Palaeozoic stromatoporoid taxonomy:
Challenging the concepts

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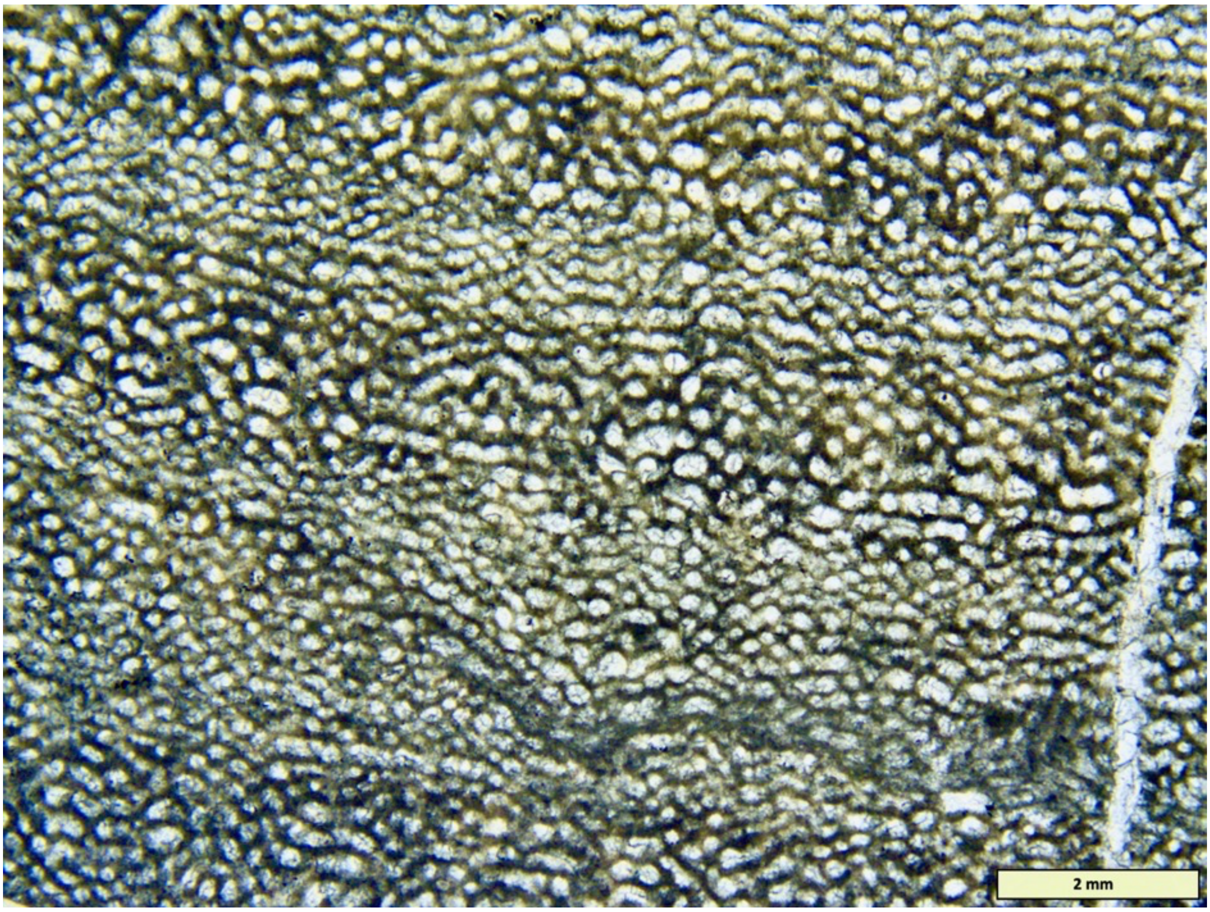
An atlas of images of three Silurian stromatoporoids, with discussion, addressing key challenges in stromatoporoid classification



This document is a compendium of annotated images and interpretations intended as a research tool for palaeontology and sedimentology

Frontispiece image

Vertical thin section microscope photo of a stromatoporoid named as *Ecclimadictyon macrotuberculatum* in a monograph of British Silurian stromatoporoids (Kershaw et al. 2021), note the scale in the bottom right corner, and the small calcite cement-filled fracture in lower right side that is a later event, nothing to do with the fossil structure. This photo is repeated in **Section 4.11** in the atlas, with annotation, but here it is presented with no annotation, to provide a nice clean picture for the front cover of the atlas; don't you think it is an amazing photo?
This picture shows unexplained and controversial aspects of stromatoporoids:

1) ***Unexplained***: the specimen's architecture is complex and variable but shows distinct banding patterns formed by alternating layers of thinner and thicker elements. The field of view shows three bands of thicker elements and three bands of thinner elements. Within the lowermost thin-element band is a disturbance in the banding, and this may be a growth interruption horizon in this part of the skeleton. Otherwise the alternating bands of thinner and thicker elements seem to be regular (as is shown in additional images of this particular specimen, in the atlas) and may relate to external controls on the growth of the stromatoporoid. Banding in stromatoporoids is well documented and historically has been assumed to represent annual growth (presumed driven by unspecified seasonal climatic changes). However, no direct evidence supports this assumption, and the underlying cause of the banding remains unknown. Alternative environmental factors may be responsible, but lack supporting data, and are essentially speculative. Moreover, stromatoporoids display several different kinds of banding in stromatoporoids, of which only one is shown here.
2) ***Controversial***: apart from the differences in thickness of skeletal elements seen in the banding, close examination reveals that the geometry of this architecture is not uniform. In the central thick-element band, some laminae are continuous, with a crumpled appearance; there are pillars between successive laminae. This arrangement is consistent with a stromatoporoid genus called *Clathrodictyon*. However, within the same band, near to the continuous laminae, the same central thick-element band also has laminations that are ***not*** continuous, and in places develop a zigzag appearance; these are more consistent with a stromatoporoid genus called *Ecclimadictyon*. Elsewhere in the specimen are curved laminae, which in some places have long empty spaces between the laminae; these have some consistency with a third stromatoporoid genus called *Camptodictyon*. These three genera are well-established in the literature, yet the presence of their three kinds of architecture in a single thin section presents a conundrum. Clearly this specimen cannot contain three different genera; they must all be one genus, but is it one of these three, or is it potentially a different one altogether? Thus the naming of this taxon as *Ecclimadictyon macrotuberculatum* by Kershaw et al. (2021) may be an oversimplification that did not take into account its structural variation.

This atlas analyses this and other samples and tries to make sense of how these variations relate to stromatoporoid taxonomy.

How to cite this atlas

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<u>SUMMARY</u>

intended for specialists and non-specialists

This document is presented as an open discussion to encourage broader thinking; it does not provide definitive answers, although there are some recommendations that may help in determining the next steps. Hopefully this study will help to refine the key questions we should be asking about the taxonomy of stromatoporoids and its applications in palaeontology. We encourage comments and feedback on this work. If, after reading this atlas, you find that you cannot sleep at night, then we fully understand and sympathise.

This Summary is NOT an abstract, it is an integral part of the document, containing some points not mentioned again in the atlas; you may need to refer back to this Summary throughout reading the atlas. This atlas contains a lot of similar-looking pictures, and you need to pay attention to the detail of subtle but significant variations in order to appreciate the arguments presented and the importance of their significance. This is a "stay awake" document that will improve your understanding of taxonomy in stromatoporoids, hence in all fossils, and without doubt will improve your life in general.

Taxonomy (description, classification and naming of organisms) is essential for analysis of organisms, required to understand their genetic relationships, biology and ecological interactions in communities. Living organisms' taxonomy is achieved largely by study of their physical characters, but may include some other aspects such as breeding interactions, and where appropriate molecular genetic analysis. A common criterion for defining species is the ability to interbreed, although this concept applies to organisms that reproduce sexually. However, in fossils, taxonomy relies almost entirely on physical characters, and interbreeding cannot be recognised. The standard approach assumes that individual fossils with great physical similarities are closely related and may be equivalent to the species concept used for living organisms. This principle holds where variation of physical characters between similar individuals is minimal; but in cases where variation in physical characters overlaps between individuals, then defining taxonomic boundaries becomes highly problematic. This document explores the challenges of taxonomic definition caused by character overlap, using fossil sponges as a case study. Although our focus is on sponges, the concepts considered here are applicable to fossil organisms that have complex variation of physical characters.

Stromatoporoids are a type of fossilised sponge, having skeletons composed of calcium carbonate mineral. Stromatoporoids are commonly referred to as one of the forms of *hypercalcified sponges*, a term that is not related to the classification of sponges. Sponges are traditionally classified into three major groups, called Classes: Demospongiae (most have spicules made of silica); Calcarea (have spicules made of calcium carbonate) and Hexactinellida (have a network made of silica). This threefold division is highly simplistic and in reality the classification is more complex, but its simplicity is sufficient for the clarity of this discussion. Hypercalcified sponges, with their calcium carbonate skeletons, are distinct from the Calcarean Class of sponges (that have calcium carbonate spicules); in almost all cases the latter have a soft spongy structure characterised by most sponges. In contrast, hypercalcified sponges have a secondary stony skeleton of calcium carbonate, superimposed on the primary soft skeleton, with soft tissue restricted to the surface layers. Nevertheless, some living Calcarean sponges are also hypercalcified and one of them is a stromatoporoid form (*Murrayona*); other living sponges with a stromatoporoid-type skeleton belong to the Demospongiae class of sponges. Although stromatoporoid-form sponges occur rarely as living organisms, they were very abundant in several episodes of Earth history, preserved as fossils in limestones deposited in warm shallow marine environments. It is these fossilised stromatoporoids that are the topic of this study.

Sponges are normally identified from their spicules, tiny mineralised structures embedded in their structures that help to strengthen the sponge; the wide range of shapes of spicules define the different orders and families of sponges. However, this system works only for sponges with spicules, but some modern sponges lack spicules, so are identified from the shapes of their body structures. One such example is the modern hypercalcified sponge genus *Vaceletia* (which is not a stromatoporoid-form of sponge, but is instead a sphinctozoan-form and is not studied in this atlas). For fossil stromatoporoids, most of the ones that occur in Mesozoic strata have spicules and so can be identified within the modern spicule-based classification system, but this is not the case for the Palaeozoic stromatoporoids, that lack spicules, except for a single specimen that does actually contain spicules (Da Silva et al., 2014)! But one specimen is not enough, so instead the Palaeozoic stromatoporoids are classified using their hypercalcified skeletons, and fall into 7 principal groups, referred to as *orders* by stromatoporoid specialists. However, because they lack spicules, these orders may or may not have the same kind of biological validity as modern orders of organisms, and thus stromatoporoid fossils within these orders may or may not be closely related. This classification is therefore phenetic (uses criteria of the morphology of the fossil but not related to any evolutionary changes). The true biological relationships between Palaeozoic stromatoporoid taxa may never be resolved due to the absence of spicules in these fossils.

Within one of these traditional orders of Palaeozoic stromatoporoids, the Order Clathrodictyida, are several genera, and three of these genera are the subject of this study; they are called *Clathrodictyon*, *Ecclimadictyon* and *Camptodictyon*. *Clathrodictyon* is characterised by continuous thin horizontal sheets called laminae, that are slightly distorted to create the impression they are a little crumpled when viewed in vertical section (VS) under the microscope; the laminae are separated by vertical struts called pillars. The laminae are not actually physically crumpled, it was just the way they grew. *Ecclimadictyon*, in contrast, is composed of horizontally-orientated laminations that are strongly crumpled in appearance in VS in some parts of a specimen, to a zig-zag arrangement in others. The result is that the successive laminations come into contact with one another upwards and downwards in the VS view, with little evidence of pillars, that may be very short, but missing in most of the skeleton. *Camptodictyon* has somewhat wavy laminae that transition to a zigzag pattern in places, has pillars in other parts, and has elongated galleries that the other two genera do not show; so *Camptodictyon* looks different again from the other two genera.

Why are these apparently simple and obvious differences between these three traditional genera interesting or even important in the study of stromatoporoids; and who cares? The answer to this question is straightforward: although there are indeed specimens of each genus that show these differences consistently without any overlap of their structural forms, there is common occurrence of cases where two, and in some cases all three, of these forms of skeletal structure can be found within the same specimen, and therefore within the same thin section, as illustrated in the Frontispiece photo of this atlas. Some problems emerge:

1) Can these three genera be consistently reliably distinguished? The answer is that there is an argument that they may be separated in assemblages where there is no overlap between the structure of all three types of skeletal structure where they occur in different individuals; but in assemblages where they show sufficient variation that overlap occurs within a specimen, then they cannot be reliably separated.
2) In cases where these genera cannot be reliably separated because of overlap between their fossil structures, what is the impact of this issue on recognising them as distinct biological entities as in the fossil record? In such cases, they cannot be consistently considered biologically different, creating uncertainty about which taxonomic name to use. There is also a further point:
3) in specimens where there is *NO* overlap in structure, are *those* specimens reliably distinguishable as different genera? Remember that we are dealing with sponges that lack spicules, and so their classification uses only the calcareous skeleton that is known to be unrelated to the biological classification in modern sponges. So how reliable could the calcareous skeleton be in definition of biological species in fossils? The problem is that we don't know; there is some evidence from modern sponges that specimens with the same calcareous skeleton are the same taxon, from the modern *Vaceletia*, a hypercalcified sphinctozoan sponge that does not have spicules, and is generally agreed to be a single taxon. The same applies to the modern *Astrosclera* (a living stromatoporoid-grade sponge), some populations of which do not have spicules but are still recognised as *Astrosclera*. But for fossil stromatoporoids, distinction as genera may or may not apply and we lack the critera to prove it. The result is that, hypothetically, multiple biological taxa may be represented by a single type of calcareous hypercalcified skeleton. Here, it means that different specimens, with identical calcium carbonate skeleton could, in theory, belong to different species. In this idea, there may be more than one species capable of growing an indistinguishable calcareous skeleton. Although it seems unlikely, nobody knows the answer to this vexing question, but it needs to be asked in order to broaden the exploration of taxonomy in stromatoporoids and potentially test current concepts of stromatoporoid genotypes. This issue lies at the root of the problem of the subject of stromatoporoid taxonomy, exemplified by this study: not only are the seven traditional orders of stromatoporoid structure unconfirmed as taxonomically separate entities, but so are the traditionally-recognised genera (and hence species) within those orders. As a result, the **holotypes** of these fossils may well be meaningless as standards of taxonomic identification, leaving us uncertain about how many biologically-distinct taxa really exist in these fossils. By the way, stromatoporoids are not the only fossils that present this issue, but here we focus on the stromatoporoids, because we love them.
4) Another interesting observation in stromatoporoids relates to this debate: in any assemblage of fossil stromatoporoids, there are normally only a few taxa (traditional genera and species). In the most diverse assemblages, there are not more than about 20 taxa, and commonly there are less. When this is compared with modern sponge assemblages (dominated by soft sponges, not the hypercalcified sponges, which are rare), those modern assemblages have high diversity of dozens of genera commonly found together. Unfortunately when they die, these modern soft sponges break down and disappear, because they lack a

hard skeleton. Does this mismatch between the numbers of taxa in modern sponge assemblages and fossil stromatoporoid communities mean that the ancient assemblages of hypercalcified sponges are only a ***part*** of the total sponge assemblage that was present in the ancient environments? If so, then what is the implication of this aspect to those many studies that try to assess the biological diversity and abundance in ancient organism assemblages/ecosystems? It makes us question whether models of diversity based on databases have any useful meaning if a part (perhaps substantial part) of the original living assemblage is missing from the fossil record.

So, why does all this matter? Researchers studying hypercalcified sponges should care; this issue affects other hypercalcified sponges, not just stromatoporoids, but also the other four groups of hypecalcified sponges, called chaetetids, sphinctozoans, inozoans and archaeocyaths. Also, those good folks who work on fossil databases should take note. Fossil assemblages are typically composed of the hard parts of organisms and soft-bodied organisms are essentially missing. As a result, assessment of the sponges' diversity within an assemblage may well be compromised by such differences in preservation potential of the organisms.

What is the conclusion of this study? The overlap in calcareous skeletal structures of *Clathrodictyon*, *Ecclimadictyon* and *Camptodictyon* in many specimens undermines their reliability as distinct genera. Therefore, these issues mean that it may well be of poor scientific value to fine-tune the taxonomy down to biological genus and thus species levels. The various documented species within these genera become insecure (if you can't separate genera, then logically it is not possible to separate species within those genera). This issue extends beyond these three genera and may affect other stromatoporoids [perhaps all stromatoporoids].

Despite these concerns, a classification scheme is needed because there ARE clear distinctions between many stromatoporoids at the level commonly considered to be genera; many of them look very different and certainly are different taxa. For example, the genus called *Labechia* is hugely different from *Clathrodictyon, Ecclimadictyon* and *Camptodictyon* and is entirely reasonably considered biologically different at the lowest taxonomic levels. Thus, much of the existing diversity information remains valid, but it all needs to be reassessed in order to find out where the uncertainties are. Some taxa, such as *Clathrodictyon, Ecclimadictyon* and *Camptodictyon*, may be better viewed as form-groups, meaning that several undefined biological taxa may exist within the range of skeletal variation across the group. One approach is to develop the grade scheme applied to hypercalcified sponges down to the traditional order and family level of stromatoporoid classification, and perhaps down to genus and species levels, by considering each taxon as a subdivision within the grade of stromatoporoids. Thus, instead of thinking of these fossils as being biologically classed into the normal Linnean hierarchy of divisions, replace this with a classification that emphasises what is visible, and consider them as grades of skeletal organisation, even at the lowest taxonomic levels. Hence the taxa of stromatoporoids are not implied to be biologically related, even though they might be.

Perhaps the biggest problem in stromatoporoid taxonomy is the common usage of small areas of specimens to describe and define the taxa, in the historical publications of stromatoporoid literature. The holotypes of *Clathrodictyon* and *Ecclimadictyon* used in this document and stored in the Natural History Museum, London, are perfect examples of this problem: rock chips ca 10 x 20 mm were used for those thin sections in the 19th Century. This approach needs to be replaced by images of large areas of stromatoporoid skeletons, and in the case of small stromatoporoids it is feasible to capture the entire stromatoporoid on a single large thin section. Thus, the lateral and vertical variation within a single stromatoporoid (or at least in large areas using large thin sections) can be viewed in vertical section, and lateral variation across the specimen within a single transverse section; the full range of variation can be demonstrated and used in the classification of the taxon. For large stromatoporoids (too large for a single thin section), vertical and lateral variation can be viewed using large thin sections and multiple thin sections to capture potential variation from different parts of the same specimen. Large thin sections have been shown to demonstrate skeletal variation of critical value in palaeoecological studies. On that basis, maybe the best thing to do is to throw away the holotypes of *Clathrodictyon* and *Ecclimadictyon*, and start again with new samples; but of course the tradition of the taxonomic process in palaeontology would never allow that to happen.

So, if you agree with the arguments presented here, and feel like abandoning stromatoporoid taxonomy, remember that these fossils do have a huge amount of skeletal variation of at least important broad-scale classification value, but require a common-sense understanding of the relationship between biology and the preservation of organic remains. Stromatoporoids are remarkably useful in ancient sedimentary environment analyses and record processes and events affecting the sea bed, in which taxonomy plays a part because of the control exerted by genetic properties on growth form in many cases. In general terms, such aspects as determination of whether the seafloor sediment underwent early lithification, and local sedimentation events, are recorded in stromatoporoid skeletons, that also in part relates to their taxonomy. Some stromatoporoid taxa preferentially encrusted hard surfaces, others seem to have thrived on soft sediment. Such features are well documented in the literature. In other words: “don’t throw out the baby with the bathwater”.

We hope this open-ended discussion document leads to greater thought and research into stromatoporoid as taxonomic entities and therefore enhance their application in palaeontological studies.

CONTENTS LIST

Title and cover image … … … … … … … 1-2
Summary … … … … … … … … … 3-7
Contents list … … … … … … … … … 8
General information and acknowledgments … … … … 9

Section 1: Introduction and Aims … … … … … 10-12
1.1. Backstory … … … … … … … … 10-11
1.2. Aim of this study … … … … … … … 11-12

Section 2: Introducting the cast … … … … … … 13-27
2.1. *Clathrodictyon* … … … … … … … … 13-17
2.2. *Ecclimadictyon* … … … … … … … … 17-21
2.3. *Camptodictyon* … … … … … … … … 21-27

Section 3: The problem of *Ecclimadictyon* definition described in Kershaw et al. (2021) … … … … … … … … 28-32

Section 4: Overlaps of stromatoporoid skeletal structure across the three taxa (*Clathrodictyon, Ecclimadictyon, Camptodictyon*) … … … 33-87
4.1. *Clathrodictyon* and *Ecclimadictyon* holotypes … … … 33-38
4.2. NHMUK PI P5722-222 – *Clathrodictyon vesiculosum* … … 39-42
4.3. NHMUK PI P5725-223 – *Clathrodictyon vesiculosum* … … 43-45
4.4. NHMUK PI P5728-221 – *Clathrodictyon vesiculosum* … … 45-51
4.5. NHMUK PI P5731-219 – *Clathrodictyon vesiculosum* … … 51-54
4.6. NHMUK PI P5955-220 – *Clathrodictyon vesiculosum* … … 55-57
4.7. NHMUK PI P5970-241 – *Clathrodictyon vesiculosum* … … 58-59
4.8. NHMUK PI P5493-240 – *Clathrodictyon vesiculosum* … … 60-64
4.9. WN15-39 – *Ecclimadictyon macrotuberculatum* … … … 65-67
4.10. LSM11-01-part 1 – *Ecclimadictyon macrotuberculatum* … … 68-76
4.11. LSM11-01-part 2 – *Ecclimadictyon macrotuberculatum* … … 77-83
4.12. LSM11-01-part 3 – *Ecclimadictyon macrotuberculatum* … … 84-87

Section 5: But don't throw out the baby with the bathwater … 88-95
Other stromatoporoids from Kershaw et al. (2021)

Section 6: Analysis: how to make sense of the variations of stromatoporoid structure illustrated within taxa in this atlas? … … … 96-99
6.1. Implications of this study for stromatoporoid taxonomy … … 96-97
6.2. An answer to the issue of stromatoporoid taxonomic classification? 97
6.3. More things to consider … … … … … … 98
6.3.1. What is a stromatoporoid? … … … … … … 98
6.3.2. How to study stromatoporoid taxa … … … … … 98
6.4. Stromatoporoid assemblages and correlations challenges … 99

Section 7: Conclusions: a way forward … … … … 100-101

Final Comment and references … … … … … … 102-103

GENERAL INFORMATION AND ACKNOWLEDGMENTS

 Please note that the scientific content of this atlas has not been peer-reviewed.

COMMENT ON PHOTOS FROM NATURAL HISTORY MUSEUM SPECIMENS

Thin section photos of NHMUK thin sections were taken using a mobile phone pointed down the eyepiece of a microscope; they are adequate for the purposes of this atlas, but contain marginal areas out-of-focus, although these should not impede your understanding of the structures.

ABBREVIATIONS USED IN THIS ATLAS

TS: transverse section (either a hand specimen or a thin section)
VS: vertical section (either a hand specimen or a thin section)
NHMUK: Natural History Museum, London

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SECTION 1:
INTRODUCTION AND AIMS

1.1. Backstory

You need to know the backstory before coming to the aims. The inspiration for this document began many years ago with two items of discovery, followed by one recent key event:

Item 1: During SK's PhD work in 1970s, that included Ludlow (upper Silurian) stromatoporoid-rich biostromes on Gotland, Sweden, two stromatoporoid taxa were difficult to separate. These taxa, *Stromatopora bekkeri* (conveniently abbreviated here to ***Sb***) and *Parallelostroma typicum* (***Pt***), were illustrated by Mori (1970). In contrast, the other taxa in those biostromes were relatively easy to characterise, highlighting that, ***within a single assemblage***, some stromatoporoids are not difficult to identify, yet others are very problematic. Thus, when you have become familiar with the assemblage, some species are instantly recognisable whereas others require careful study and comparisons. In 1978 SK asked Kei Mori (a Japanese specialist on stromatoporoids who made his PhD on Gotland stromatoporoids in 1960s) about the difficulty of distinguishing ***Sb*** and ***Pt***; Mori agreed that in some cases it is a problem. [By the way, because of Stearn's (1993) paper redefining the genus *Stromatopora*, ***Sb*** is now not included in the genus *Stromatopora*, but subsequent unpublished thoughts and discussions have not resulted in a decision about what genus it should be called: for the record it is ***not*** *Parallelostroma* and has been called *"Stromatopora" bekkeri* (therefore ***"S"b***) in subsequent publications, pending decision about what to call it.]

But ***how can it be*** that not only are these two stromatoporoids, which can be difficult to distinguish in thin sections, classified as different species, but they are in different ***genera***? Remarkably they may also be in different traditional ***orders*** of stromatoporoids [*Stromatopora* is in the Order Stromatoporida, *Parallelostroma* is in the Order Syringostromellida]. However, because we don't know what genus to call *"Stromatopora" bekkeri* therefore we don't know what traditional stromatoporoid order it is in. In the light of the notion of fossil taxonomy explained in the Summary at the beginning of this document, such an issue between *"S"b* and *Pt* doesn't make sense from a taxonomic viewpoint. So right from the outset of his journey with stromatoporoids in the 1970s, SK was aware of the uncertainty surrounding stromatoporoid taxonomy. There is another Figshare atlas in preparation to illustrate the issue of *"S"b*.

Item 2: The thoughtful ideas presented by great late Colin Stearn (1989) regarding his recognition that stromatoporoid structure commonly shows variation even within one specimen, to the extent that different parts of a single stromatoporoid may be classified as different species or even different orders (Stearn's 1989 paper is worth reading). Worry, worry, worry.

The recent key event: in January 2025, in an email to SK, Juwan Jeon (South Korean stromatoporoid worker) drew attention to a perceived error by Kershaw et al. (2021) in classification of Silurian stromatoporoids from the Wenlock of UK. More on this later. Accepting that this error is justifiable, this event motivated SK to dig up the long-buried (but not decomposed) corpses of old problems of stromatoporoid taxonomy in an attempt to re-evaluate this issue and come to some sensible outcomes. The results of these investigations are reported in this file.

1.2. Aim of this study

The result of the items and event described in Section 1.1 is this document, which **aims** to offer a solution to the problem of the application of stromatoporoid taxonomy using the vehicle provided by 3 genera. The findings may reshape our understanding of genus and species concepts in stromatoporoids, and how holotypes may be chosen to define taxa in stromatoporoids.

The most important point for the reader to take home is that this document is presented as an open-ended discussion which casts doubt on the principles and practice of stromatoporoid taxonomy as it has been applied in many, many published studies. On one hand this document is not a formal peer-review publication, so it can't change anything about the way stromatoporoids are classified in formal publication. But on the other hand its controversial content has the potential to change everything and force a complete re-assessment of all we have thought about the systematics of these amazing and beautiful fossils. Depending on how you view this text and evidence, it may be necessary to reconsider some important aspects. Two key examples are:

1) determination of the diversity of stromatoporoids in an assemblage;
2) the interpretation of the palaeobiogeographic distribution of stromatoporoids in relation to positions of ancient continents: are apparently identical stromatoporoid taxa found on different ancient continents really the same taxa?

Other critical considerations, which we leave open for future discussion, include the degree of morphological plasticity in stromatoporoid characteristics. Consider these points:

1) Could a morphometric or statistical approach help define more meaningful taxonomic groups?
2) Do observed variations reflect different growth stages or ecophenotypic plasticity? There are some attempts at these aspects in the literature, that may be worth further exploration.
3) Extending these ideas further, is it possible that widely-recognized stromatoporoid taxa actually represent multiple, unrelated species that have convergently developed similar skeletal structures? Is that possible, and if not then how can you prove it is not?
4) Should taxonomic studies prioritize examination of the range of skeletal variation within ***complete*** stromatoporoid specimens, to replace the common practice of using small rock chips taken from anywhere within a specimen? The latter results in isolated thin sections that mostly do not show the range of variation within a single specimen; whole specimen study may better capture morphological variation, particularly in the definition of holotypes.
5) Perhaps stromatoporoid taxonomy should shift toward more flexible classifications based on a range of structure rather than rigid genus-species divisions that use only parts of the variation.

Expanding this discussion beyond stromatoporoids, how might these issues impact taxonomic practices in palaeontology and evolutionary biology? Given the uncertainties in taxonomic assignments, how reliable are conclusions drawn from such datasets regarding past ecosystems, climate, evolutionary trends, and extinction rates?

The problems described above present challenges beyond stromatoporoid classification. They raise deep and broad questions about the way palaeontology defines and categorizes extinct organisms. But for the present purpose, we drill down into the detail of stromatoporoid taxonomy and try to make sense of it.

SECTION 2:
INTRODUCING THE CAST

We have chosen three stromatoporoid genera for this study, this choice derives from the query raised by Juwan Jeon regarding the taxonomy of *Clathrodictyon* as discussed by Kershaw et al. (2021). We will explain the query itself after describing and illustrating the three stromatoporoid genera. So please remain sitting on the edge of your seat: your insatiable curiosity will be satisfied in due course.

2.1. Clathrodictyon

Clathrodictyon is defined in Nestor (2015, p. 755)[=the 2015 Treatise on Hypercalcified Sponges]. However, *Clathrodictyon* is a taxon named by Nicholson & Murie (1878), so it dates back to that time. The word *Clathrodictyon* derives from Latin and Greek and its two components are: *clathro = a lattice; dictyon = a net*.

Hence the fossil has the appearance of a lattice and a net when seen in vertical thin section, as illustrated in Figs. 2.1.1-2.1.5. Fig. 2.1 shows an overview of the VS and Fig. 2.1.2 shows a closeup of the right-hand part of the holotype, indicating the location of the photo used by Nestor (2015, p.756, Fig. 416-1a).

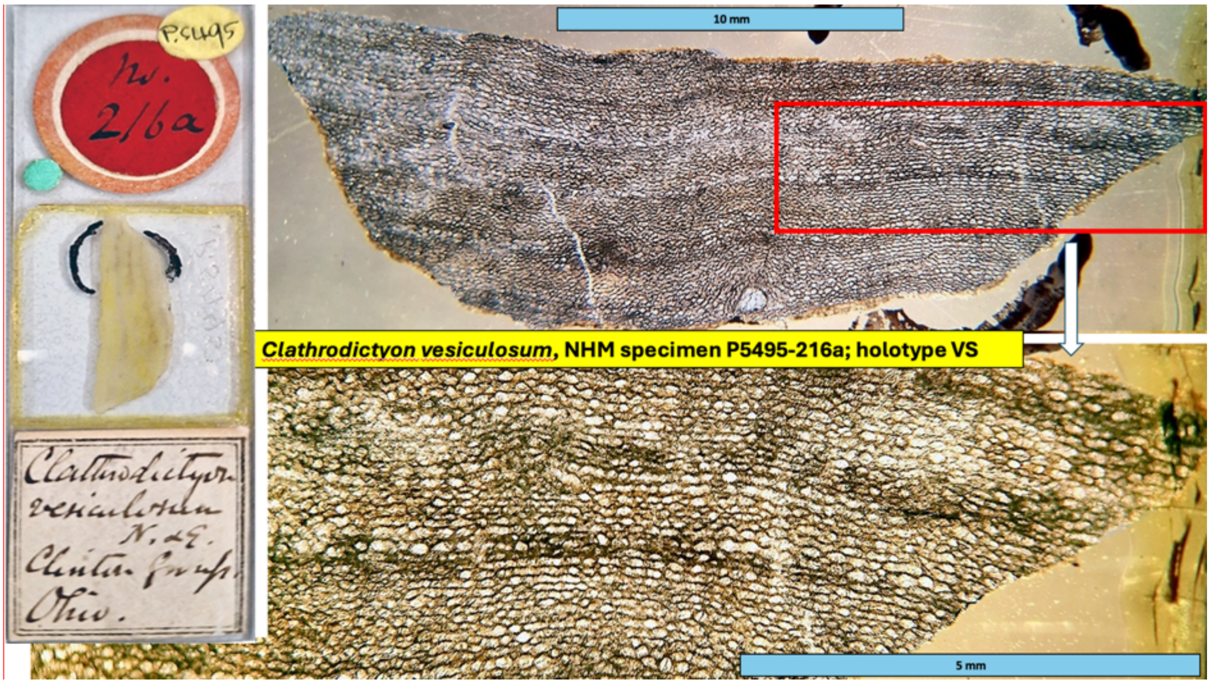


Fig. 2.1.1. Vertical thin section of the holotype specimen of *Clathrodictyon*, represented here as the type species *Clathrodictyon vesiculosum*. (*vesiculosum* is derived from Latin meaning of a bladder, reflecting the vesicular nature of the gallery spaces caused by the crumpled character of the laminae). Note the thin section is 75 x 25 mm, demonstrating the very small size of the holotype sample; this issue is discussed in the text. Formal specimen number is NHMUK PI P5495-216a.

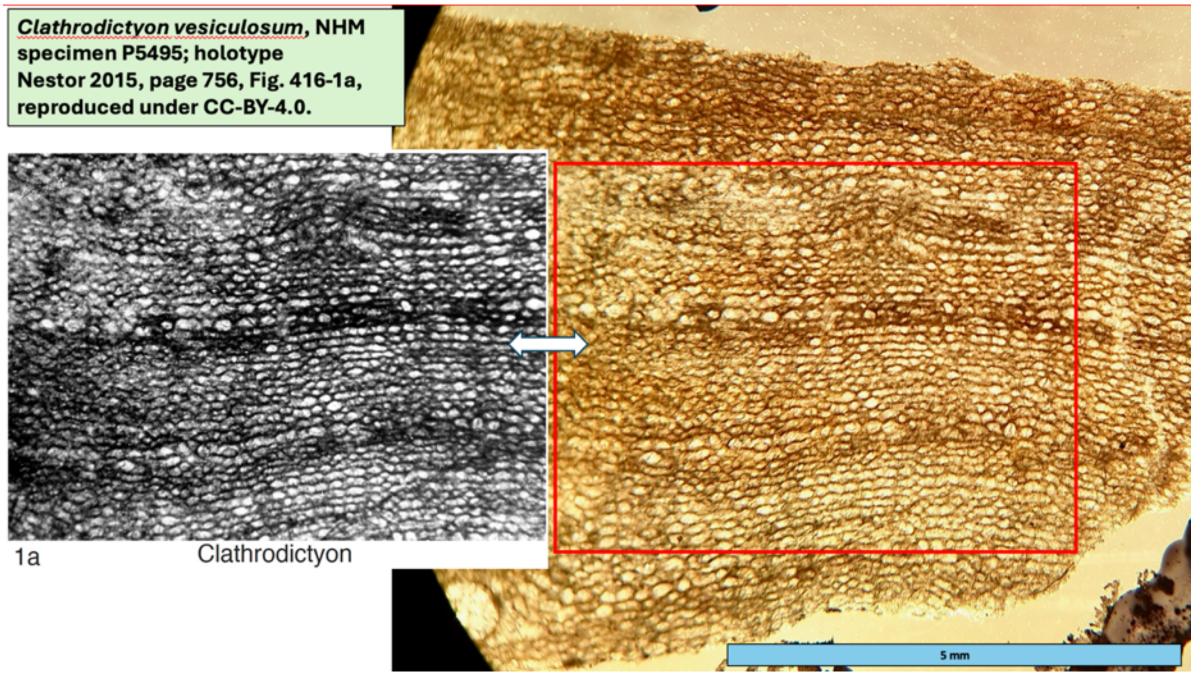


Fig. 2.1.2. Vertical thin section of the holotype specimen of *Clathrodictyon*, together with the photograph of the same area published in Nestor (2015) [the 2015 Treatise on Hypercalcified Sponges]. Notice that the photo used to define this holotype is only 5 mm wide. Formal specimen number is NHMUK PI P5495-216a.

Enlargements of the area of the holotype are shown in Fig. 2.1.3, where the continuous laminae that define *Clathrodictyon* are present. However, the caption draws attention to the lowermost part of the figured area where the laminae begin to lose their continuous character; thus, this part of the photo departs a little from this defined character of *Clathrodictyon*. Indeed, part of that structure has a partially zigzag architecture, which takes it closer to the definition of *Ecclimadictyon*, seen in Section 2.1.2.

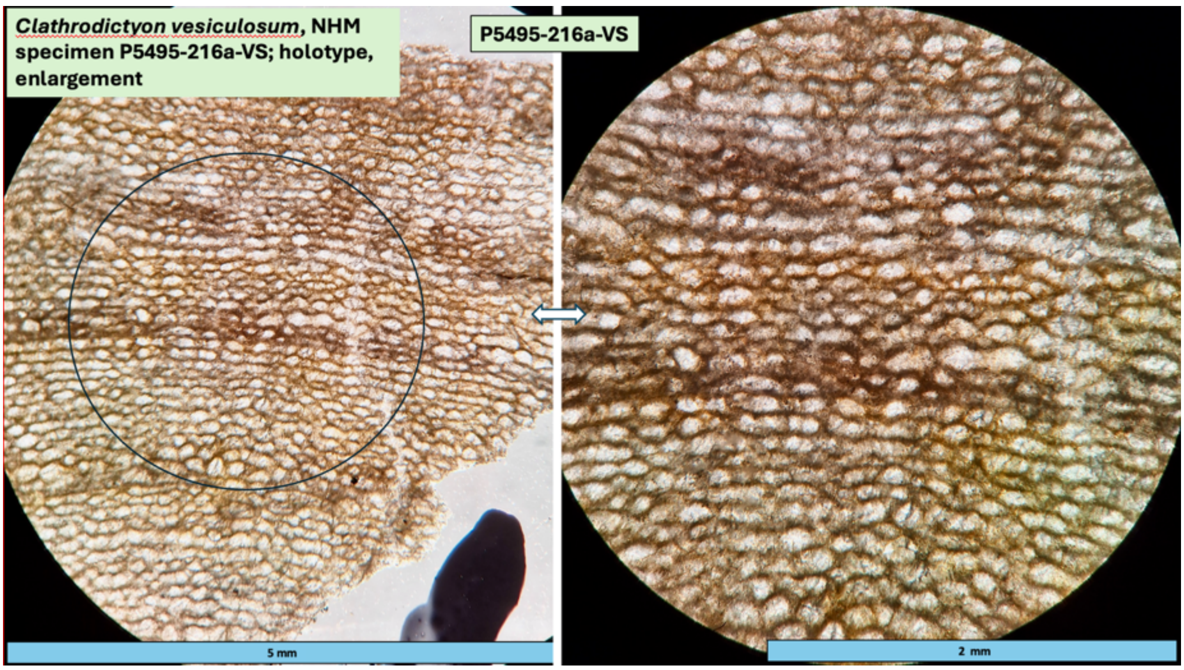


Fig. 2.1.3. Details of the vertical thin section of the holotype specimen of *Clathrodictyon*, showing in most of its area the continuous laminations characterised by *Clathrodictyon* according to its definitions

in Nestor (2015). The dark circle in the left-hand image is enlarged on the right. Note, however, in the right-hand image, lower part, the continuous laminations are not so well developed, and are not so consistent with the definition of *Clathrodictyon*, discussed in the text. Formal specimen number is NHMUK PI P5495-216a.

Figs. 2.1.4-2.1.7 illustrate the TS of *Clathrodictyon vesiculosum*, showing the laminae in transverse section, but in particular the small round pillars.

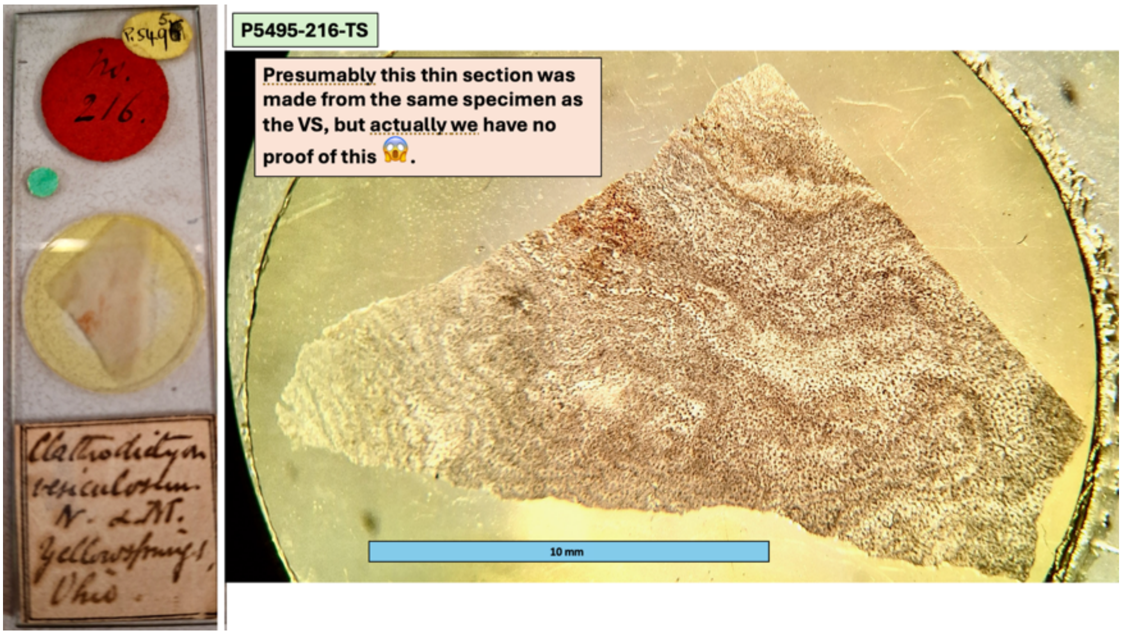


Fig. 2.1.4. Transverse thin section (TS) of the holotype specimen of *Clathrodictyon*, showing its laminae and pillar appearance in TS. The whole thin section is 75 x 25 mm, showing how small is the chip in this holotype sample. Formal specimen number is NHMUK PI P5495-216.

Fig. 2.1.5 highlights the area used in Nestor (2015, p. 756, Fig. 416-1b) and Figs. 2.1.6 and 2.1.7 show details.

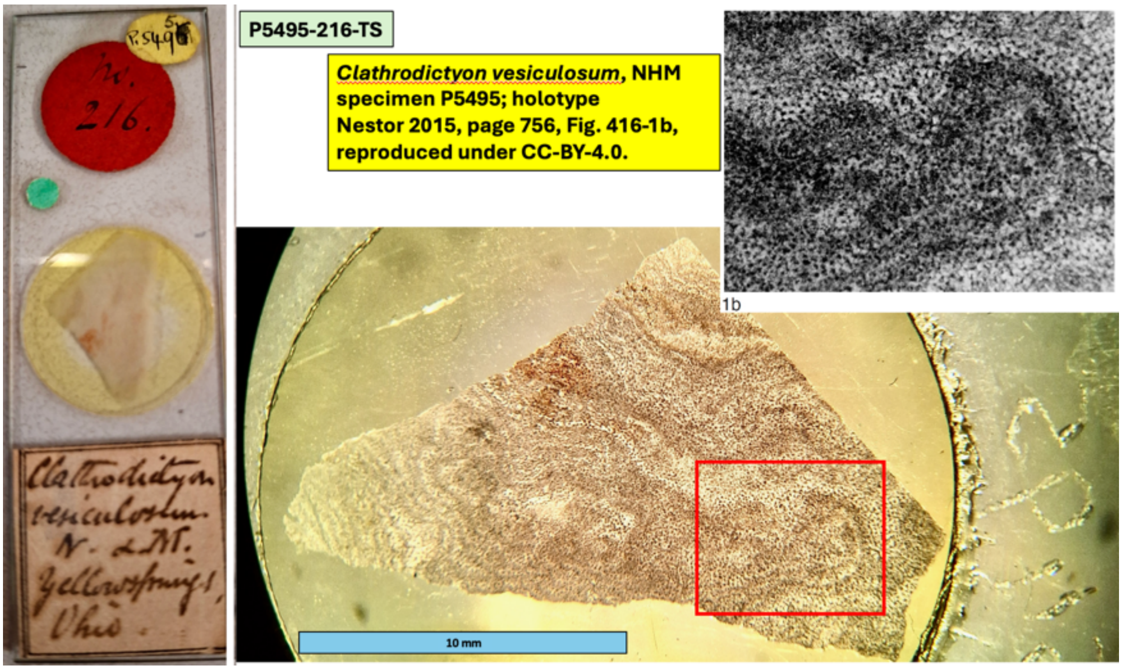


Fig. 2.1.5. Transverse thin section (TS) of the holotype specimen of *Clathrodictyon*, together with the photo published in Nestor (2015) of the TS view, area highlighted in the red box. Formal specimen number is NHMUK PI P5495-216.

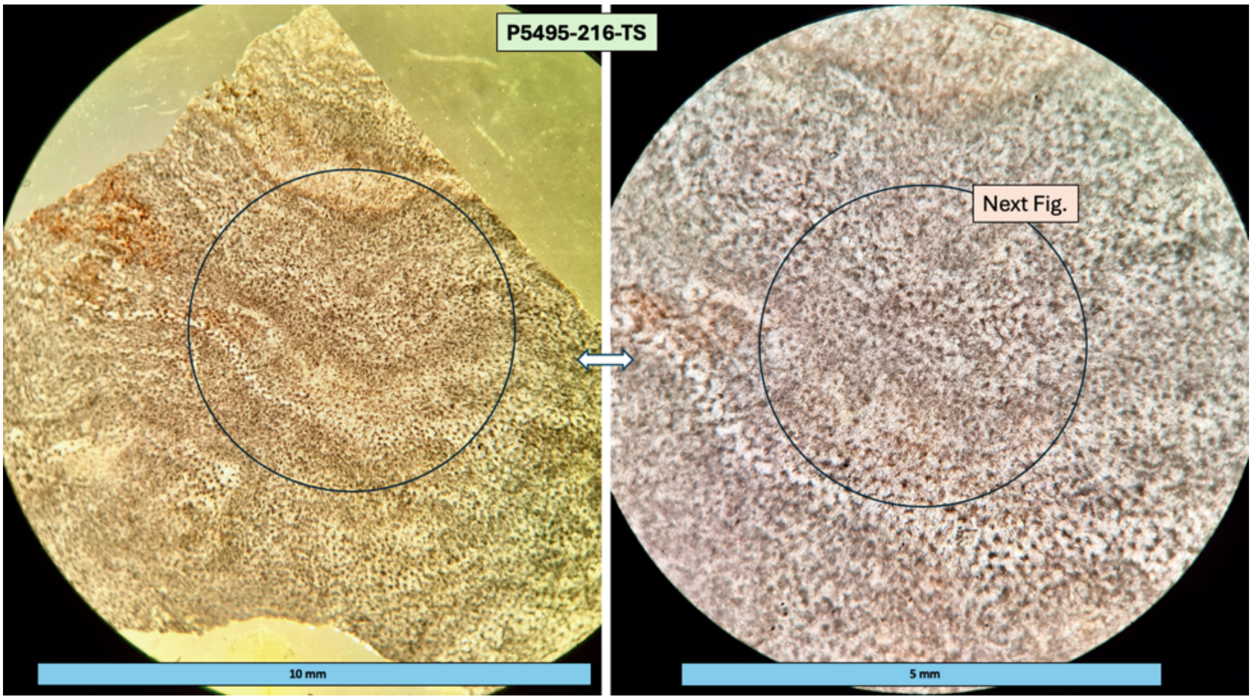


Fig. 2.1.6. Transverse thin section (TS) of the holotype specimen of *Clathrodictyon*, enlarged to show the details of pillars. The dark circle in left-hand image is enlarged on the right; the dark circle in right-hand image is enlarged in Fig. 2.7. Formal specimen number is NHMUK PI P5495-216.

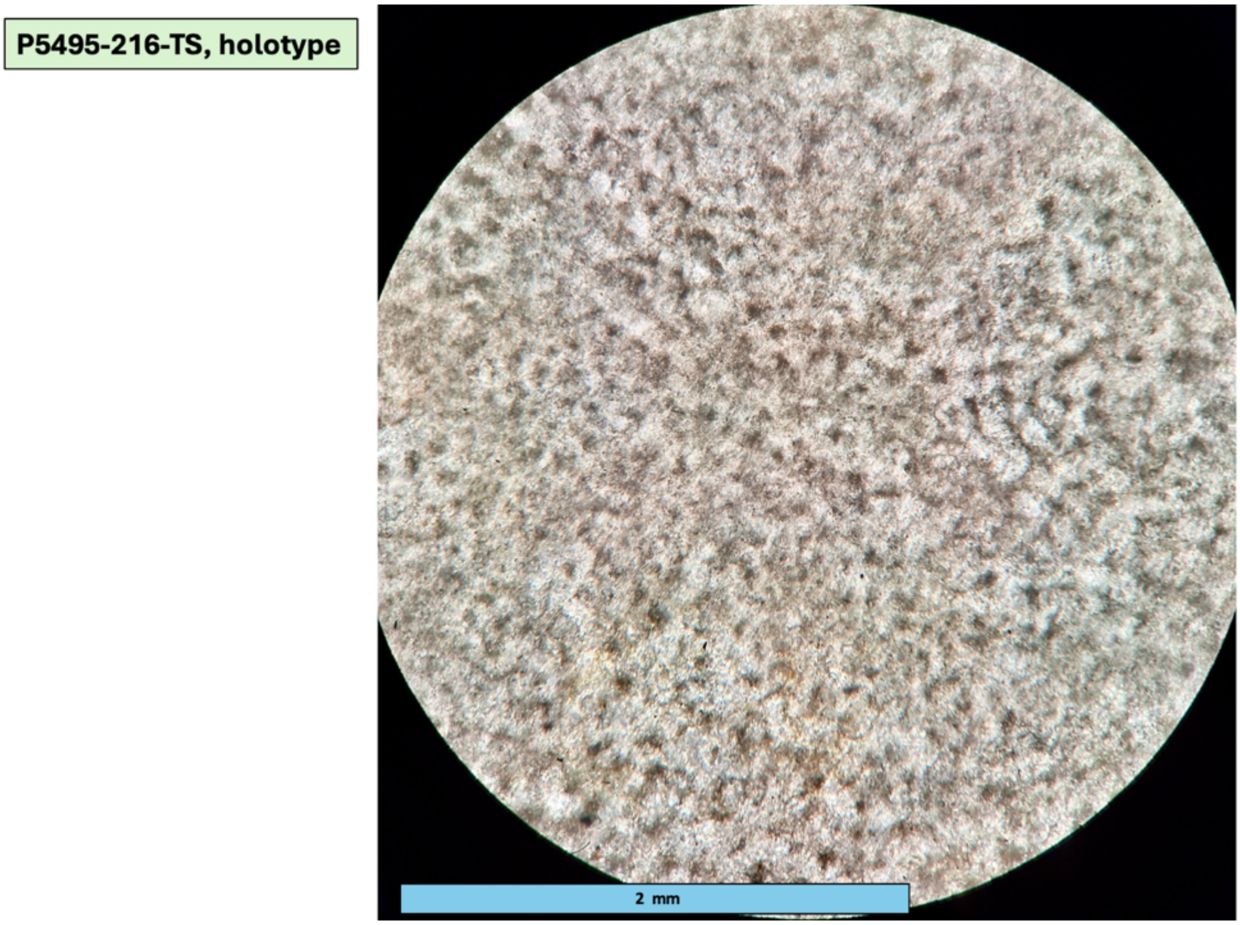


Fig. 2.1.7. Enlargement of transverse thin section (TS) of the holotype specimen of *Clathrodictyon*, enlarged to show the details of pillars. Formal specimen number is NHMUK PI P5495-216.

