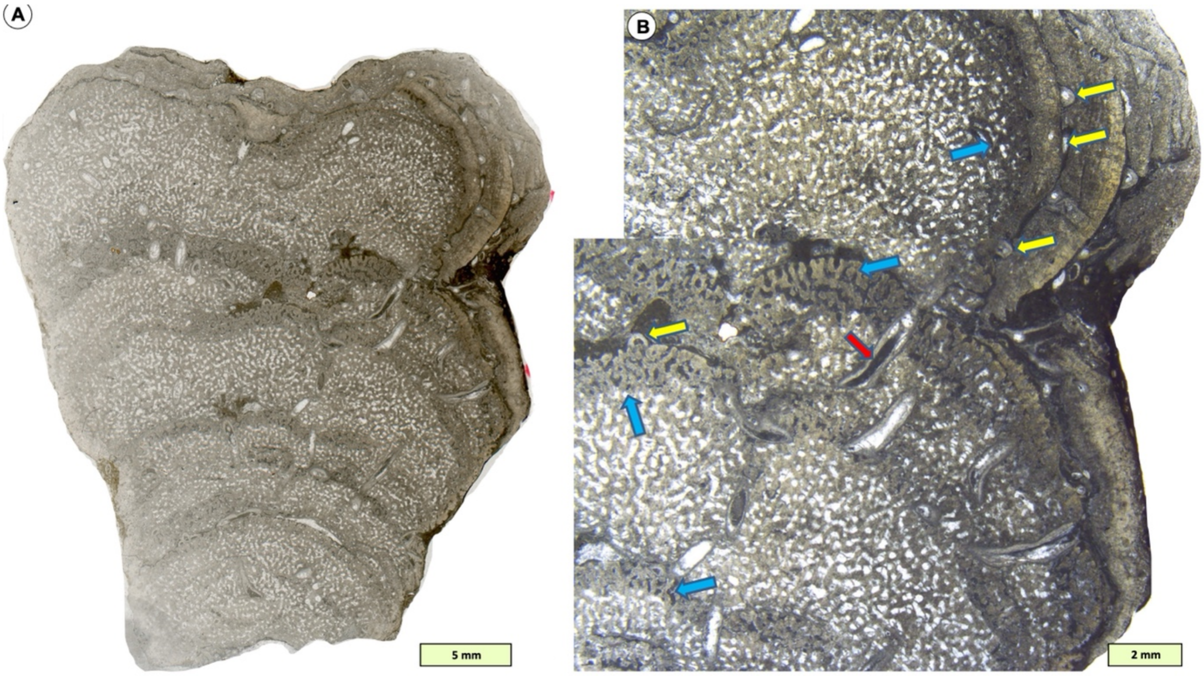

Fig. 8.4. VS whole thin section [A] and enlargement [B] of two stromatoporoids, the first one with an open architecture, which has four interruption events each one showing induration of the upper part of the stromatoporoid with sediment (blue arrows). Syringoporid tabulates are present in the first stromatoporoid (red arrow). A second stromatoporoid, with a finer skeletal structure, encrusted the side of the first one. Yellow arrows show encrusting auloporids at interruption surfaces. File: GothemshammarStrom-04.

Fig. 8.5. Example of a domical stromatoporoid with numerous interruption surfaces and syringoporid tubes that contain geopetal sediment (yellow arrows), indicating the stromatoproid was overturned before the tubes were infilled. Thus the specimen is illustrated in an inverted position. File: GothemshammarStrom-05.