In the traditional scheme of stromatoporoid taxonomy, *Clathrodictyon* is a genus in the **Order Clathrodictyida**, which Nestor (2015, p. 755) characterized as having "*Skeleton consists of continuous, single layer, inflected to planar laminae and short to superposed pillars; microstructure compact; interspaces are galleries.*"

Within this order, *Clathrodictyon* is placed in the **Family Clathrodictyidae** defined by Nestor (2015, p.755) as having "Skeletal elements weakly differentiated; laminae irregularly inflected, bending down into short pillars; galleries open, lenticular or irregular in longitudinal section."

Clathrodictyon itself is described (Nestor 2015, p. 755) as "*Growth form domical to laminar; laminae irregularly wrinkled; pillars short, in many cases oblique or funnel shaped, rodlike at base; galleries lenticular or irregular in longitudinal section; astrorhizae common.*"

Thus, to summarise, *Clathrodictyon* has continuous laminae that consist of single layers (contrasting some other stromatoporoids that have laminae with multiple layers), and in some cases the laminae are planar, in other cases they are inflected (which means they are not planar but have some irregularities). Laminae are irregularly wrinkled in *Clathrodictyon* but by definition they are continuous. Pillars are short and with some variation, but essentially originate from laminae bending down.

All these diagnostic features of *Clathrodictyon* are visible in the photos of the holotype specimen shown in Figs. 2.1.1-2.1.7 above (but there is a surprise coming, so please stay awake).

2.2. Ecclimadictyon

Ecclimadictyon is described in Nestor (2015, p. 758, based on Nestor, 1964). However, the taxon was originally called *Clathrodictyon fastigiatum* by Nicholson (1887); but in 1964 it was formalised as *Ecclimadictyon* by Nestor. In the Russian-language literature where *Ecclimadictyon* is defined (Nestor, 1964), the text lacks explanation for the reason for the name *Ecclimadictyon*; we suspect that the '*ecclima'* refers to the zigzag structure, that goes up and down based on the Latin meaning of '*Clima'* meaning *slope*; *'dictyon'* means a *net*. Anyway, *Ecclimadictyon* is an established genus in stromatoporoid studies, so there is no purpose in addressing the name, best to leave it as it is.

The following figures illustrate the holotype of *Ecclimadictyon*, that is fortuitously in the NHMUK and was accessible for direct examination and photography.

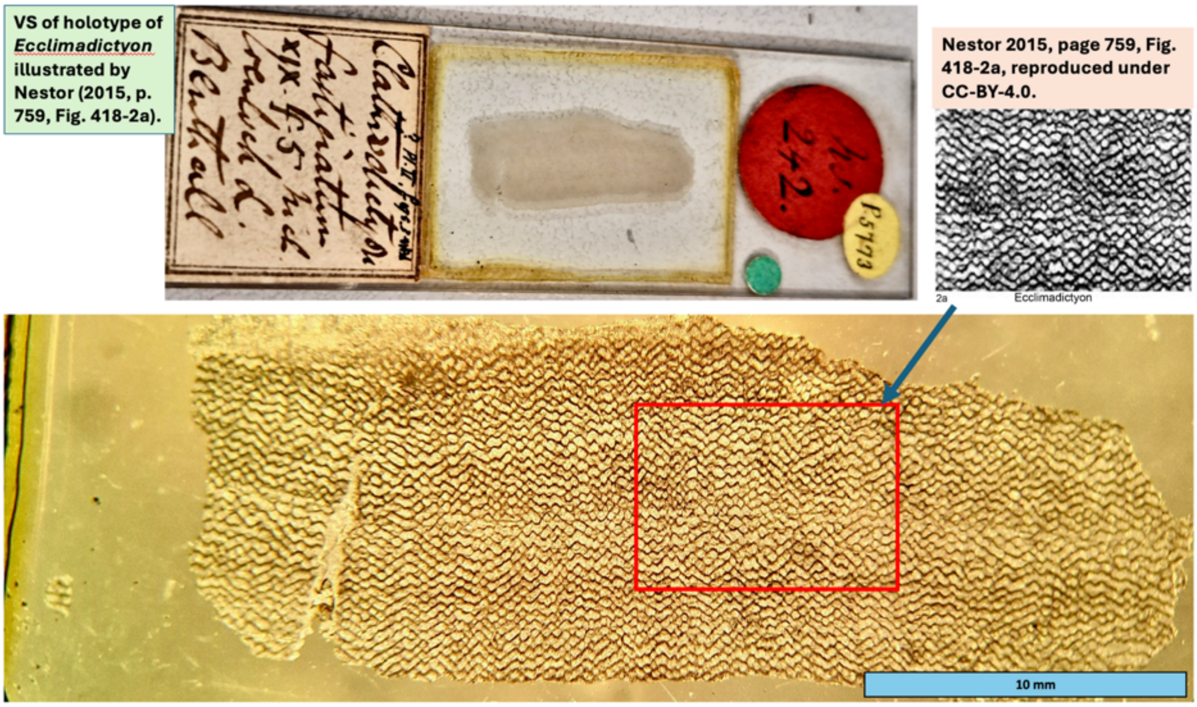


Fig. 2.2.1. Vertical thin section of the holotype specimen of *Ecclimadictyon*, represented here by the type species *Ecclimadictyon fastigiatum* from Nicholson (1887). (The word *fastigiatum* is derived from Latin meaning parallel structures with parts projecting upwards, reflected by the zigzag character of the laminae in this taxon). The red box shows the location of the photo used by Nestor (2015, p.759, Fig. 418-2a) to illustrate the genus in the Treatise; that photo is reproduced under CC-BY-4.0. The thin section is 75 x 25 mm, showing the small size of this holotype sample. Formal specimen number is NHMUK PI P5733-242.

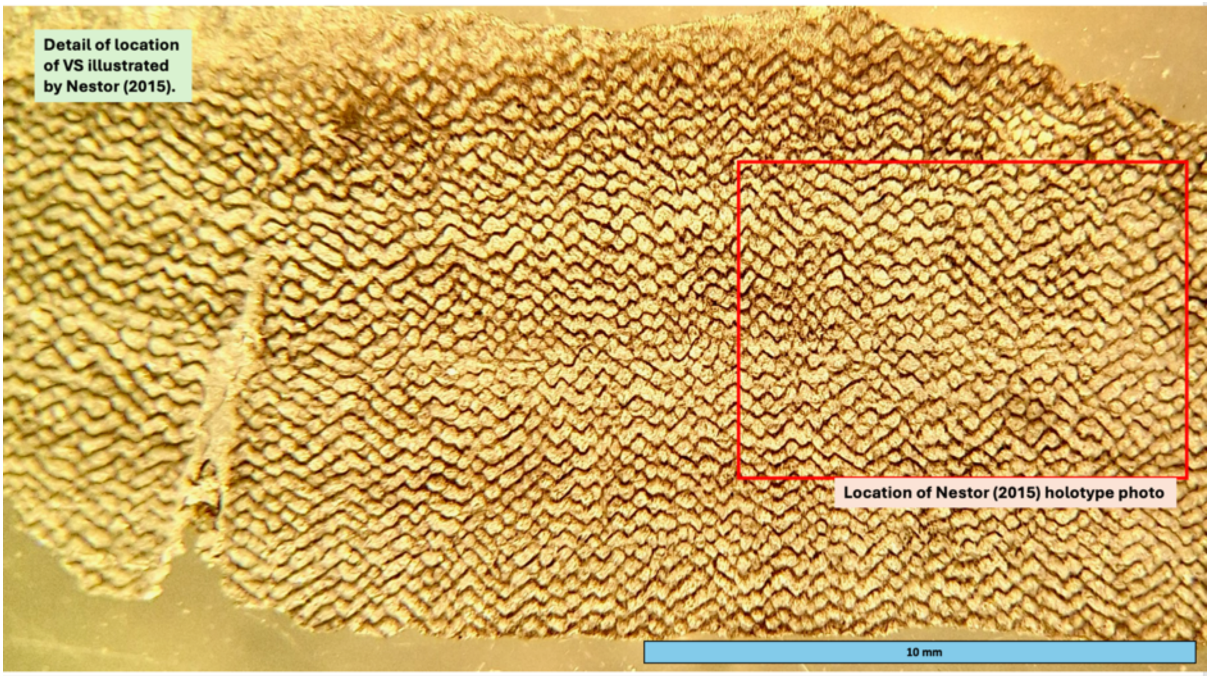


Fig. 2.2.2. Enlargement of the VS of *Ecclimadictyon* holotype, showing more detail of its architecture; the red box shows the location of the photo in Nestor (2015). Formal specimen number is NHMUK PI P5733-242.

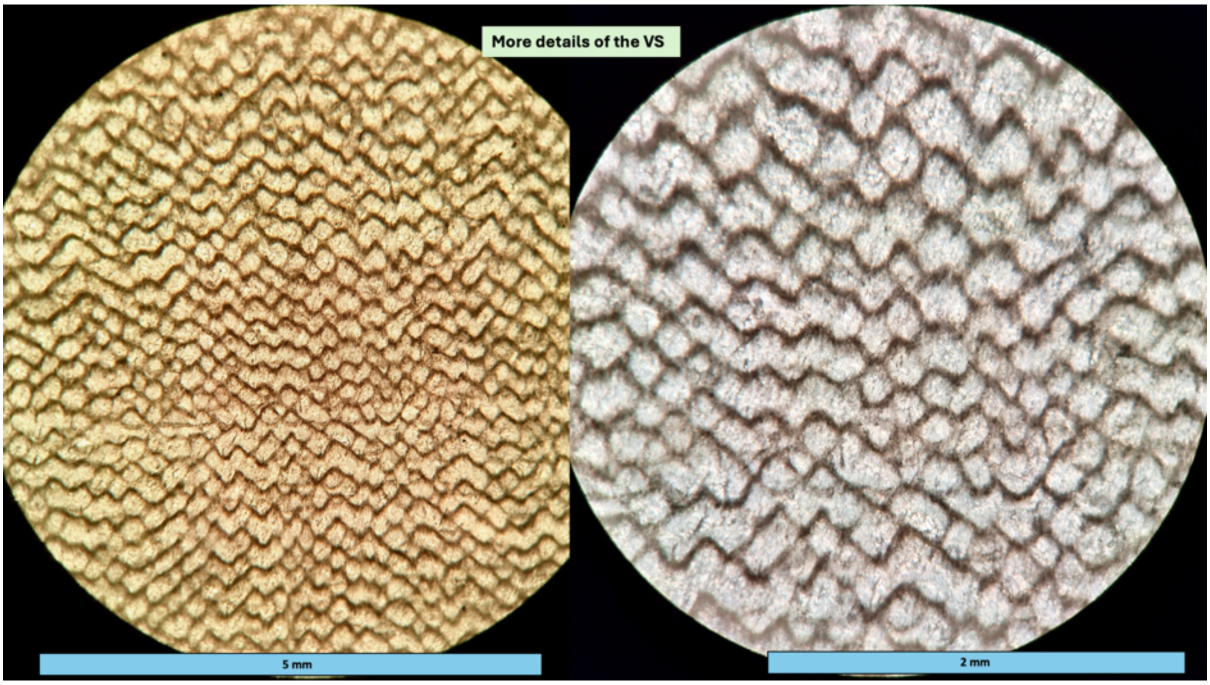


Fig. 2.2.3. Additional details of the VS thin section of the holotype of *Ecclimadictyon*; right-hand photo is an enlargement of the central part of the left-hand photo. Note how the zigzag arrangement of laminae broadly follows the concept of continuous laminae that is a key feature of the traditional Order Clathrodictyida, but not all of the laminae in these photos can be traced across the entire width of the pictures, discussed in the text. Formal specimen number is NHMUK PI P5733-242.

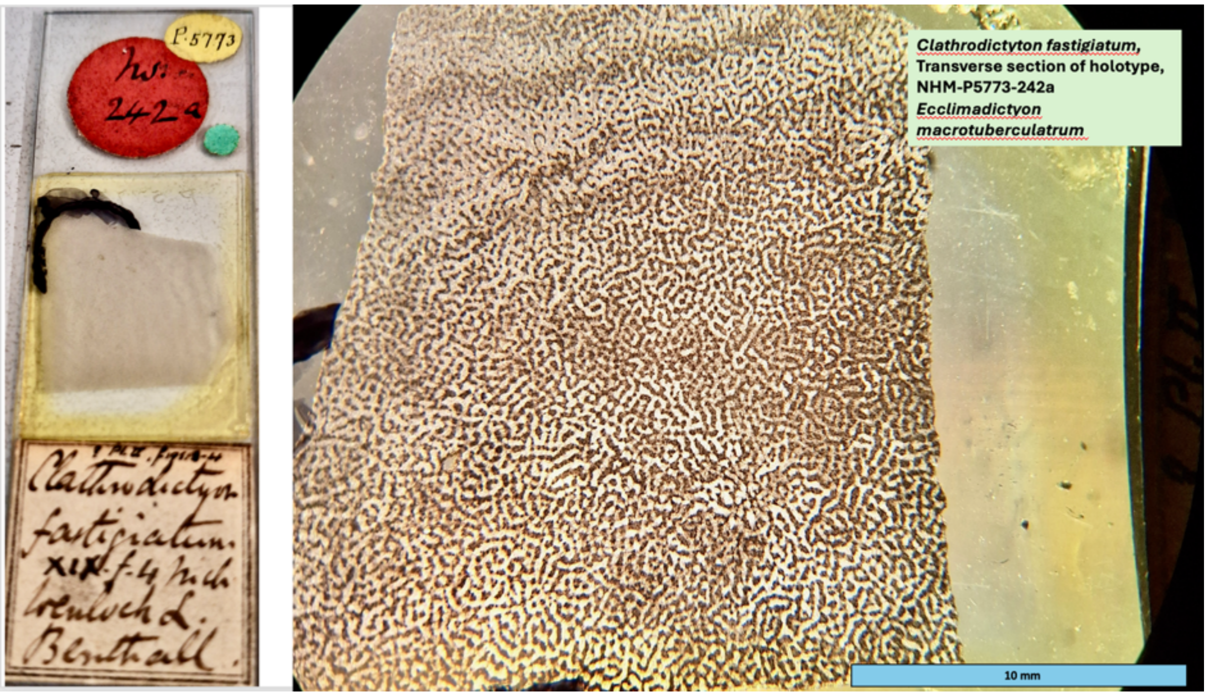


Fig. 2.2.4. TS thin section photos of the holotype of *Ecclimadictyon*, showing the transverse section view of the intersection of the laminations with horizontal plane, indicating that the upward-pointing and downward-pointing tips of the laminations form a haphazard arrangement of short ridges. The systematic description of *Ecclimadictyon* from Nestor (2015) is repeated at the end of this Section 2.2. which states that *Ecclimadictyon* has short pillars. In most of this photo, distinct pillars are not apparent, except sporadically, in contrast to the consistent occurrence of pillars seen in the TS of *Clathrodictyon* in Section 2.1. However, in the upper part of this picture, pillars are visible, where they occur at the very tips of the zigzag laminae, fortuitously sectioned in that particular area. Formal specimen number is NHMUK PI P5733-242a.

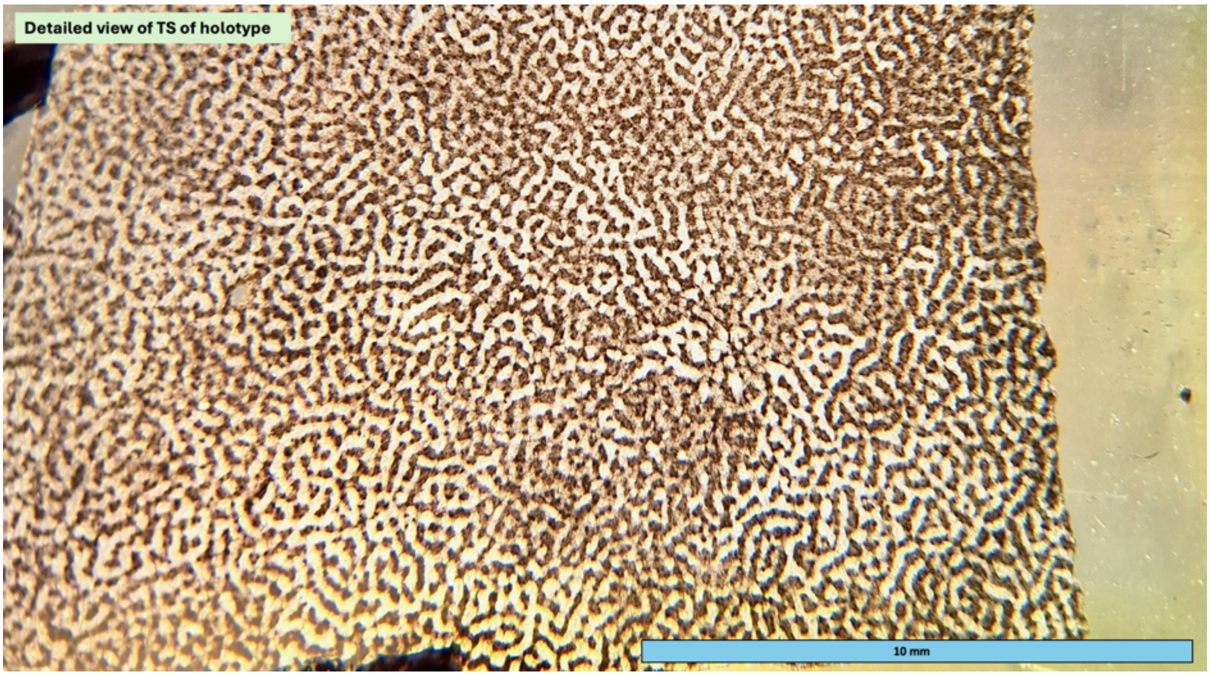


Fig. 2.2.5. Enlargement of TS thin section photo of holotype of *Ecclimadictyon*, showing more detail of the intersection between laminations and the horizontal plane, indicating that the upward-pointing and downward-pointing tips of the laminations form a haphazard arrangement of short ridges. Formal specimen number is NHMUK PI P5733-242a.

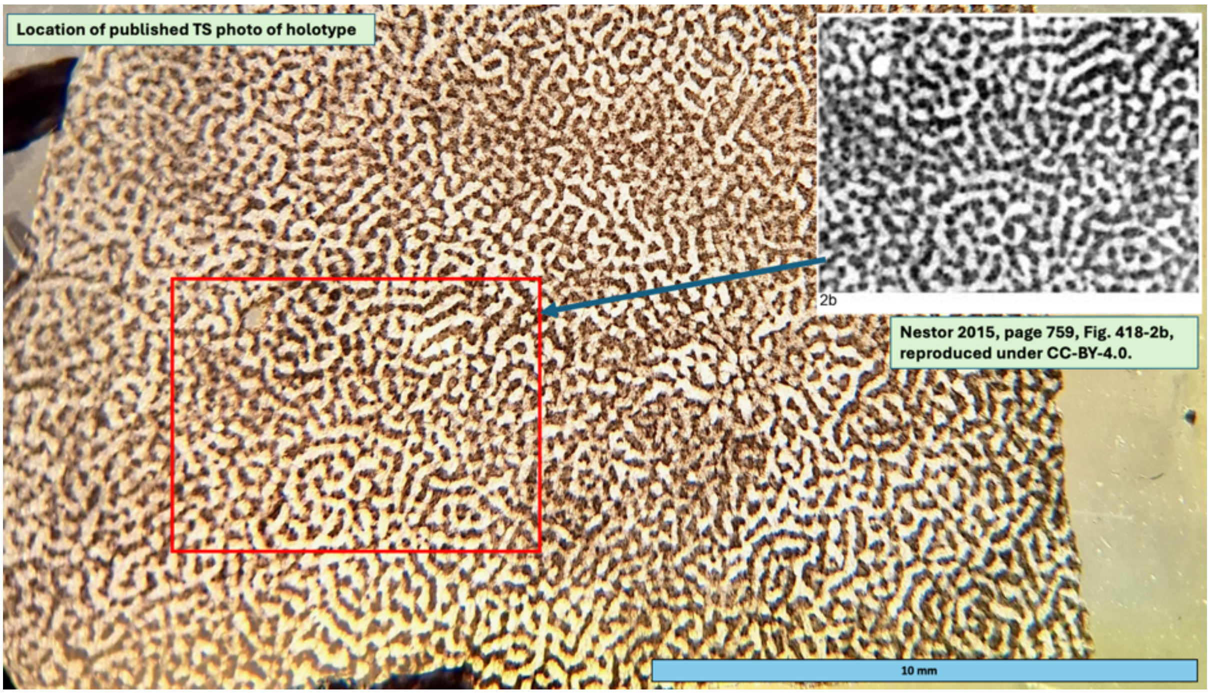


Fig. 2.2.6. Repeat of Fig. 2.2.5, showing enlargement of TS thin section photo of holotype of *Ecclimadictyon*; the red box shows the area used by Nestor (2015) in the photo of the holotype in the Treatise, reproduced under CC-BY-4.0. Note that there are very few distinct pillars shown in this photo, compared to the variation in pillar visibility seen in Fig. 2.2.4. Formal specimen number is NHMUK PI P5733-242a.

Ecclimadictyon, in the traditional scheme of stromatoporoid taxonomy, is also a genus in the **Order Clathrodictyida**. This order is characterised by Nestor (2015, p. 755) as: "*Skeleton consists of continuous, single layer, inflected to planar laminae and short to superposed pillars; microstructure compact; interspaces are galleries.*"

Ecclimadictyon is placed in the **Family Actinodictydae** which is described in Nestor (2015, p.758) as: "*Skeletal elements very weakly differentiated; laminae crumpled (zigzag), forming cassiculate network; pillars indistinct or oblique; galleries labyrinthine, subangular in longitudinal section; megapillars and paralaminae may be present.*"

Ecclimadictyon is defined by Nestor (2015, p. 758) as: "*Growth form laminar to domical; laminae crumpled, forming cassiculate network; pillars oblique or indistinct; galleries labyrinthine, subangular in longitudinal section; astrorhizae fasciculate, irregular.*

[**Cassiculate** is an English word derived from Latin *cassiculus* meaning 'net'; commonly applied to spiders webs. Cassiculate was used by Stearn (1993) to describe the structure of the stromatoporoid *Stromatopora* and he likened cassiculate structure to the appearance of a chain-link fence; it's not a bad analogy!]

[**Fasciculate** derives from Latin meaning bundle or cluster, and it is not clear how this applies to the astrorhizae of *Ecclimadictyon* (or indeed of any stromatoporoid)].

It is an interesting reflection that the Order Clathrodictyida is defined as having continuous single layer laminae and yet *Ecclimadictyon* placed in this order has a cassiculate network. The photos of *Ecclimadictyon* in VS show that the laminae are continuous in only some places in the skeleton and raise a question about whether it is appropriate for *Ecclimadictyon* to be in the Order Clathrodictyida. To what extent do the laminae need to be continuous to fix a specimen in *Ecclimadictyon*? This is something you can think about. The variability in pillar expression observed in thin sections may reflect ontogenetic or taphonomic influences, or possibly a different mode of skeletal growth compared to its relatives.

2.3. Camptodictyon

Camptodictyon is a relatively recent addition to stromatoporoid taxonomy. The genus was introduced in the monograph by Nestor et al. (2010) on stromatoporoids from Anticosti island in eastern Canada, p. 85: *Camptodictyon* n. gen. The name is based on Greek *kampto*, a bend, curve, and *diktyon*, net, reflecting the curved laminae that characterize this genus.

We have not been able to study directly the holotype of *Camptodictyon*, so rely on the photos in Nestor (2015, p.760, Fig. 419-3a,b), reproduced here as Fig. 2.3.1. However, some thin sections of *Camptodictyon* kindly provided by Shenyang Yu, Qufu Normal University, Rhizhao, Shandong Province, China, enable the inclusion of new images in this atlas.

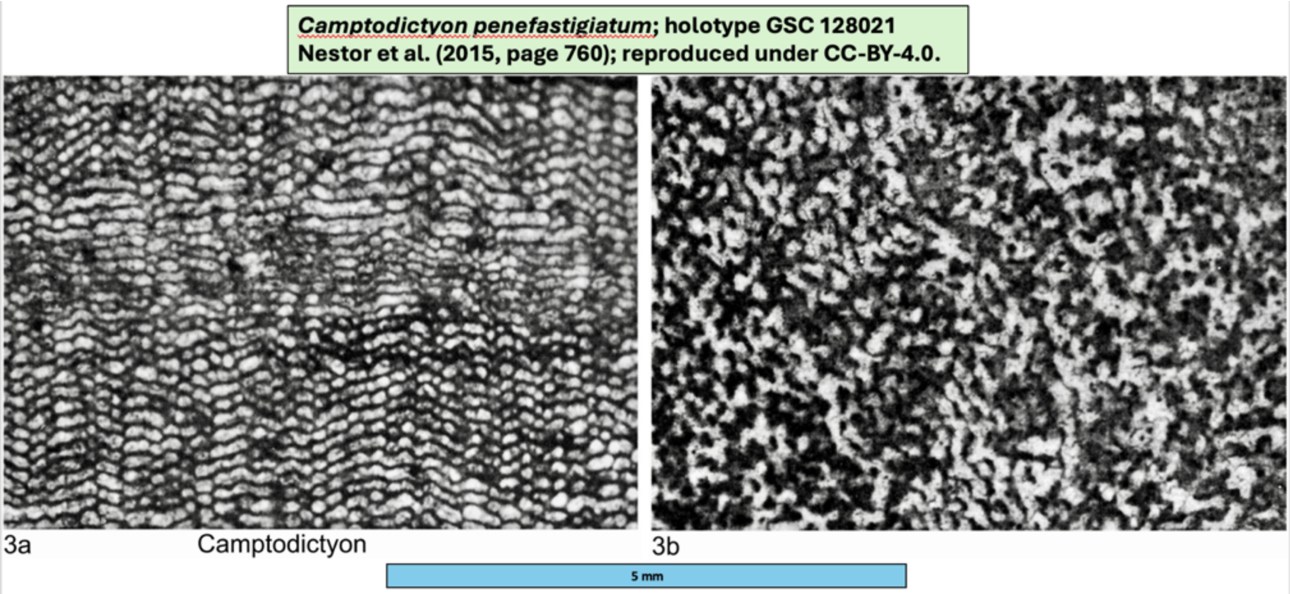


Fig. 2.3.1. Vertical (left) and transverse (right) microscope thin section photographs of holotype of *Camptodictyon* reproduced from Nestor (2015, Fig. 419-3a,b) under CC-BY-4.0 creative commons licence. Note the variability in the VS; small areas resemble *Ecclimadictyon* but overall, the common occurrence of continuous laminae and elongated gallery spaces provides a reason to call it *Camptodictyon*. Observe the band in the middle of VS (left image), where laminae are more closely spaced than in the upper and lower regions. In TS (right picture) the irregular dark areas indicate tangential section through portions of laminae intersecting the thin section plane. Spoiler alert: comparison with photos later in this atlas may make you wonder whether *Camptodictyon* is a valid genus. Specimen number GSC 128021 (GSC = Geological Survey of Canada, Ottawa, Ontario, Canada).

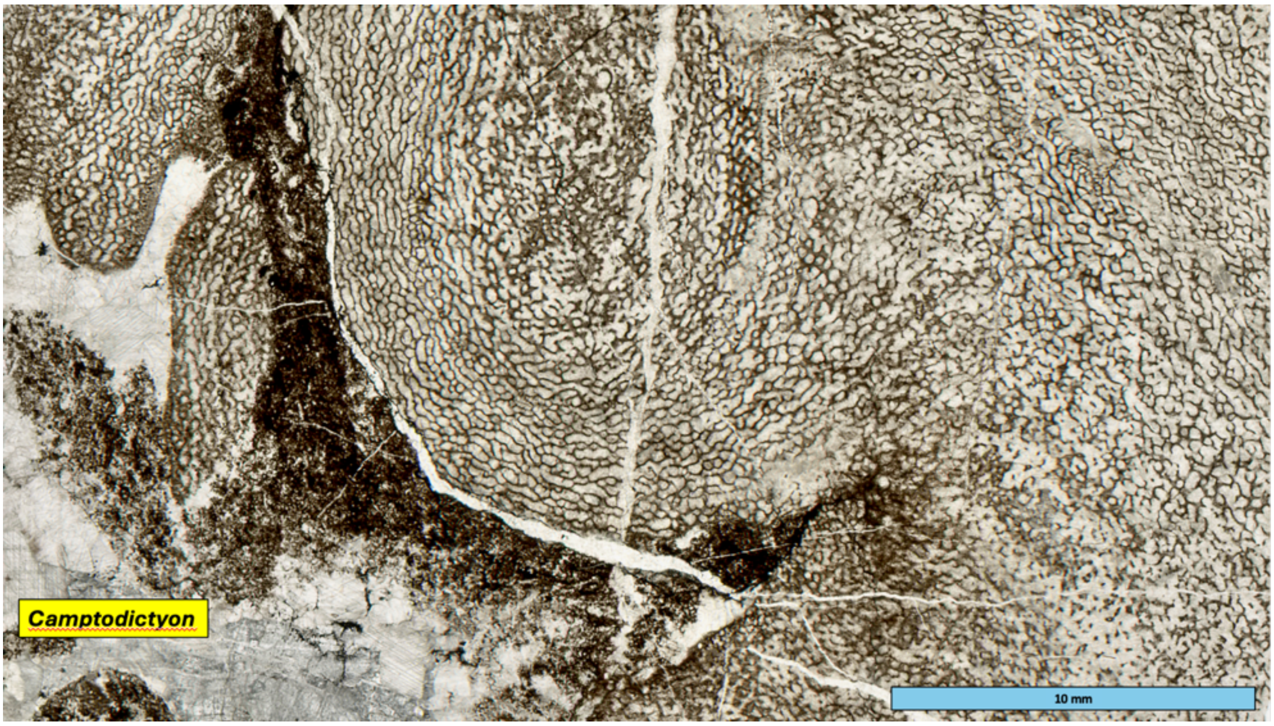


Fig. 2.3.2. Thin section of *Camptodictyon* from a specimen with a highly curved morphology, resulting is a mixture of full VS, full TS and oblique sections through the skeleton. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

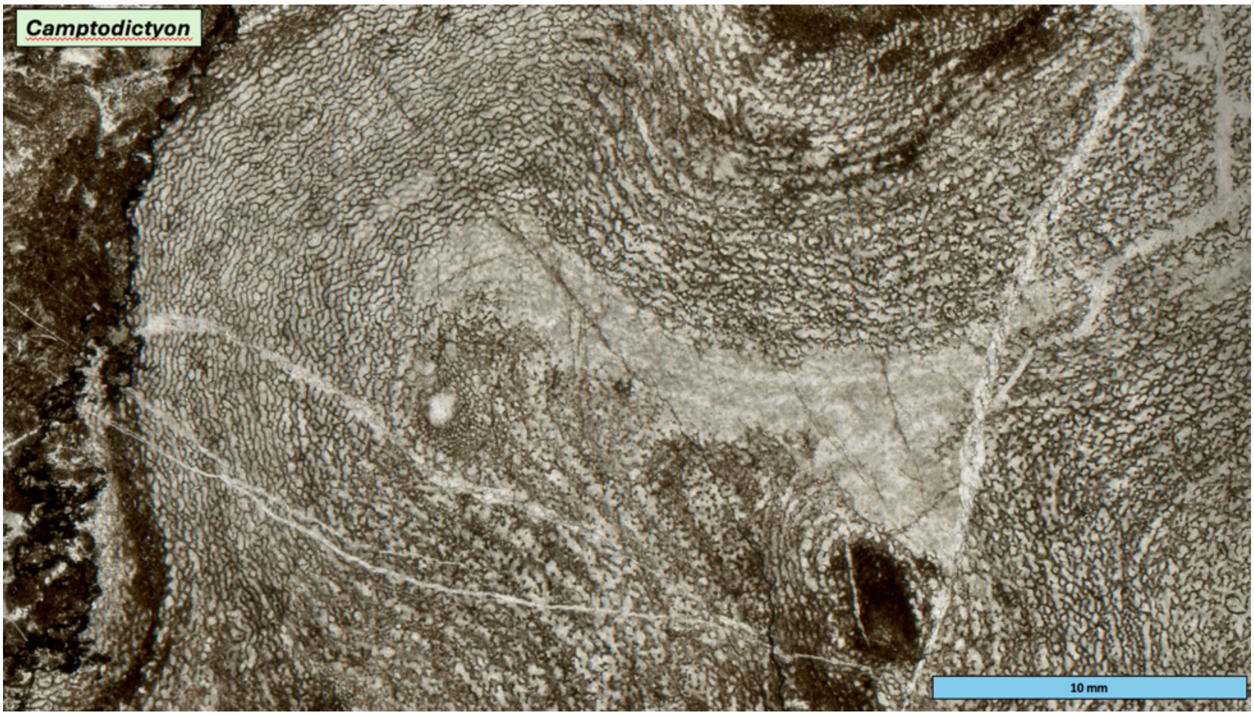


Fig. 2.3.3. Thin section of *Camptodictyon* from a similarly curved specimen, also showing mixed orientations of sections (full VS, full TS and oblique section) through the skeleton. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

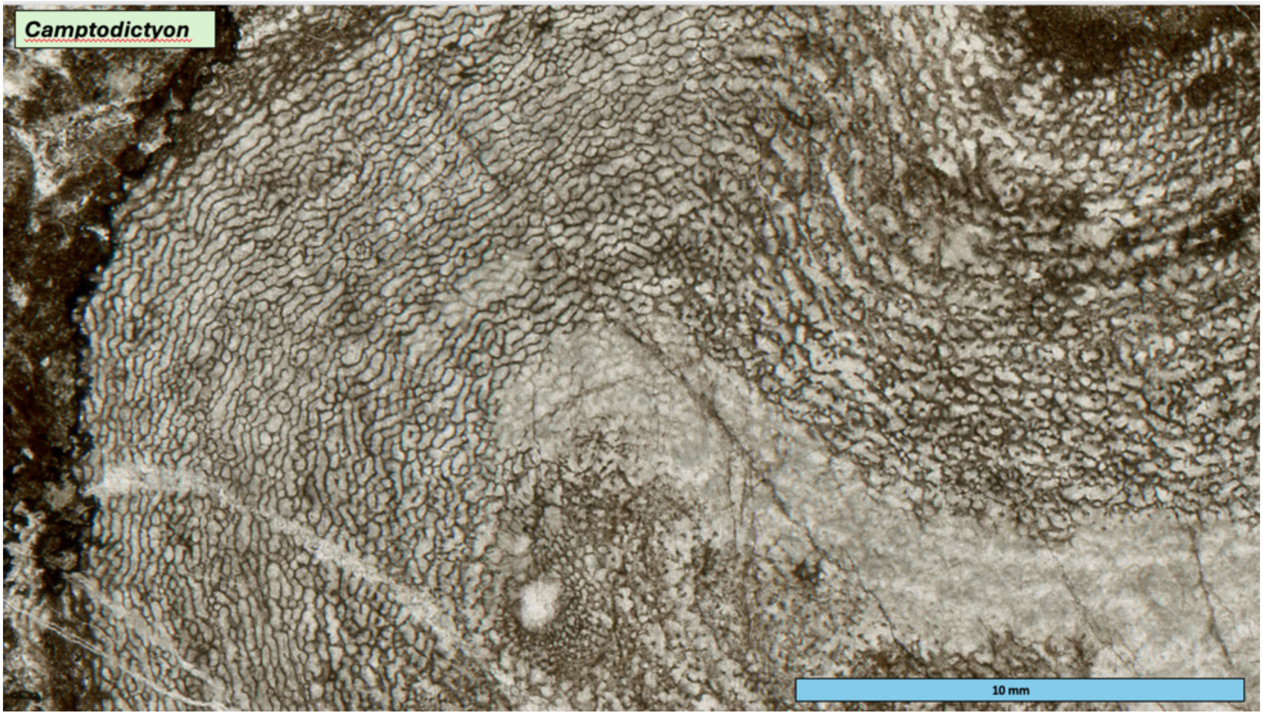


Fig. 2.3.4. Enlargement of upper central area of Fig. 2.3.3, showing detail of the *Camptodictyon* structure, emphasising a range of architecture including continuous and discontinuous laminae, elongated galleries and in places the structure has the zigzag character that resembles *Ecclimadictyon*. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

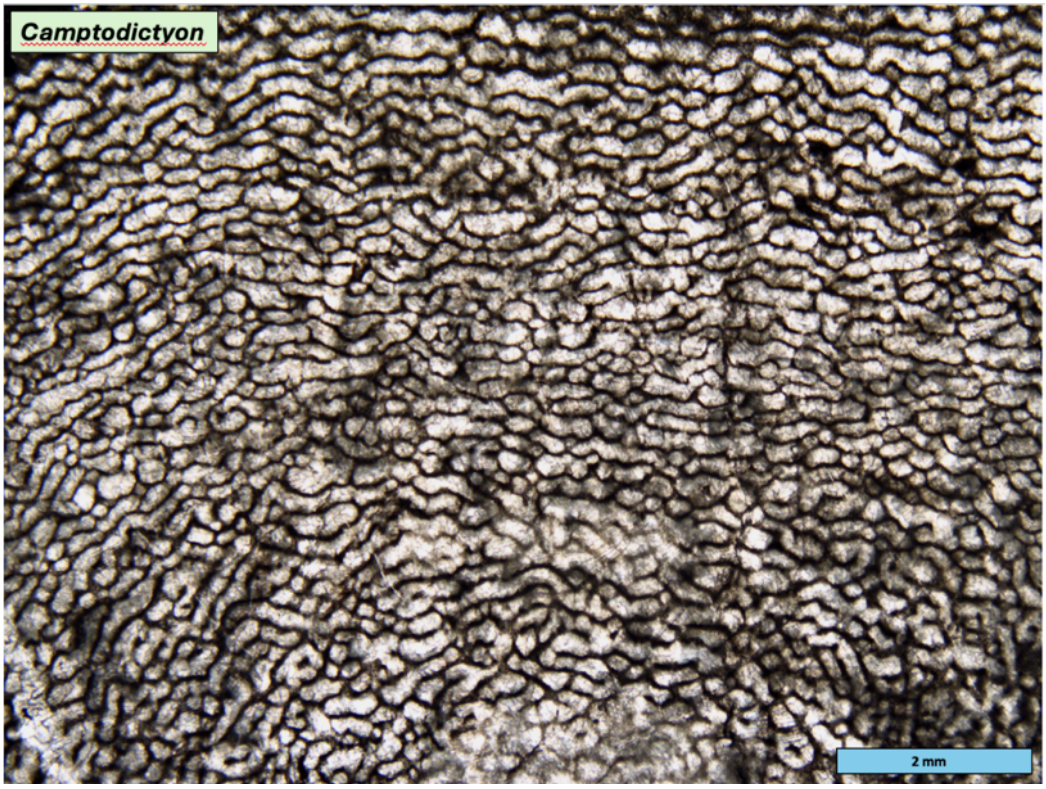


Fig. 2.3.5. Vertical thin section showing detail of the *Camptodictyon* structure, emphasising a range of architecture including continuous and discontinuous laminae, elongated galleries and in places the structure has the zigzag character that resembles *Ecclimadictyon*. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

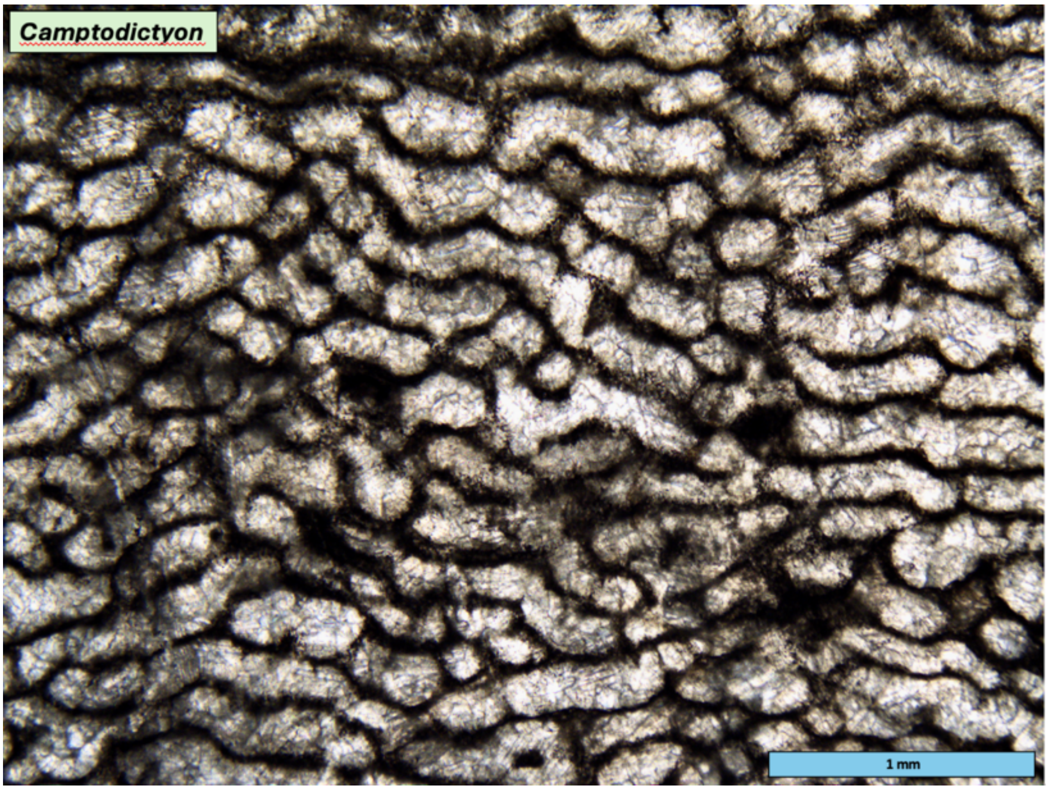


Fig. 2.3.6. Enlargement of upper right corner of Fig. 2.3.5, showing VS detail of the *Camptodictyon* structure, emphasising a range of architecture including continuous and discontinuous laminae,

elongated galleries and in places the structure has the zigzag character (e.g. centre left of the photo) that resembles *Ecclimadictyon*. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

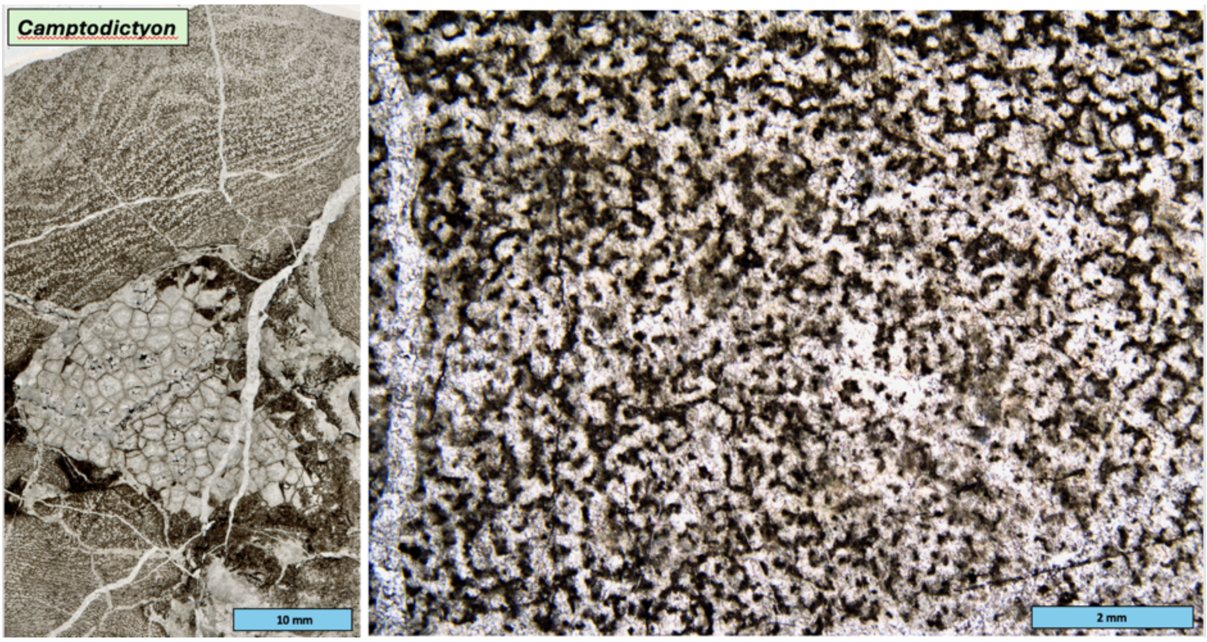


Fig. 2.3.7. Left image: whole thin section showing transverse section (TS) view of *Camptodictyon* and a tabulate coral. Right image: enlargement of upper right corner (cement-filled fraction on left shows location); note a mixture of pillars (dark dots) and partial tangential sections through laminae that interrupt the plane of section. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

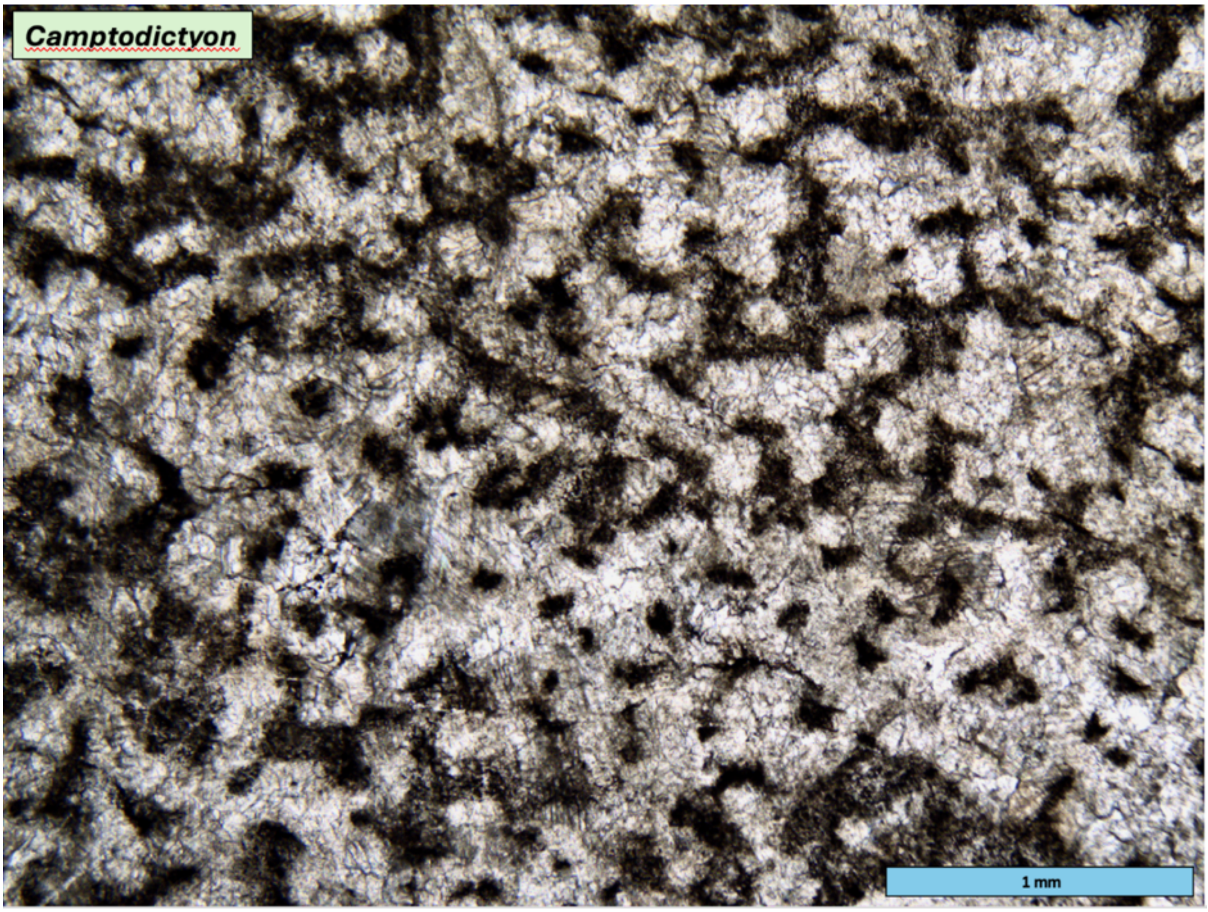


Fig. 2.3.8. Enlargement of upper right corner of Fig. 2.3.7, showing TS detail of the *Camptodictyon* structure. Shiqian Formation, Upper Ordovician; Shiqian, NE Guizhou Province, China; sample provided by Shenyang Yu.

Camptodictyon, in the traditional scheme of stromatoporoid taxonomy, is also a genus in the **Order Clathrodictyida**, members of which are characterised in Nestor (2015, p. 755) as: "*Skeleton consists of continuous, single layer, inflected to planar laminae and short to superposed pillars; microstructure compact; interspaces are galleries.*"

Camptodictyon (as with *Ecclimadictyon*) is placed in the **Family Actinodictydae** which is described in Nestor (2015, p.758) as: "*Skeletal elements very weakly differentiated; laminae crumpled (zigzag), forming cassiculate network; pillars indistinct or oblique; galleries labyrinthine, subangular in longitudinal section; megapillars and paralaminae may be present.*"

Camptodictyon itself is described by Nestor (2015, p. 758) as follows: *"Growth form laminar to domical; laminae chevronlike (sic) folded to smoothly microundulating; pillars imperfect, oblique inflexions of laminae, partly superposed, forming longer zigzag-shaped pseudopillars; galleries labyrinthine, round, oval or meandriform in longitudinal section, often superposed forming subvertical rows, separated from each other by zigzag pseudopillars; astrorhizae inconspicuous."*

The Order Clathrodicyida is traditionally characterised by continuous laminae, but it is interesting to note that *Camptodictyon*, as with *Ecclimadictyon* described in

Section 2.2, does not have consistently continuous laminae. Indeed, laminae in *Camptodictyon* are continuous for only relatively short distances in the skeleton, as in *Ecclimadictyon*, and raises the question as to whether this is fully compatible with the character of continuous laminae prescribed for Order Clathrodicyida. Once again, this invites reflection: to what extent can taxa with variably continuous laminae be considered fully consistent with the traditional definition of Clathrodictyida? It's something to keep in mind as you explore further examples in this atlas.

SECTION 3:
THE PROBLEM OF *Ecclimadictyon* DEFINITION DESCRIBED IN KERSHAW ET AL. (2021)

In the monograph by Kershaw et al. (2021) on British Silurian stromatoporoids, a description of the taxon *Ecclimadictyon macrotuberculatum*, (p. 72) is provided, beginning with the synonym list shown below:

> "*Ecclimadictyon macrotuberculatum* (Riabinin, 1951) Pl. 8; Text-figs 8B, 14B, 16, 40
>
> 1878 *Clathrodictyon vesiculosum* Nicholson & Murie; pp. 220, 221, pl. 2, figs 11–13.
> 1951 *Clathrodictyon fastigiatum* Nicholson var. *macrotuberculatum* n. var. Riabinin; p. 22, pl. 15, fig. 5, pl. 16, figs 1, 2."

However, there are some problems here:

1) Incorrect inclusion. A mistake was made; the first entry (1878 *Clathrodictyon vesiculosum* Nicholson & Murie; pp. 220, 221, pl. 2, figs 11–13.) should not have been included because it refers to a different genus, *Clathrodictyon,* which is treated separately in Section 2.1 of this atlas;
2) Incomplete taxonomic history. The second entry (1951 *Clathrodictyon fastigiatum* Nicholson var. *macrotuberculatum* n. var. Riabinin; p. 22, pl. 15, fig. 5, pl. 16, figs 1, 2), which was renamed by Nestor (1964) as the holotype of *Ecclimadictyon*, does not fully explain the history of description of this taxon.

In literature, numerous alternative descriptions of the taxonomy of this fossil are provided. We have chosen two descriptions. The first is by Mori (1970), and the second, more comprehensive one, by Nestor et al. (2010). These descriptions are duplicated below, placed in speech marks to indicate they are the exact wording from those two sources. Note that in neither case is *Clathrodictyon vesiculosum* mentioned:

Mori (1970, p. 96-97):

> "Genus ***Ecclimadictyon*** NESTOR, 1964
> TYPE SPECIES. - *Clathrodictyon fastigiatum* NICHOLSON, 1886.
>
> *Ecclimadictyon macrotuberculatum* (RIABININ) Pl. V, figs. 3, 4
> 1951. *Clathrodictyon fastigiatum* NICH. var. *macrotuberculatum,* n. var. - RIABININ, p. 22, pl. 15, fig. 5; pl. 16, figs. 1, 2.
> 1964. *Ecclimadictyon macrotuberculatum* (RIABININ) - NESTOR, p. 68, pl. 24, figs. 3- 5; pl. 27, figs. 2, 4.
> 1968. *Ecclimadictyon macrotuberculatum* (RIABININ)"

Nestor et al. (2010, p.76):

> "Genus *Ecclimadictyon* Nestor 1964

Ecclimadictyon: Nestor 1964, pp. 60-61; Stearn and Hubert 1966, p. 37; Petryk 1967, p. 16; Mori 1968, pp.60-61; Flügel and Flügel-Kahler 1968, pp. 543-544; Webby 1969, p. 659; Flügel 1969, p. 214; Kazmierczak 1971, p. 56; Bogoyavlenskaya 1973, p. 29; Bolshakova 1973, pp. 63-64; Nestor 1976, p. 53; Webby 1979a, pp. 101-103; Dong and Yang 1980, p. 399; Bogoyavlenskaya and Khromykh 1985, p. 76; Webby and Zhen 1997, p. 27; Nestor in Stearn et al. 1999, p. 26.
Type species. *Clathrodictyon fastigiatum* Nicholson 1887, p. 8; the lectotype is No. P5773 (Nicholson 1886b, pl. 2, figs. 3, 4), deposited in the Natural History Museum, London; Much Wenlock Limestone Fm, upper Wenlock, England."

[**Author COMMENT**: note here that *Clathrodictyon fastigiatum* is stated as the lectotype, whereas in Nestor (2015, p.758) it is called the holotype. As far as we have been able to find out by looking in Nicholson's literature, sample NHMUK PI P5773, which we illustrate in this atlas, is the holotype. However, this difference in terminology has little effect, since a lectotype stands in for the holotype when there was no holotype specimen designated in the original publication.]

Continuing with description from Nestor (2010):

Nestor et al. (2010, p.78):

"*Ecclimadictyon macrotuberculatum* (Riabinin 1951) Pl. 1 8e,f; Figs. 16c, 23 f
1951 *Clathrodictyon fastigiatum* Nicholson, var. *macrotuberculata* Riabinin, p. 22, pl. 15, fig. 5; pl. 16, figs. 1 , 2.
1964 *Ecclimadictyon macrotuberculatum* (Riabinin); Nestor, pp. 68-69, pl. 24, figs. 3-5; pl. 27, figs. 2, 4.
1966 *Ecclimadictyon macrotuberculatum* (Riabinin); Nestor, pp. 15-16, pl. 5, figs. 1, 2.
1968 *Ecclimadictyon macrotuberculatum* (Riabinin); Mori, pp. 64-65, pl. 8, figs. 3, 4; pl. 9, figs. 1, 2; pl. 10, fig. 2.
1970 *Ecclimadictyon macrotuberculatum* (Riabinin); Mori, pp. 97-98, pl. 5, figs. 3, 4.
1971 *Ecclimadictyon macrotuberculatum* (Riabinin); Lesovaya, pp. 1 19-120, pl. 34, fig. 1.
1982 *Ecclimadictyon macrotuberculatum* (Riabinin); Wang, p. 27, pl. 2, figs. 1 1, 12.
Type specimen. The holotype is No. 89/185 (Riabinin 1951, pl. 15, fig. 5; pl. 16, figs. 1 , 2), deposited in the research institute VNIGRI, St. Petersburg; late Rhuddanian, Karinu Mbr, Tamsalu Fm, Karinu, Estonia."

For information, below is the Russian text transcribed from Riabinin (1951, p. 22), referenced above in these synonym lists, followed by a translation from Russian using GoogleTranslate:

"*Clathrodictyon fastigiatum* Nich., var. *macrotuberculata* n. var.
Табл. XV, фиг. 5 и табл. XVI, фиг. 1, 2
В коллекции имеется два обломка ценостеума. Наиболее крупный желвак, размерами 23 х 15 х 8 см, имеет неправильную шишковатую форму с округлыми возвышениями диаметром 3,2-4 см. Нижняя поверхность не сохранилась.
В приготовленных прозрачных шлифах видно строение цено-стеума, типичное для *Clathrodictyon fastigiatum* Nich. Следов астрориз не видно.

Описываемый экземпляр выделен как вариетет вида *Cl. fasti-giatum*, так как отличается от типичного вида лишь формой цено-стеума (не пластинчатая, а крупнобугорчатая форма).
Местонахождение — карьер Карину, образцы 189 и 190а, коллекция Я. С. Никитина; возраст — райккюльские слои (G_3).”

“Clathrodictyon fastigiatum Nich., var. macrotuberculata n. var. Plate XV, Fig. 5 and Plate XVI, Figs. 1, 2
There are two fragments of coenosteum in the collection. The largest nodule, measuring 23 x 15 x 8 cm, has an irregular knobby shape with rounded elevations 3.2-4 cm in diameter. The lower surface is not preserved. In the prepared transparent sections, the structure of the coenosteum is visible, typical for Clathrodictyon fastigiatum *Nich. Traces of astrorhizae are not visible. The described specimen is isolated as a variety of the species* Cl. fastigiatum*, since it differs from the typical species only in the shape of the coenosteum (not a lamellar, but a large-tuberculate form).*
Location: Karinu quarry, samples 189 and 190a, collection of Ya. S. Nikitin; age: Raikkyul layers (G_3).”

Read this translation carefully; note how it states that this species differs from *Clathrodictyon fastigiatum* defined by Nicholson ONLY by the shape of the whole fossil [here he uses ‘coenosteum’, now an outdated and discontinued term to describe the entire stromatoporoid fossil]. It is well-known amongst stromatoporoid taxonomists that the shape of the entire fossil is not diagnostic for the taxon. Therefore, the “var. *macrotuberculata*” is an invalid taxonomic name; it follows that *Ecclimadictyon macrotuberculatum* is also invalid, and perhaps it should have been named only *Ecclimadictyon fastigiatum*. Nevertheless, to avoid any confusion, we keep to *Ecclimadictyon macrotuberculatum* for the purposes of this atlas.

[Note that Riabinin used the spelling “*macrotuberculata”,* which has been changed to *“macrotuberculatum”* in Mori (1970) and Nestor et al. (2010).]

FURTHERMORE: below in Fig. 3.1.1 is an extract from the illustration of thin sections from Riabinin (1951) of plate XVI, figs 1 & 2, which are quoted in the above synonym lists as being the critical illustrations of *Clathrodictyon fastigiatum* Nich*.,* var*. macrotuberculata n. var. = Ecclimadictyon macrotuberculatum.*

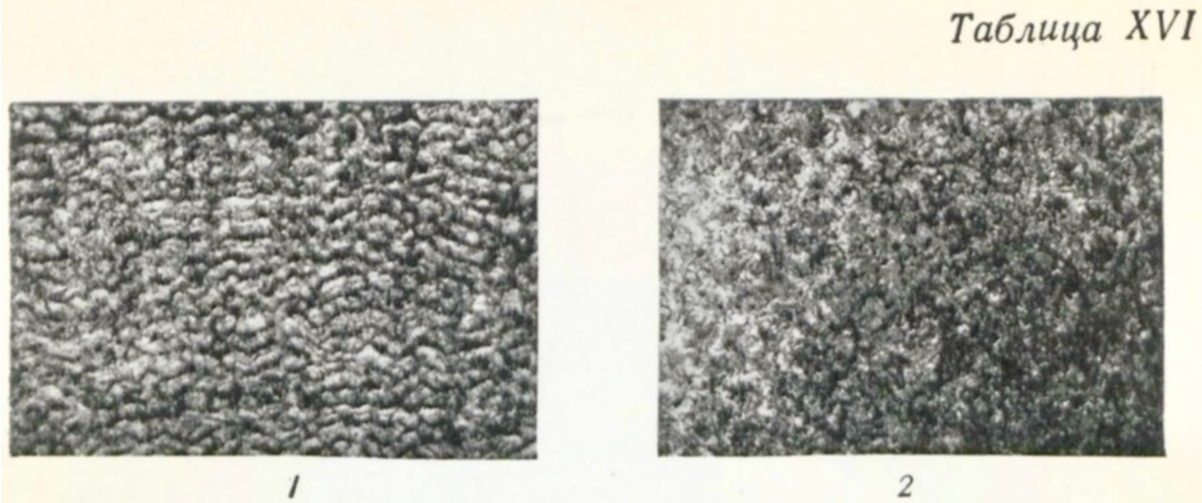


Fig. 3.1.1. Extract from Riabinin (1951, plate 16, figs. 1 & 2), cited in the synonym lists above, showing "*Clathrodictyon fastigiatum* Nich., var*. macrotuberculata* n. var.". This is now called *Ecclimadictyon macrotuberculatum* by Mori (1970) and Nestor et al. (2010), as described in the synonym lists above. Please note that the images have been enhanced to improve their visual appearance. These are considered the definitive photos of this taxon. Note there is no scale in the original publication; the plate description simply states it as x10. These images were taken from a pdf, we do not have the actual book to measure the scale. However, you can get an approximate idea of scale by comparing the pictures with those of the NHMUK and other stromatoporoids illustrated in this atlas.

We hereby assert that the images presented in Riabinin (1951), specifically those shown in Fig. 3.1.1, are inadequate to define a taxon. The TS image, in particular, is of such poor quality that the structure cannot be discerned clearly. These pictures also illustrate too limited an area of the skeleton to be useful in taxonomic identification; there is no scope to show variation of skeletal structure. Additionally, Riabinin (1951, p. 22) does not provide a diagnosis description of the taxon. We reiterate that the use of "*var. macrotuberculata*" describing the whole stromatoporoid fossil is an invalid taxonomic discriminator. So, this variety, "*var. macrotuberculata*", does not exist in any formal or legitimate sense. These images should never have been used to define the taxon, as they lack the necessary quality and detail, and this specimen should never have been used to define a variant: ***indeed, given that "var. macrotuberculata" refers to a knobby shape of the whole fossil, and not part of its internal skeletal structure, why has the invalidity of this variety of the taxon not been noticed before?*** Maybe prior researchers did not have access to the translation from Russian of Riabinin's (1951, p.22) text.

Regarding the systematic description of *Ecclimadictyon macrotuberculatum* by Kershaw et al. (2021) in Silurian strata of England, two key points:

A) The authors of this atlas, who are authors of Kershaw et al, 2021, British Silurian stromatoporoids monograph, acknowledge the mistake of including *Clathrodictyon vesiculosum* as a synonym and thank Juwan Jeon for pointing this out (but this is not the end of the story, as you will see later in the atlas).
B) Juwan Jeon also noted that there seems to be some difference between the holotype image of *Ecclimadictyon* in Nestor (2015) and the illustration of *Ecclimadictyon* in the Kershaw et al. (2021) monograph.

These two points were part of the motivation for this atlas. In response, we revisited the definition of *Ecclimadictyon* and, just for comparative purposes, examined the

Clathrodictyon holotype in Nicholson Collection in the Natural History Museum, London (NHMUK) to look for comparisons, illustrated above. Therefore, SK revisited the NHMUK and studied and photographed the holotypes of both *Clathrodictyon* and *Ecclimadictyon* in the NHMUK collections. SK also examined the other thin sections from Nicholson Collection described by Nicholson as *Clathrodictyon vesiculosum* (=*Clathrodictyon sensu stricto*) and *Clathrodictyon fastigiatum* (redefined by Nestor, 1964 as *Ecclimadictyon*). We also looked again at the images and samples presented in the Kershaw et al. (2021) monograph. The results are, in contemporary English euphemism "very interesting".

Read the next text carefully, it opens a can of worms:

The results of revisiting the NHMUK holotype revealed that the *Ecclimadictyon* holotype (*Clathrodictyon fastigiatum*) contains a consistent structure that matches its description in Nestor (2015), BUT:

1) **Variation in the Kershaw et al. (2021) material:**
   The material described as *Ecclimadictyon* in Kershaw et al. (2021) displays considerable structural variation not reflected in the holotype. While some areas of thin sections look like the holotype, other regions more closely resemble *Clathrodictyon,* as defined in Nestor (2015). Furthermore, some other areas resemble *Camptodictyon* as defined in Nestor (2015). These variations are illustrated in Section 4 of this atlas.
2) **Partial representation in Nestor (2015):**
   The image used by Nestor (2015) for illustration of *Clathrodictyon* in the 2015 Treatise is only part of the specimen; re-examination revealed that other parts of the same thin section [noting it is a ***tiny*** rock chip!!!] depart from the definition of *Clathrodictyon* and more closely resemble *Ecclimadictyon*.
3) **Unpublished notes by Nestor (1989):**
   During a 1989 visit to the NHMUK to study stromatoporoid taxonomy, Heldur Nestor* left behind handwritten notes in the top drawer of the stromatoporoid slide cabinet. In those notes (part of which are reproduced in Section 4) Nestor stated that only the holotype of *Clathrodictyon vesiculosum* is correctly identified amongst the numerous specimens of that species named by Nicholson; the others are another taxon, and Nestor recommended them as *Ecclimadictyon.* This is highly enlightening; it shows Nestor recognized that Nicholson made mistakes in his identifications, but it also implies that, of the specimens in the NHMUK, only the holotype is classified as *Clathrodictyon.* This raises a deeper issue: **IF** the holotype itself partially deviates from the diagnostic features of *Clathrodictyon* (as illustrated in Section 4), then the validity of the holotype's classification must be questioned.

We invite readers to review the photographic evidence in Section 4; make your own judgment on this provocative, perhaps even heretical, suggestion, that the holotype of *Clathrodictyon* is faulty.

*Heldur Nestor (1935–2019) was a distinguished Estonian geologist and paleontologist, renowned for his expertise in Palaeozoic stromatoporoids. He completed his geology studies at Tartu State University in 1959 and earned his doctorate in geology from Moscow State University in 1979 with a dissertation on the evolution and habitats of Palaeozoic stromatoporoids. He was a key contributor to the *Treatise on Invertebrate Paleontology*. His work significantly advanced the understanding of the biogeography and evolution of these ancient organisms.

SECTION 4:
OVERLAPS OF STROMATOPOROID SKELETAL STRUCTURE ACROSS THE THREE TAXA (*Clathrodictyon, Ecclimadictyon, Camptodictyon)*

In this section we demonstrate the problems in defining these three taxa because they overlap in structure. While many of the images presented here may appear superficially similar, they contain critical evidence that illustrates the blurred boundaries among these taxa. The examples shown, sourced from the NHMUK collections and additional samples, reveal a mix of both obvious and subtle morphological differences. Altogether, they prompt a fundamental question: ***what constitutes a genus in stromatoporoid taxonomy?*** These comparisons are intended to encourage critical reflection on the validity of the traditional definitions of these genera.

4.1. Clathrodictyon and Ecclimadictyon holotypes

In this section we compare the holotypes of these two genera, in the following figures.

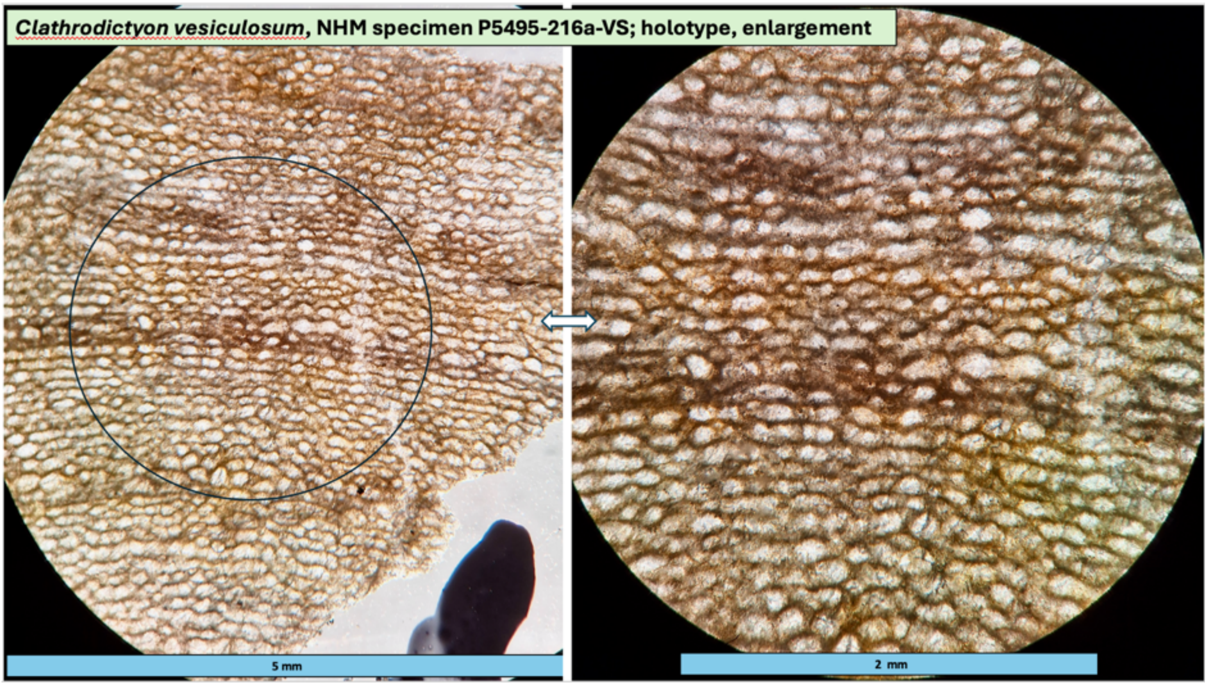


Fig. 4.1.1. Repeat of Fig.2.1.3 as a reminder of the skeletal structure of the holotype of *Clathrodictyon vesiculosum* as illustrated by Nestor (2015). Formal specimen number is NHMUK PI P5495-216a.

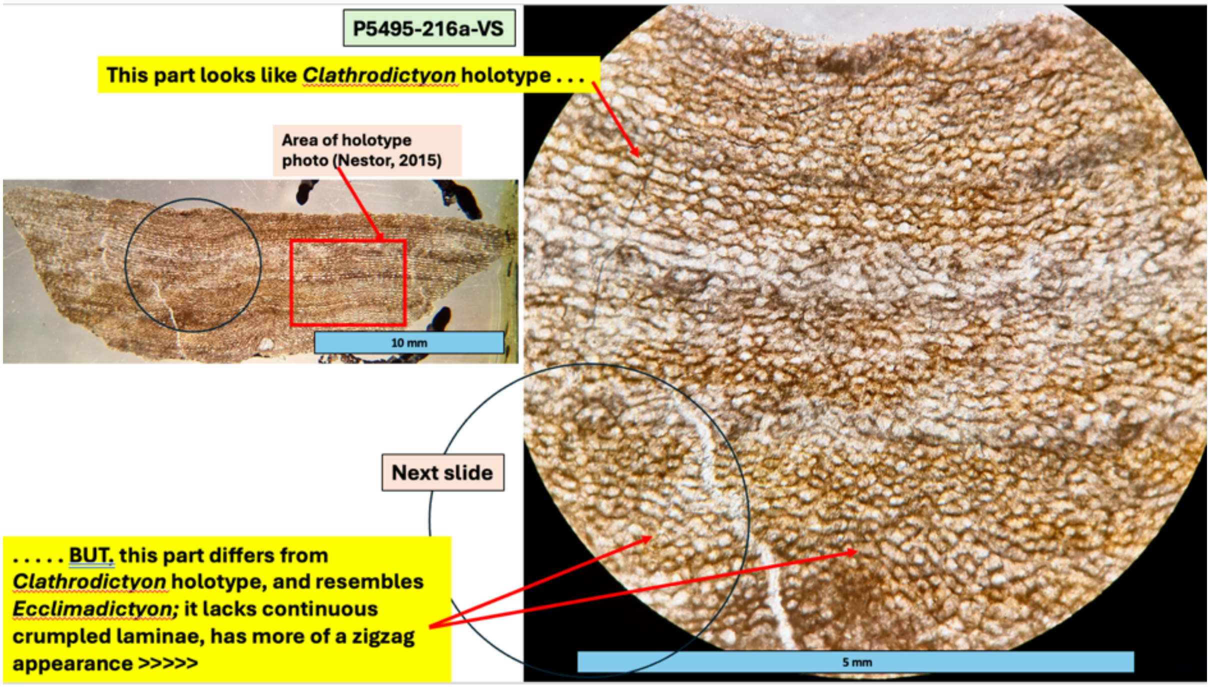


Fig. 4.1.2. View of the left-hand side of the thin section of *Clathrodictyon vesiculosum* holotype specimen, showing comparison between the crumpled laminae features that define *C. vesiculosum* in the upper part of the right-hand image, *versus* a more irregular portion that approaches the skeletal structure of *Ecclimadictyon* at the bottom of the image; see enlargement in Fig. 4.1.3. Formal specimen number is NHMUK PI P5495-216a.

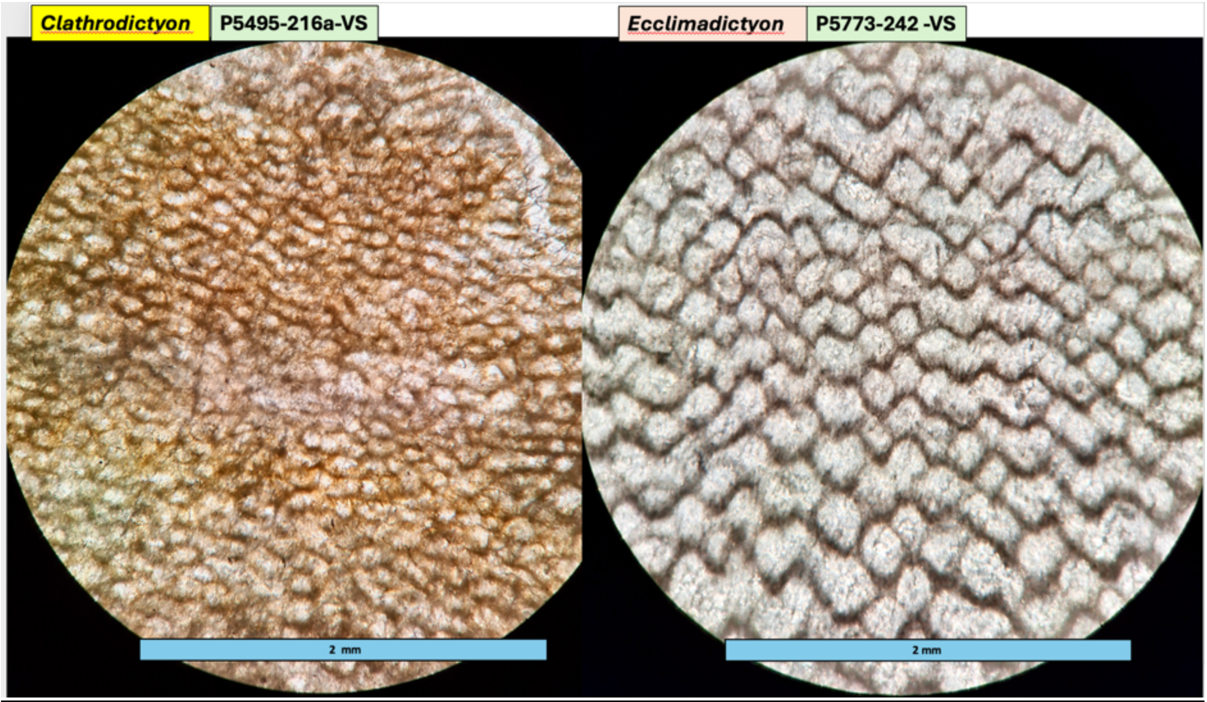


Fig. 4.1.3. Left-hand image is the enlargement from Fig. 4.1.2, showing the *Clathrodictyon vesiculosum* holotype specimen. Note the highly crumpled laminae in most of the area of this image, contrasting the continuous laminae of the holotype. Some continuous laminae are visible on the right side of the left-hand photo, but the rest of the image area does not show continuous laminae; making it more consistent with the description of *Ecclimadictyon*. Formal specimen number NHMUK PI P5495-216a. **Right-hand image** repeats the detail of *Ecclimadictyon* holotype from Fig. 2.2.3, though it shows a slightly different area of the holotype. Note that although the skeletal elements in this image of *Ecclimadictyon* are generally more widely spaced than in the left-hand image, there is some

variation, particularly in the central region, where the spacing is finer. This raises the question of how significant is size in distinguishing these elemental characters. If the only difference is size, such as the larger elements in *Ecclimadictyon* compared to *Clathrodictyon*, what evidence supports the recognition of a distinct taxon? Some later illustrations in this atlas show considerable size variations in the skeletal elements of *Ecclimadictyon.* Formal specimen number is NHMUK PI P5773-242.

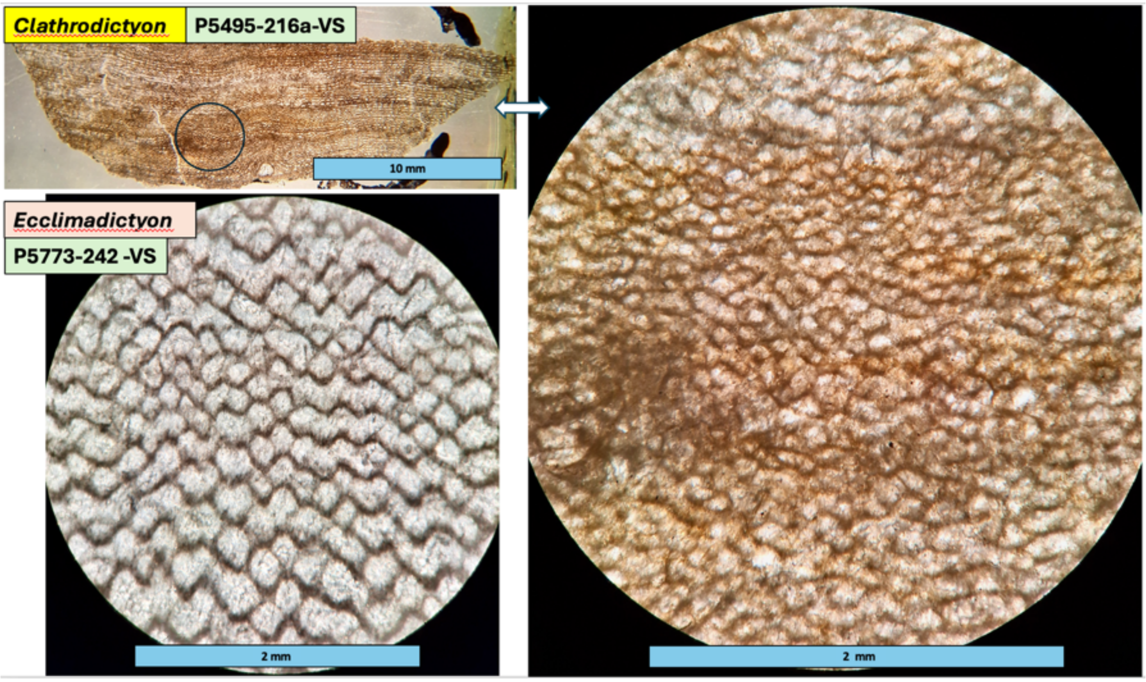


Fig. 4.1.4. Upper left photo of *Clathrodictyon vesiculosum* holotype specimen, showing location of detail in the **right-hand photo (**specimen NHMUK PI P5495-216a). **Lower left photo** shows *Ecclimadictyon* holotype (NHMUK PI P5773-242) for comparison (note scale difference between the two enlargement photos). As in Fig. 4.1.2, the *Clathrodictyon* structure in this part of the *Clathrodictyon* holotype departs considerably from the continuous crumpled laminae seen in the holotype photo from Nestor (2015), and much of it resembles *Ecclimadictyon* (NHMUK PI P5773-242)*.* The lower and upper edges of right-hand image shows element spacing similar to the holotype of *Ecclimadictyon*.

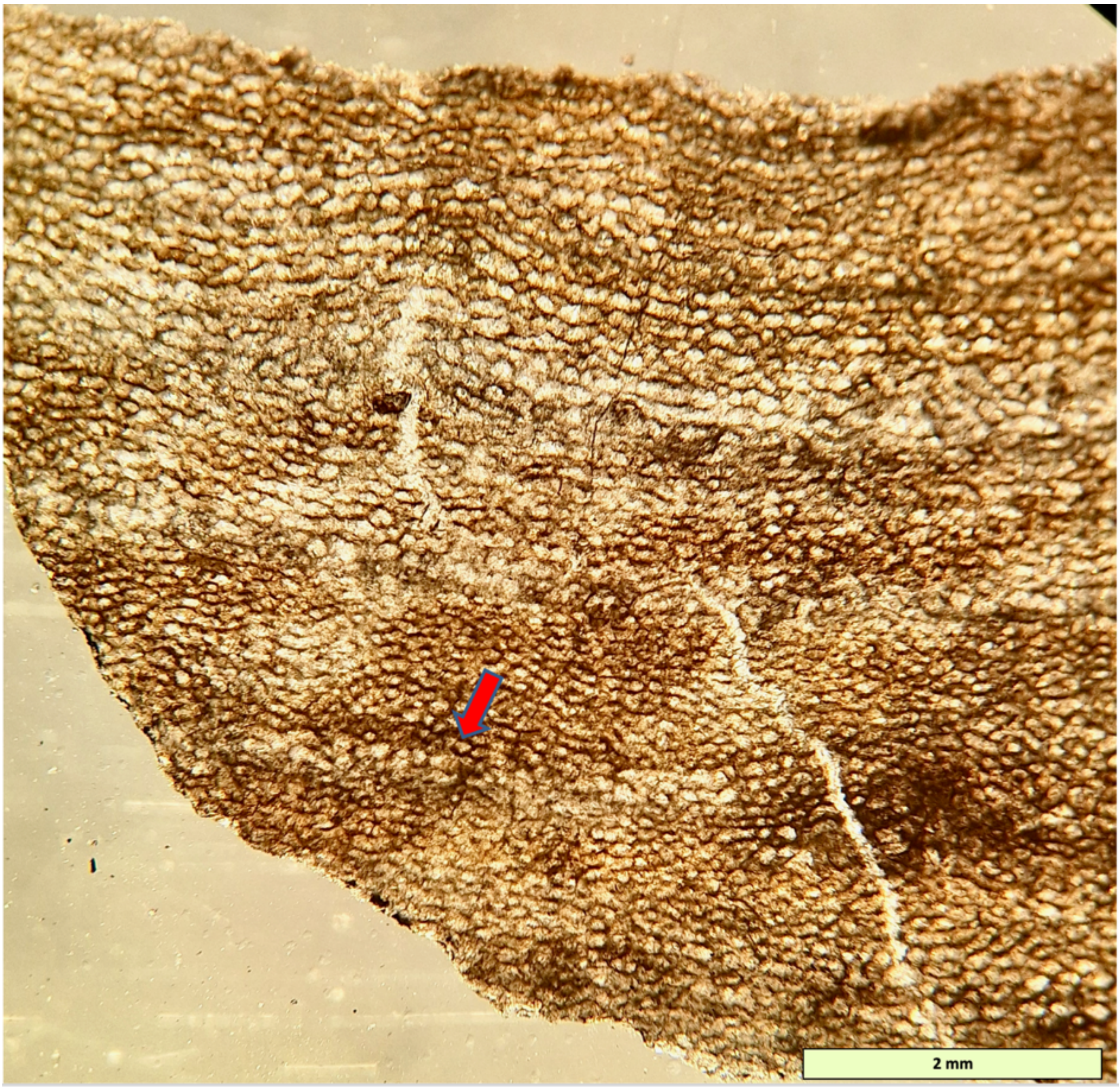


Fig. 4.1.5a. Another photo of *Clathrodictyon vesiculosum* holotype VS, showing detail of variation of continuous crumpled laminae (consistent with *Clathrodictyon*) in the upper part of the picture, contrasting the more crumpled zigzag laminae in the lower part (resembling *Ecclimadictyon*). Red arrow shows a matched point with the enlargement in Fig. 4.1.5b. Formal specimen number NHMUK PI P5495-216a.

Fig. 4.1.5b. Enlargement of lower part of Fig. 4.1.5a, detailing the more crumpled zigzag laminae in the lower part of the VS thin section (resembling *Ecclimadictyon*). Red arrow shows a matched point with the photo in Fig. 4.1.5ba. Formal specimen number NHMUK PI P5495-216a.

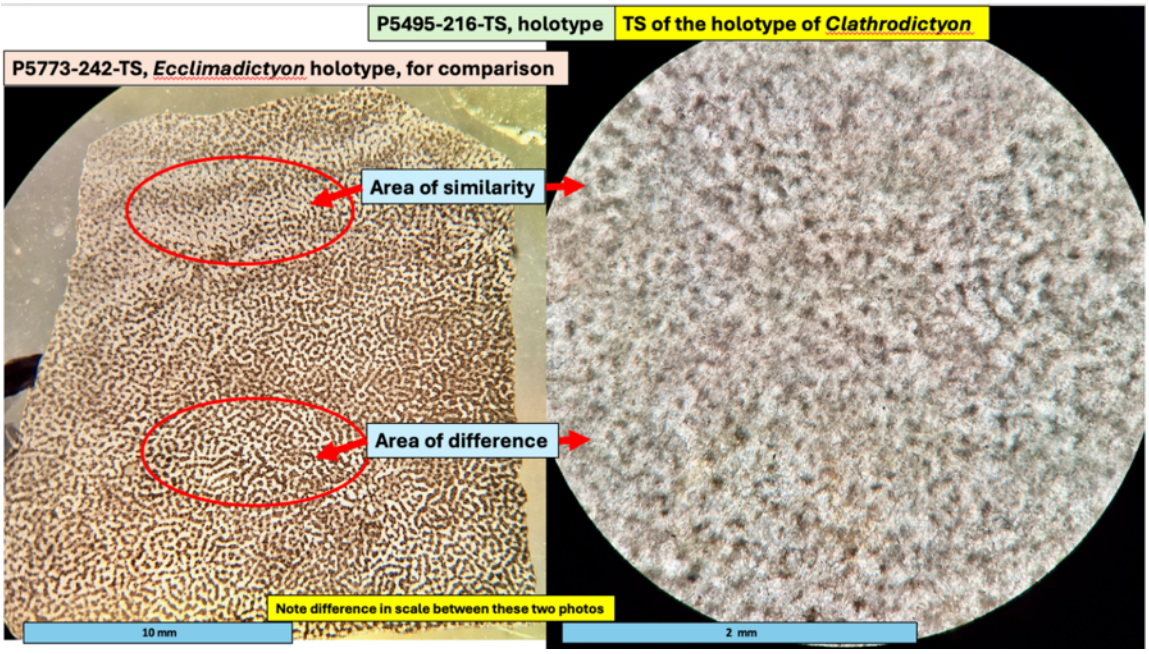
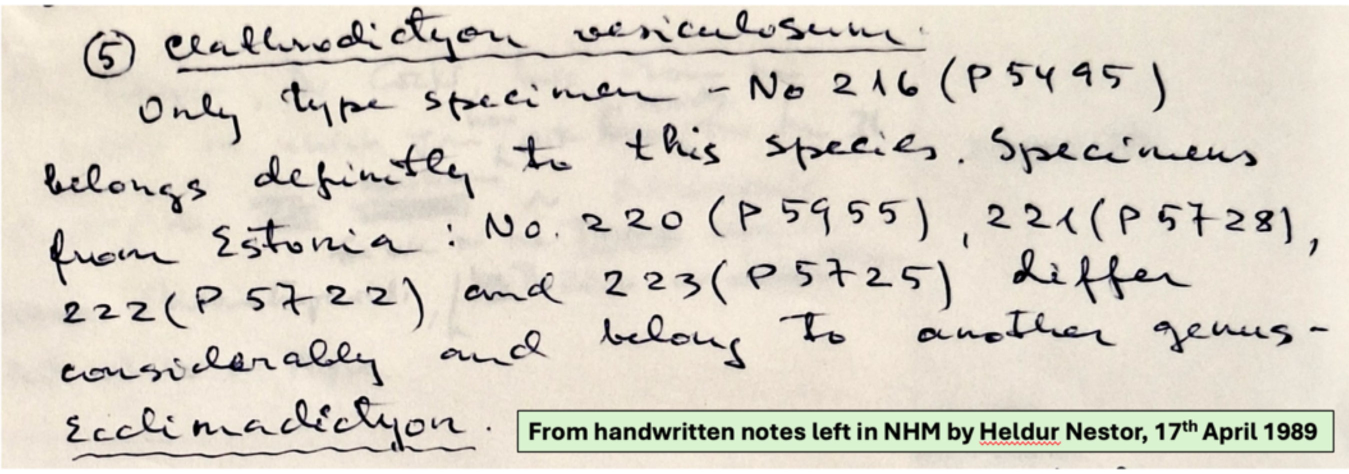


Fig. 4.1.6. Left-hand photo: Transverse section of *Ecclimadictyon* holotype (specimen NHMUK PI P5773-242), highlighting areas with apparent individual pillars (upper) and areas where the elements are amalgamated (lower); the upper areas have similarity to **right-hand photo** *Clathrodictyon* holotype TS (NHMUK PI P5495-216).



(5) Clathrodictyon vesiculosum.
Only type specimen - No 216 (P5495)
belongs definitly to this species. Specimens
from Estonia: No. 220 (P5955), 221 (P5728),
222 (P5722) and 223 (P5725) differ
considerably and belong to another genus -
Ecclimadictyon.

From handwritten notes left in NHM by Heldur Nestor, 17th April 1989

Fig. 4.1.7. Extract from hand-written notes left in the NHMUK, written by Heldur Nestor 17th April 1989. This information is very revealing, because it demonstrates that Nicholson identified all these specimens as *Clathrodictyon vesiculosum.* However, the indication is that only one of them is *Clathrodictyon*, the others are regarded as *Ecclimadictyon* by Nestor, and therefore would be expected to have been called *C. fastigiatum* by Nicholson. These notes also reveal that Nestor was selective in his definition of the *C. vesiculosum* taxon, basing his identification on only the ***right-hand part*** of the NHMUK PI P5495-216a holotype VS, whereas he did not take account of the left-hand part of the holotype VS, so did not include variation of the skeletal structure in the definition of the genus.

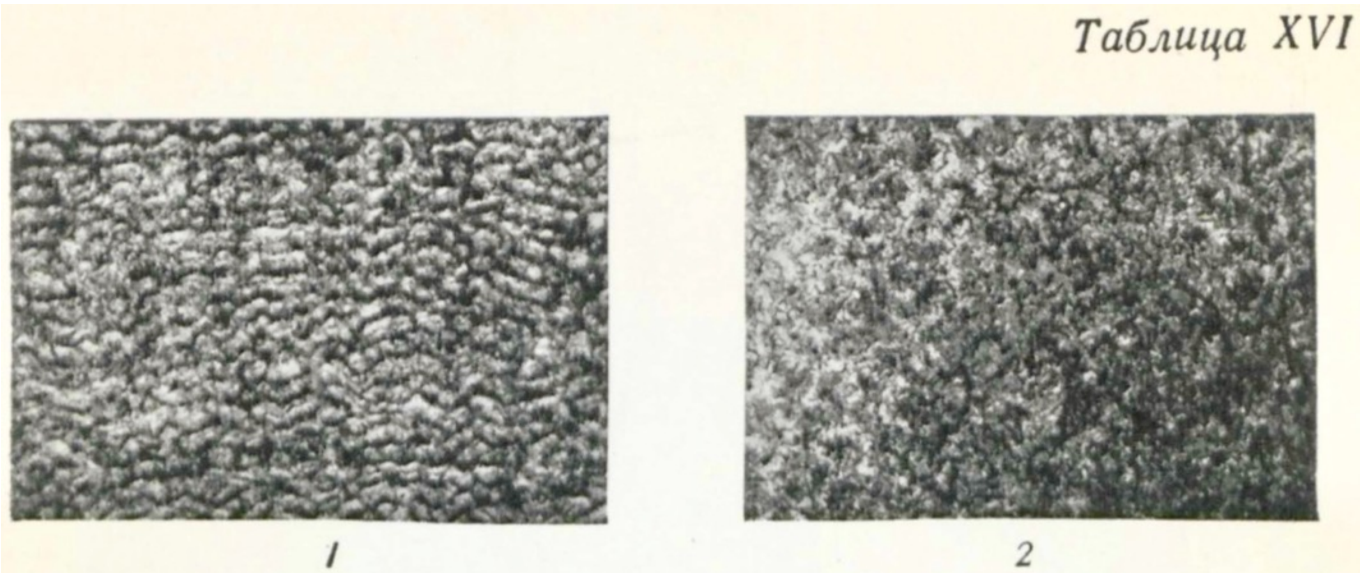


Fig. 4.1.8. Duplicate of Fig. 3.1.1., showing "*Clathrodictyon fastigiatum Nich.,* var*. macrotuberculata* n. var*.*" as proposed by Riabinin (1951, plate 16, figs 1 & 2). Although this is now called *Ecclimadictyon macrotuberculatum* by Mori (1970) and Nestor et al. (2010), as described in Section 3, the VS has some similarity with *C. vesiculosum*, and *Camptodictyon*, but the TS does not show clear structure. Thus these images are poor representions of *Ecclimadictyon macrotuberculatum* , and the TS image (on the right side) in particular is too poor to reveal any useful detail. Note also that the term "var*. macrotuberculata*" refers to large knobby structure of the whole fossil, and is therefore descriptive of the morphology of the fossil, not of its skeletal structure. Hence "var*. macrotuberculata*" is invalid as a taxonomic descriptor; *Ecclimadictyon fastigiatum* is likely a more accurate name.

4.2. NHMUK PI P5722-222 – Clathrodictyon vesiculosum

This is another specimen of *C. vesiculosum* from Nicholson's Estonia collections, from Kaugatoma Bank in Estonia, of Silurian age.

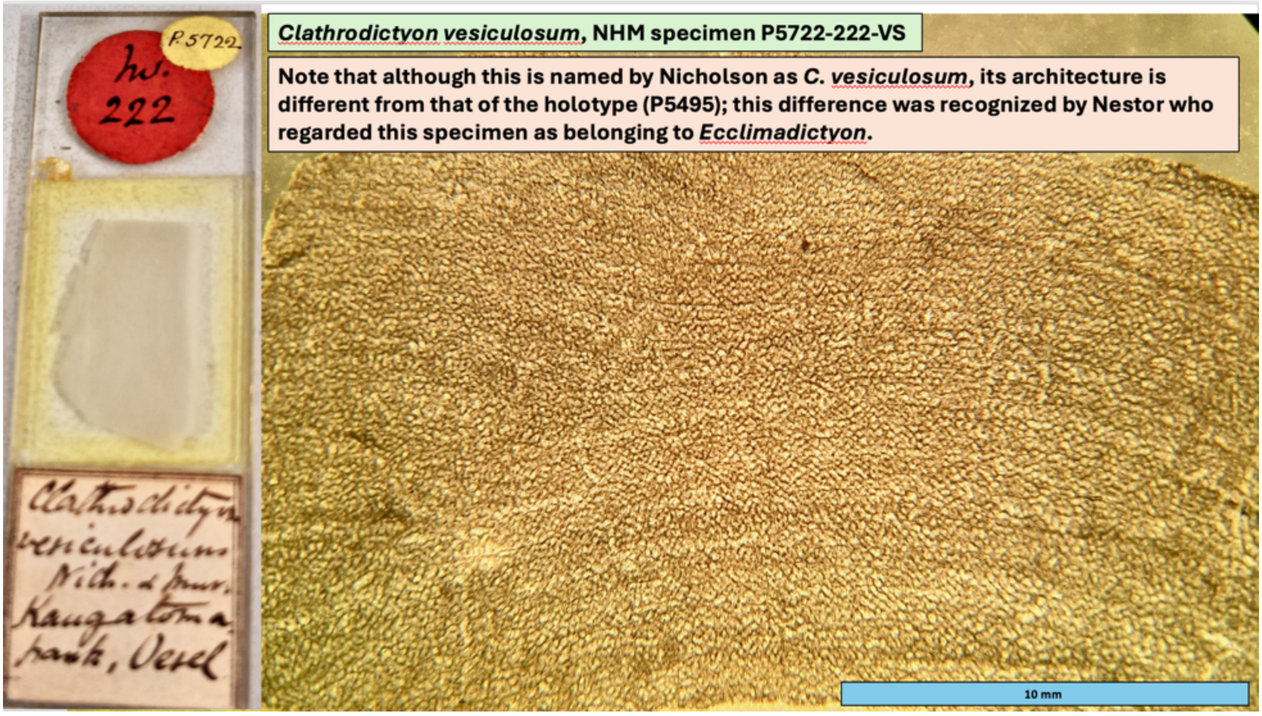


Fig. 4.2.1. Specimen of *C. vesiculosum* (NHMUK PI P5722-222) exhibiting a skeletal structure that more closely resembles *Ecclimadictyon*. Enlargements are shown in the subsequent figures.

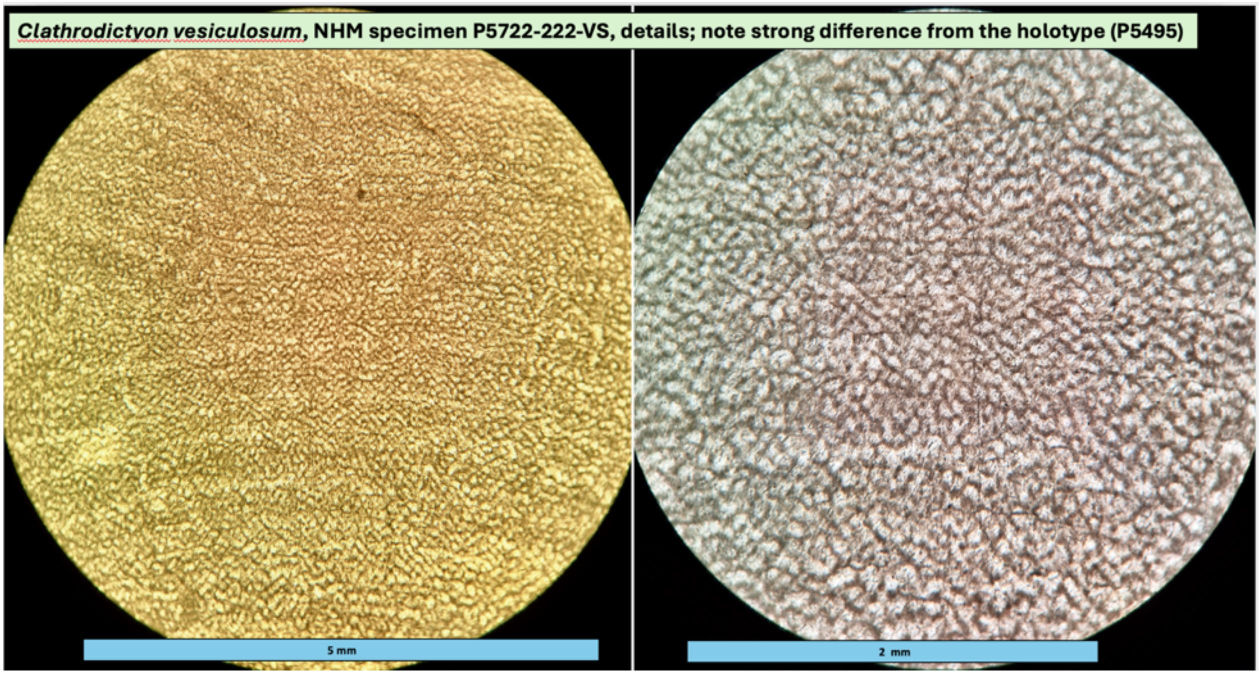


Fig. 4.2.2. Enlarged views of *C. vesiculosum* (NHMUK PI P5722-222) from Fig. 4.2.1, showing a skeletal structure more typical of *Ecclimadictyon*. The crumpled continuous laminae that are diagnostic of *C. vesiculosum* are not present in these photos.