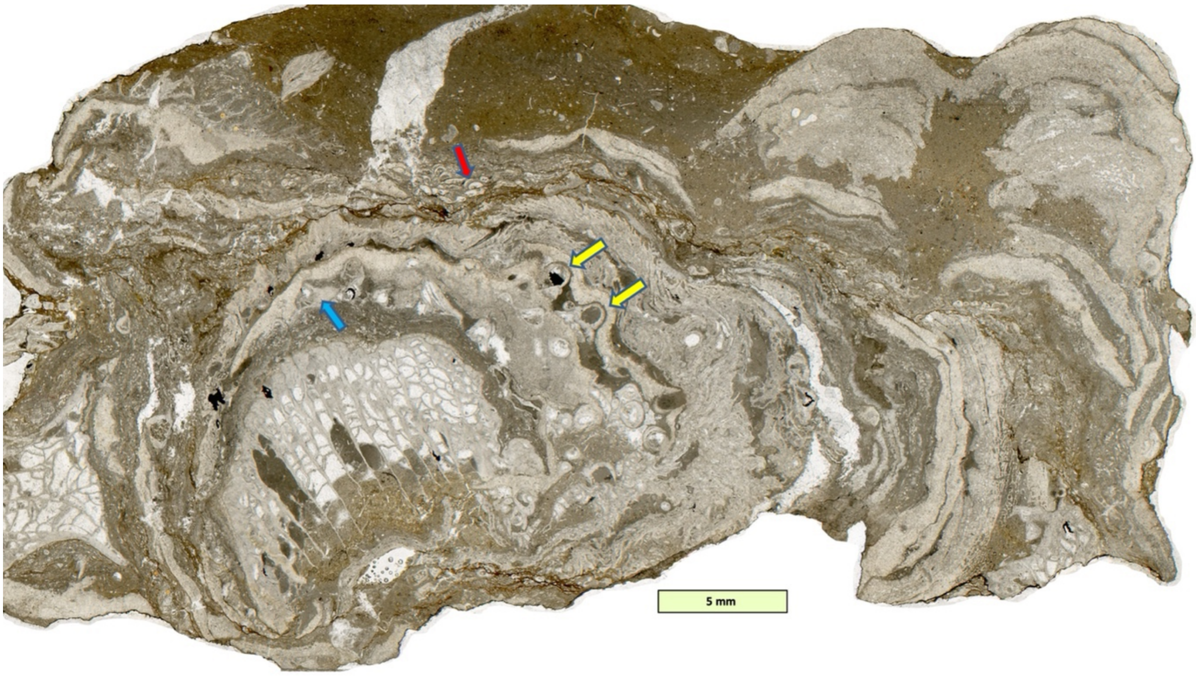

Fig. 8.6. VS whole thin section view of a complex detailed sample that includes a rugose coral (lower centre-left) as the bioclast upon which the growth sequence developed. Subsequently, the precise sequence is open to some interpretation, but one possible sequence follows. A layer of possible microbial micrite coats the coral, and encrusting auloporids developed on the resulting surface (blue arrow). Then a stromatoporoid with intergrown and encrusting tubes presumed to be auloporids (yellow arrows), followed by a layer of calcimicrobes (red arrow). The specimen was overturned and encrusted (bottom, below the rugose coral) before being uprighted again; finally small stromatoporoids developed (upper right), showing coalescence at the top. File: GothemshammarStrom-06.

9. CONCLUSION

1) This compilation should give you a broad view of the nature of symbiotic relationships in stromatoporoids, and their great value in helping to analyse the biology, life histories, interruptions, interactions and palaeoenvironments.

2) The evidence in this document supports a general model for syringoporid tabulates that their larvae were floating around in the sea and settled on particular stromatoporoid taxa that had characteristics which allowed the syringoporids to develop (we don’t know what those characteristics are). Thus they seem to have settled onto live stromatoporoid surfaces and survived; this is in contrast to many tube symbionts in stromatoporoids, which did not survive, but were overgrown by the stromatoporoid (see Kershaw et al. 2018 for evidence and discussion). So, either the syringoporids had something that was useful to the stromatoporoids (we don’t know what), or the syringoporids had a mechanisms to prevent the stromatoporoids from rejecting and overgrowing them; maybe the syringoporids could just grow a bit faster and keep away from the stromatoporoid living tissues. However, there is some indication of difference in stromatoporoid taxa; for Pc, the syringoporids continue to the top of the specimens, but there are two samples of Sv where the syringoporids are present in the lower portion of the stromatoporoid but become much less

common in the upper part (see Figs. 4.5 & 6.7, but in Fig. 3.7 the syringoporids are present through the sample). Nevertheless, the fact that syringoporids first appear in stromatoporoids at different levels in the individual stromatoporoid growth history is an indication that the syringoporids discovered the stromatoporoids by chance, thus the relationship was not an obligate one, but gave the syringoporids a better survival ability. Consequently this could mean that the syringoporids were commensals, as previously interpreted by many authors; but the problem is that we have only the mineralised skeletons, so we don't know if there was a mutualistic interaction between them.

3) For rugose corals the situation seems to have been rather similar to syringoporids. It is also interesting that when growth interruptions occurred (e.g. sedimentation events), the stromatoporoid, rugose and syringoporids were affected in different ways in different samples; in some cases rugosans survived, in other cases syringoporids survived, in other cases both survived, in other cases all died. Stromatoporoids in some cases survived growth interruption and recovered, in other cases, the surface was re-encrusted by new stromatoporoid growth. This complexity and individuality of events and processes shows the changeable dynamic situations for each stromatoporoid, and thus underlines a statement early in this document, that all stromatoporoids are individuals and each has its own story to tell.

4) However, the key point is that most, maybe all, cases illustrated here are open to interpretations and give you the opportunity to consider different possibilities. Thus, for example, can you discriminate reliably between associations that were mutualistic, or one sided? For one-sided cases was the relationship a commensal or parasitic one? For my own view, I have never recognised any parasites amongst all the corals and other tubes, in stromatoporoids; that is no modification of stromatoporid structure close to the symbiont that would indicate an adverse effect on the stromatoporoid due to presence of the symbiont. Thus none of the cases illustrated in this document show any features that could be easily considered as parasitic; but these are animals that are preserved as only mineralised skeletons and they lived hundreds of millions of years ago, so there is much scope for different opinions. There is a lot of information here that may be applied to other assemblages, so I hope it is useful.

Steve Kershaw

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