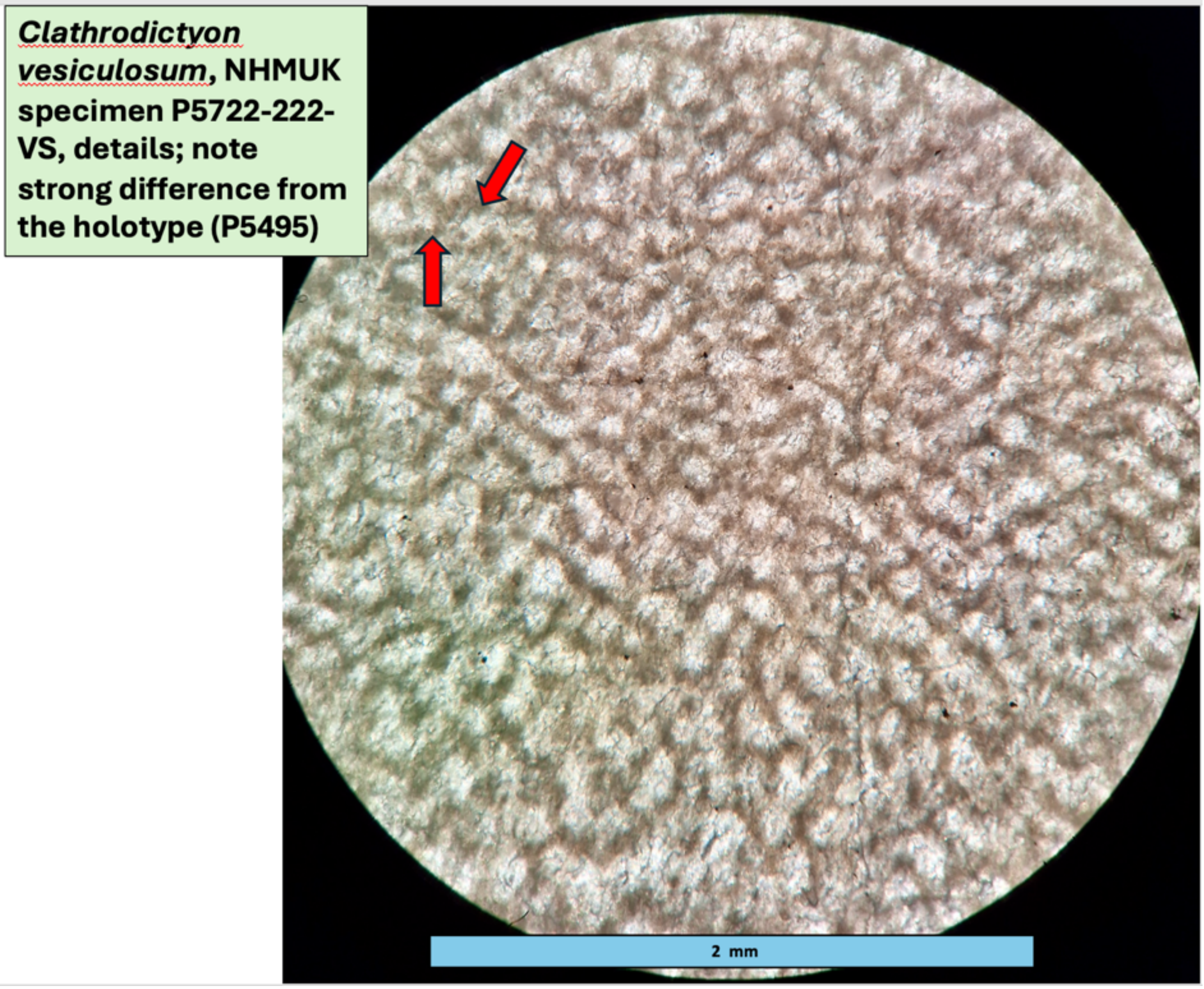


Fig. 4.2.3. Detail of Fig. 4.2.1, of *C. vesiculosum* VS*,* with a skeletal structure more closely resembling *Ecclimadictyon*. Only two of the crumpled continuous laminae (red arrows) that are diagnostic of *C. vesiculosum* are present in this image; all the remainder looks more like *Ecclimadictyon*. Formal specimen number is NHMUK PI P5722-222.

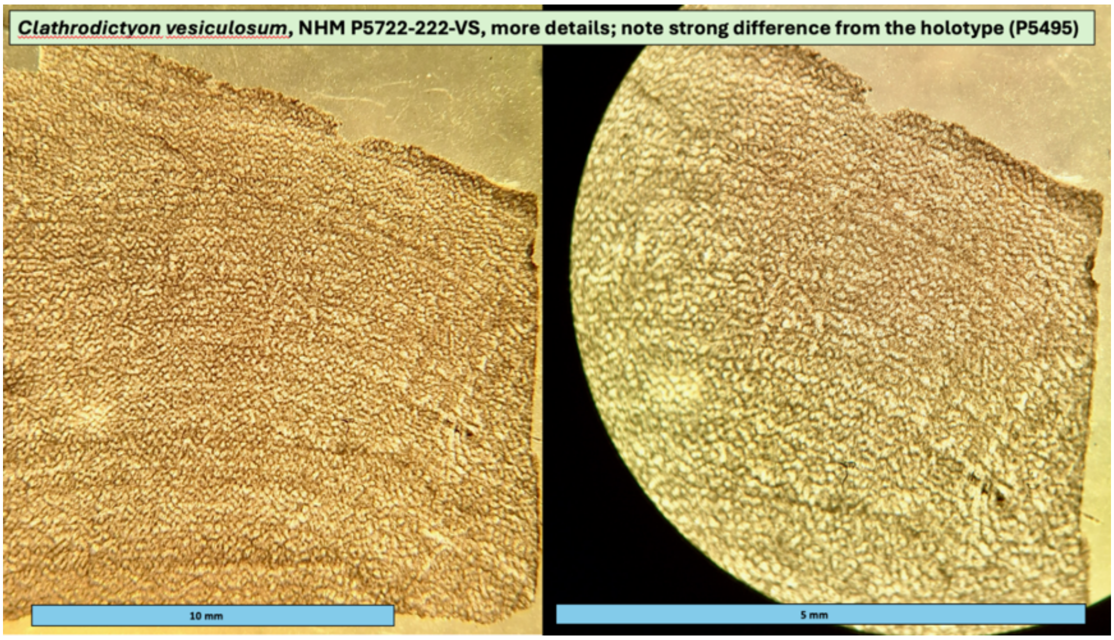


Fig. 4.2.4. Another area of VS shown in Fig. 4.2.1, of *C. vesiculosum,* with a skeletal structure more closely resembling *Ecclimadictyon*. Note the presence of astrorhizal system, visible as vertically-orientated spaces that look tubelike. Also note that although there is indication of horizontal layering, the crumpled continuous laminae that are diagnostic of *C. vesiculosum* are not present in these photos. Specimen NHMUK PI P5722-222.

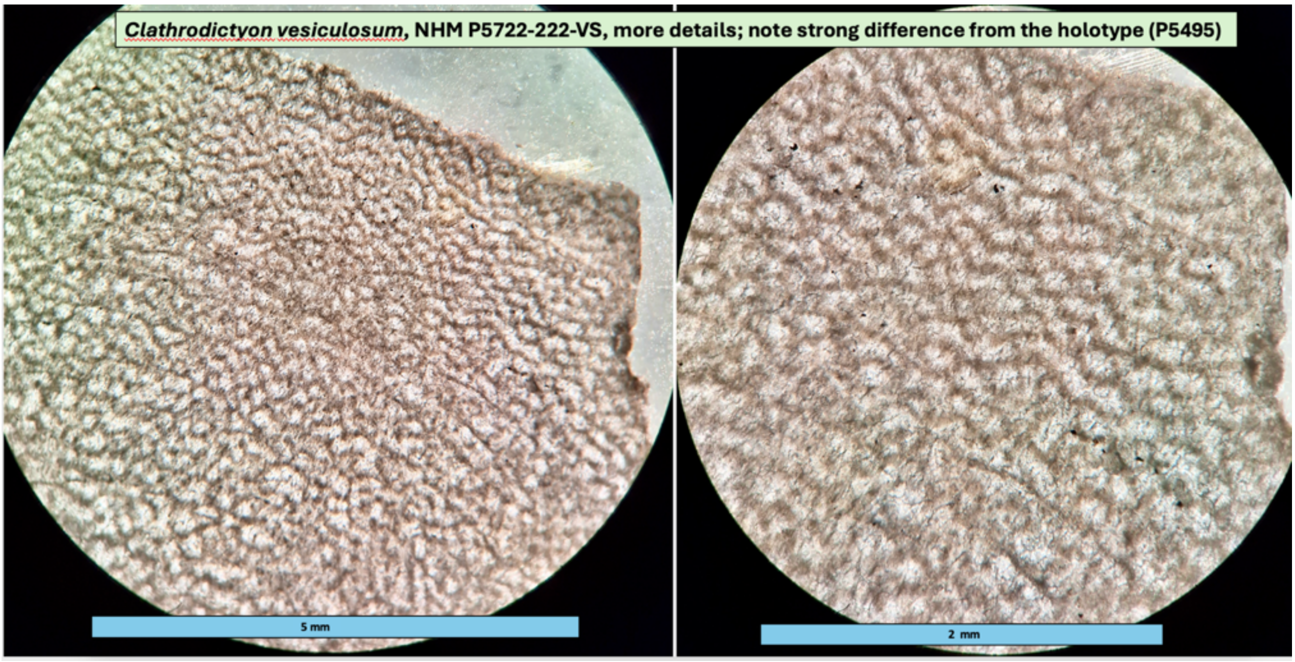


Fig. 4.2.5. Another area of VS shown in Fig. 4.2.1, of *C. vesiculosum,* with a skeletal structure comprising zig-zag laminae, more closely resembling *Ecclimadictyon*. The crumpled continuous laminae that are diagnostic of *C. vesiculosum* are almost completely absent in these photos. Formal specimen number is NHMUK PI P5722-222.

Fig. 4.2.6. TS of *C. vesiculosum,* with a skeletal structure that shows pillars consistent with *C. vesiculosum* in some areas. However, other areas may represent transverse cuts through the upper or lower parts of the zigzag structure seen in VS. Overall the structure more closely resembles *Ecclimadictyon*. Specimen NHMUK PI P5722-222.

4.3. NHMUK PI P5725-223 – Clathrodictyon vesiculosum

The following figures illustrate an additional specimen of *C. vesiculosum* identified by Nicholson, showing more variations, for comparison with other samples in this atlas.

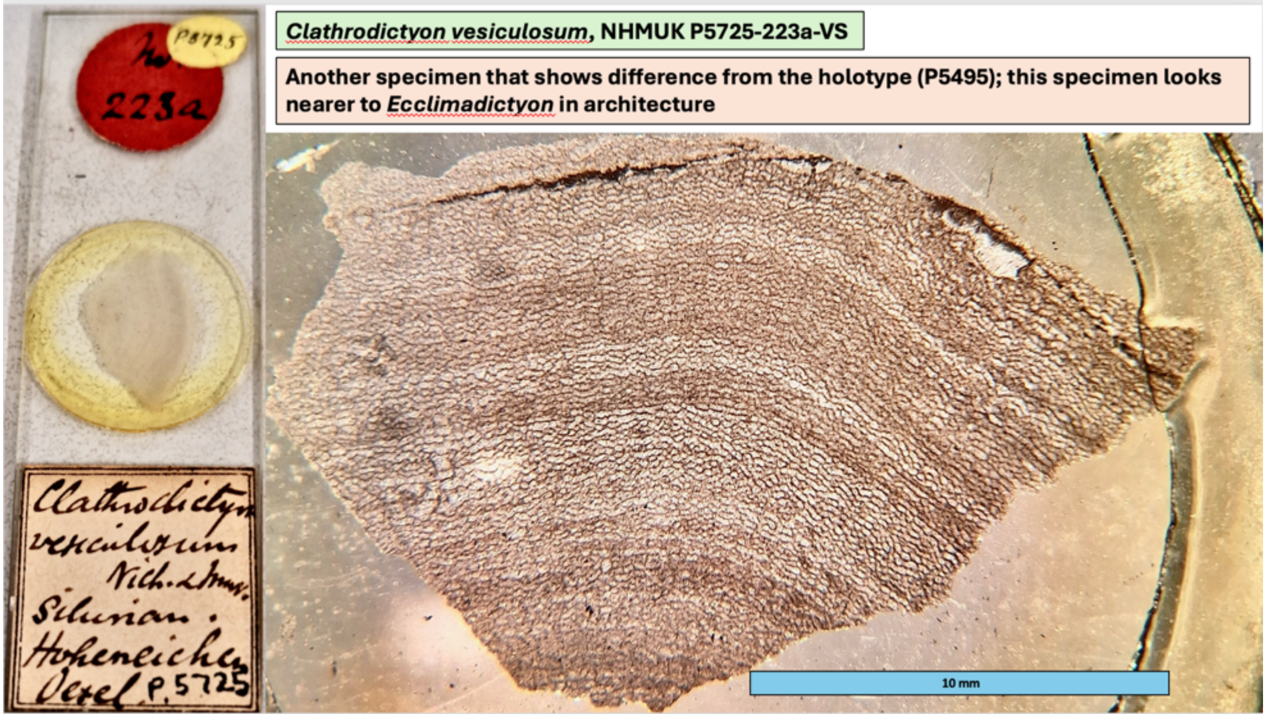


Fig. 4.3.1. VS of *C. vesiculosum,* with a skeletal structure that shows crumpled laminae and pillars consistent with *C. vesiculosum* in parts, but other parts there is resemblance to *Ecclimadictyon* and also in some areas is resemblance to *Camptodictyon*. Formal specimen number is NHMUK PI P5725-223a.

Fig. 4.3.2. Enlargement of Fig. 4.3.1, *C. vesiculosum* VS, with a skeletal structure that shows crumpled laminae and pillars consistent with *C. vesiculosum* in parts, but other parts there is

resemblance to *Ecclimadictyon* and also in some areas is resemblance to *Camptodictyon*. Formal specimen number is NHMUK PI P5725-223a.

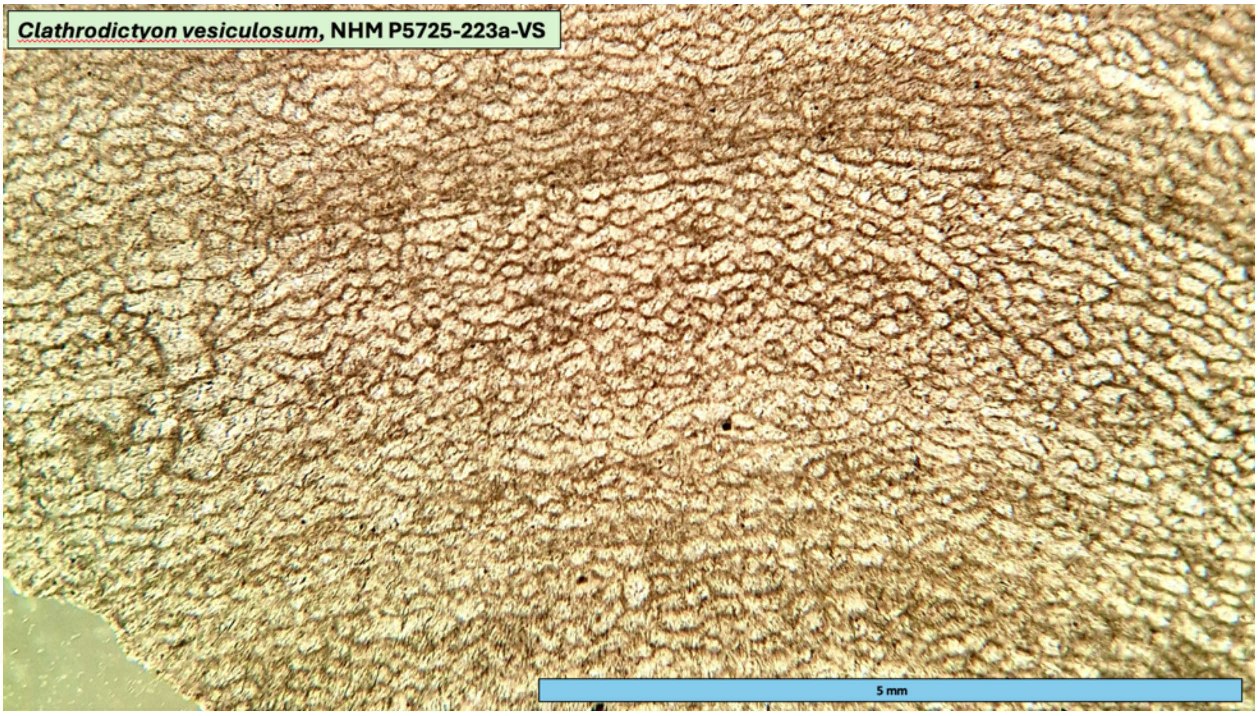


Fig. 4.3.3. Enlargement of another area of Fig. 4.3.1, *C. vesiculosum* VS, with a skeletal structure that shows crumpled laminae and pillars consistent with *C. vesiculosum* in parts, but other parts there is resemblance to *Ecclimadictyon* and also in some areas is resemblance to *Camptodictyon*. Formal specimen number is NHMUK PI P5725-223a.

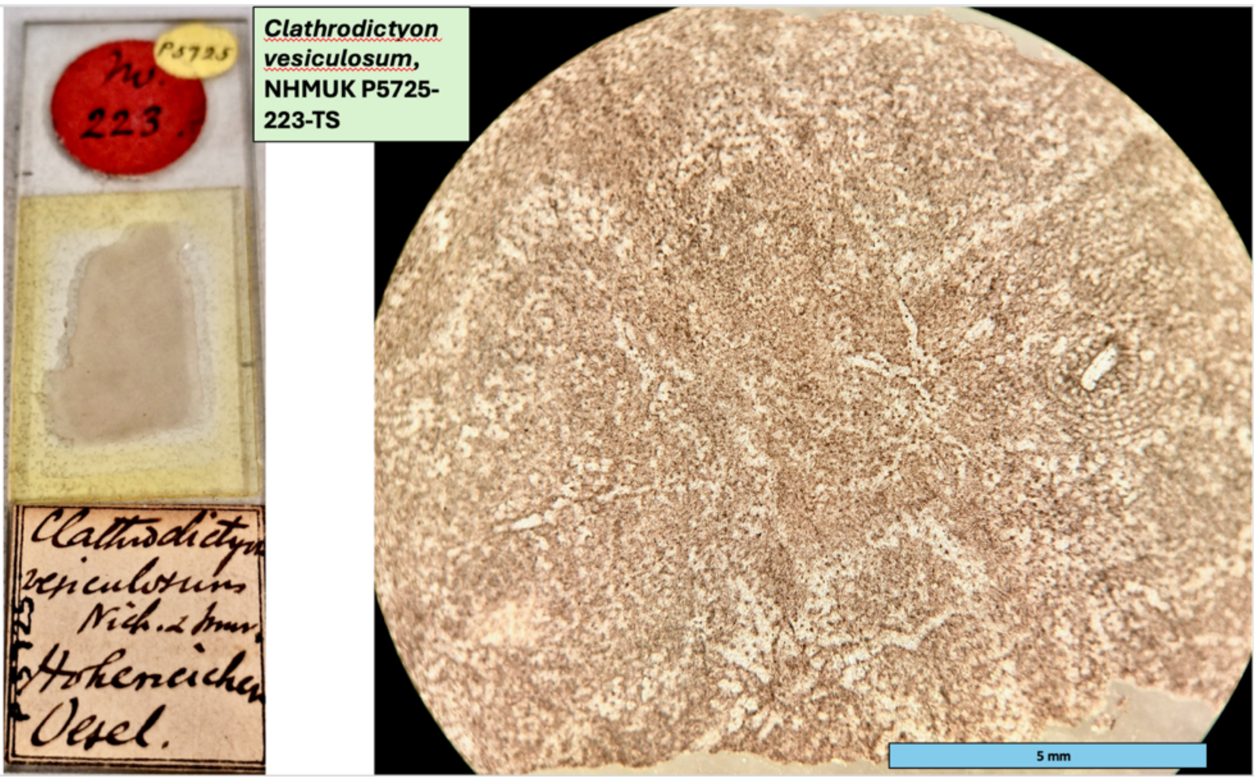


Fig. 4.3.4. TS view of *C. vesiculosum,* showing pillars consistent with *C. vesiculosum* in some regions, but other areas of more diffuse structure indicating the cross section has intersected the laminations in TS, consistent with the VS views. Formal specimen number is NHMUK PI P5725-223.

4.4. NHMUK PI P5728-221 – Clathrodictyon vesiculosum

This sample of *C. vesiculosum* from Estonia illustrates variation in preservation and also shows the contact between stromatoporoid base and its underlying sediment.

Fig. 4.4.1. General view of 4 thin sections of *C. vesiculosum* from Nicholson Collection at the NHMUK, details illustrated in the succeeding figures. Formal specimen numbers NHMUK PI P5728-221, plus a-c.

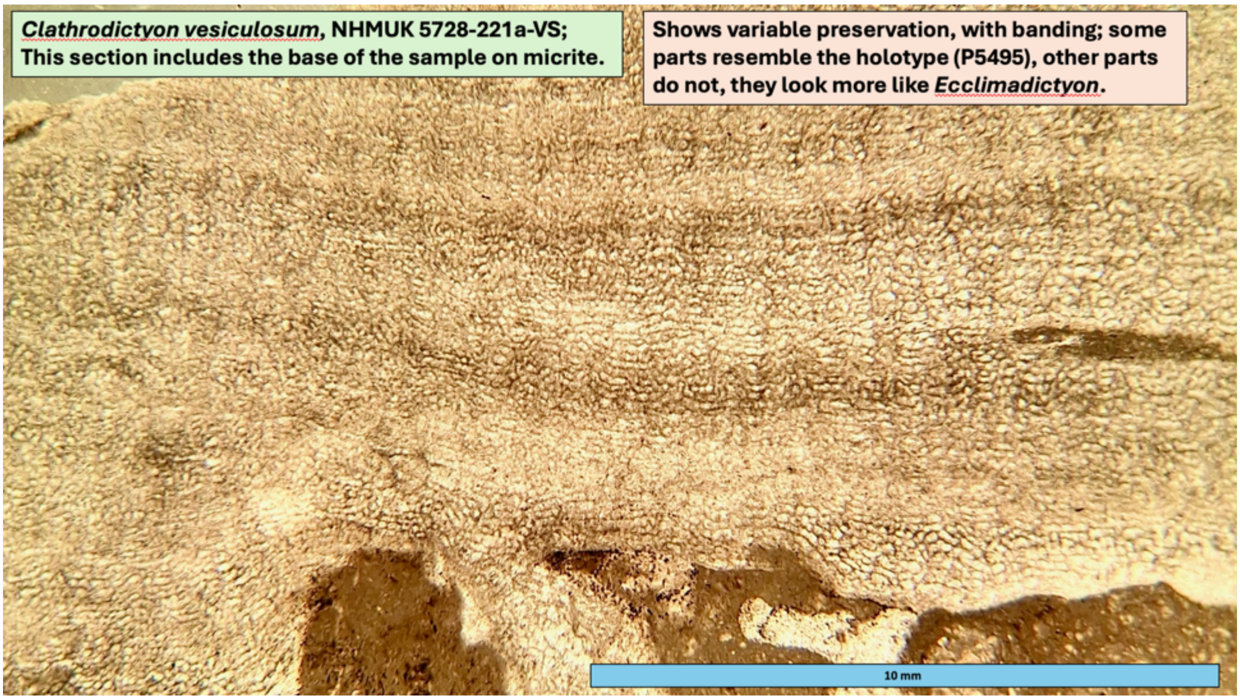


Fig. 4.4.2. VS of *C. vesiculosum* showing variation in preservation in bands. Differences in the size of skeletal elements are also visible. More details in the following figures. Formal specimen number is NHMUK PI P5728-221a.

Fig. 4.4.3. Detail of Fig. 4.4.2, *C. vesiculosum* VS, showing variation in preservation in bands; some variation in size of skeletal elements is also visible. Note that most of the skeleton does not show continuous crumpled laminae that are the key characteristic of *Clathrodictyon*. More details in the following figures. Formal specimen number is NHMUK PI P5728-221a.

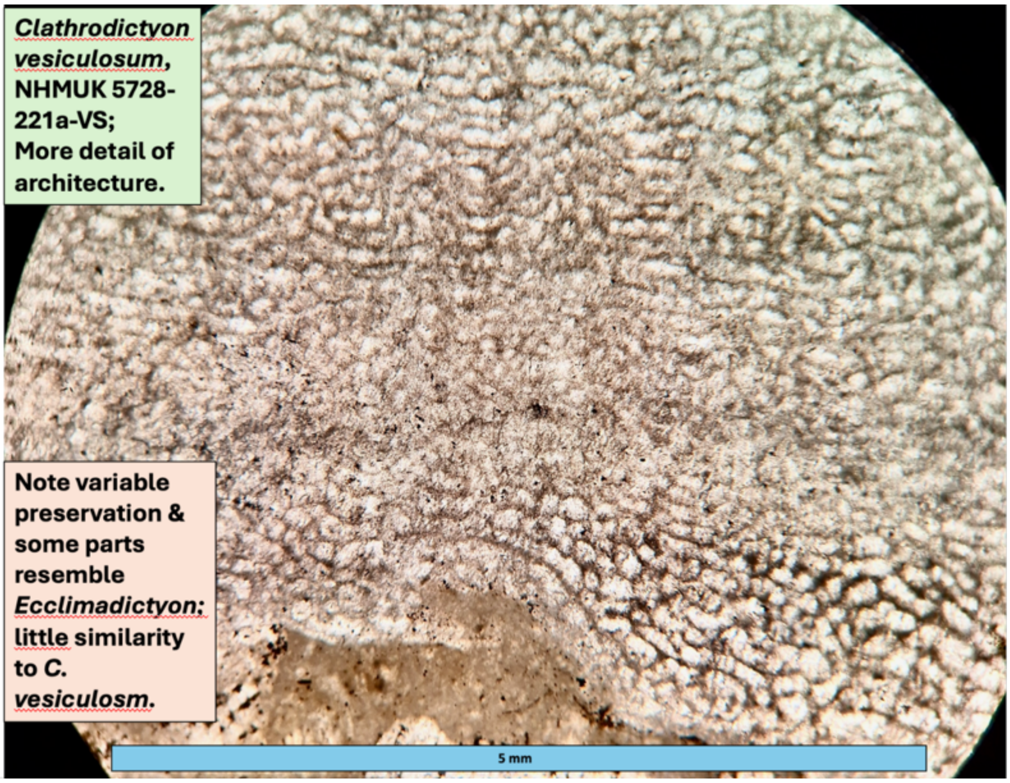


Fig. 4.4.4. Enlargement of Fig. 4.4.3, *C. vesiculosum* VS, showing variation in preservation in bands; some variation in size of skeletal elements is also visible. Note that most of the skeleton does not show continuous crumpled laminae that are the key characteristic of *Clathrodictyon*, and this thin section shows structure more resembles *Ecclimadictyon*. Formal specimen number is NHMUK PI P5728-221a.

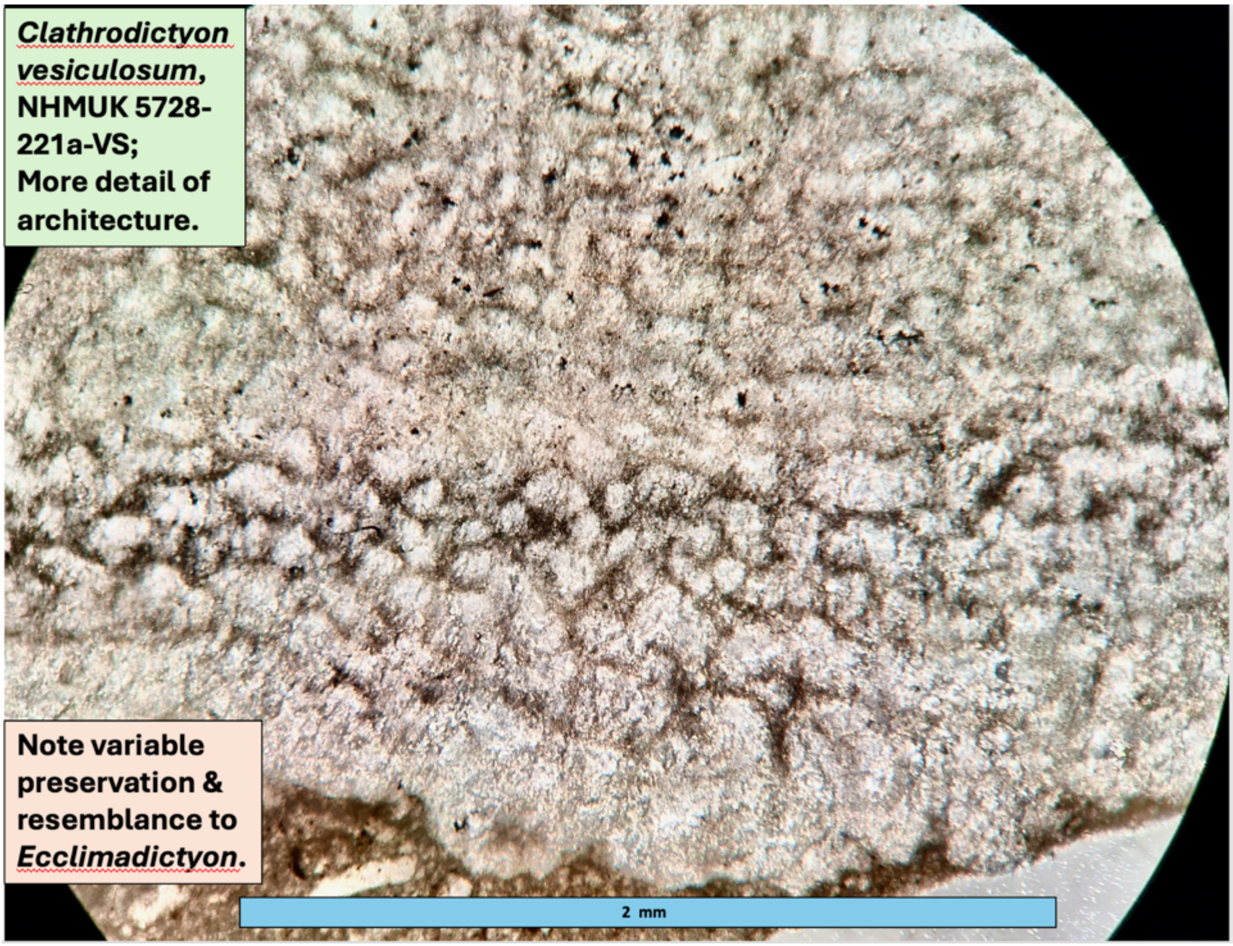


Fig. 4.4.5. Close-up of Fig. 4.4.4, *C. vesiculosum* VS, with very little evidence of continuous crumpled laminae, the key characteristic of *Clathrodictyon.* Instead, thin section shows structure that more resembles *Ecclimadictyon*. Formal specimen number is NHMUK PI P5728-221a.

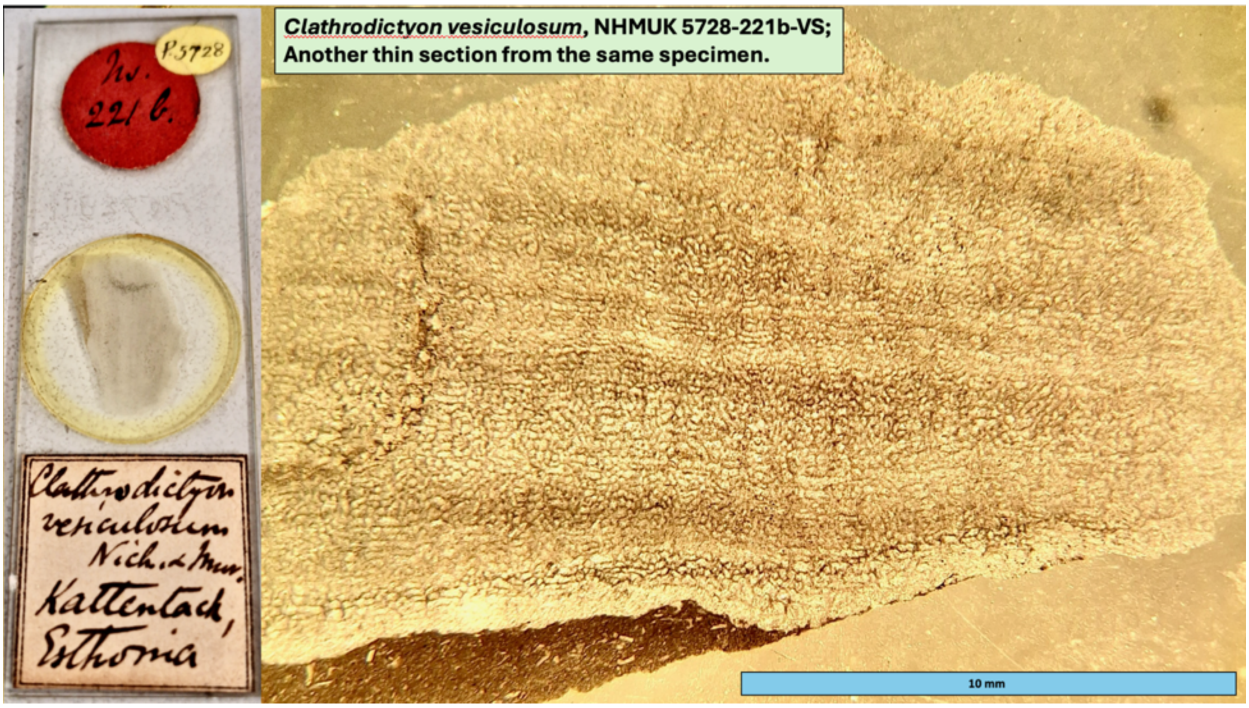


Fig. 4.4.6. Another VS of *C. vesiculosum* showing a general view of skeletal variation in banding. Formal specimen number is NHMUK PI P5728-221b.

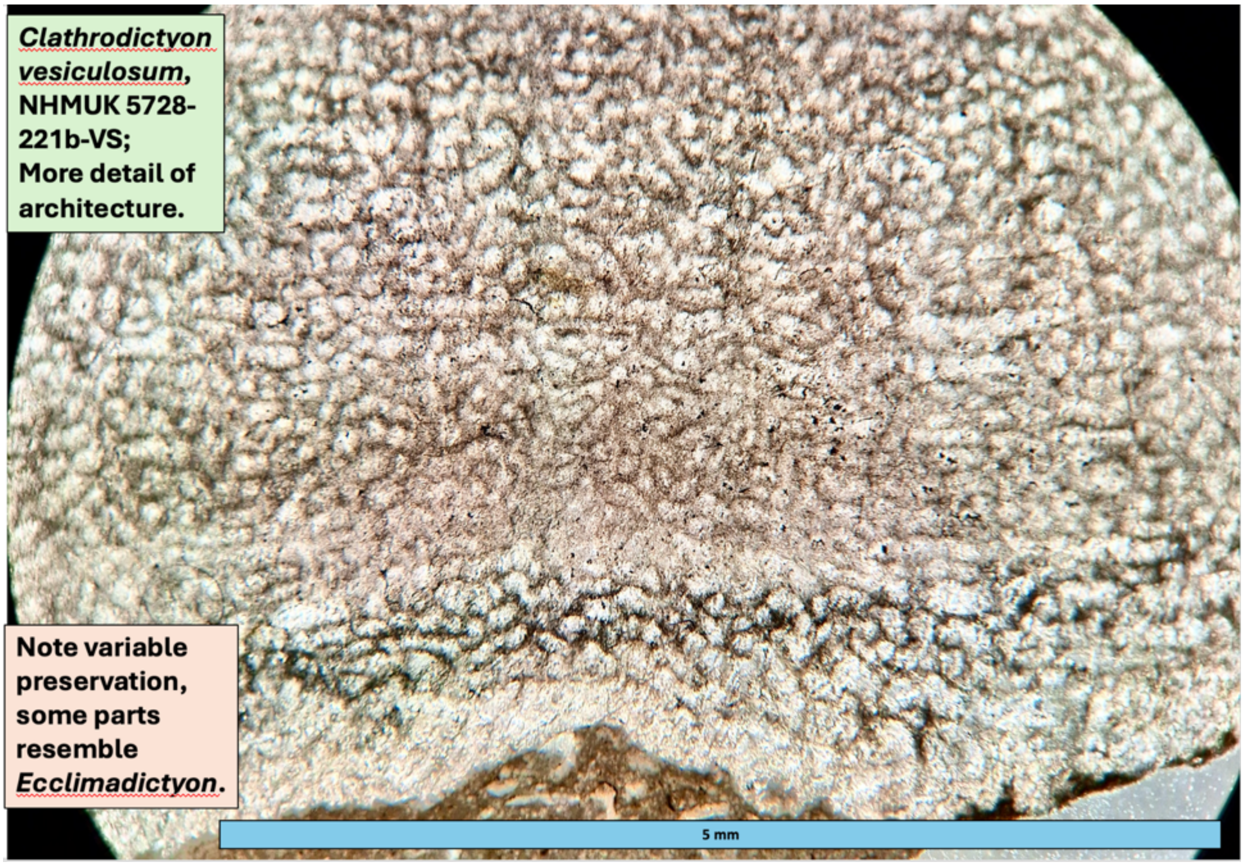


Fig. 4.4.7. Enlargement of Fig. 4.4.6., *C. vesiculosum* VS, showing variation in banding and only part shows continuous laminae, with greater resemblance to *Ecclimadictyon*. Formal specimen number is NHMUK PI P5728-221b.

Fig. 4.4.8. TS of *C. vesiculosum* in which individual pillars are uncommon, and thus not representative of *Clathrodictyon*. Formal specimen number is NHMUK PI P5728-221.

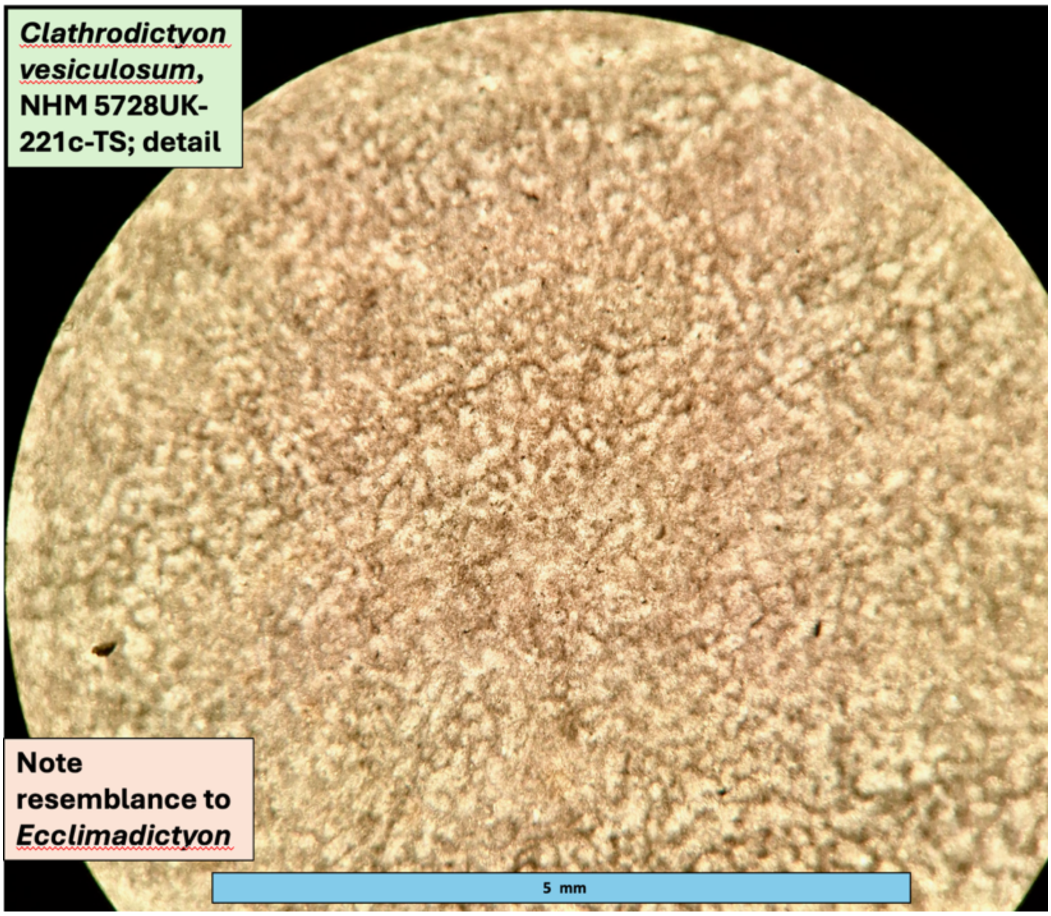


Fig. 4.4.9. Enlargement of *C. vesiculosum* TS in which individual pillars are uncommon. As a result, the overall structure is not representative of *Clathrodictyon*. Formal specimen number is NHMUK PI P5728-221.

4.5. NHMUK PI P5731-219 – Clathrodictyon vesiculosum

Another example from Nicholson Collection, showing some variation from the previous cases in this section of the atlas.

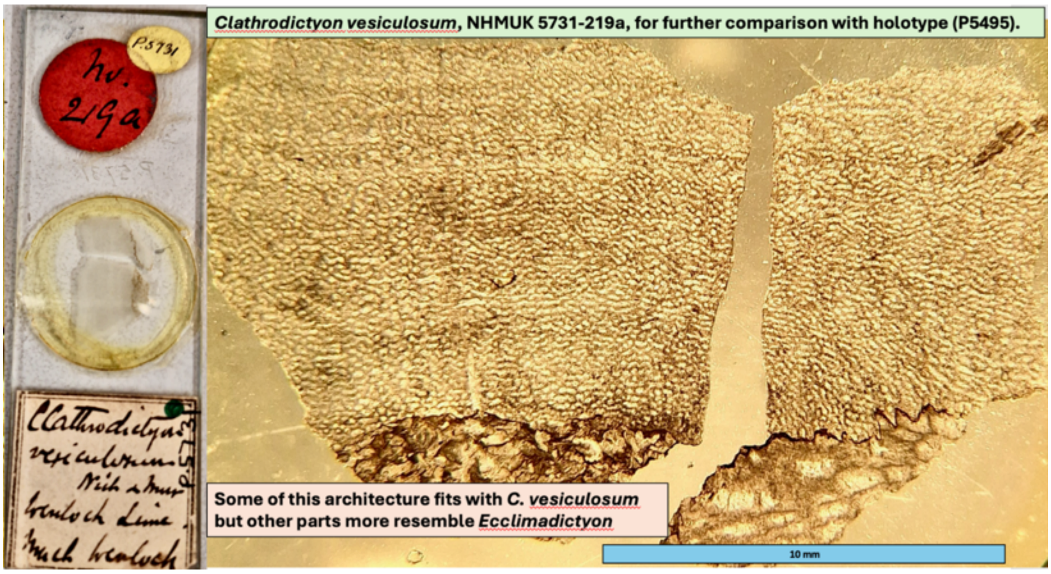


Fig. 4.5.1. General view of *C. vesiculosum* VS; much of the structure displays continuous crumpled laminae consistent with the identification of *Clathrodictyon*, although has thicker laminae than other samples in the studied material. Formal specimen number is NHMUK PI P5731-219a.

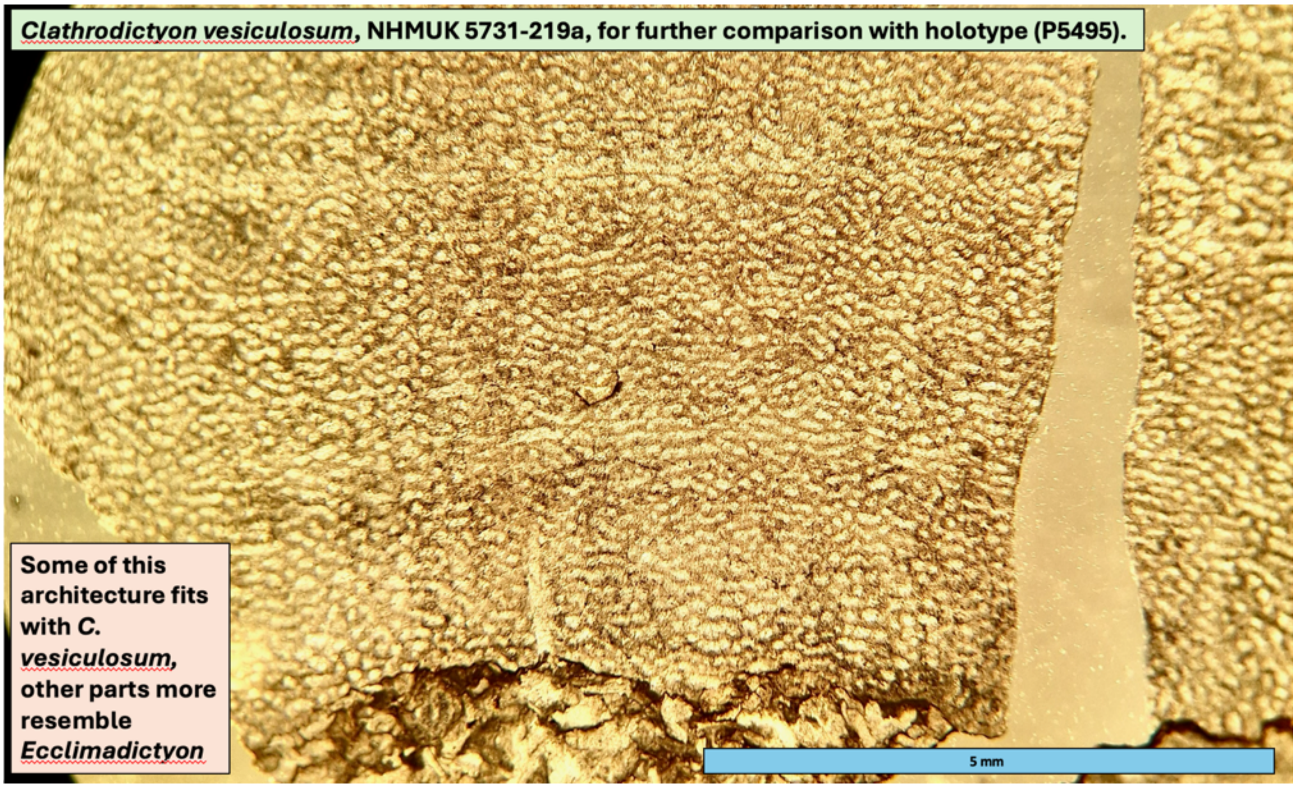


Fig. 4.5.2. General view of *C. vesiculosum* VS. While regions of the structure show continuous crumpled laminae consistent with the identification of *Clathrodictyon*, but much of it does not. Also this specimen has thicker laminae than other samples in the studied material. Formal specimen number is NHMUK PI P5731-219a.

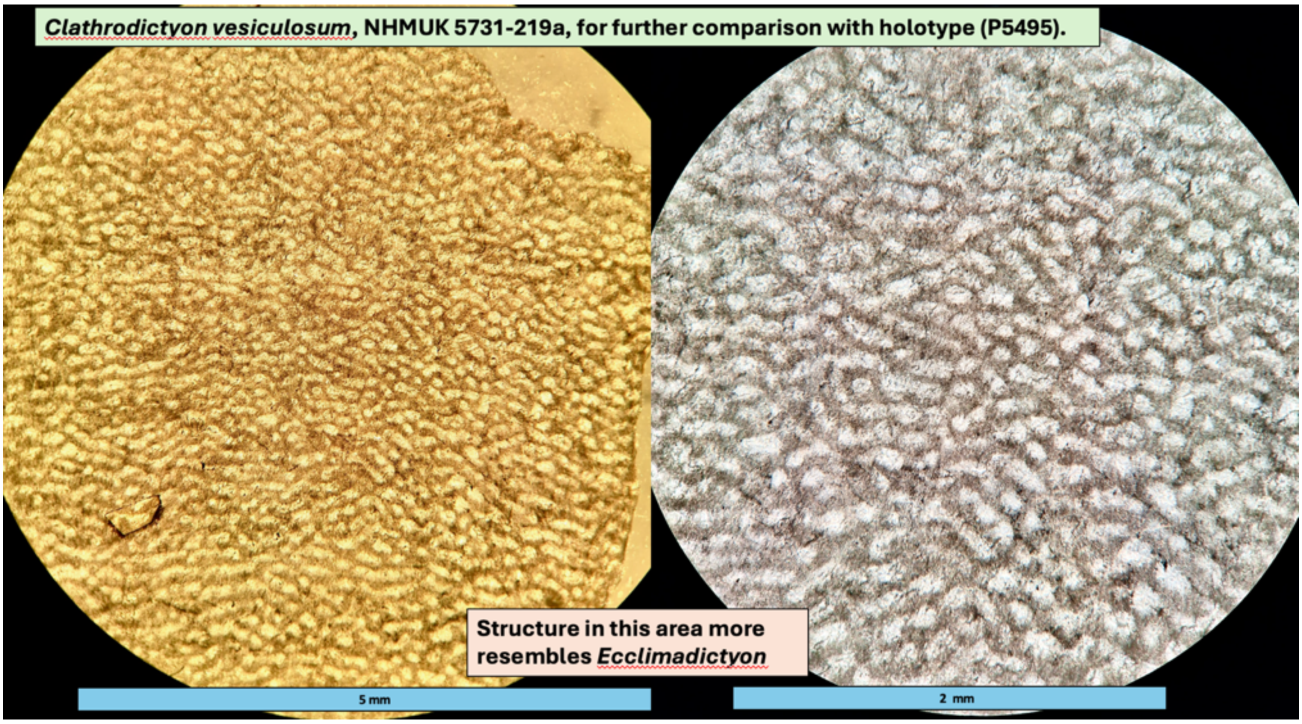


Fig. 4.5.3. Enlargements of *C. vesiculosum* VS; in detail this specimen does not show continuous laminae of *Clathrodictyon*; there is more resemblance to *Ecclimadictyon*, yet does not conform to the zigzag structure of *Ecclimadictyon*. It is possible that it represents another taxon altogether. Formal specimen number is NHMUK PI P5731-219a.

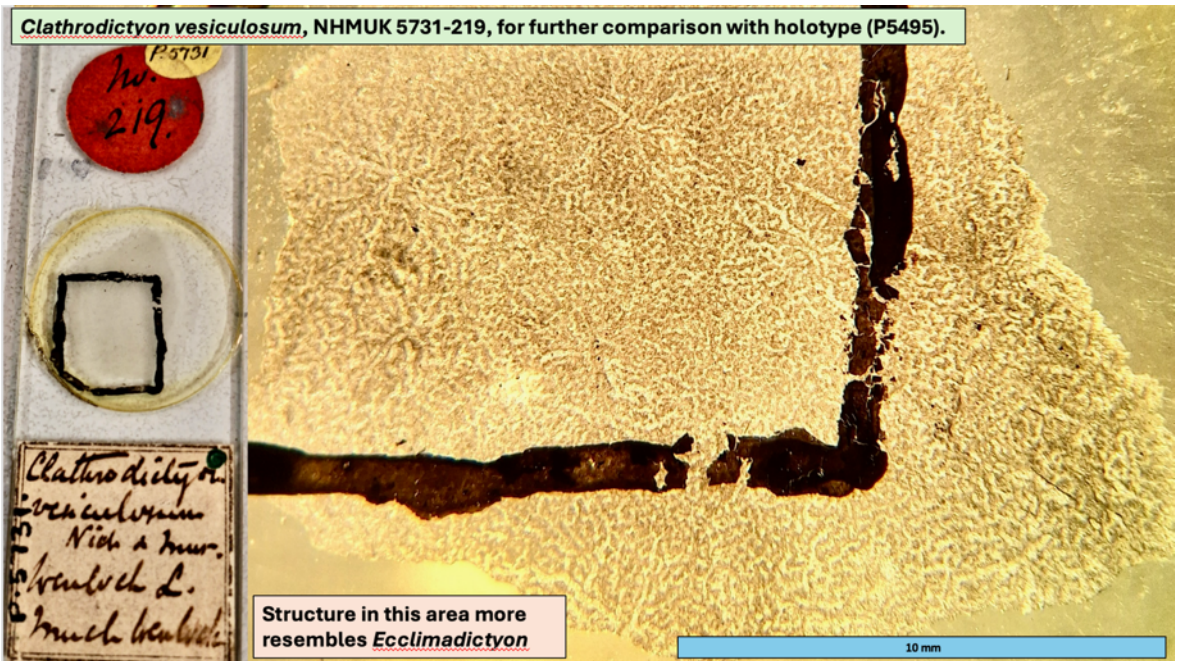


Fig. 4.5.4. General view of *C. vesiculosum* TS, lacking the small round pillars characteristic of the holotype of *Clathrodictyon*. Formal specimen number is NHMUK PI P5731-219.

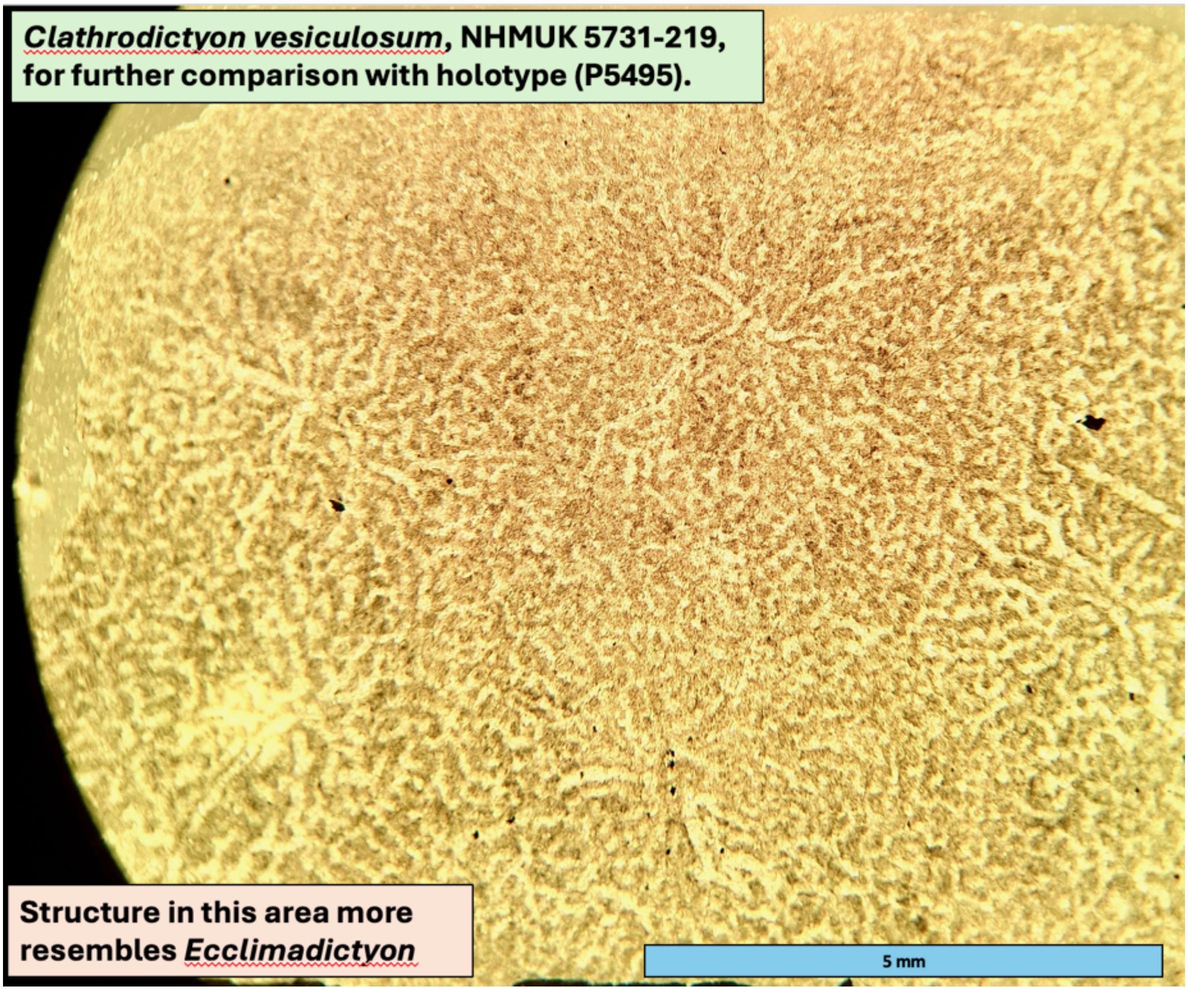


Fig. 4.5.5. Enlargement of *C. vesiculosum* TS shown in Fig. 4.5.4. While common pillars are present, the detail emphasises the lack of small round pillars characteristic of the holotype of *Clathrodictyon.* Formal specimen number is NHMUK PI P5731-219.

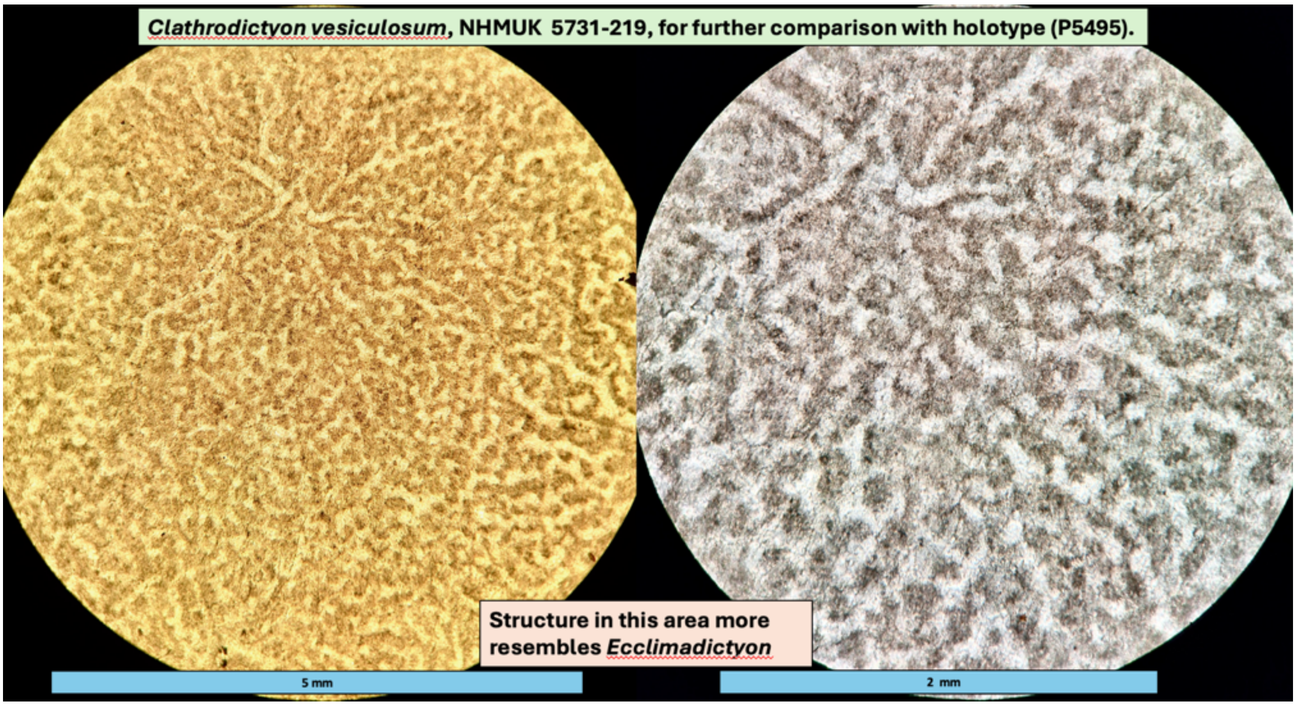


Fig. 4.5.6. Close-up of *C. vesiculosum* TS, showing common pillars. This detail emphasises the lack of small round pillars characteristic of the holotype of *Clathrodictyon.* Formal specimen number is NHMUK PI P5731-219.

4.6. NHMUK PI P5955-220 – Clathrodictyon vesiculosum

Another specimen of *C. vesiculosum* illustrating variation of skeleton in relation to banding.

Fig. 4.6.1. General view of *C. vesiculosum* VS, showing variation of skeletal structure in bands. Formal specimen number is NHMUK PI P5755-220.

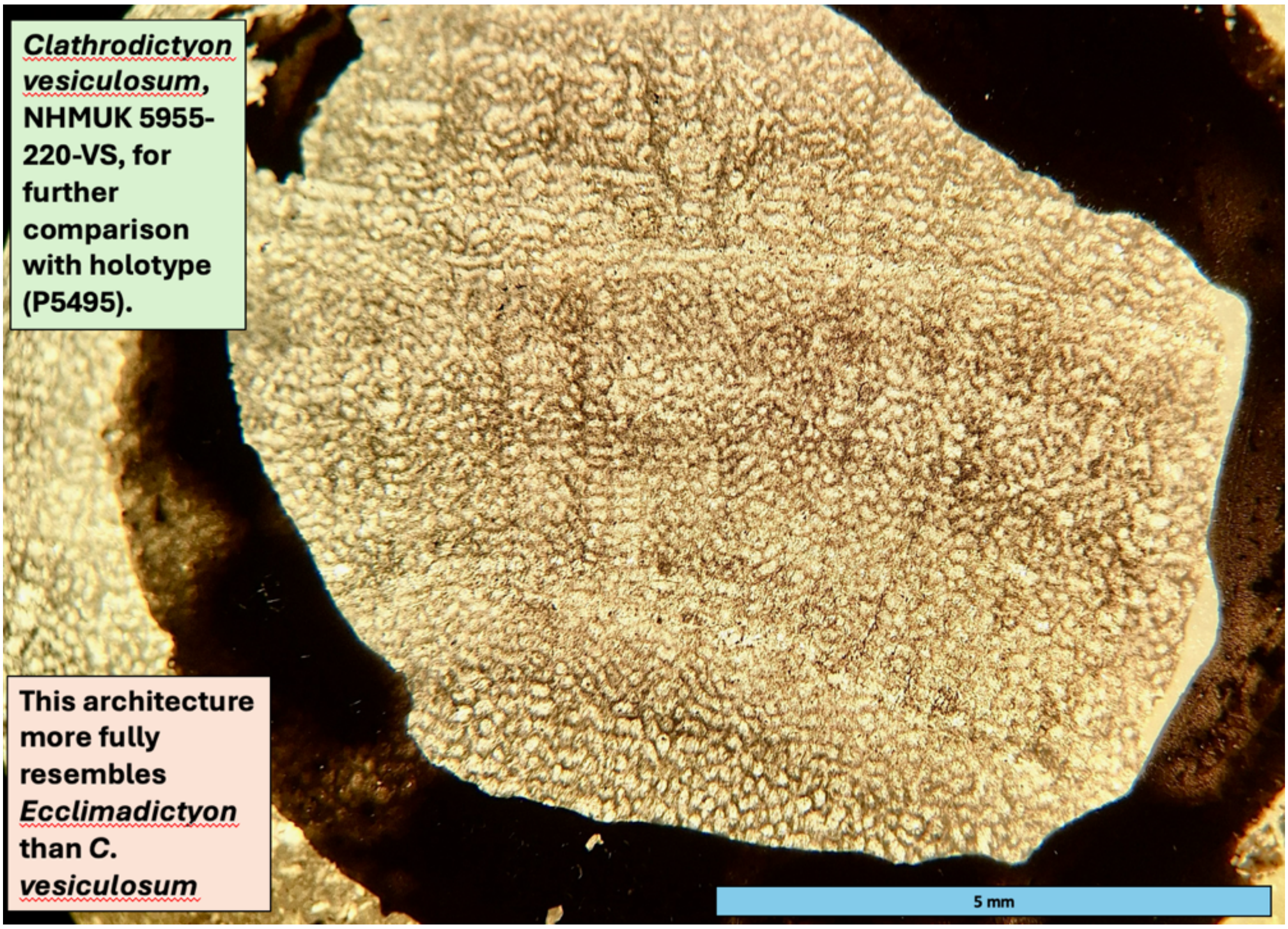


Fig. 4.6.2. Enlargement of *C. vesiculosum* VS illustrating variation of skeletal structure in bands. How much of this view conforms with the definition of *Clathrodictyon*? Answer [spoiler alert]: not so much 😩. Formal specimen number is NHMUK PI P5755-220.

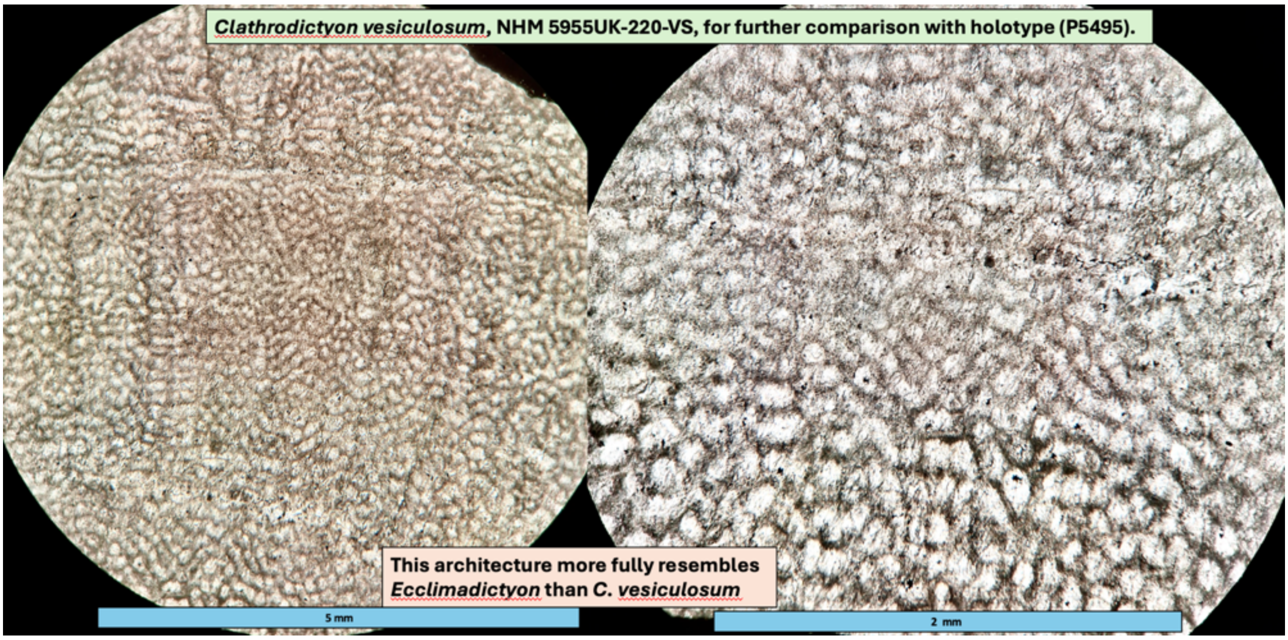


Fig. 4.6.3. Details of *C. vesiculosum* VS, **Fig. 4.6.2,** showing variation of skeletal structure across bands. The right-hand image shows reduced spacing between elements in the central region of the specimen, reflecting likely growth variation in the organism's life. Formal specimen number is NHMUK PI P5755-220.

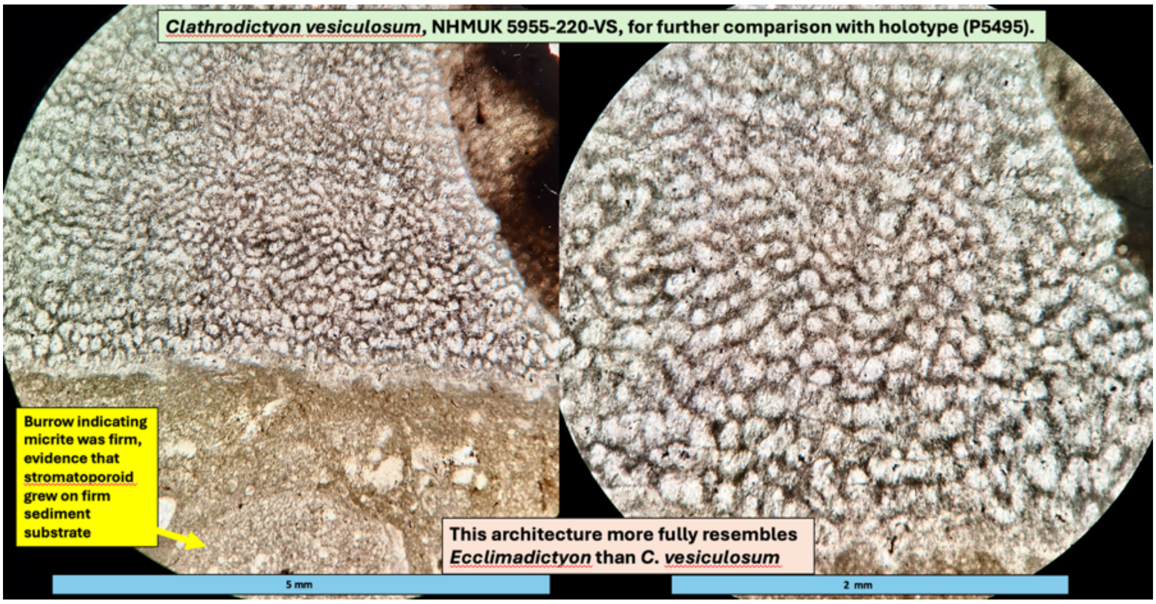


Fig. 4.6.4. Enlargement of lower left part of Fig. 4.6.1, *C. vesiculosum* VS, showing lack of continuous laminae. At the base of the specimen (on the left), sediment with a sharp-edged burrow provides evidence of firm substrate on which the stromatoporoid grew on. Formal specimen number is NHMUK PI P5755-220.

4.7. NHMUK PI P5970-241 – Clathrodictyon fastigiatum

Sample of *Clathrodictyon fastigiatum* from the Nicholson Collection, which was reclassed by Nestor (2015) as *Ecclimadictyon*. However, note in the following figures that there is overlap with *C. vesiculosum*. This specimen also exhibits prominent structural variation in bands, suggesting the influence of external growth controls on the arrangement of the skeletal elements, producing phases of growth. Although the causes of these structural changes have never been identified in stromatoporoids, they are of considerable importance in the development of a taxonomic definition of the fossil.

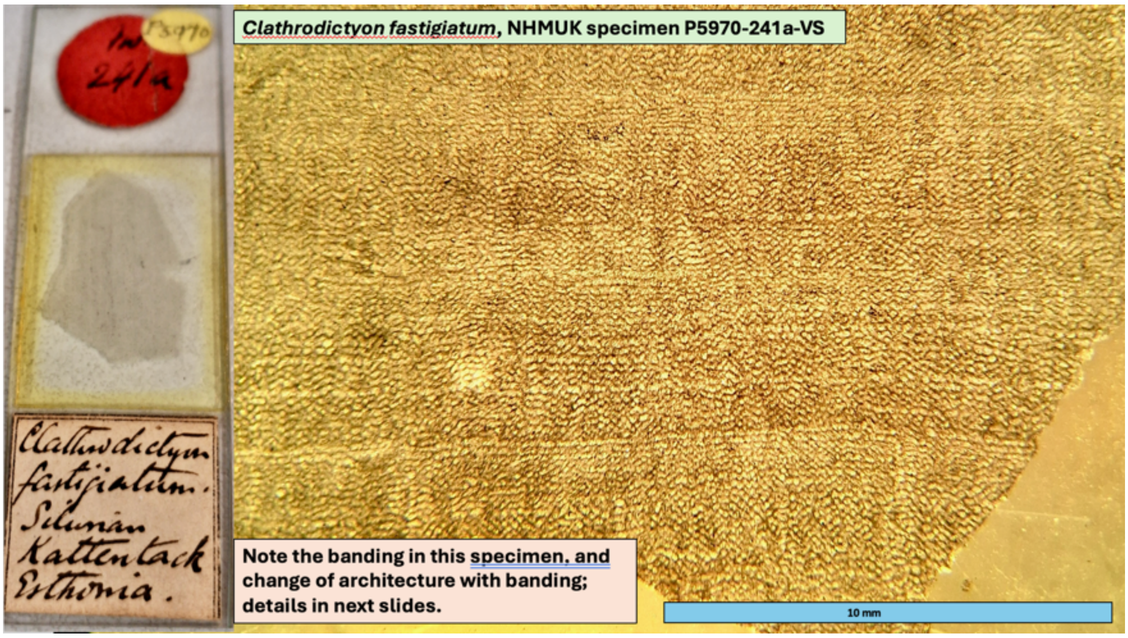


Fig. 4.7.1. General view of *Clathrodictyon fastigiatum* VS showing apparent continuous laminae, and prominent variations in bands. Formal specimen number is NHMUK PI P5970-241a.

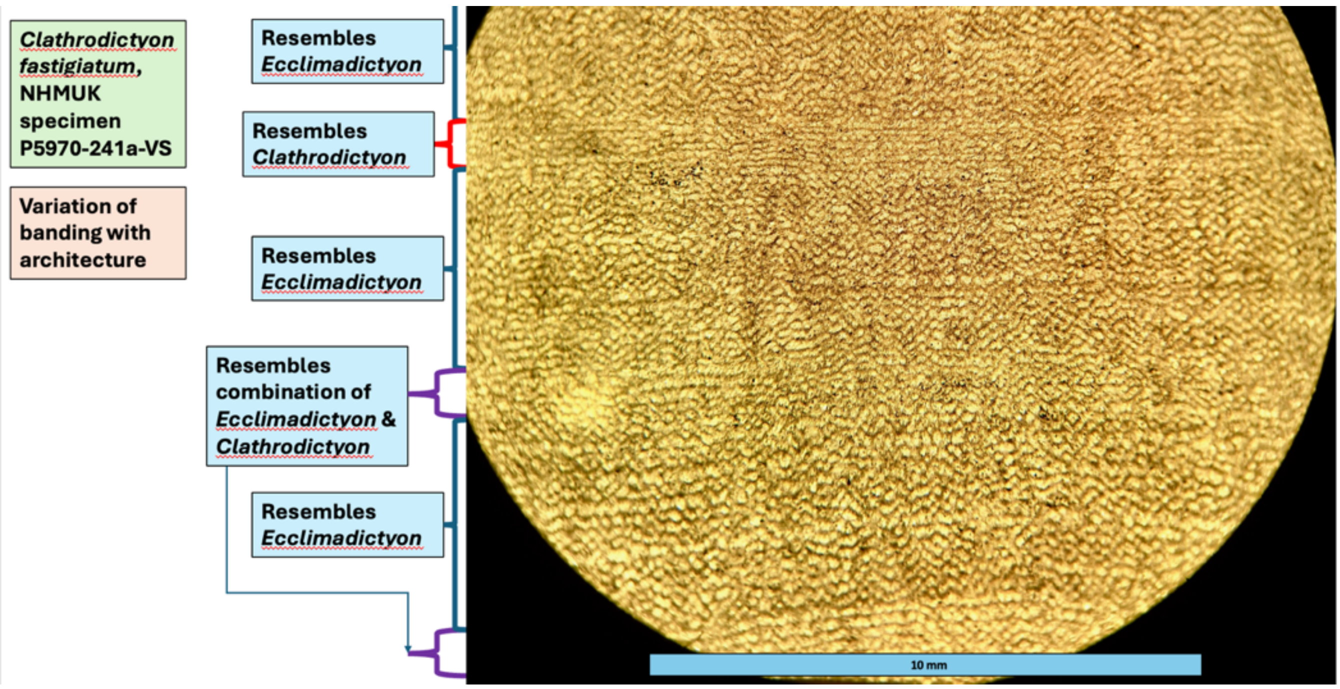


Fig. 4.7.2. Enlargement of *Clathrodictyon fastigiatum* VS, **Fig. 4.7.1.** showing apparent continuous laminae, and prominent variations in bands. Annotations on the left of the image highlight interpretive comparisons between to *C. vesiculosum* and *C. fastigiatum*. Formal specimen number is NHMUK PI P5970-241a.

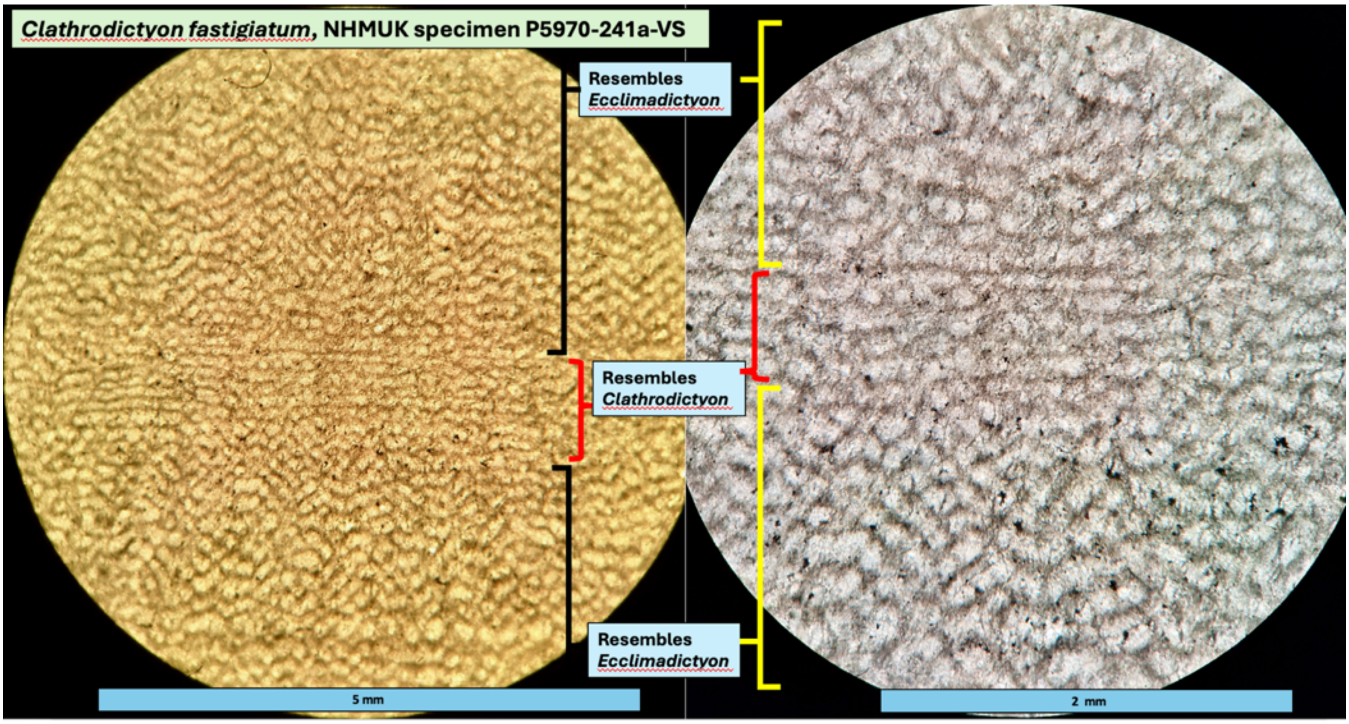


Fig. 4.7.3. Detail of *Clathrodictyon fastigiatum* VS, **Fig. 4.7.2**, showing continuous laminae in the middle of the images, consistent with *Clathrodictyon vesiculosum*, but the upper and lower parts are more consistent with *Ecclimadictyon.* Formal specimen number is NHMUK PI P5970-241a.

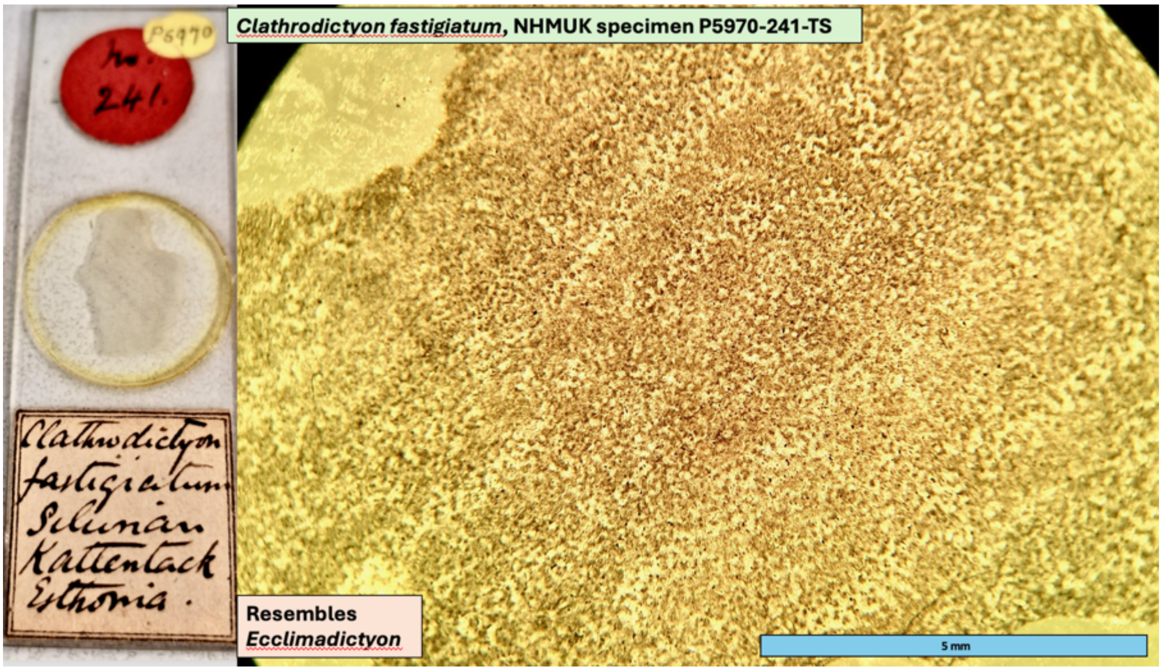


Fig. 4.7.4. General view of *Clathrodictyon fastigiatum* TS. Note similarity with TS views of *C. vesiculosum* in other figures in the atlas. Formal specimen number is NHMUK PI P5970-241.

4.8. NHMUK PI P5493-240 – Clathrodictyon fastigiatum

This specimen of *Clathrodictyon fastigiatum* is notable because its structural variability, displaying features reminiscent of *Camptodictyon* in some areas, and *Ecclimadictyon* in others, as shown in the following figures.

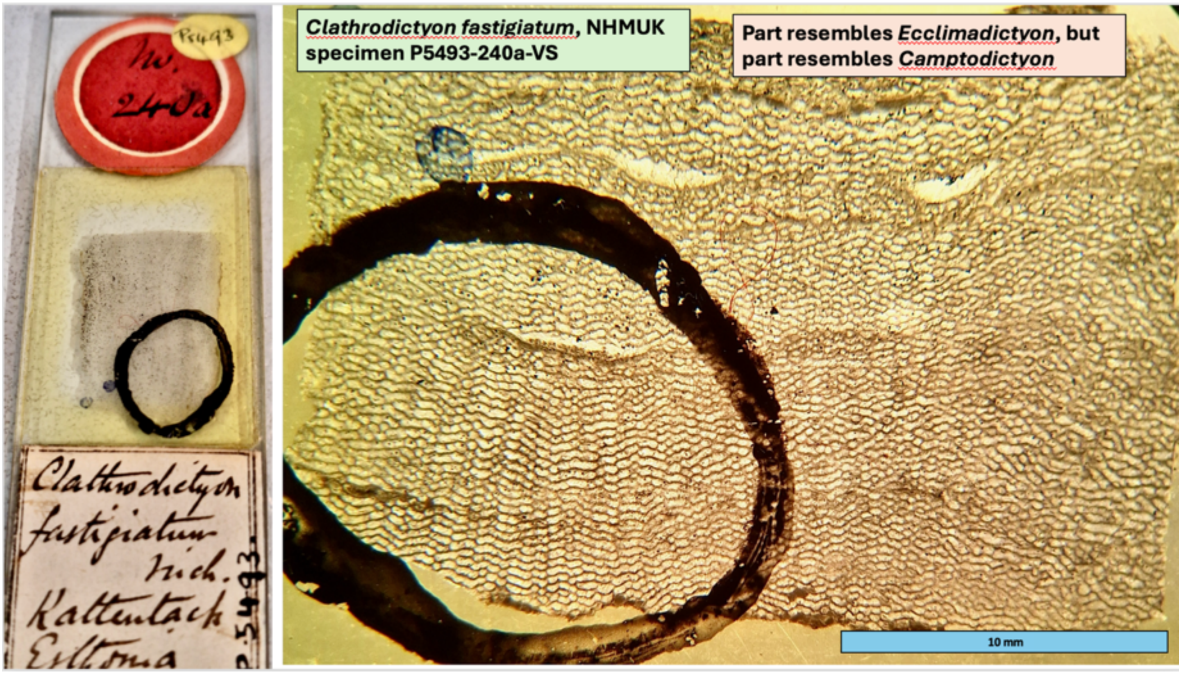


Fig. 4.8.1. General view of *Clathrodictyon fastigiatum* VS. Note similarity of its skeletal structure to *Camptodictyon*, inside the black circle. Within the same area, on the upper part, there is an elongate geopetal cavity partially filled with sediment, indicating a growth interruption event at that level in the history of the sample. Another growth interruption is shown higher up outside the black circle, as three elongate spar-filled cavities (look like spooky eyes watching you). In this upper area, the skeleton has an *Ecclimadictyon* resemblance. Formal specimen number is NHMUK PI P5493-240a.

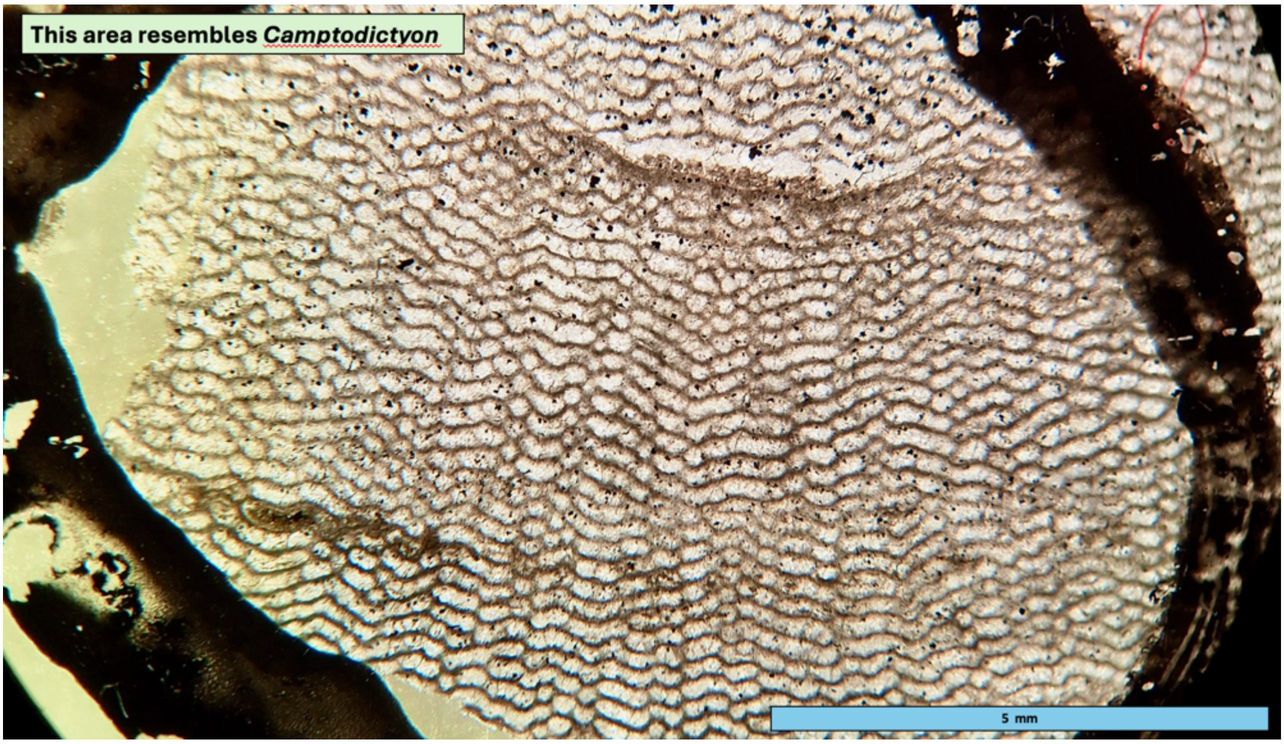


Fig. 4.8.2. Enlargement of black circle area of *Clathrodictyon fastigiatum* VS, **Fig. 4.8.1.,** providing more clarity of similarity to *Camptodictyon*. Note there is yet another minor growth interruption event marked by a thin dark line of sediment in the skeleton, near the bottom of the image. Formal specimen number is NHMUK PI P5493-240a.

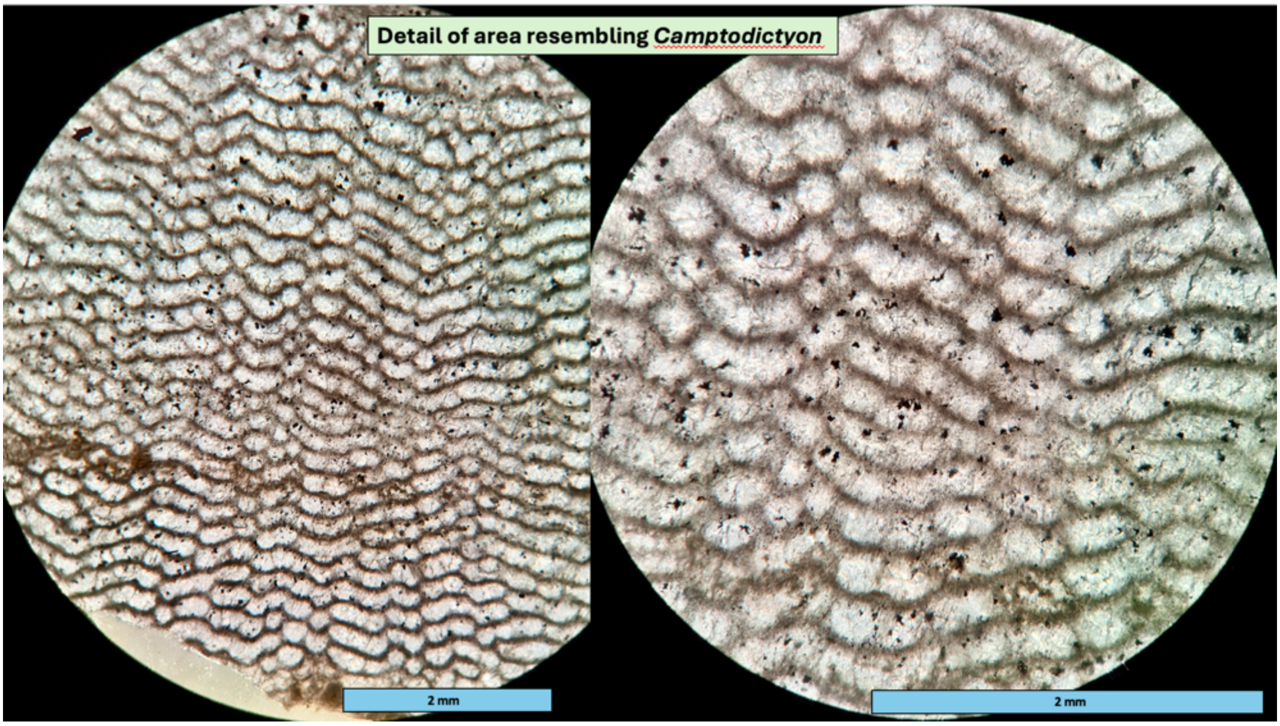


Fig. 4.8.3. Additional detail of the area inside the black circle, **Fig. 4.8.2,** *Clathrodictyon fastigiatum* VS, showing more clarity of similarity to *Camptodictyon*. Formal specimen number is NHMUK PI P5493-240a.

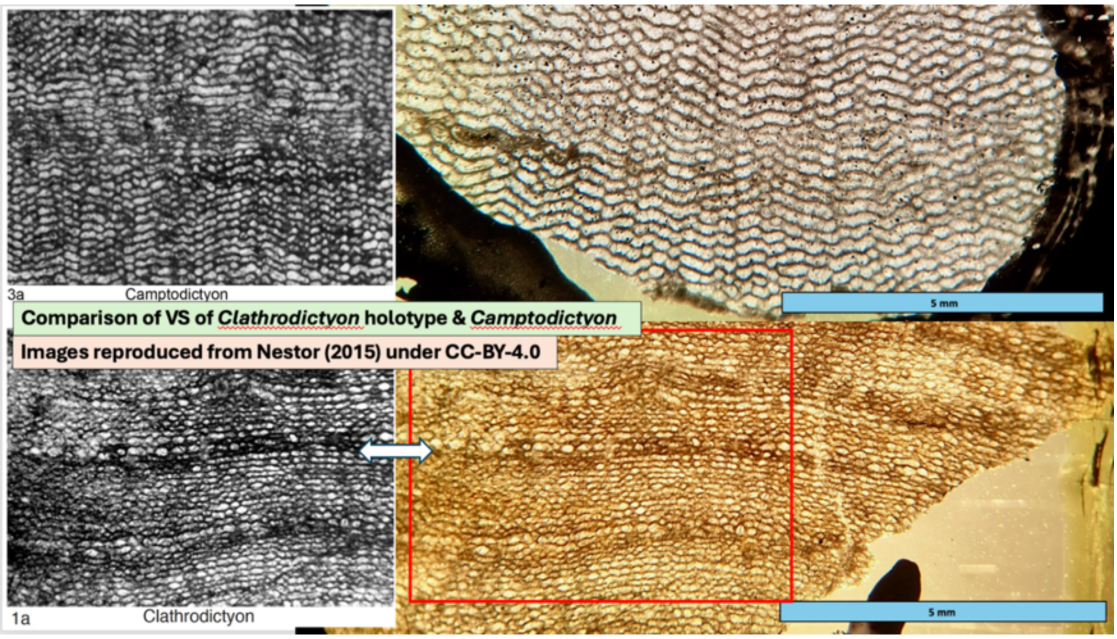


Fig. 4.8.4. Comparative images showing the VS thin sections of *Camptodictyon* and *Clathrodictyon*, both from Nestor (2015, reproduced here under the CC-BY-4.0 licence). These images highlight the contrast between the two holotypes, as well as between the two NHMUK specimens (lower one is the holotype of *Clathrodictyon*, noting that this picture is only part of the entire holotype specimen, and does not reveal its variation, as illustrated and discussed previously).

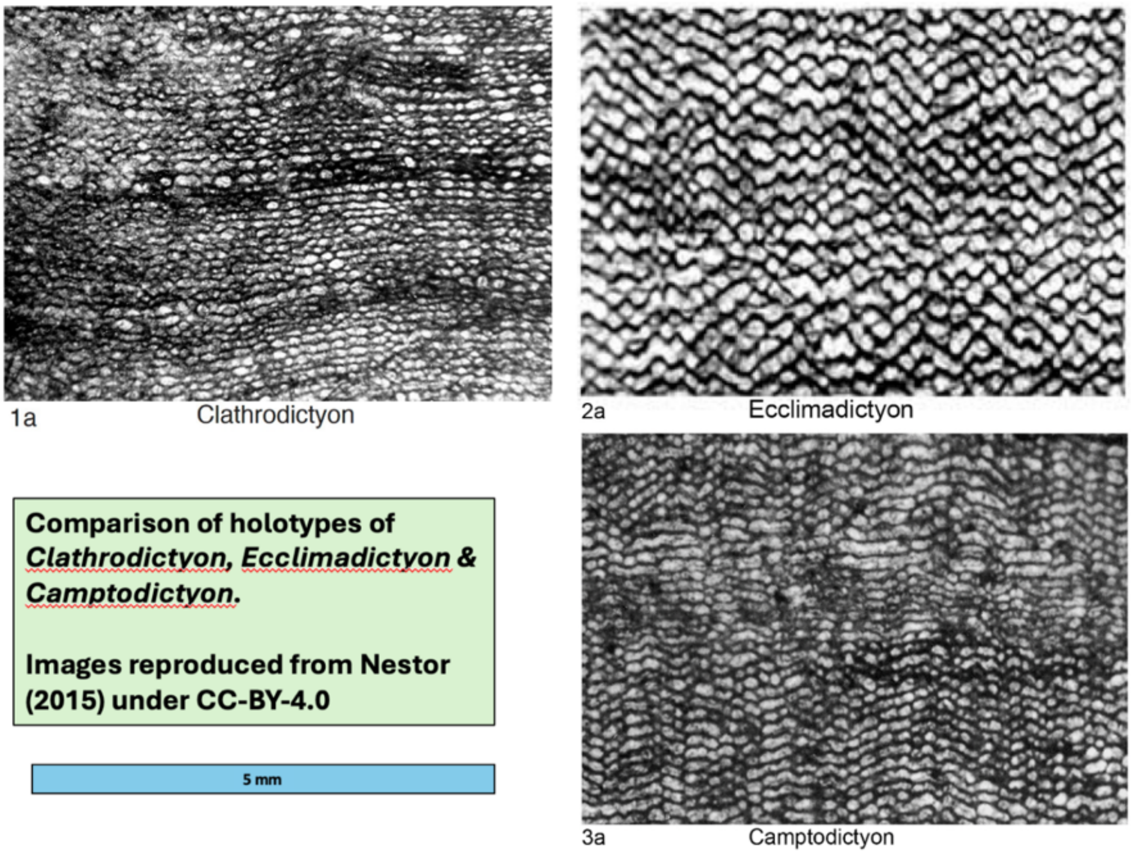


Fig. 4.8.5. Comparative images showing VS views of the *Clathrodictyon*, *Ecclimadictyon* and *Camptodictyon* holotypes, from Nestor (2015, reproduced here under the CC-BY-4.0 licence). These images show the contrast between the three genera as defined in the 2015 *Treatise*, but note that even within the holotype picture of *Camptodictyon* are areas resembling *Clathrodictyon* (centre) and *Ecclimadictyon* (top and lower right).

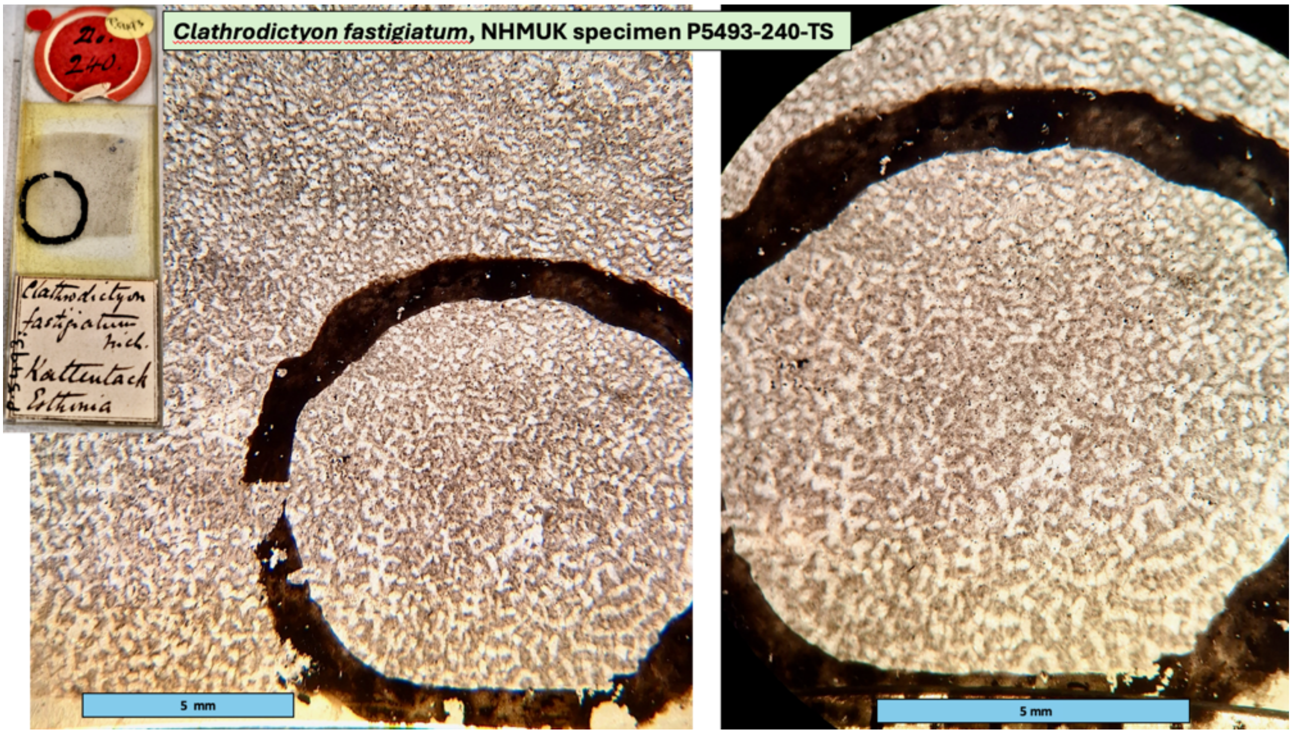


Fig. 4.8.6. TS view of *Clathrodictyon fastigiatum*. Formal specimen number is NHMUK PI P5493-240.

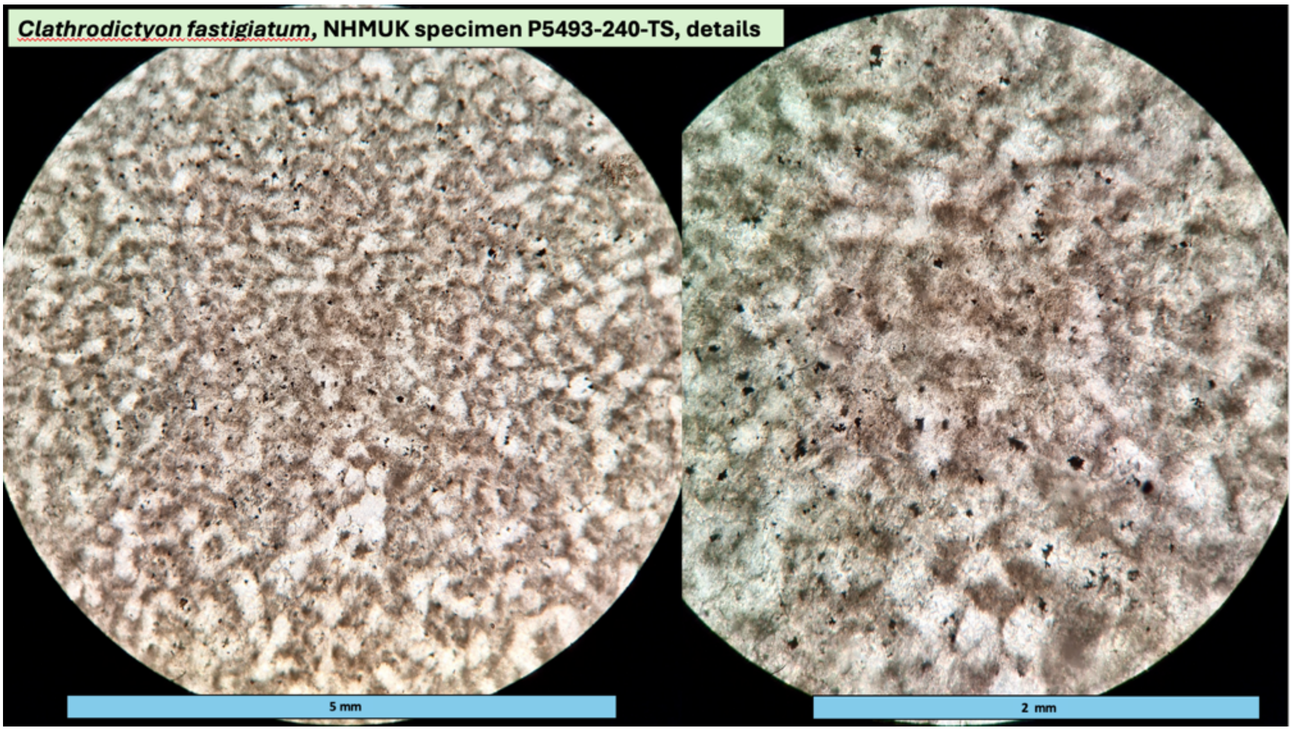


Fig. 4.8.7. Details of *Clathrodictyon fastigiatum* TS view, **Fig. 4.8.6**., highlighting finer aspects of skeletal structure. Formal specimen number is NHMUK PI P5493-240.

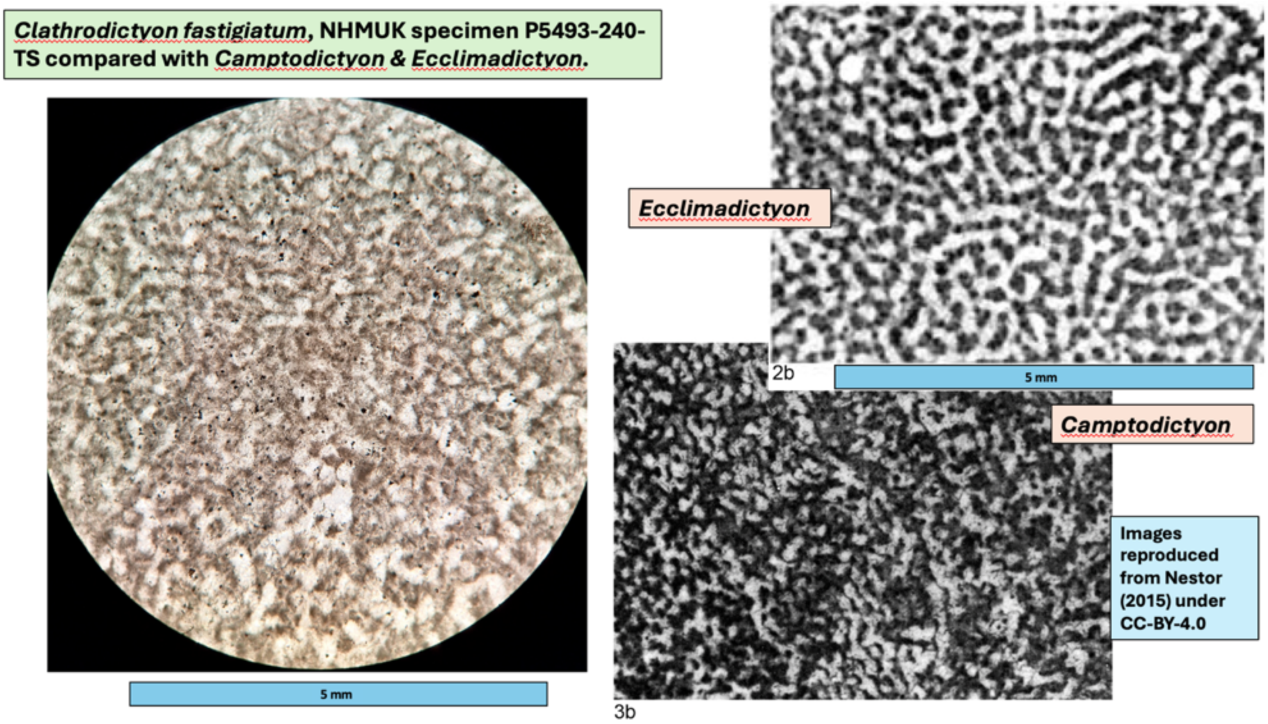


Fig. 4.8.8. Comparison of *Clathrodictyon fastigiatum* TS view with TS views of *Ecclimadictyon* and *Camptodictyon* holotypes (reproduced from Nestor, 2015, under CC-BY-4.0 licence). The TS of the specimen NHMUK PI P5493-240 more closely resembles the holotype of *Camptodictyon.*

4.9. WN15-39 – Ecclimadictyon macrotuberculatum

In this section is illustrated one of the specimens from Kershaw et al. (2021) identified by them as *Ecclimadictyon macrotuberculatum*. It is from the Much Wenlock Limestone Formation, Silurian; Wren's Nest locality, West Midlands, England.

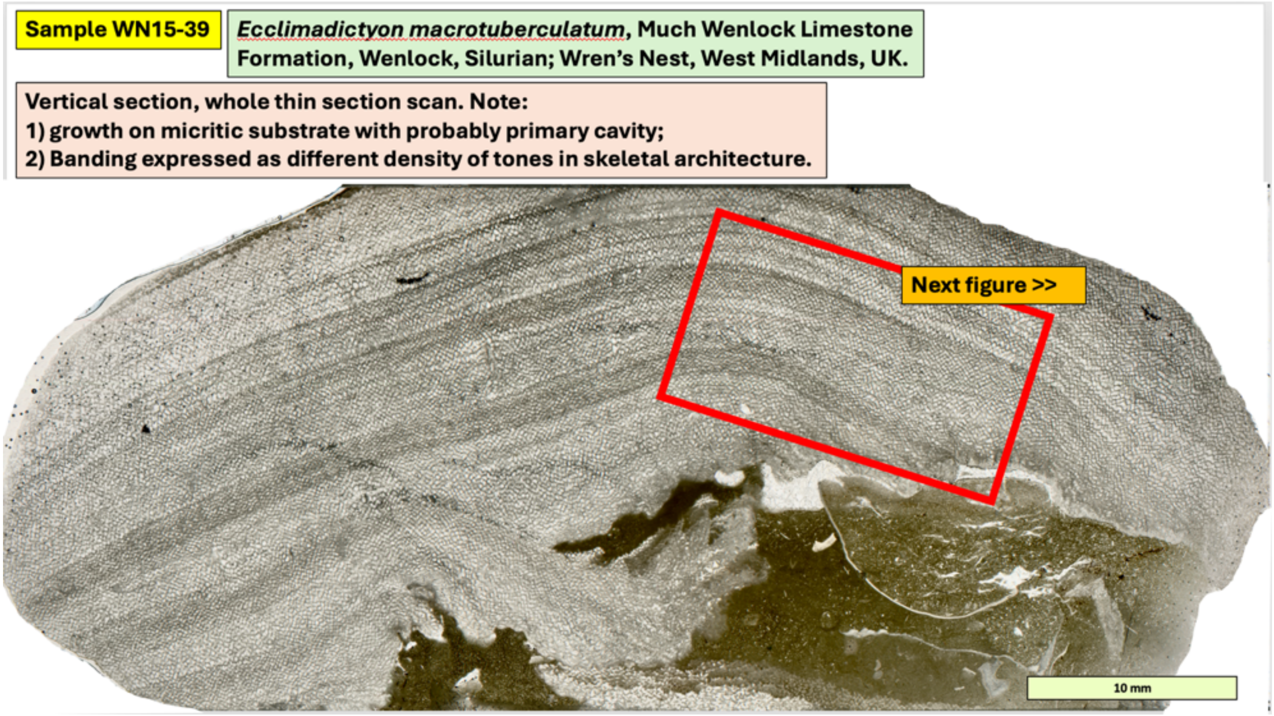


Fig. 4.9.1. Whole thin section view of *Ecclimadictyon* VS. It displays the central region of the specimen, but its margins broke off and were not collected due to cementation within the surrounding rock. The specimen shows the common occurrence of a complex basal region in stromatoporoids; seemingly it grew on a sediment surface but part of it has a geopetal cavity, potentially indicating an original basal cavity. At least two growth interruption events in the lower centre are visible, but pass laterally to the left into uninterrupted skeleton, a common feature in stromatoporoids. This lateral variation may indicate that stromatoporoids had an efficient sediment-removal mechanism (also known in modern sponges). Banding in the remaining part of the thin section may indicate sediment-driven growth interruption events that left no evidence, and emphasises the need for marginal areas to investigate whether sediment may be the cause of growth interruption. The following figures show details of this banding variation that may have been caused by sedimentation which was subsequently removed by the recovering sponge surface. Specimen WN15-39, a counterpart of which is deposited in the Sedgwick Museum, Cambridge; the sample illustrated here is from SK's personal collection.

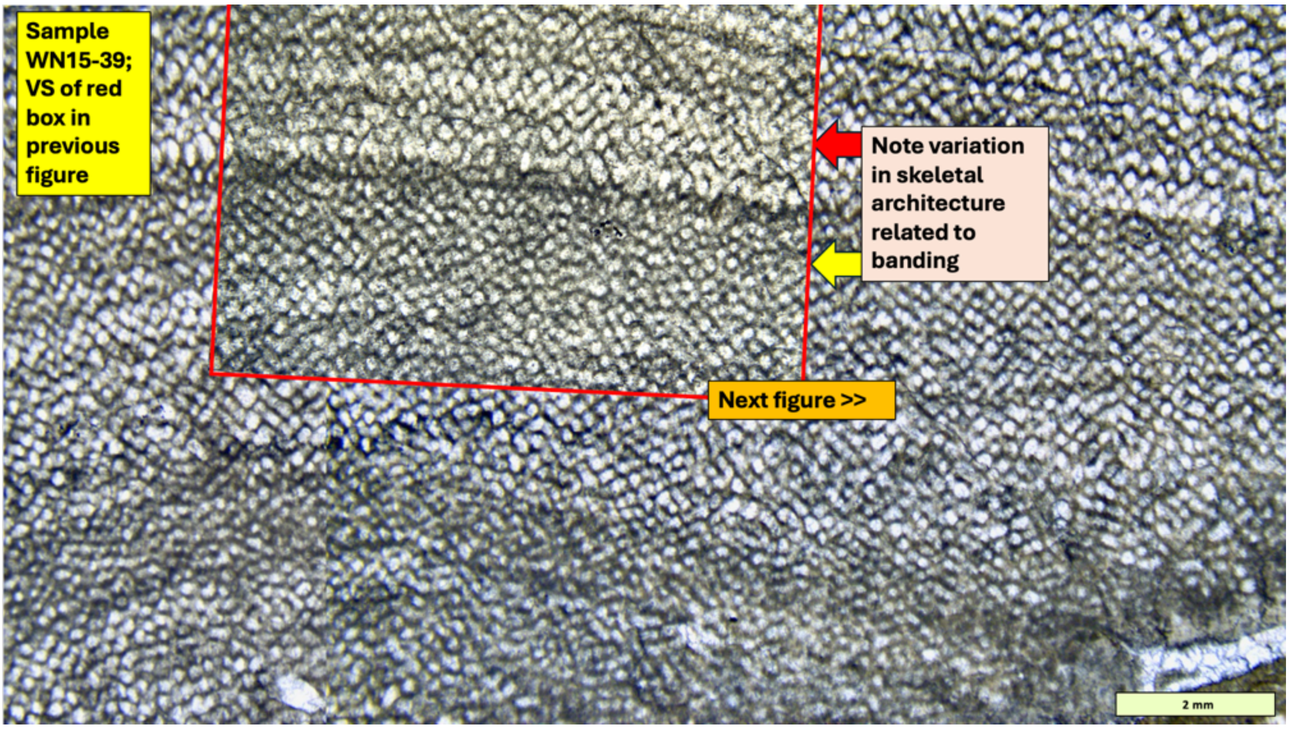


Fig. 4.9.2. (If you have not already done so, please first read caption of Fig. 4.9.1 that is relevant to this figure.). Enlargement of Fig. 4.9.1 showing VS of *Ecclimadictyon.* Banding within the skeletal elements is clearly visible, as is variation in the spacing between these elements, which correlate with the banding pattern. Compare the closely-spaced lamination above the bottom of the image (about ¼ of the distance up the picture) with the widely-spaced banding near the top of the image, that is about twice the spacing of the lower area. This variation in skeletal element arrangement in banding indicates change in the growth attributes of the sponge. There is no indication of the controls on these changes, whether they are due to external forces (e.g. sedimentation, nutrient supply) or related to internal biological processes within the sponge. Regardless of the cause, these changes occurred within the lifespan of one organism, so the taxonomy does not change with the skeletal variations. Specimen WN15-39, a counterpart of which is deposited in the Sedgwick Museum, Cambridge.

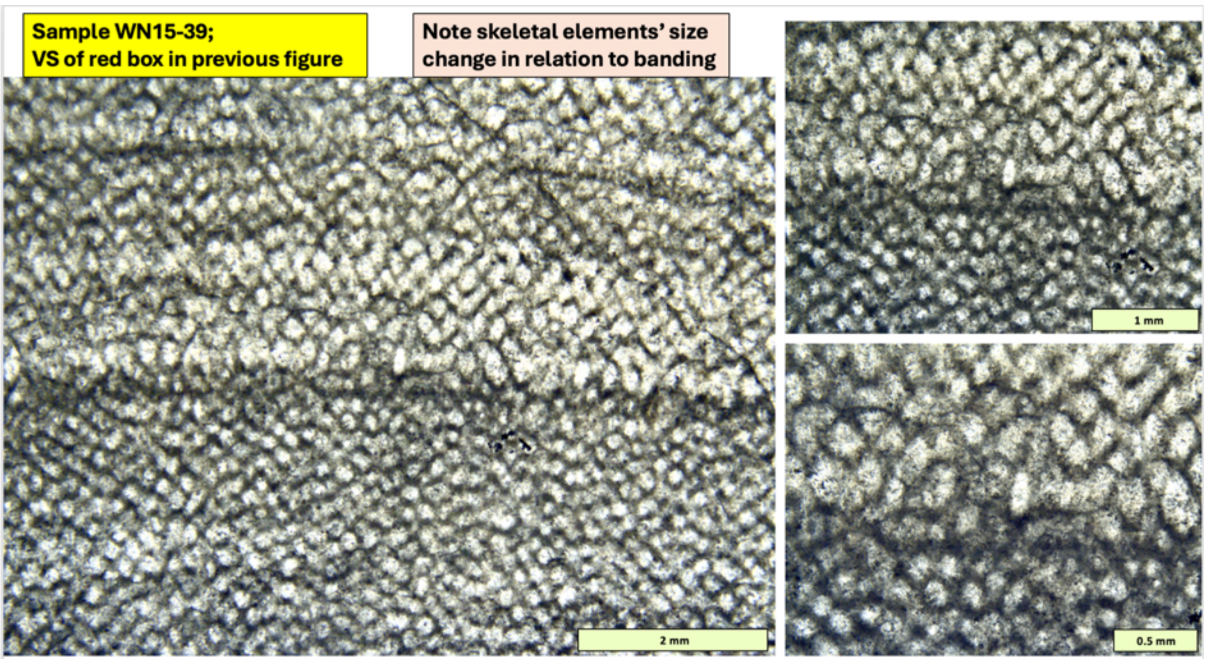


Fig. 4.9.3. Left-hand image is enlargement of red box in Fig. 4.9.2, and the two right-hand images are further enlargements, emphasising change in spacing of skeletal elements, related to the

banding in the stromatoporoid, reflecting growth-related variation. Specimen WN15-39, a counterpart of which is deposited in the Sedgwick Museum, Cambridge.

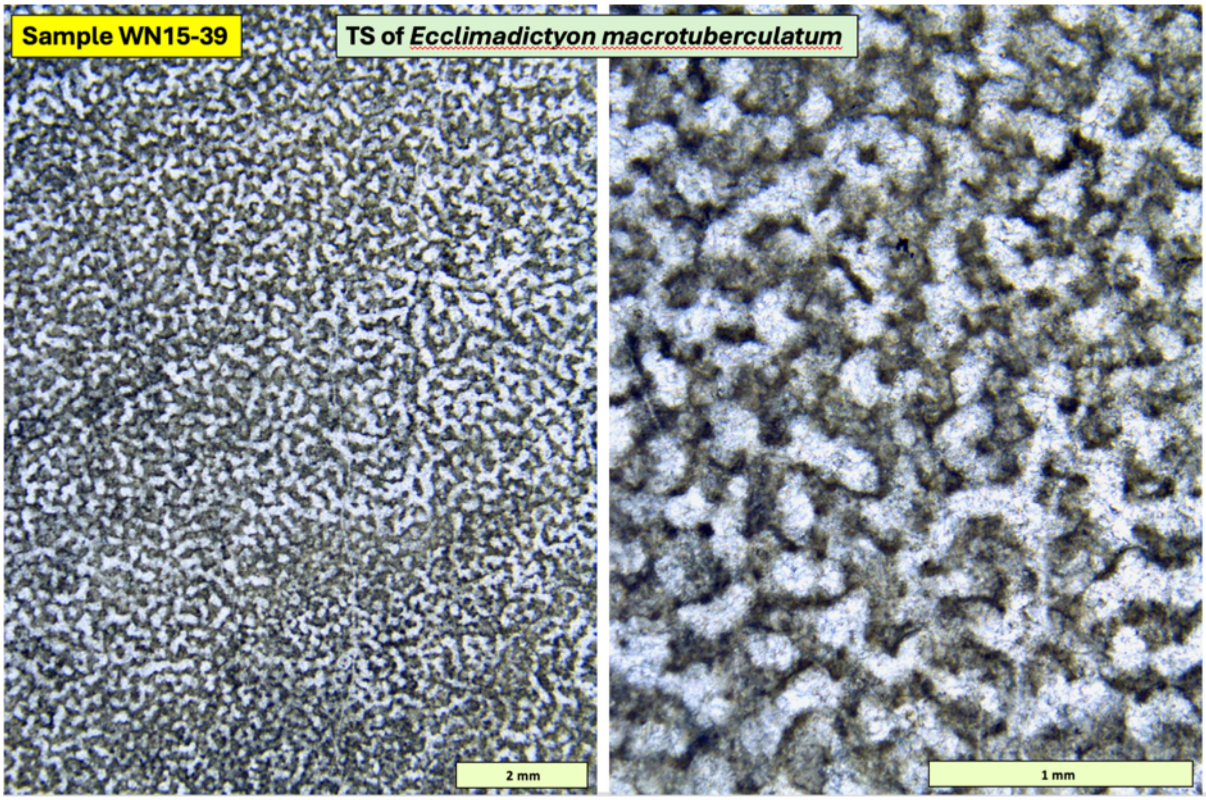


Fig. 4.9.4. TS views of sample WN15-39, identified in Kershaw et al. (2021) as *Ecclimadictyon macrotuberculatum*. Specimen WN15-39, a counterpart of which is deposited in the Sedgwick Museum, Cambridge.

4.10. LSM11-01-part 1 – Ecclimadictyon macrotuberculatum

The following series of figures in parts 1-3 show the specimen LSM11-01, which was used by Kershaw et al. (2021) to illustrate this taxon. This is an interesting and controversial sample, as you will see if you carefully study the following images. This section (LSM11-01-part 1) presents images from the thin section used by Kershaw et al. (2021, Plate 8). The other two parts show photographs of additional thin sections made from the same specimen, providing a more complete view of its structural variation.

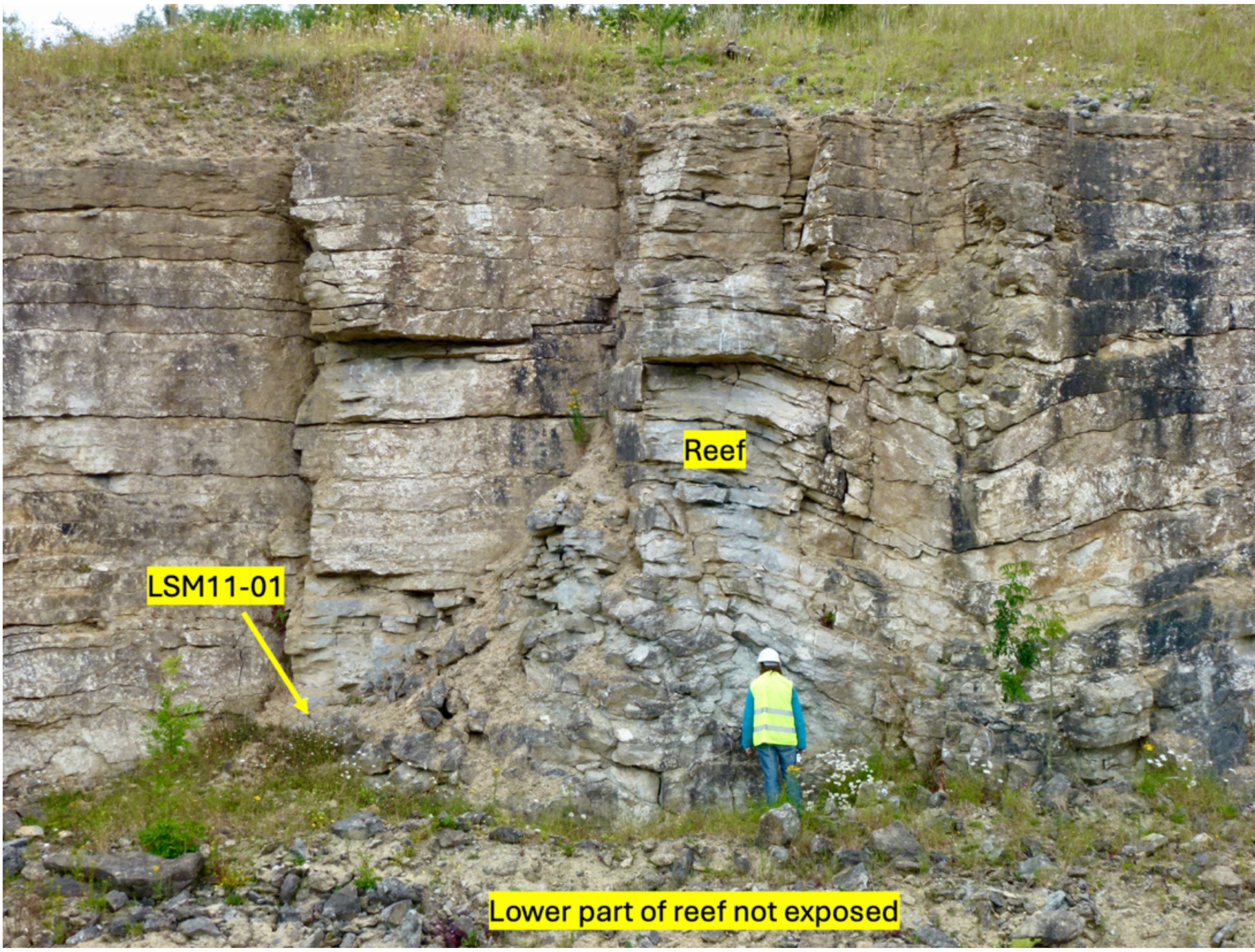


Fig. 4.10.1. Field view of reef in Lea Quarry South, Wenlock Edge, Shropshire, in England, taken in 2011. Location of sample collected *in situ* in reef flank area, south side of a single reef that cropped out in the middle of the quarry. Sample permissions information is given in Kershaw et al. (2021).

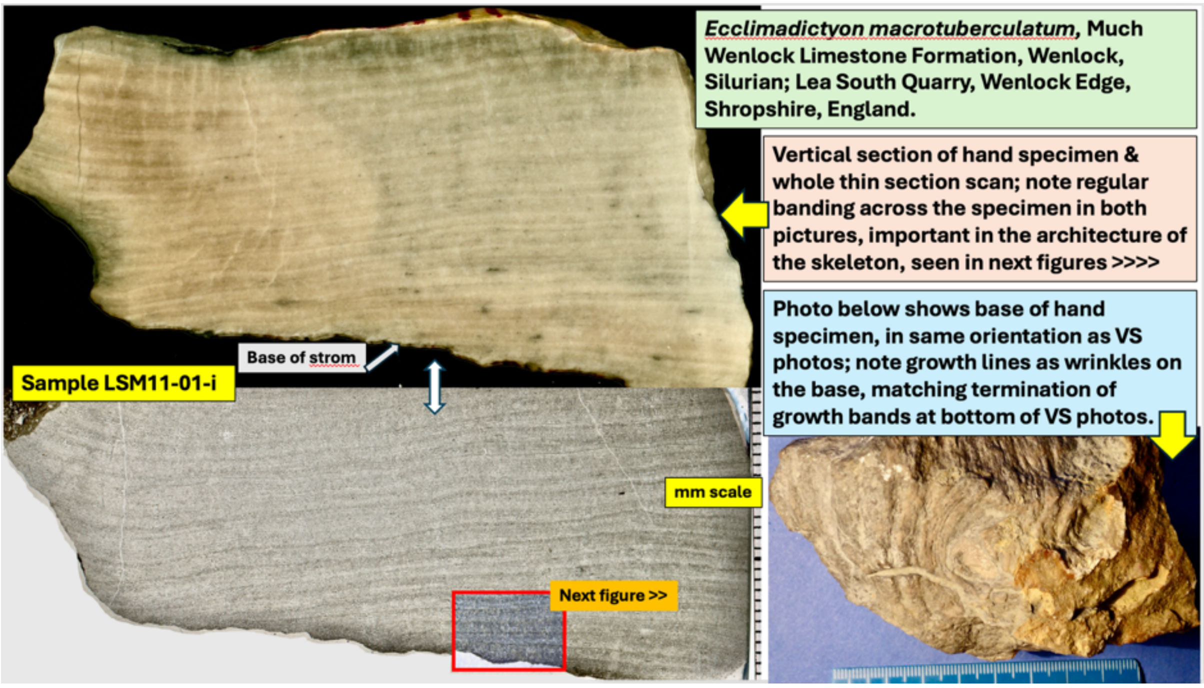


Fig. 4.10.2. Upper left photograph: VS of stromatoporoid cut block LSM11-01. **Lower left photograph:** whole-scan image of a thin section prepared from the block's surface. In both images, the base of the stromatoporoid is present, and it is clear from these pictures that the stromatoporoid grew both vertically and laterally, with an overlapping of laminations towards the left side, indicating directional expansion. **Lower right photograph:** base of the block, showing part of the concentric wrinkles on the base of the stromatoporoid corresponding to the downward inflections in the other two photos. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

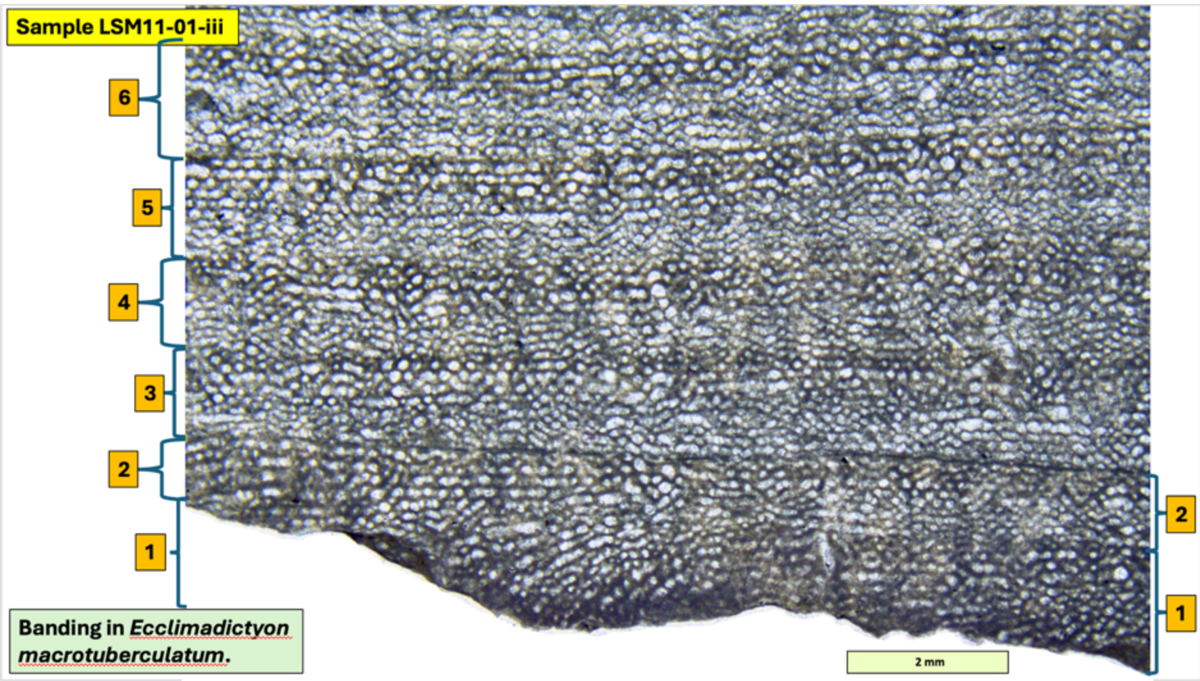


Fig. 4.10.3. VS thin section of LSM11-01-iii. Note the prominent banding that may be due to either external forces or internal processes in the stromatoporoid. Band #1 is the basal band and shows lateral overgrowth from right to left. The remaining bands seem to have developed vertically on the basal band, but presumably also have lateral components; however, these are not determinable because the margins of the stromatoporoid were not collected (compare with Fig. 4.10.2 upper left photo). Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

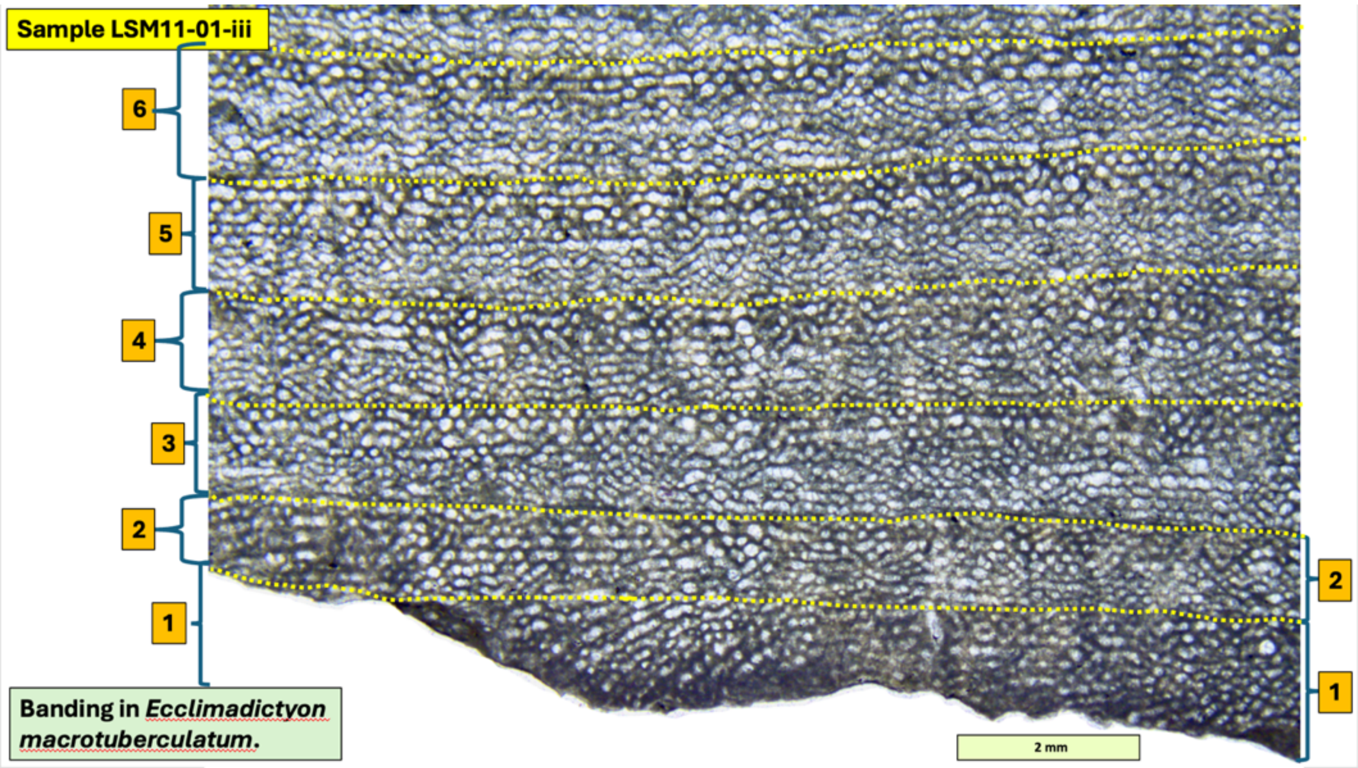


Fig. 4.10.4. VS thin section of LSM11-01-iii. The same as Fig. 4.10.3, with a suggested interpretation of band contacts shown in yellow dotted line, for clarity (but see below at end of this caption). Note that the bands seem to comprise two parts: a lower part with smaller-scale elements, overlain by an upper part with larger-scale elements. The smaller-scale elements show less continuity of laminae than the larger-scale elements, which may impact the taxonomic interpretation of the specimen.

One hypothesis is that the smaller-scale elements represent a recovery phase from a trauma, while the overlying larger-scale elements indicate return to normal growth, with this process repeated in successive bands. Of course, there is no supporting evidence for this interpretation, so other explanations would be likely just as valid; however, clearly this specimen is a single taxon, yet it has elements of *Clathrodictyon* and *Ecclimadictyon* within the same thin section raising questions about taxonomic boundaries.

Another interpretation of the bands is to view the bands as couplets, each consisting of a thinner-element layer followed by a thicker-element layer. Notably, the contact between a thicker-element layer and the overlying thinner-element layer often appears sharper than the basal contact of the thicker-element layer below. This may suggest periodic shifts in growth dynamics, with more abrupt changes occurring at the tops of thicker-element bands, though not all contacts are sharply defined, which complicates any phase-based interpretation (especially for those brave enough to tackle stromatoporoid growth phases😱).

These characteristics reflect that the stromatoporoid, while alive, was responsive to changes/fluctuating conditions, that may be internal to its growth properties or driven by external influences of unknown nature. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

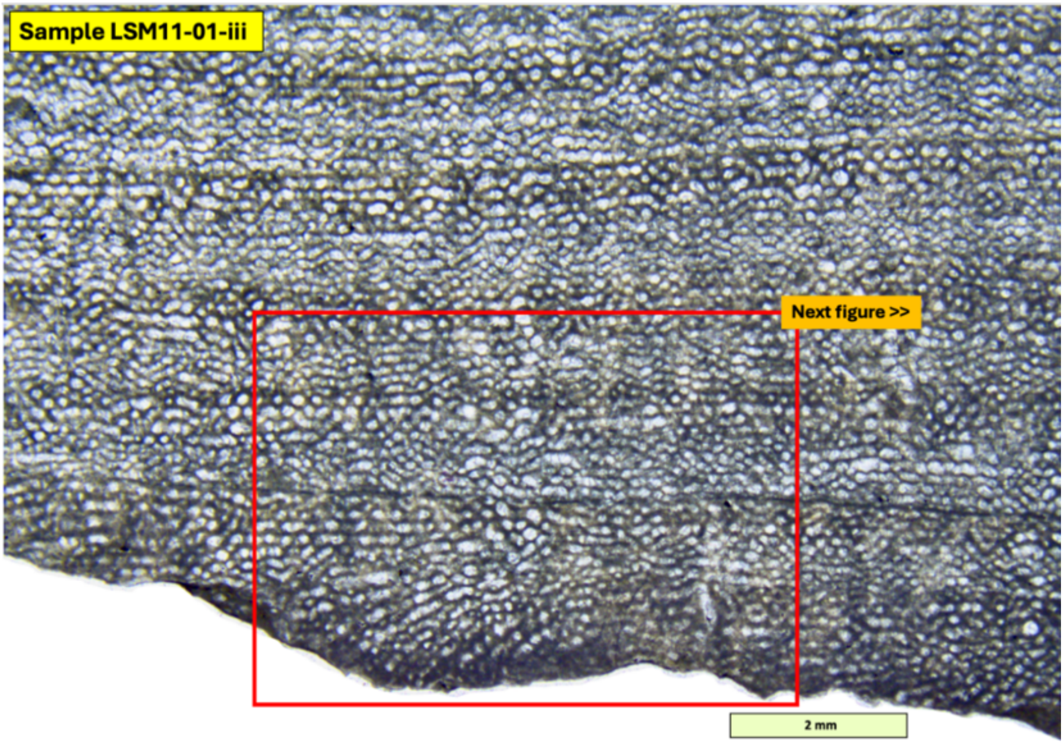


Fig. 4.10.5. The same as Fig. 4.10.3, *Ecclimadictyon macrotuberculatum*, showing location of enlargement in Fig. 4.10.6. Note this image highlights an area of the specimen that is consistent with *Clathrodictyon vesiculosum*, with continuous crumpled laminae, as discussed earlier in this atlas. However, other areas lack the continuous laminae, particularly in the smaller-scale elements in lower parts of bands as seen in Fig. 4.10.4. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

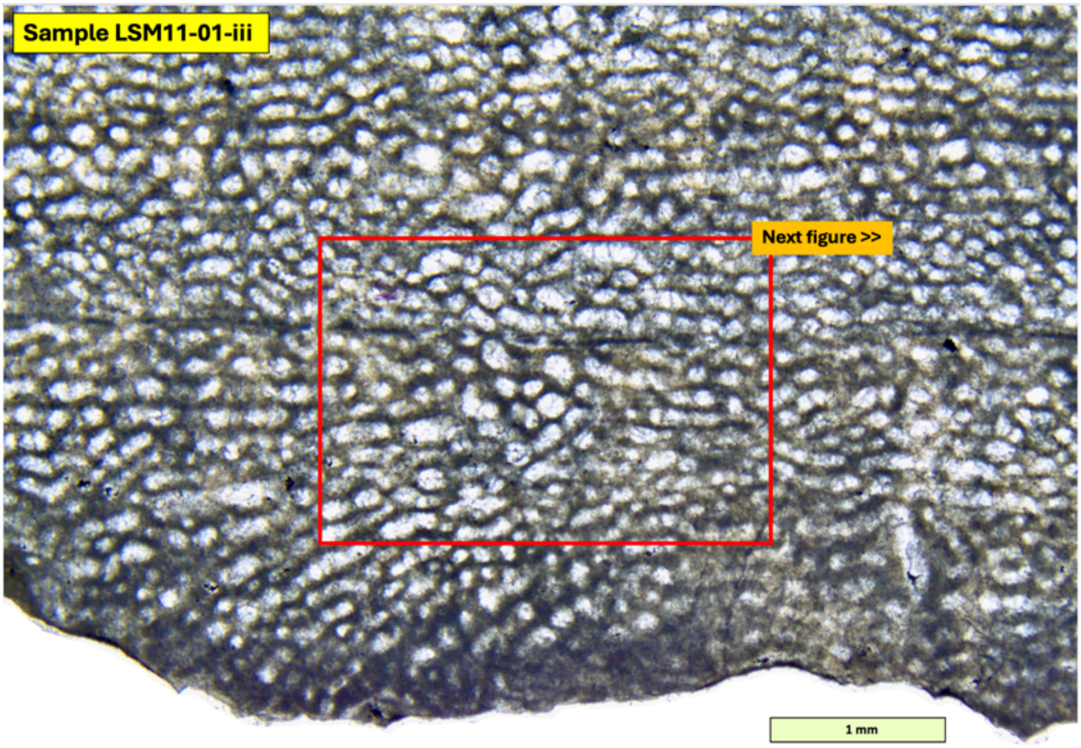


Fig. 4.10.6. VS thin section of LSM11-01-iii, red box in Fig. 4.10.5. This detailed view illustrates the transition in skeletal structure from a *Clathrodictyon*-like fabric, characterized by continuous crumpled laminae, to an *Ecclimadictyon*-like morphology, where laminae are more discontinuous and irregular. The variation within this small area highlights the morphological complexity of the

specimen and further reflects the taxonomic ambiguity observed. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

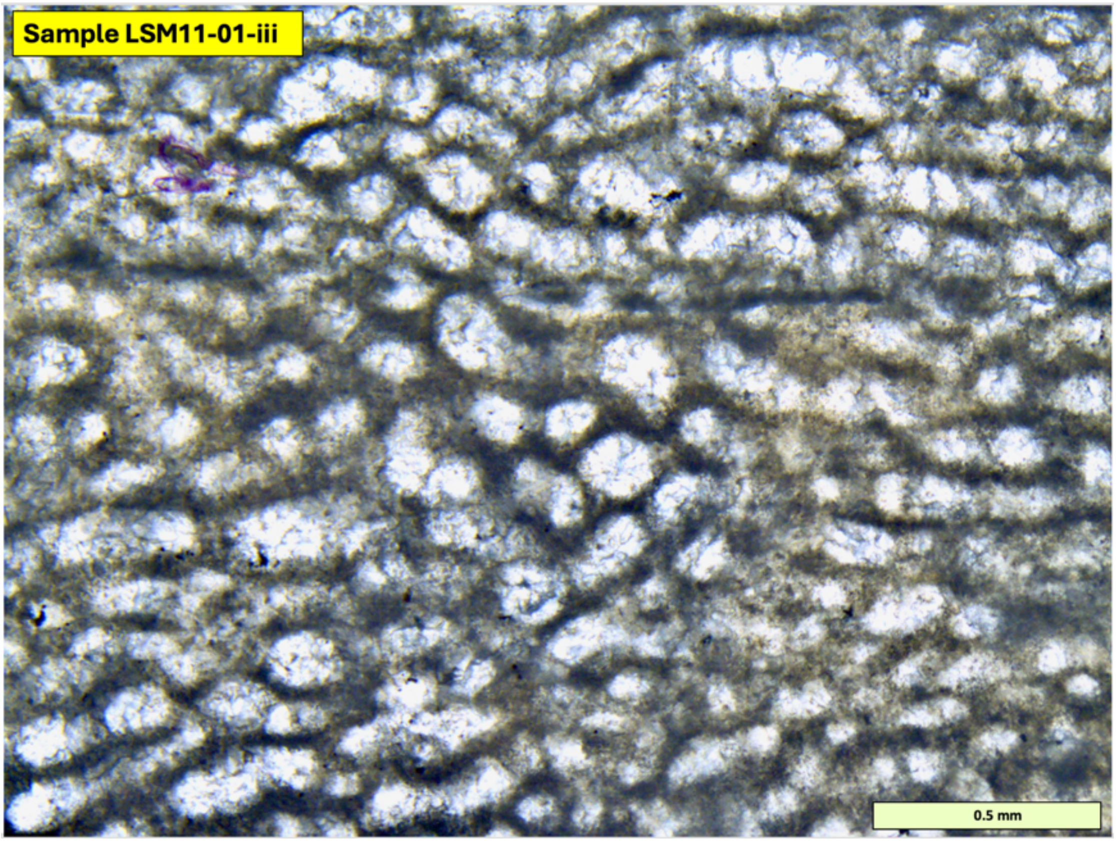


Fig. 4.10.7. Further detail of this specimen in VS, in this area there is limited consistency with the definition of *Clathrodictyon* (continuous crumpled laminae). The lack of laminar coherence in this area further emphasizes the internal variability of the specimen and complicates straightforward taxonomic assignment. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

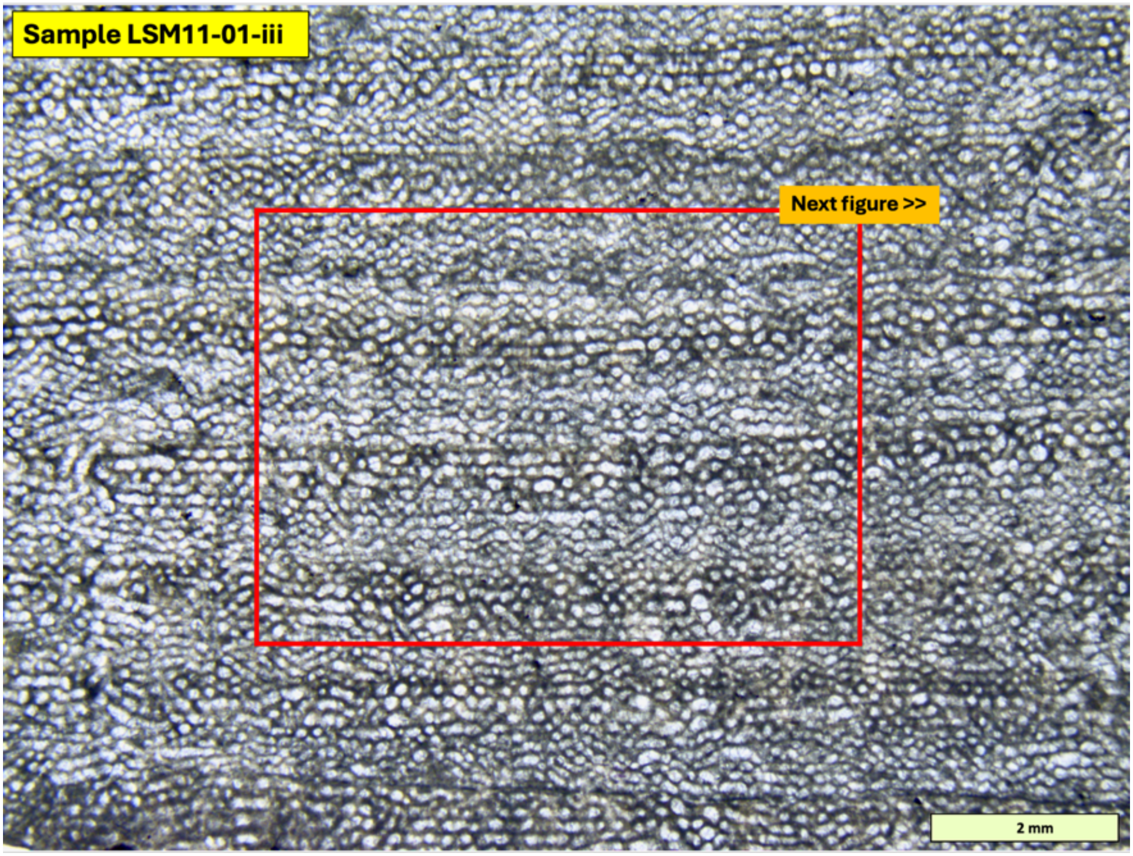


Fig. 4.10.8. VS thin section of LSM11-01-iii, showing a different area of the same thin section as in the previous figures. This image also shows detail of the variation from *Clathrodictyon*-like structure to *Ecclimadictyon*-like structure; there is also a hint of *Camptodictyon*-like structure in some areas. The *Clathrodicyton*-like structure seems to be present predominantly within the darker-toned bands that have thicker elements. This pattern reinforces the observed correlation between structural type and banding characteristics. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

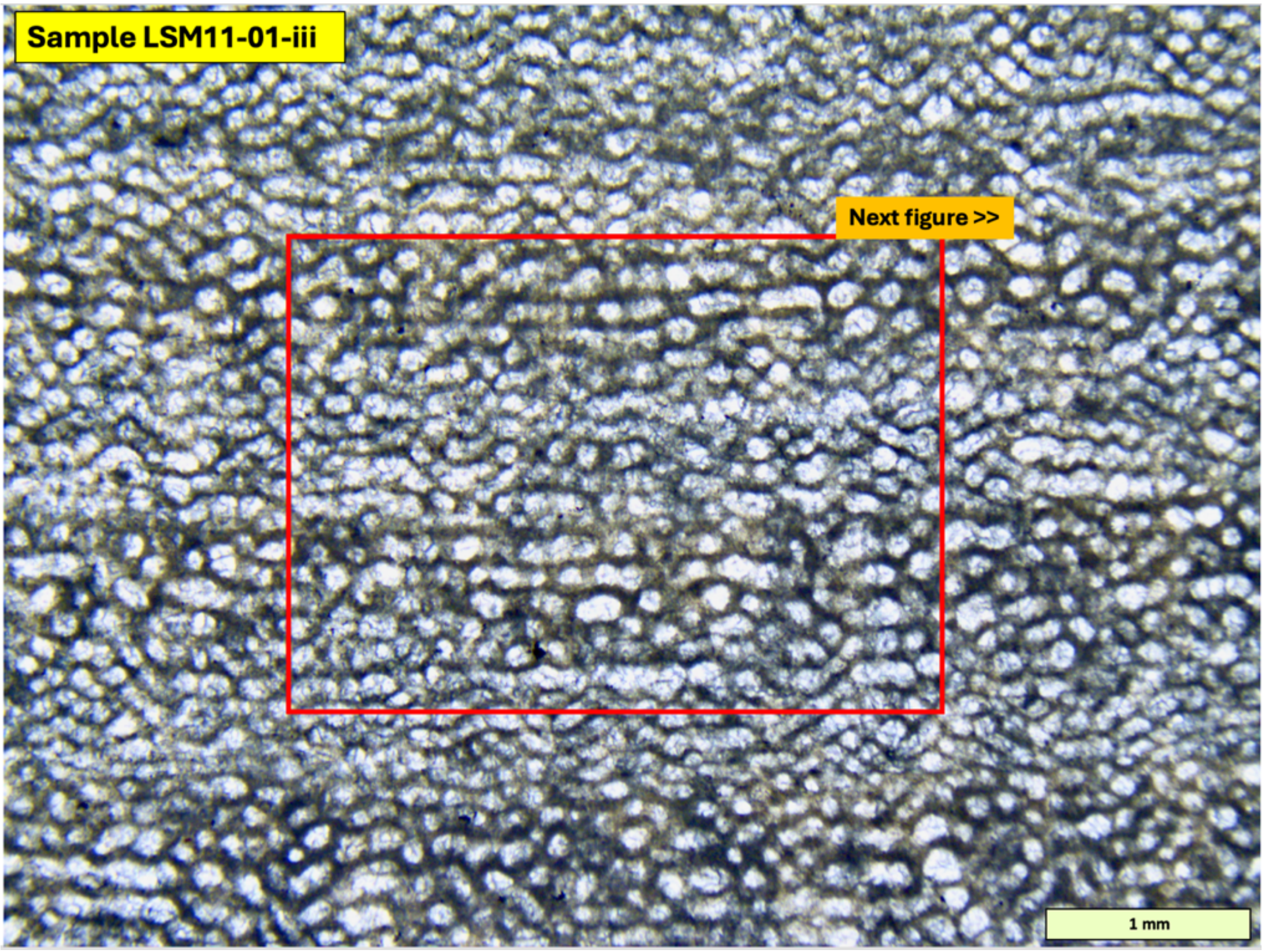


Fig. 4.10.9. Enlargement of red box in Fig. 4.10.8. This close-up view highlights the detailed transition from *Clathrodictyon*-like, characterized by more continuous and crumpled laminae, to a more open, irregular *Ecclimadictyon*-like structure. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

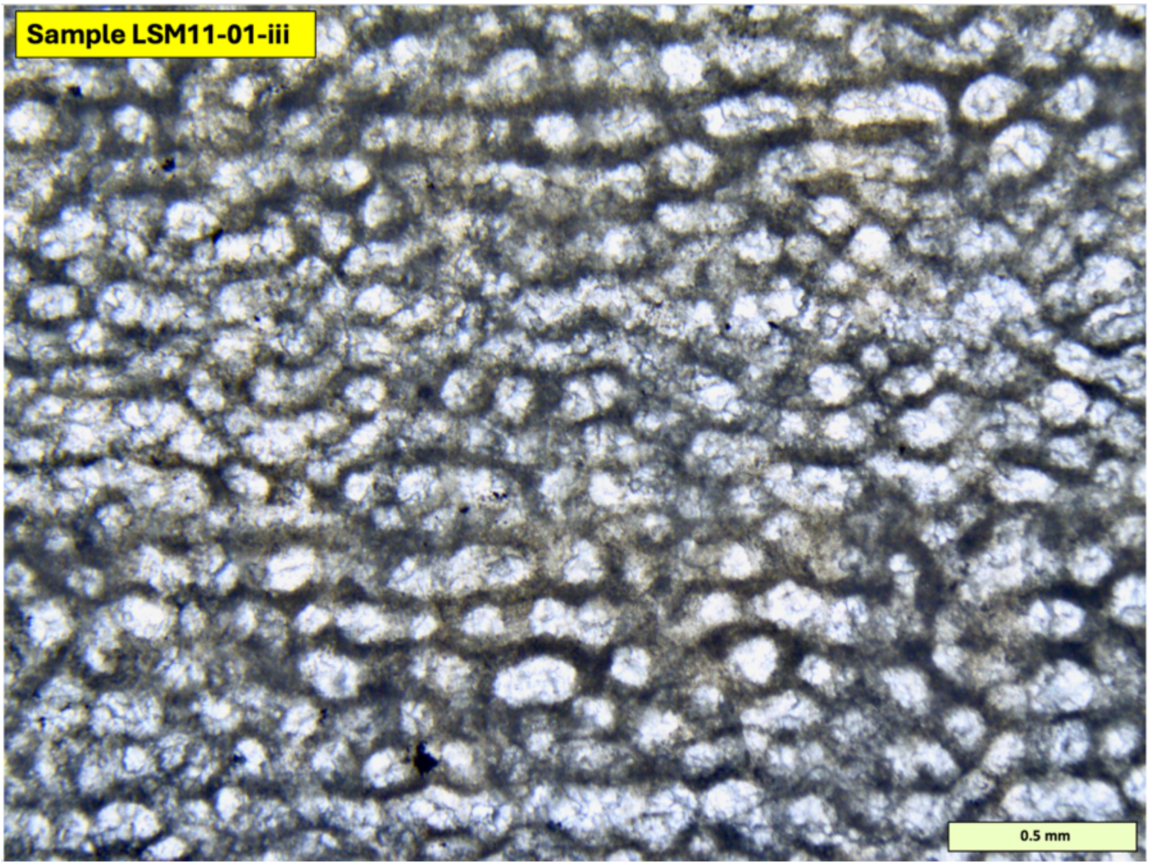


Fig. 4.10.10. Detail from red box in Fig. 4.10.9, emphasising *Clathrodictyon*-like structure in the lower and upper parts of the photo (in the parts that have thicker elements, contrasting the lack of continuous laminae in the middle (thinner elements), that have greater resemblance to *Ecclimadictyon*-like structure. Some questions to ask yourself are: 1) To what extent does the crumpled laminae character of *Clathrodictyon* need to be different from the holotype image in Nestor (2015) before you would accept that it is no longer appropriate to call it *Clathrodictyon*? Would a threshold such as >50% deviation be reasonable?; and: 2) If nearly all of the stromatoporoid had the *Ecclimadictyon*-like structure, then what name would you give it? (presumably the answer would be *Ecclimadicton*). See also the Analysis Section 6 for further discussion. Specimen LSM11-01-iii, Sedgwick Museum, Cambridge.

Fig. 4.10.11. Whole thin section scan of TS. This image presents a complete view of the thin section, providing context for the vertical sections and detailed areas shown in the following figures. Specimen LSM11-01, Sedgwick Museum, Cambridge.

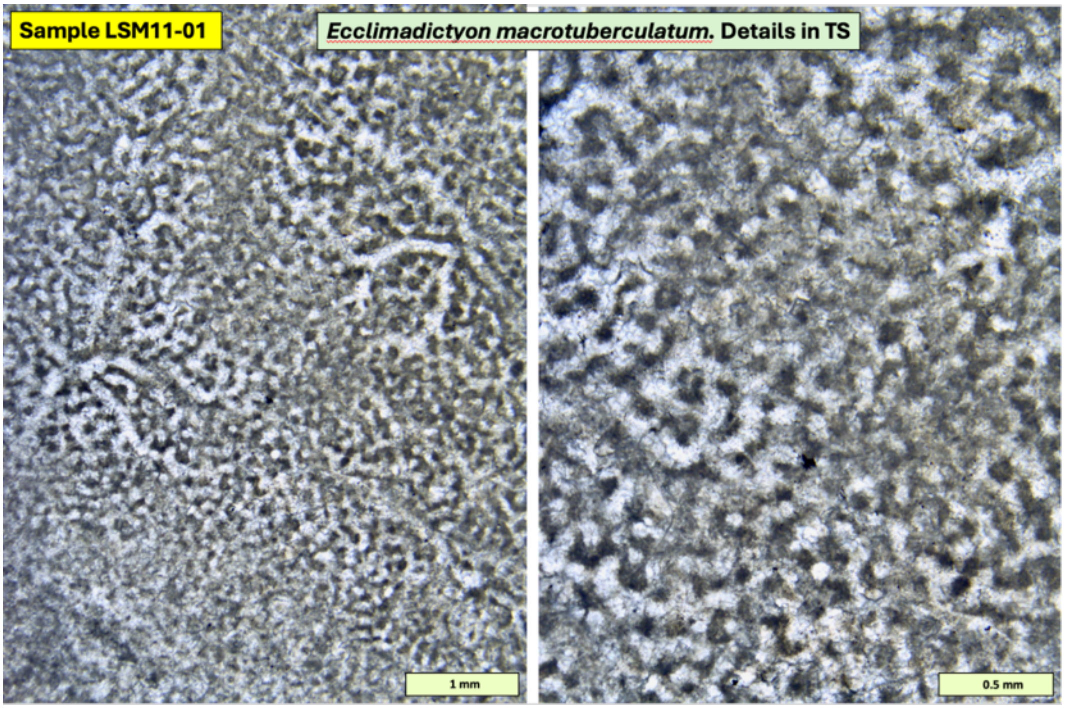


Fig. 4.10.12. Details of TS of specimen LSM11-01, showing prominent pillars, many of which resemble those of *Clathrodictyon*. Compare with the holotype of *Clathrodictyon* in Figs. 2.1.6 & 7. It could be argued that this TS warrants inclusion in *Clathrodictyon*, but the story is not over yet, as you will see in later images from other thin sections made from this amazing sample. Specimen LSM11-01, Sedgwick Museum, Cambridge.

4.11. LSM11-01-part 2 – Ecclimadictyon macrotuberculatum

This section illustrates a parallel thin section to the one in Section 4.10, and includes the Frontispiece picture.

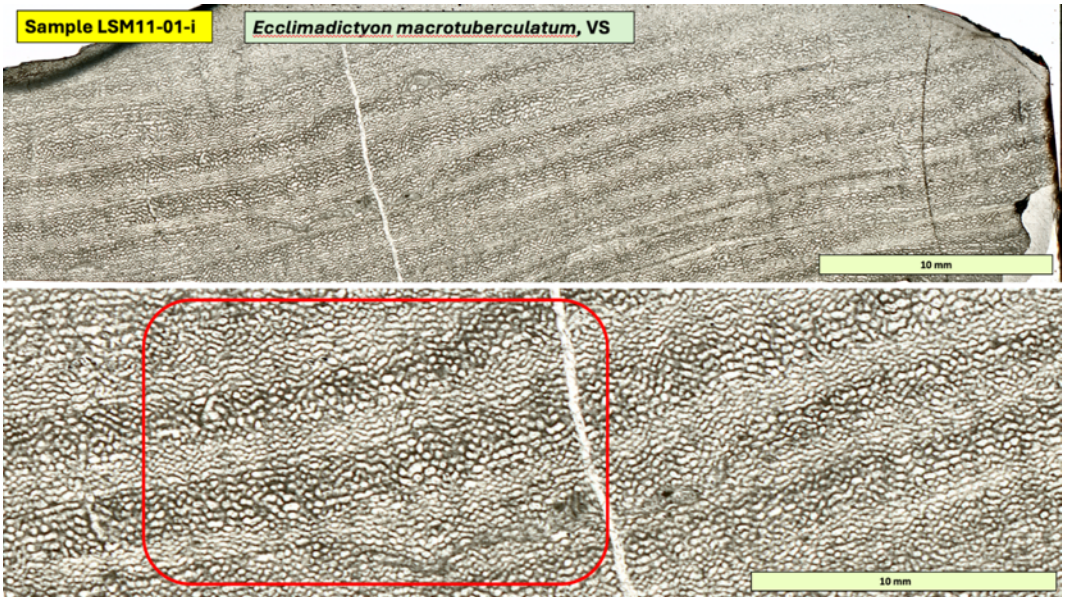


Fig. 4.11.1. Upper photograph: VS of LSM11-01-i, showing regular banding associated with phases of skeletal growth as shown in Section 4.10. Note that although the banding looks regular, there are some layers with disruptions, and overlapping laminations (that look like cross bedding (e.g. top left). **Lower photograph:** enlargement of lower left-central part showing location of Fig. 4.11.2, that is the Frontispiece image of this atlas. Specimen LSM11-01-i, SK personal collection.

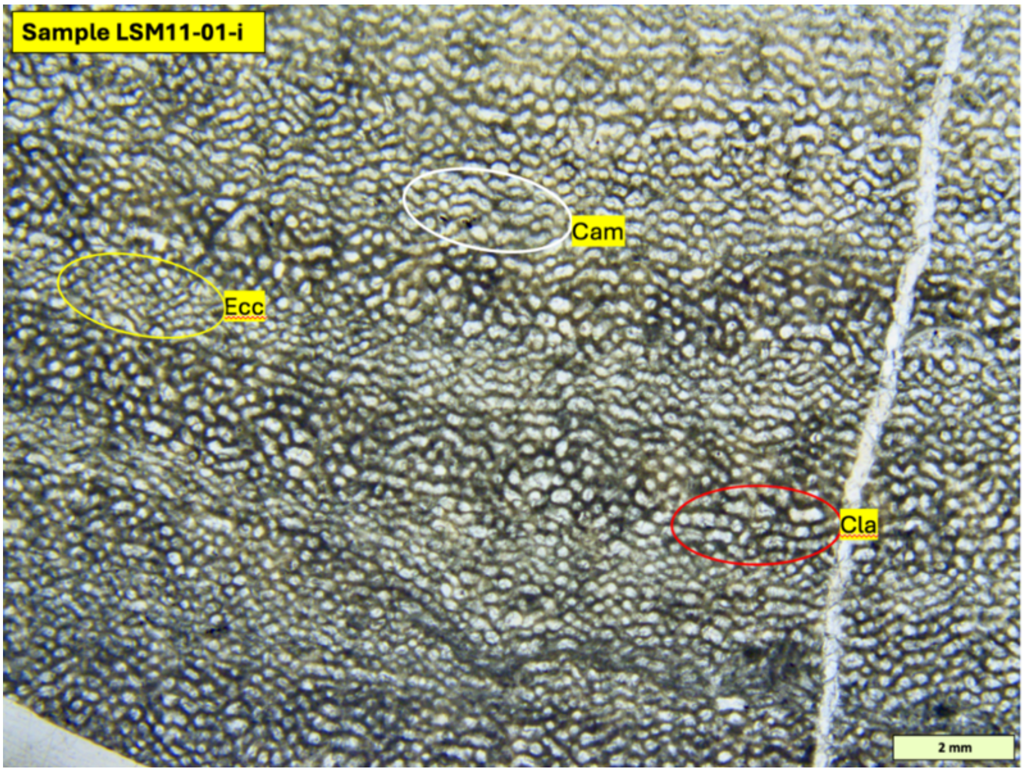


Fig. 4.11.2. Enlargement of red box in LSM11-01-i, showing VS, with details of banding and skeletal structure, that show variations. Three ellipses encompass regions consistent with descriptions of the genera *Clathrodictyon* (Cla), *Ecclimadictyon* (Ecc) and *Camptodictyon* (Cam). Note the disruption of skeletal structure in the lower central area, which appears to be a hiatus in the growth history at this level. This image partially overlaps the area of the Frontispiece image of this atlas. Specimen LSM11-01-i, SK personal collection.

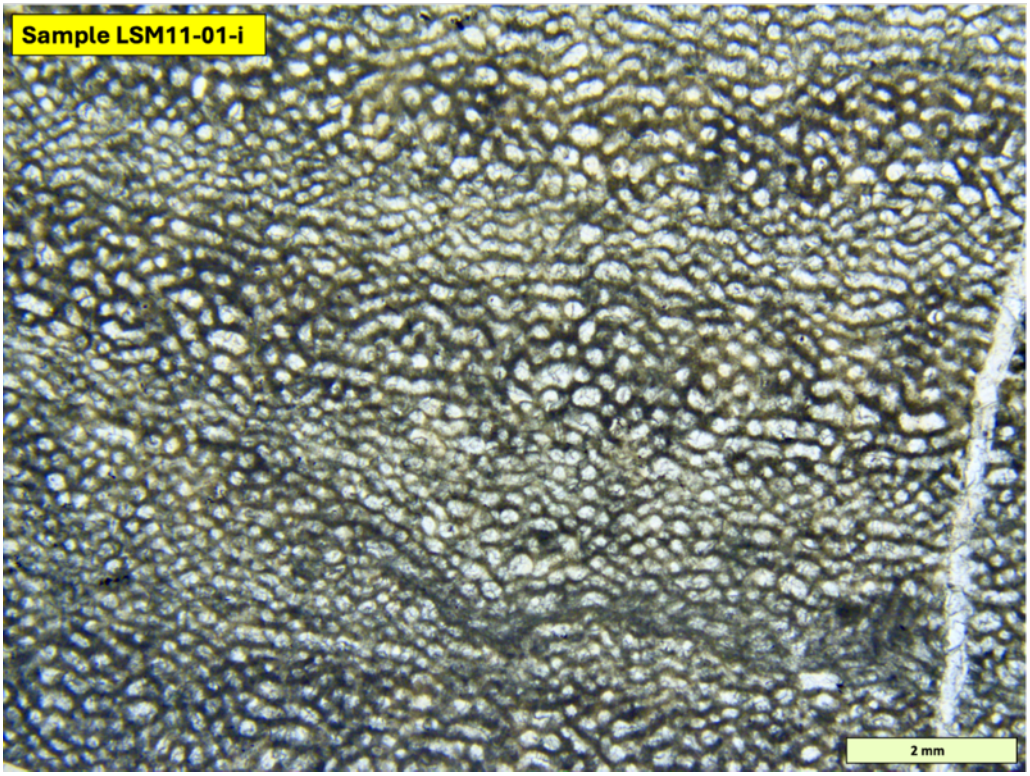


Fig. 4.11.3. Enlargement of Fig. 4.11.2, showing variations in structure of potential taxonomic implications. Specimen LSM11-01-i, SK personal collection.

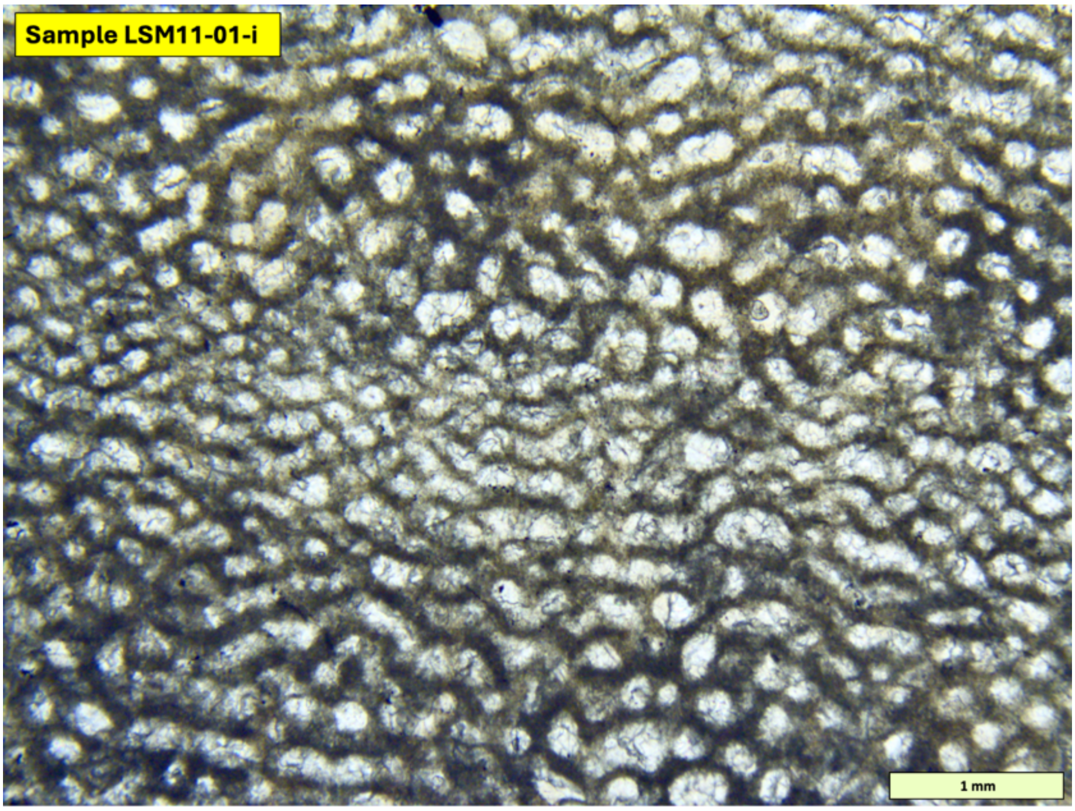


Fig. 4.11.4. Enlargement of Fig. 4.11.3, highlighting structural variations with potential taxonomic significance. Note the variation of element thickness, as part of the banding in the sample. Specimen LSM11-01-i, SK personal collection.

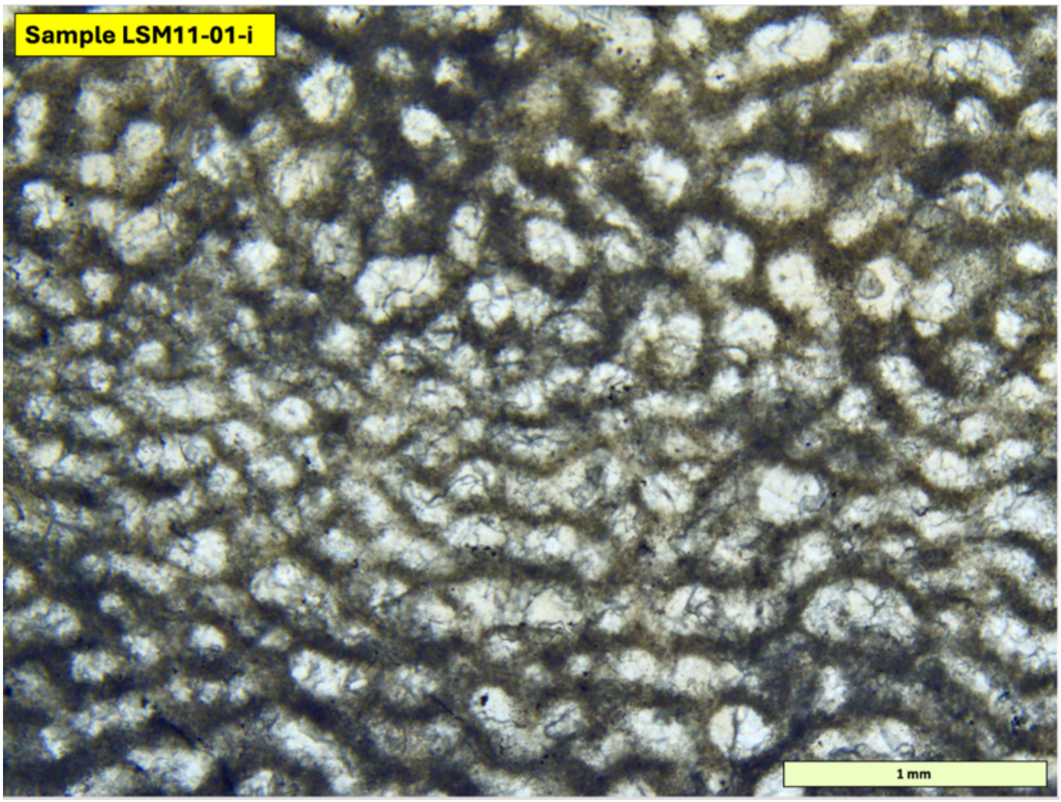


Fig. 4.11.5. Detail of Fig. 4.11.4, showing structural variations with potential taxonomic implications. Note the variation of element thickness, as part of the banding in the sample. Specimen LSM11-01-i, not deposited.

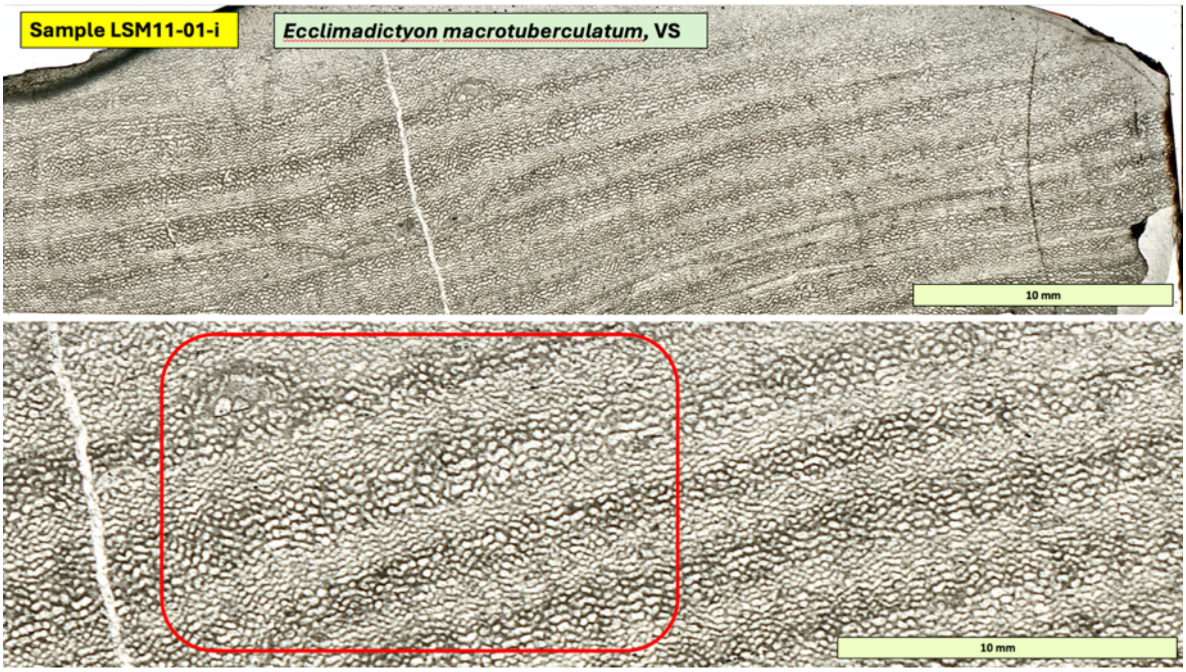


Fig. 4.11.6. Upper image: VS of LSM11-01-i, showing regular banding patterns indicative of successive phases of skeletal growth, as discussed in Section 4.10. Although the banding looks regular, there are some layers with disruptions, and overlapping laminations (that look like cross bedding (e.g. top left). **Lower image:** detail of lower central part showing location of Fig. 4.11.7. Specimen LSM11-01-i, SK personal collection.

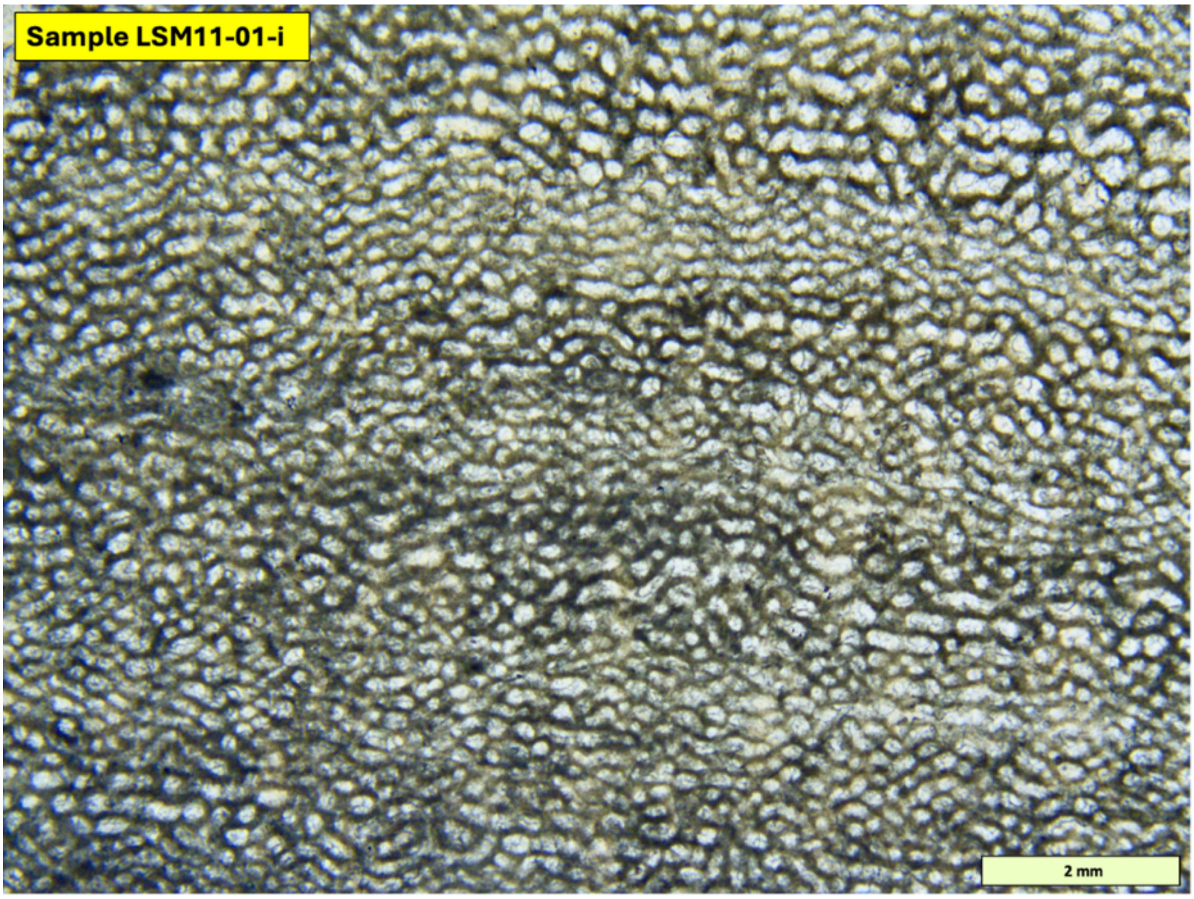


Fig. 4.11.7. Enlargement of VS of LSM11-01-i from Fig. 4.11.6, showing regular banding of phases of skeletal growth as shown in Section 4.10. Specimen LSM11-01-i, SK personal collection.

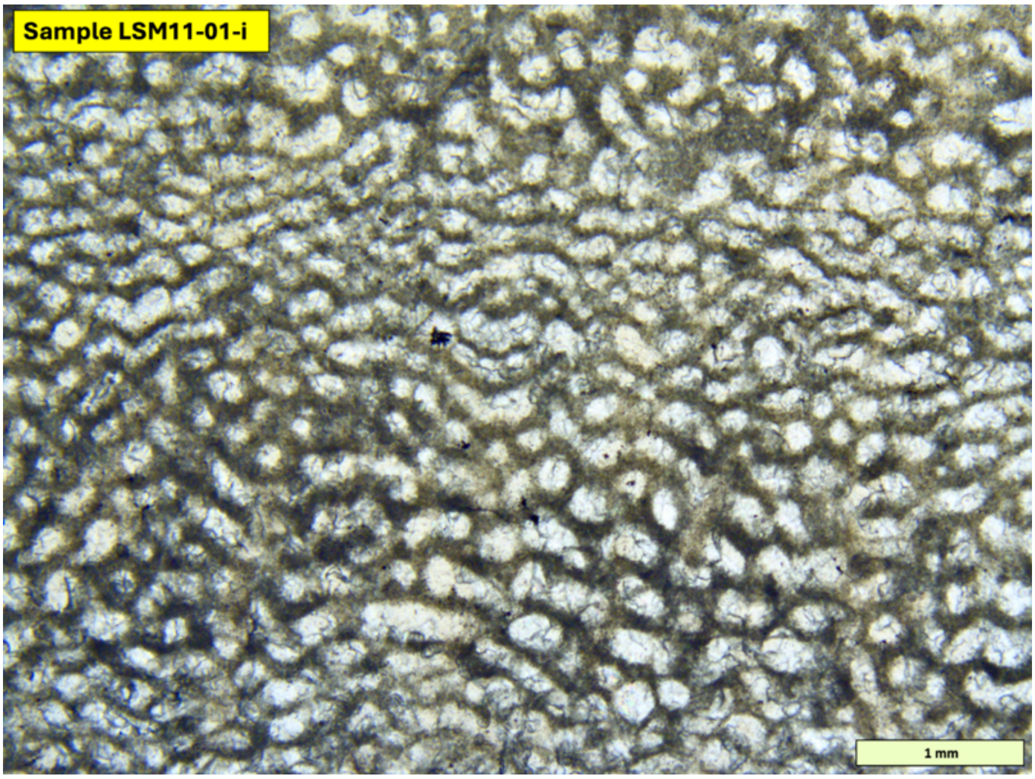


Fig. 4.11.8. Enlargement of Fig. 4.11.7, showing details of phases of skeletal growth as shown in Section 4.10. Please take note of the potential taxonomic implications of the observed phase variation between the thinner-element band in the middle, compared to the thicker-element zones in upper and lower parts of the image. Specimen LSM11-01-i, SK personal collection.

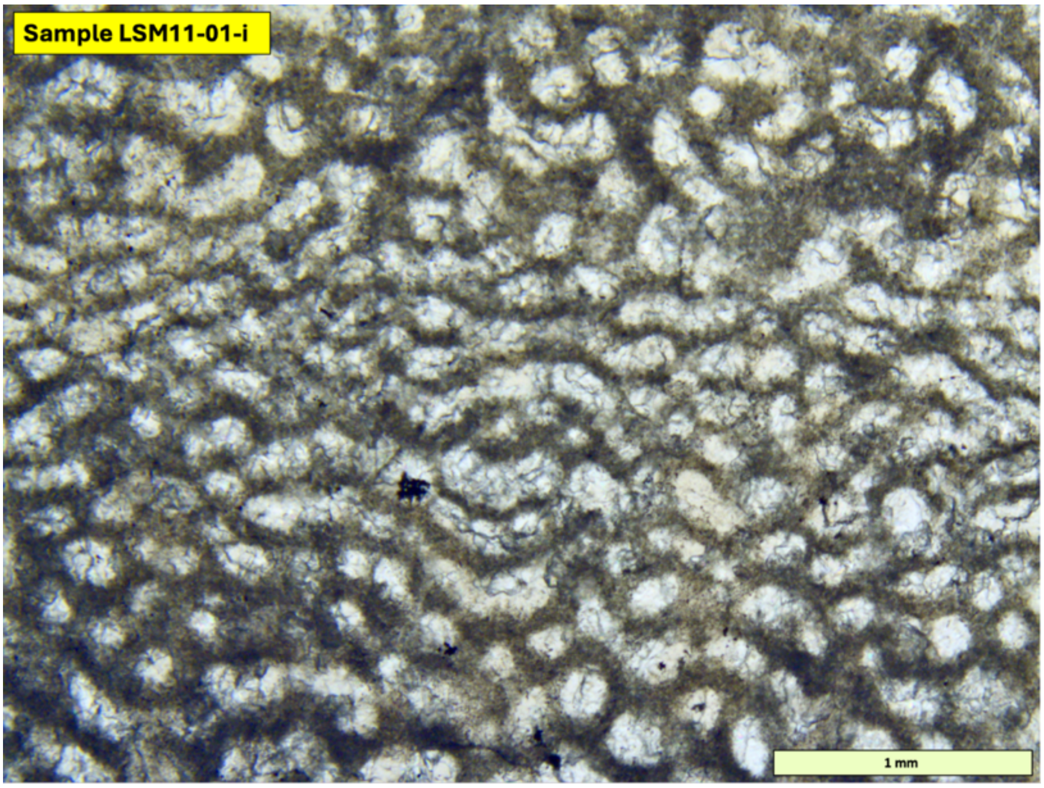


Fig. 4.11.9. More details of Fig. 4.11.8, revealing additional detail in phases of skeletal growth as shown in Section 4.10. This close-up emphasizes the potential taxonomic implications of the phase variation between the thinner-element band in the middle, compared to the thicker-element parts in upper and lower parts of the photo. Specimen LSM11-01-i, SK personal collection.

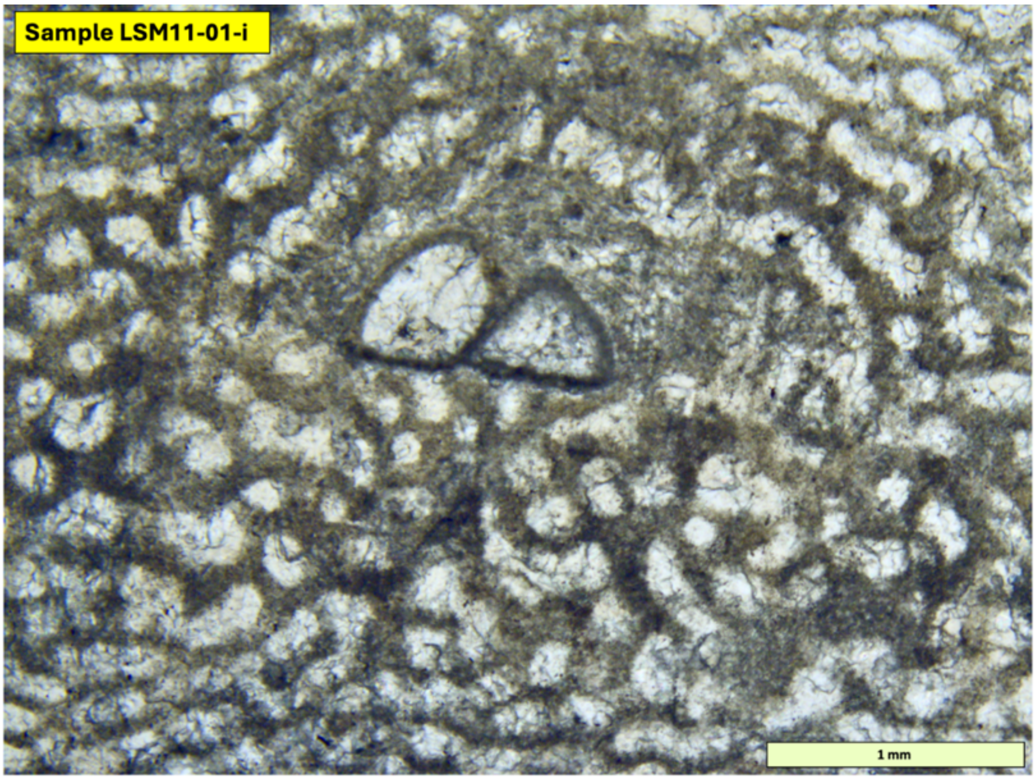


Fig. 4.11.10. Enlargement of upper left corner of Fig. 4.11.6, showing an embedded foreign shelly organism within the stromatoporoid; it is probably a spiral tubular shell, based on the abundance of such associated organisms in stromatoporoids, from the authors' prior observations. The flat base of the shell is interpreted to indicate that the shell grew on the stromatoporoid, potentially on living stromatoporoid soft tissue and killed that portion of the stromatoporoid surface. However, as is common in stromatoporoids, the shell was overgrown by the stromatoporoid's continued upward growth and encased in the skeletal network of the subsequent stromatoporoid growth. Specimen LSM11-01-i, SK personal collection.

4.12. LSM11-01-part 3 – Ecclimadictyon macrotuberculatum

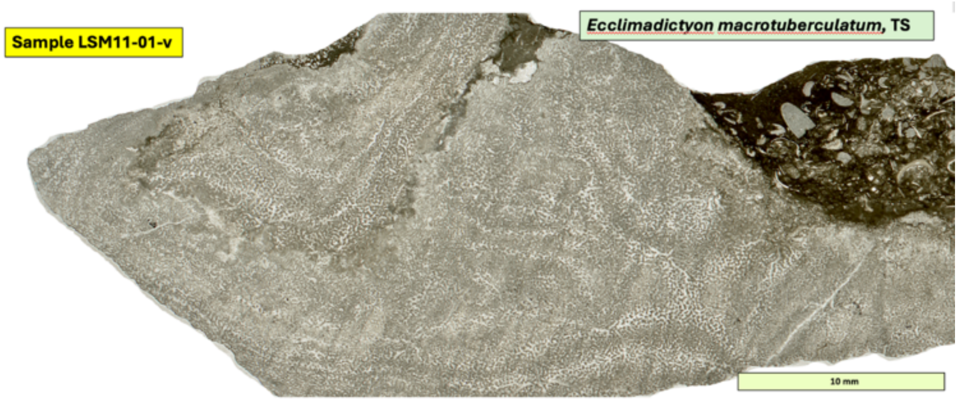


Fig. 4.12.1. Whole thin section scan of TS of LSM11-01-v, showing abundant pillars, that might be consistent with *Clathrodictyon*; but the pillars are notably thicker than those of the *Clathrodictyon* holotype illustrated in Nestor (2015). Specimen LSM11-01-v, SK personal collection.

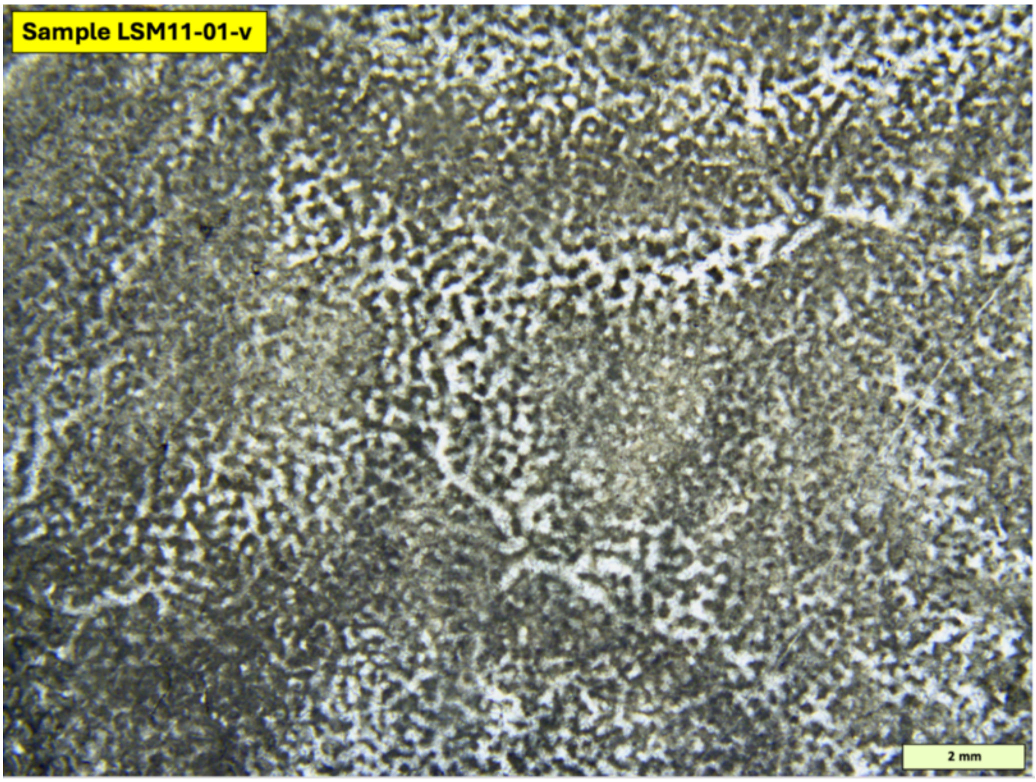


Fig. 4.12.2. Enlargement of TS of LSM11-01-v, showing thick pillars, many of which seem to be fused into elongate structures that are abundant in the holotype of *Ecclimadictyon* illustrated by Nestor (2015). So there is uncertainty as to whether this specimen is most similar to *Clathrodictyon* or *Ecclimadictyon.* Specimen LSM11-01-v, SK personal collection.

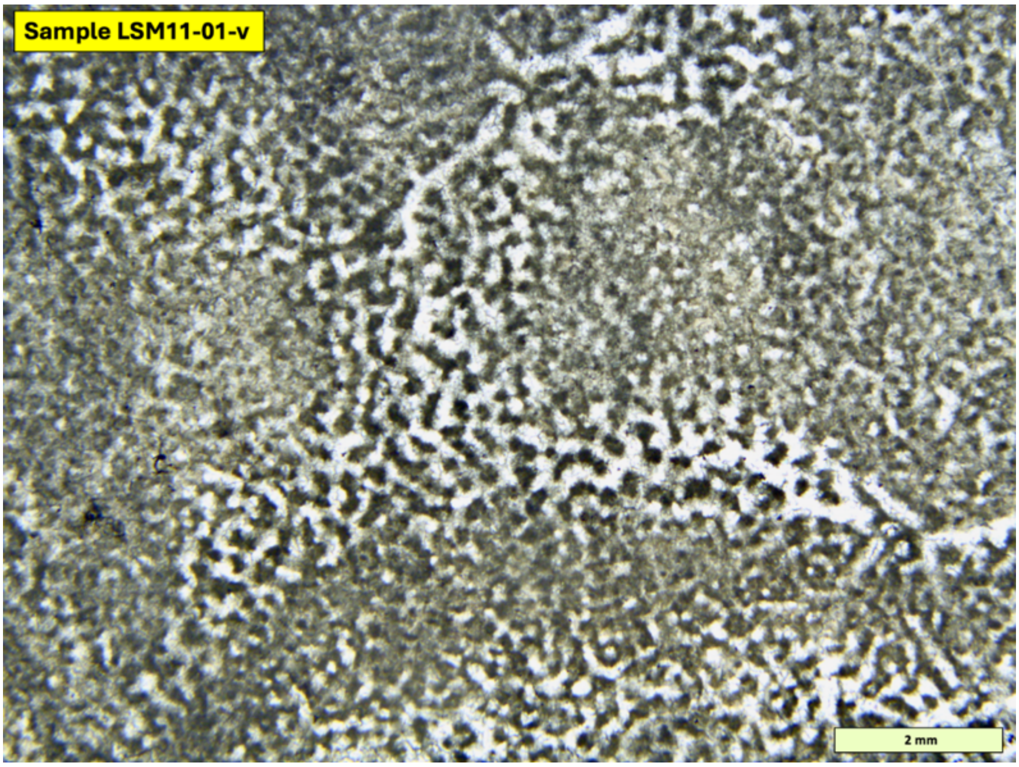


Fig. 4.12.3. Additional enlargement of TS of LSM11-01-v, showing thick pillars, many of which seem to be joined together forming elongate structures that are abundant in the *Ecclimadictyon* holotype illustrated by Nestor (2015). Consequently, there is uncertainty regarding which taxon this is most similar to, *Clathrodictyon* or *Ecclimadictyon.* Specimen LSM11-01-v, SK personal collection.

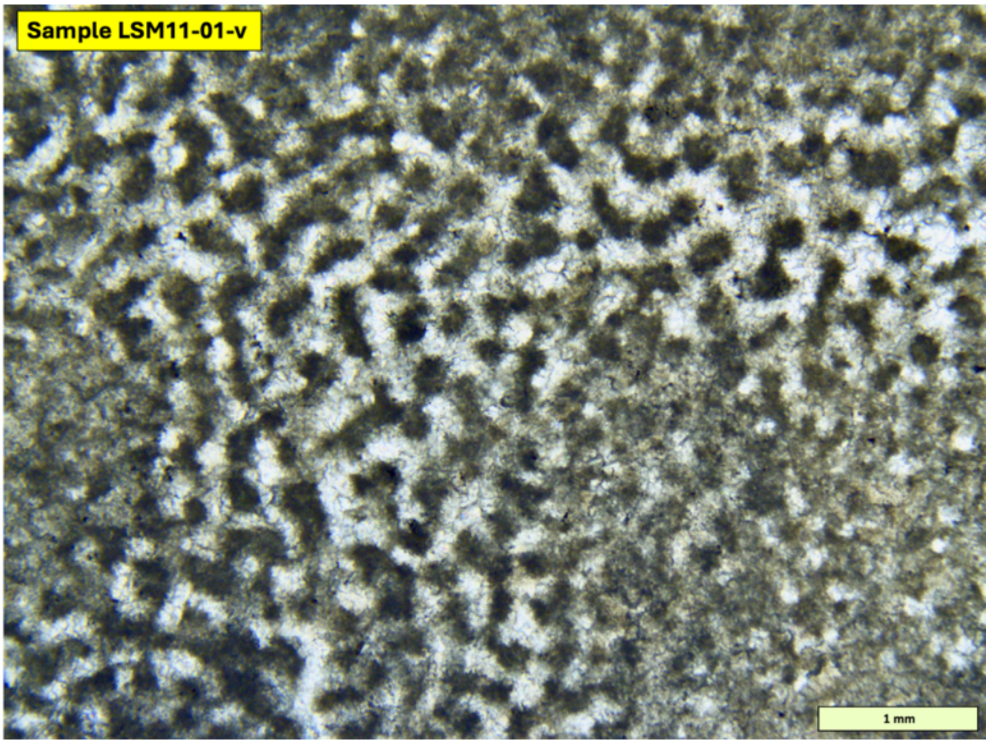


Fig. 4.12.4. Detail of TS of LSM11-01-v, showing thick pillars, many seem to be joined together forming elongate structures that are abundant in the *Ecclimadictyon* holotype illustrated by Nestor (2015). So there is uncertainty regarding which taxon this is most similar to, *Clathrodictyon* or *Ecclimadictyon.* Specimen LSM11-01-v, SK personal collection.

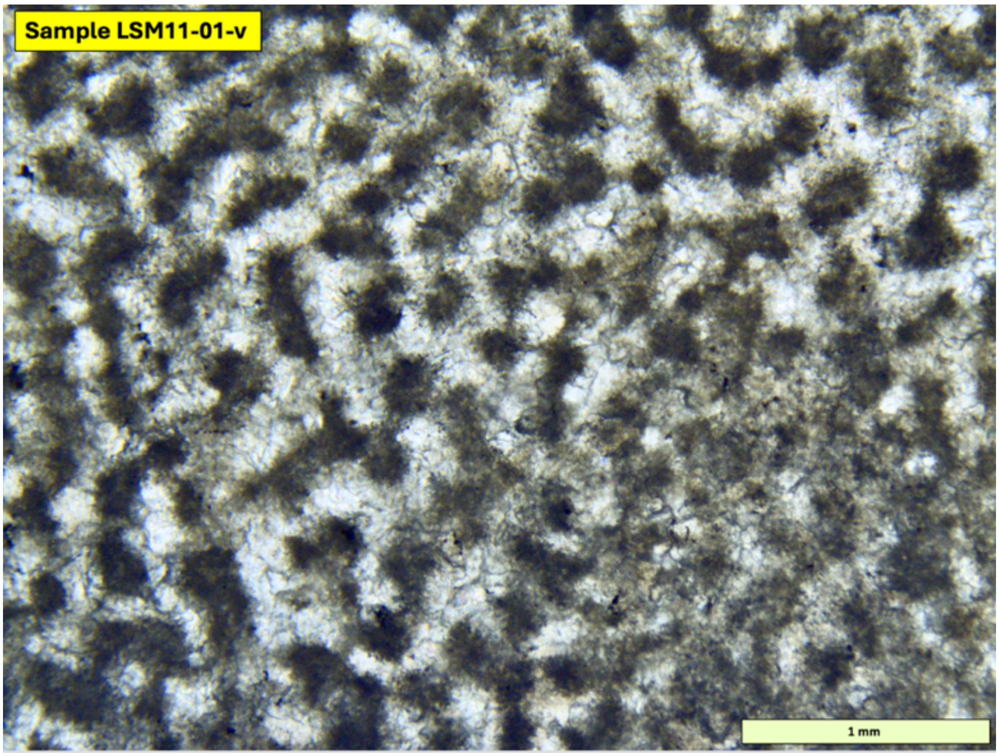


Fig. 4.12.5. Further detail of TS of LSM11-01-v, showing thick pillars, many of which appear to be joined together, forming elongate structures that are similar to those abundant in the *Ecclimadictyon* holotype illustrated by Nestor (2015). This introduces a degree of uncertainty regarding which taxon this is most similar to, *Clathrodictyon* or *Ecclimadictyon.* Specimen LSM11-01-v, SK personal collection.

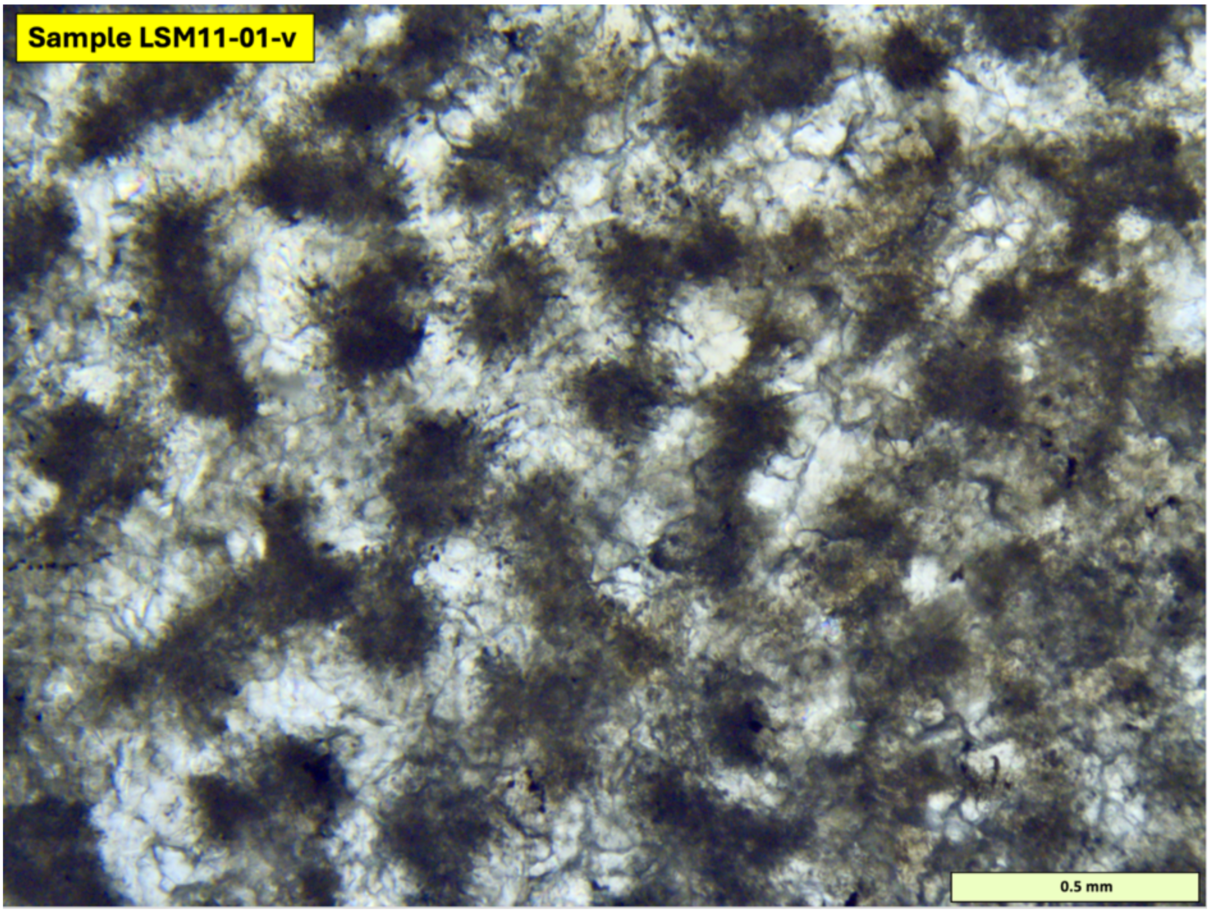


Fig. 4.12.6. More details of TS of LSM11-01-v, showing thick pillars; these may have been diagenetically enlarged. This interpretation is supported by the presence of fine crystal terminations radiating outward from the pillars into the gallery space. Specimen LSM11-01-v, SK personal collection.

SECTION 5:

BUT DON'T THROW OUT THE BABY WITH THE BATHWATER

"Don't throw out the baby with the bathwater" is a common English idiom which advises you not to discard something important when you dispose of something no longer needed. According to *Wikipedia*, this idiom originated in Germany in the 16th Century. If you agree with the indications in the prior sections of this atlas, that there is a problem with the definition of the three genera discussed, then it is necessary to consider to what extent **all** stromatoporoid taxonomy has validity. The good news is fairly obvious: there must be quite a lot of validity in stromatoporoid systematics, at least at the traditional order level of classification, because of the large variations of skeletal structure in stromatoporoid sponges.

In order to illustrate this critical point (the extensive morphological diversity), we have chosen some examples from Kershaw et al. (2021), which focus on Silurian stromatoporoids of similar age to, and commonly found occurring together with, *Clathrodictyon* and *Ecclimadictyon.* However, note that *Camptodictyon* has been previously known from only Ordovician strata, so the possibility that a skeletal structure consistent with *Camptodictyon* also occurs in the Silurian, because of its overlap with the structure of *Clathrodictyon*, may thus depend on how these taxa are defined.

The following figures (slightly modified from the open-access NHM Data Portal depository at https://data.nhm.ac.uk/dataset/british-silurian-stromatoporoid-systematic-palaeontology) show some other stromatoporoids from the Much Wenlock Limestone Formation, Wenlock, Silurian; central England. These specimens occur in the same bedded limestones and reef environments where *Ecclimadictyon* was reported by Kershaw et al. (2021); they are all deposited in the Sedgwick Museum, Cambridge, UK. However, please note that Kershaw et al. (2021) did not report *Clathrodictyon*, and this is in contrast to Nestor (2015) who stated that *Clathrodictyon* is abundant in the Wenlock of England. We surmise that many of the specimens that we called *Ecclimadictyon* were regarded by Nestor (2015) as *Clathrodictyon*. This emphasises the need for clearer taxonomic boundaries.

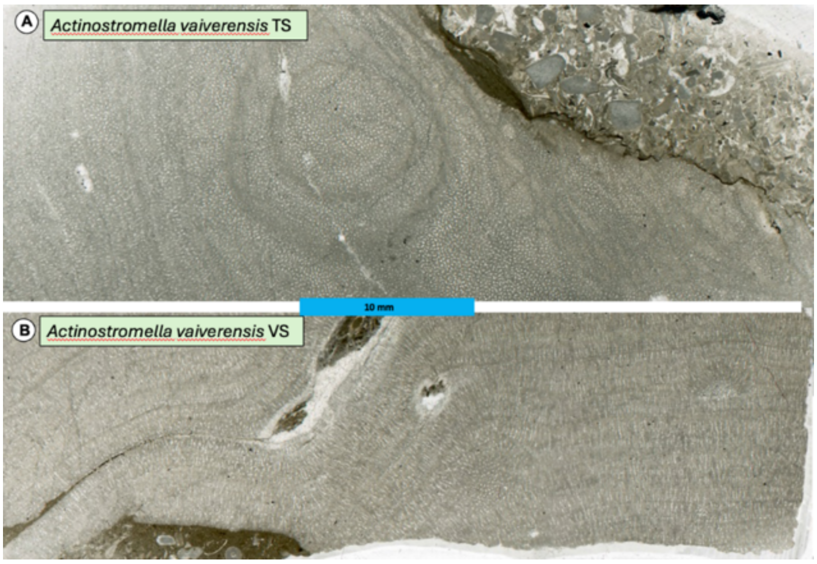


Fig. 5.1.1. VS (lower) & TS (upper) whole thin section scans of *Actinostromella vaiverensis*. Its overall architecture is clearly different from that of *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxa and is different from all other taxa within the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

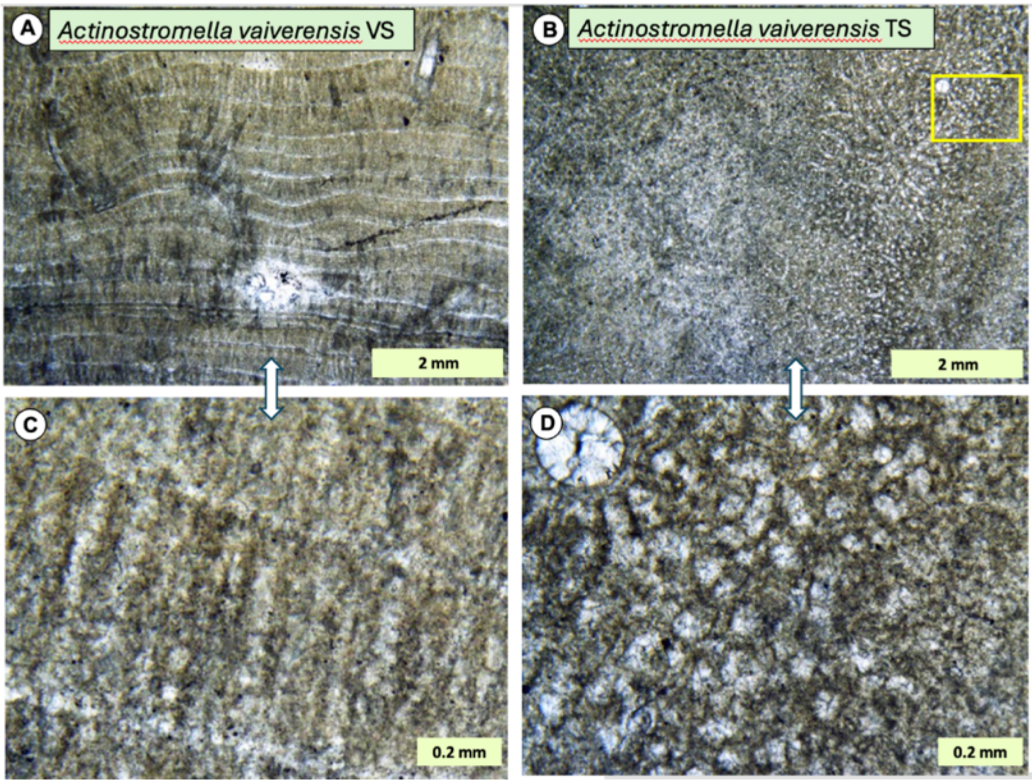


Fig. 5.1.2. VS (A & C) & TS (B & D) detail thin section images of *Actinostromella vaiverensis*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group and all other taxa within the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

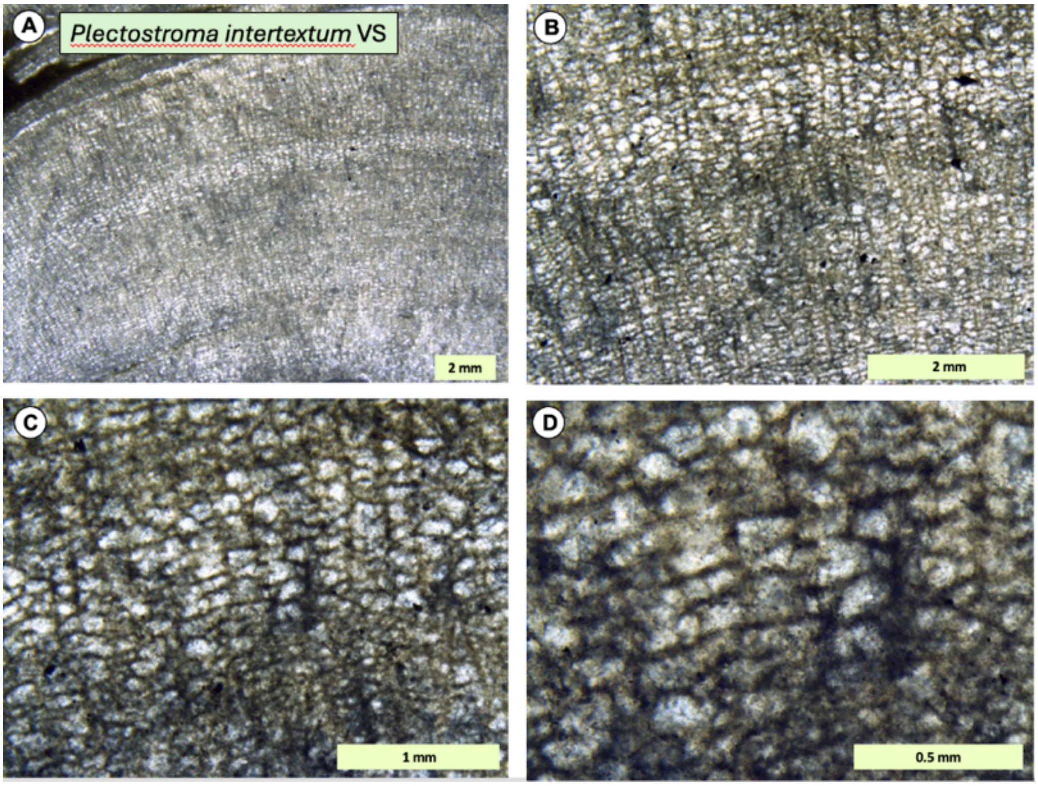


Fig. 5.1.3. VS thin sections at increasing magnifications from A to D of *Plectostroma intertextum*. Note the clear distinctions between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group, as well as from all other taxa within the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

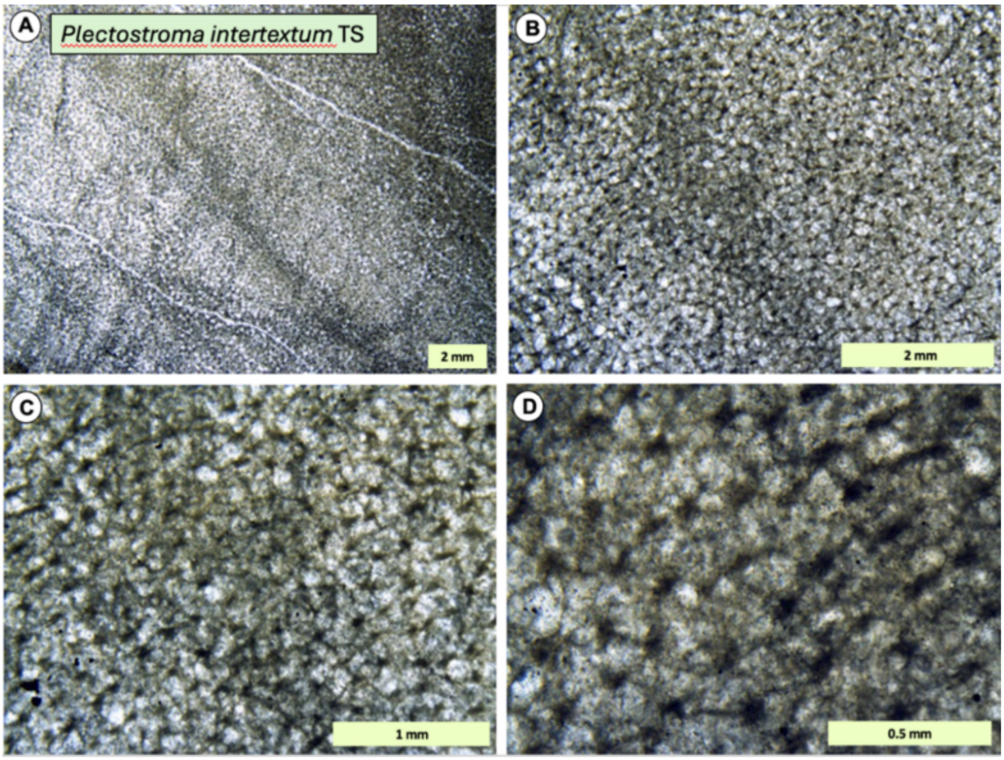


Fig. 5.1.4. TS thin sections at progressively increasing magnifications from A to D of *Plectostroma intertextum*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-*

Ecclimadictyon-Camptodictyon taxonomic group, as well as all other taxa present in the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

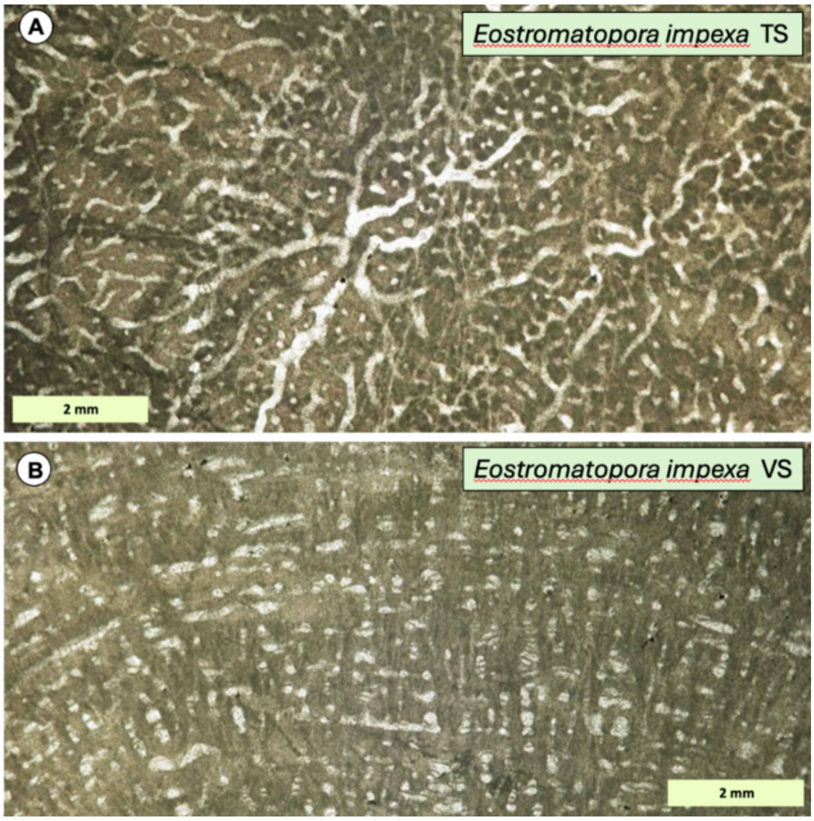


Fig. 5.1.5. TS (upper) and VS (lower) thin sections of *Eostromatopora impexa*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group, as well as from all other taxa in the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

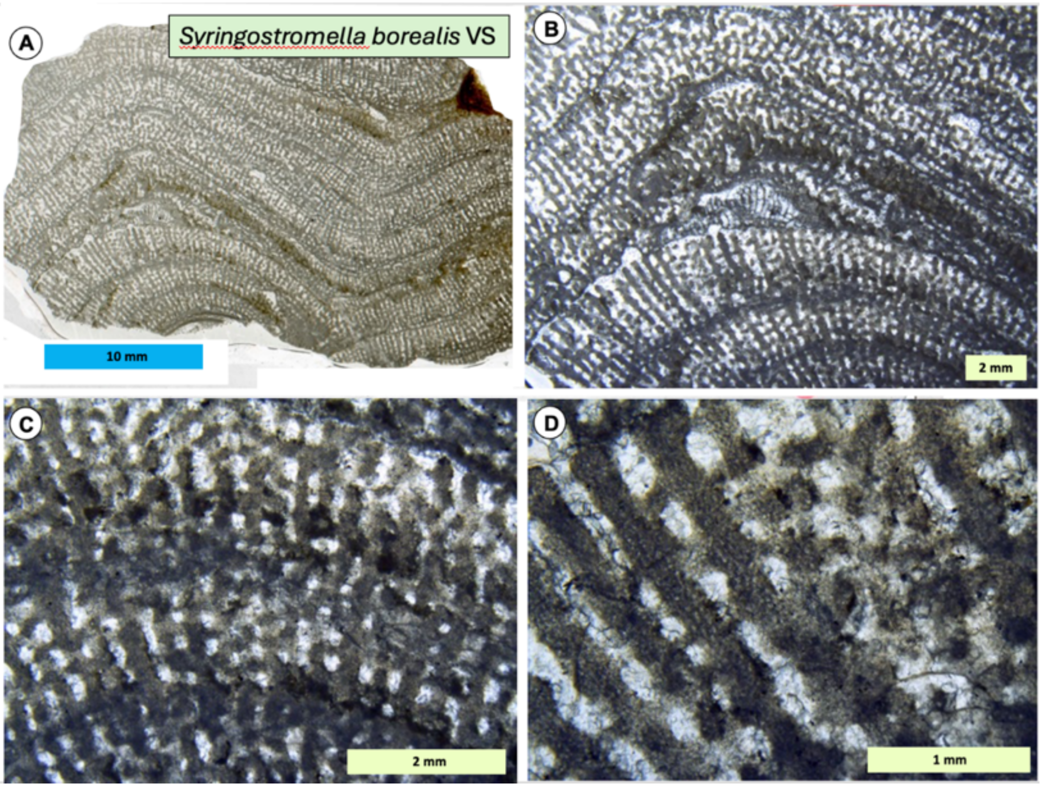


Fig. 5.1.6. VS thin sections at progressively increasing magnifications from A to D of *Syringostromella borealis*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group and all other taxa within the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

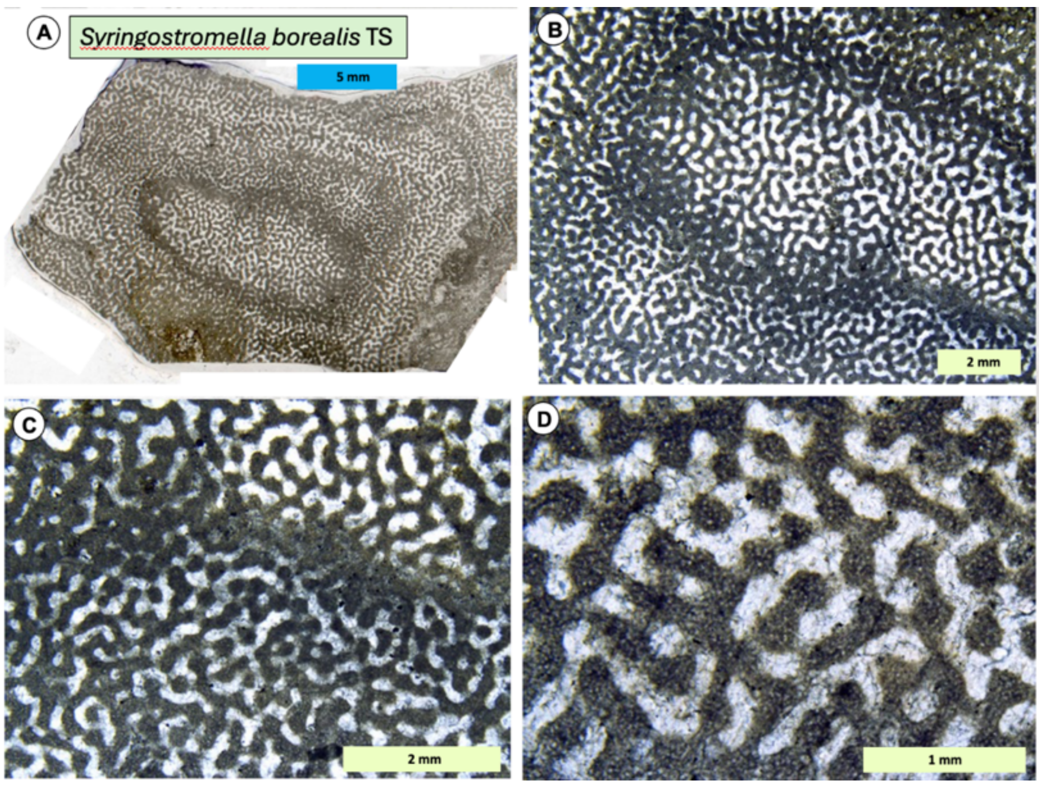


Fig. 5.1.7. TS thin sections at progressively increasing magnifications from A to D of *Syringostromella borealis*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-*

Ecclimadictyon-Camptodictyon taxonomic group and all other taxa within the assemblage. Much Wenlock Limestone, Wenlock, Silurian, England.

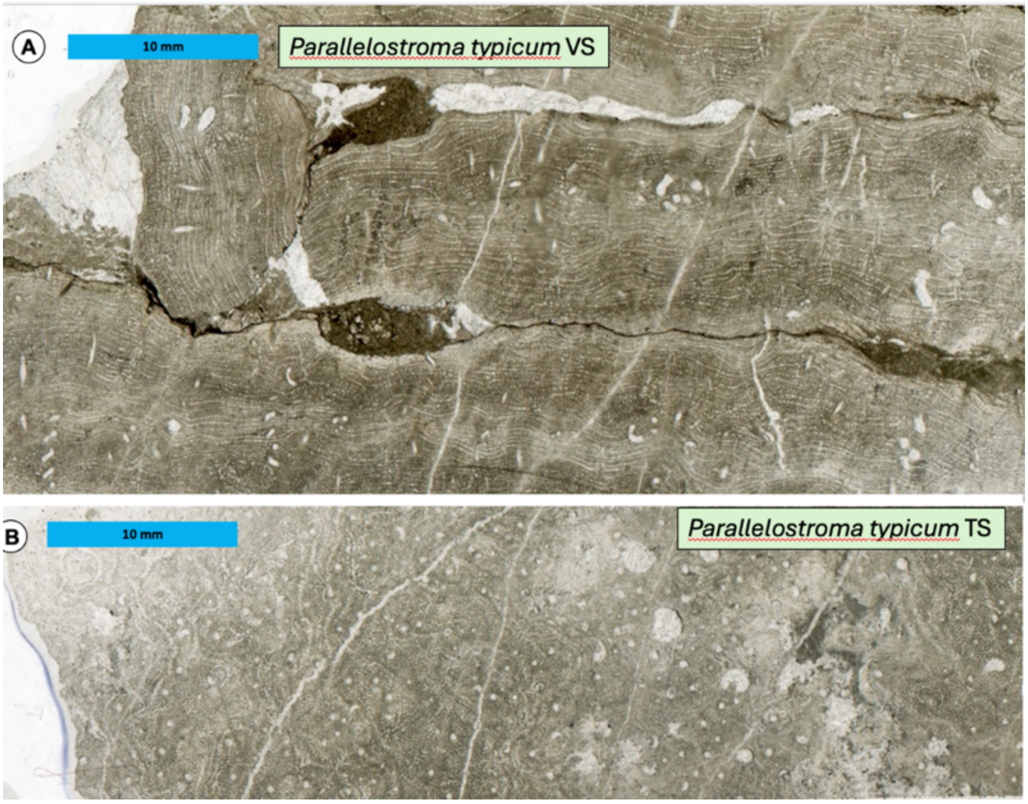


Fig. 5.1.8. Whole thin section scans (A: VS, B: TS) of *Parallelostroma typicum*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group and all other taxa within the assemblage. This specimen also has abundant intergrown tubes of both straight and spiral forms, that were symbiotic with the growth of the stromatoporoid. Much Wenlock Limestone, Wenlock, Silurian, England.

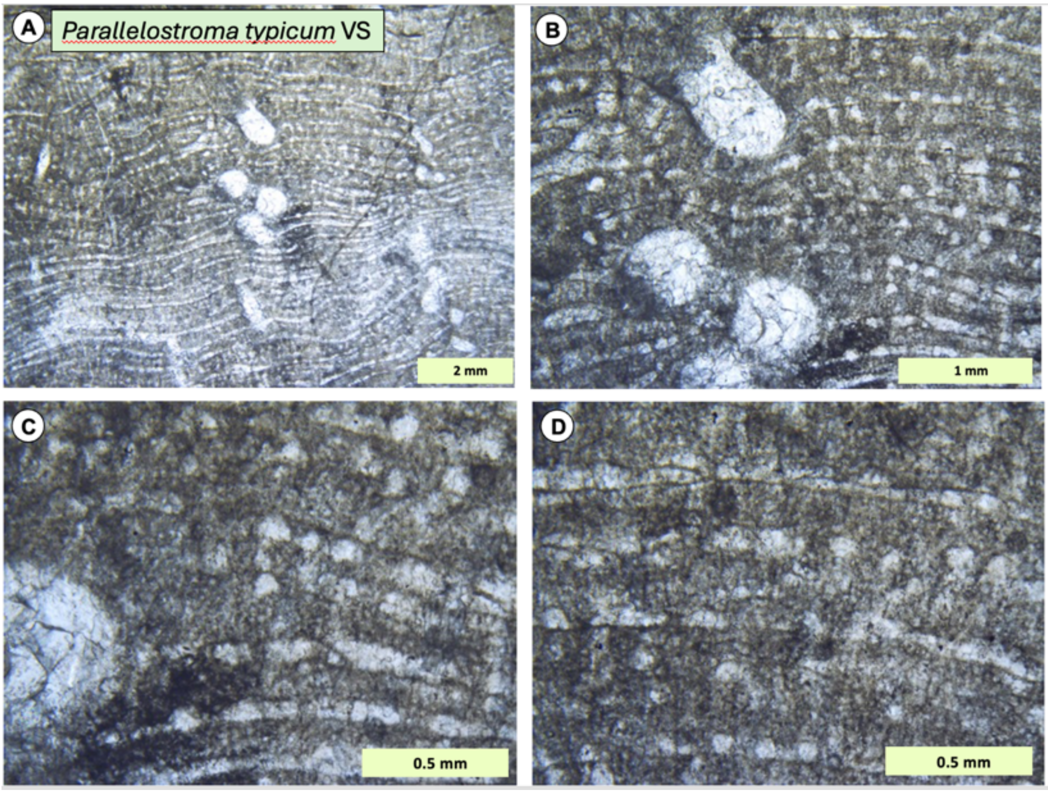


Fig. 5.1.9. VS thin sections at progressively increasing magnifications from A to D of *Parallelostroma typicum*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group and all other taxa within the assemblage. Note the symbiotic tubes in A-C. Much Wenlock Limestone, Wenlock, Silurian, England.

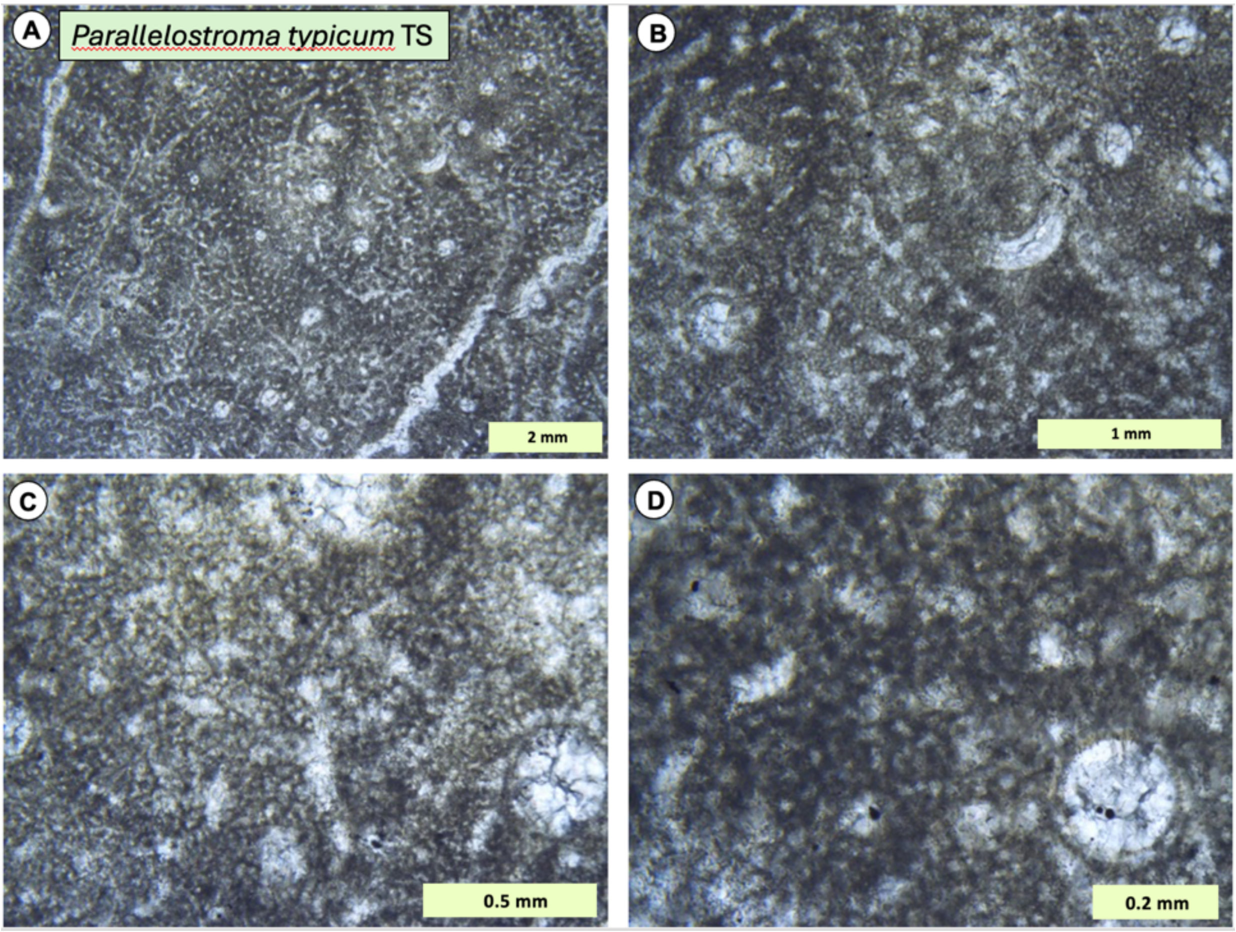


Fig. 5.1.10. TS thin sections at progressively increasing magnifications from A to D of *Parallelostroma typicum*. Note the obvious differences between this taxon and all variations of the *Clathrodictyon-Ecclimadictyon-Camptodictyon* taxonomic group and all other taxa within the assemblage. Note the symbiotic tubes. Much Wenlock Limestone, Wenlock, Silurian, England.

SECTION 6:

ANALYSIS:

How to make sense of the structural variations in stromatoporoid illustrated within taxa in this atlas?

6.1. Implications of this study for stromatoporoid taxonomy

Palaeozoic stromatoporoid taxa are based on the calcareous secondary skeleton, called hypercalcified skeleton, in the absence of spicules and molecular data that play a key role in modern sponge systematics (see West, 2015, pp 124-125 for useful discussion, in a chapter focussed on chaetetids but relevant to all hypercalcified sponges). Thus, as mentioned earlier, Palaeozoic stromatoporoid taxonomy is phenetic (based on observed features without implication of evolutionary characters). Because of their lack of spicules, stromatoporoid hypercalcified skeletons cannot be proved to be homologous with extant hypercalcified sponges (Vacelet, 1985; Wörheide, 2008; Kershaw & Li, 2024), thus the current seven orders of Palaeozoic stromatoporoids lack reliable biological meaning in classification. Consequently, the families within these orders are also unstable, and this uncertainty automatically cascades down to genera and species. In light of this, we continue to consider as valid the approach proposed by Kershaw et al. (2021), which emphasizes the use of “lowest-level taxon” to represent stromatoporoid diversity. This scheme of lowest-level taxa may or may not correspond to biological species, and they cannot be confirmed as such due to the lack of spicules and molecular evidence. Thus, each lowest-level taxon has the same status as all others. Hence, the recommendation presented in this document is that formal species, genera, families and orders, and of course the whole Class Stromatoporoidea, are abandoned; the only thing that matters is the lowest-level taxon. Consequently, we recommend that the current suite of named stromatoporoid species in all publications are considered as lowest-level taxa rather than species, to separate them from the concept of biospecies.

In terms of nomenclature, it may be useful to adopt descriptive grade terminology in place of formal Linnaean ranks. For example, “Order Labechiida” could be reframed as a “labechiid-form” or *Labechia*-grade stromatoporoid, based only on visible skeletal characteristics, without inferring biological distinction. This terminology is more honest, transparent, and empirically grounded in observable features. Applying this to the *Clathrodictyon-Ecclimadictyon-Camptodictyon* (*Cl-Ec-Ca*) taxonomic group, we suggest it could be addressed by giving it a category such as ‘form-group’, ‘grade-group’, or ‘subgrade groups’. Within the *Cl-Ec-Ca* group, it is plausible that structural variation reflects either distinct biological species or variation within a single species or genus. Similarly, a single skeletal architecture might represent multiple biological species.

Key questions to ask yourself, for consideration:

Q1) To what extent does the crumpled laminae character of a *Clathrodictyon* specimen need to be different from the holotype image in Nestor (2015), and to be more similar to *Ecclimadictyon* or perhaps *Camptodictyon,* before you would accept that it is no longer appropriate to call it *Clathrodictyon*? Perhaps >50% for example (and how would you measure it)? This means that if more than 50% of the stromatoporoid had the *Ecclimadictyon*-like structure, then presumably it could be called *Ecclimadicton*. The same applies for *Camptodictyon*.

Q2) Another way of viewing Q1: if a specimen contained >50% of its structure with a *Clathrodictyon* architecture, and therefore also contained either or both *Ecclimadictyon* and *Camptodictyon* architectures, how confident would you be that you can apply the name of *Clathrodictyon* to that fossil? (e.g. perhaps that specimen was really an *Ecclimadictyon* taxon, but part of the architecture that was present in your thin section (which represents only a small part of the entire skeleton) had a *Clathrodictyon* structure; scary.)

As a consequence of the above points, in the monograph of British Silurian stromatoporoids by Kershaw et al. (2021), the naming of *Ecclimadictyon macrotuberculatum* becomes an uncertain definition, because of its mixture of architectures. Nevertheless, this taxon is recognisable as a distinct stromatoporoid in the assemblage, even though it contains mixtures of skeletal architecture as shown in Section 4 illustrations. Furthermore, the distinction between *Ecclimadictyon macrotuberculatum* (*Em*) and *Ecclimadictyon astrolaxum* (*Ea*) highlights another complexity. Although *Em* and *Ea* are morphologically distinct enough to warrant separate names (possibly as subgrade taxa), there is no clear evidence that they represent separate biological species. They may reflect intra-species variation driven by environmental or developmental factors, or they could represent multiple biological species sharing similar skeletal morphologies. Specimen LSM11-01, examined in detail in this atlas, contains characteristics that encompass all three of the *Cl-Ec-Ca* taxa. Still, *Em* and *E*a stand apart from all other British Silurian stromatoporoids (see the evidence in figures in Section 5) and do not overlap structurally with any other taxa in the assemblage. Consequently, that dataset remains robust when interpreted as a collection of lowest-level taxa, provided no biological species assumptions are made.

We should also point out that the name of *Ecclimadictyon macrotuberculatum* remains an issue; *macrotuberculatum* derives from Riabinin's (1951) "*var. macrotuberculata"* for a specimen that has a knobbly surface [inspired the concept of macrotubercles]; but Riabinin (1951) stated that these are part of the external form of the stromatoporoid that are not part of its taxonomy. As a result, the designation "var. macrotuberculata" is likely invalid, and the correct name for this taxon may instead be *Ecclimadictyon fastigiatum*.

6.2. A way forward for stromatoporoid taxonomic classification?

From the discussion in Section 6.1. above, perhaps now we have an acceptable way to deal with stromatoporoid taxonomy. If taxa, that are considered to be different at the lowest level, DO NOT have any overlap of the forms of skeletal architecture, then this could be a good reason to consider them as being biologically distinct. Nevertheless, this does not eliminate the possibility that multiple biological species share a single skeletal architecture.

6.3. More things to consider

6.3.1. What is a stromatoporoid?

Developing the concepts of taxa further in stromatoporoids, another aspect, that is not emphasised in stromatoporoid literature, is that some fossils classified as stromatoporoids do not in fact have stromatoporoid structure (defined as having layers and holes). Probably the best example is *Lophiostroma*, composed of an almost completely solid skeleton in the holotype of *Lophiostroma schmidtii* (see Kershaw, 2022). We may also wonder about such beautiful constructions as the labechiid stromatoporoid *Pennastroma* (Webby, 2015 [the 2015 *Treatise*], p. 737) and other forms classed as labechiids, that deviate significantly from the concept of stromatoporoids as fossils with “layers and holes” (which are embodied within the word stromatoporoid). Taking this even further, it may be more logical to separate most (though not all) labechiid forms from stromatoporoids, and simply call them labechiids, as a kind of hypercalcified [presumed] sponge of unknown affinity. This conceptual shift warrants future investigation.

6.3.2. How to study stromatoporoid taxa

Traditional stromatoporoid taxonomy relies heavily on small thin sections, but our experience, partly illustrated in this atlas, shows that small thin sections commonly fail to capture the full range of structural variation. Using large thin sections, in contrast, allows assessment of the range of structure. Best is where an entire stromatoporoid can be mounted onto a single thin section, possible in small stromatoporoids; but if not, then multiple thin sections from different parts of the same specimen are highly valuable. Such an approach can be applied to holotypes; maybe a useful approach would be to use multiple thin sections from a holotype specimen rather than only one VS & one TS thin section. It might even be useful to use multiple specimens, assembling a small collection of samples to capture all the variation and thus define a holotype as a broader concept.

For historical application of holotypes, there is some evidence of selection by the researcher who defined the holotype. In the case of *Clathrodictyon vesiculosum* (*Cv*) holotype specimen NHMUK PI P5495, perhaps Nestor himself did not select the most appropriate specimen for the holotype of *Clathrodictyon* (which contains much variation, with similarity to *Ecclimadictyon* in parts), noting that it is a small thin section!! Furthermore, it seems that he selected the part of the holotype that he deemed to be most appropriate for the definition of the holotype, but he did not take account of the variability within that VS thin section in the definition of the holotype. This raises the question about whether this particular holotype should be reconsidered and possibly another specimen chosen to replace it. Although Kershaw et al. (2021) unintentionally included *Cv* as an earlier synonym of *Ecclimadictyon macrotuberculatum*, this misstep may reflect a deeper truth: part of the *Clathrodictyon* holotype structure genuinely resembles *Ecclimadictyon*. It seems, by accident, there is some validity in that inclusion of *Cv* in the synonym list of *Ecclimadictyon macrotuberculatum* (or whatever we should now call it). This point brings us full circle back to the original issue that motivated this atlas: the inclusion by Kershaw et al. (2021) of *Cv* as a synonym of *Ecclimadictyon macrotuberculatum* in the systematics section of that monograph. It is remarkable that, in the process of making this atlas, we discovered that the holotype of *Cv* actually contains variation beyond its defined structure, and that variation happens to overlap with the structure of *Ecclimadictyon* !!!

6.4. Stromatoporoid assemblages and correlations challenges

A final concern involves the broader implications for stromatoporoid assemblages and biostratigraphic correlation. Within lowest-level taxa, the problem of whether the overlap of skeletal architecture between traditionally defined genera and species has any impact on the taxonomic definition remains a problem, as stated above, but also problematic is the potential for more than one biological species to be represented by a single lowest-level taxon skeletal structure. This issue might mean that correlation of taxa between different ancient continents may or may not be secure.

It might be argued that because other kinds of fossils can be correlated between continents (e.g. species of graptolites, conodonts etc.) therefore stromatoporoid species could also travel across oceans to correlate occurrences of species. However, such comparisons are not proof that individual stromatoporoid species actually could travel across oceans to occur on different continents and we don’t know if the same skeletal architecture really represents a single species. Also, small geographic variations in stromatoporoid ‘species’ could be due to geographic differences in external environmental pressures that drove the skeletal differences, creating the impression of different taxa that may have been in reality the same taxon. The problem is how to test such wild ideas and exclude them from the picture? Thus, although some may argue that, like graptolites or conodonts, stromatoporoid species could facilitate global correlation, this presumes a level of biological and structural consistency that cannot be verified. Similar skeletal architectures in distant geographic regions may not reflect shared species but instead may be convergent responses to environmental pressures. Subtle morphological differences between regions could be interpreted as distinct taxa, even if they represent environmentally driven variation within the same biological species.

The core problem remains: without biological data (i.e. a spicule-based classification), how can we confidently exclude such possibilities?

SECTION 7:

CONCLUSIONS: A WAY FORWARD

1) From the issues and images shown in this atlas, how should we approach stromatoporoid taxonomy and its applications? How to get the best information out of stromatoporoids in paleoecological and sedimentological research? The images and issues presented in this atlas underscore the challenges of stromatoporoid taxonomy, particularly at the genus and species levels. Stromatoporoids dominated shallow-marine reefs and reef-related facies for 100 million years between the Middle Ordovician and Late Devonian periods, and play a crucial role in the interpretation of global climates in that episode. They responded to extinctions, and information from them helps with models of biosphere reaction to global catastrophes. Recent research on the Devonian terrestrialisation of plants and their effects on shallow marine systems includes consideration of stromatoporoid-rich deposits. Given their widespread presence and environmental sensitivity, stromatoporoids offer valuable insights into the evolution and dynamics of carbonate systems. However, the taxonomic uncertainties, especially at lower taxonomic levels, limit their interpretive potential unless approached with caution.

2) We urge researchers take care to NOT consider the current suite of stromatoporoid species to be confirmed as biological species, but to be aware of the possibility that they represent skeletal structural forms that are less firmly connected to biospecies. In particular, taxa that show overlap of skeletal structure with other taxa should flag a warning that the variation of structure observed may not be a reliable indication of genetic differences. Such overlap may reflect morphological plasticity, environmental influence, and potentially, taphonomic alteration, rather than distinct evolutionary lineages. The concept of lowest-level taxa, as discussed in this atlas, offers a more pragmatic framework for describing stromatoporoid diversity without assuming unwarranted biological specificity. This approach could provide a clearer foundation for interpreting stromatoporoid assemblages and their paleoenvironmental significance.

3) A practical application of stromatoporoid taxonomy may lie in **intra-assemblage analysis,** focusing on the diversity of stromatoporoid architectures (=taxa), in relation to their growth forms and sedimentary environment. Thus, within one assemblage there is great value in developing interpretations of abundance and variation of stromatoporoids and how they may have responded to the local/regional environmental conditions. Correlating these morphotypes with growth forms and depositional environments can offer valuable insights into stromatoporoid ecology and sedimentary dynamics. For example, the case study of British Silurian stromatoporoids presented by Kershaw et al. (2021), which contains the *Ecclimadictyon* taxon discussed in this document, exemplifies how a suite of morphologically distinct but contemporaneous taxa can be interpreted as a coherent community reflecting specific paleoenvironmental conditions. However, while such intra-assemblage analyses are insightful, comparisons

between coeval assemblages from different regions (e.g., comparing England with palaeogeographically nearby Gotland) must be approached with caution. Differences in preservation, sampling scale, and local environmental factors mean that apparent similarities may not necessarily reflect equivalent biological or ecological realities. This problem of comparisons is an issue that has been in the background of stromatoporoid research for many years – that an individual assemblage is a useful tool to analyse the biota and the environments **locally**, but more caution should be applied when examining similarities and differences between coeval assemblages across a region or between regions: we may not necessarily be comparing like with like.

4) Thus, future stromatoporoid research should embrace flexibility in taxonomic interpretation. Researchers should avoid relying on narrowly defined species concepts when making detailed paleoecological or stratigraphic inferences We recommend not to assume that individual species can be relied upon to make detailed interpretations, but to consider the whole issue of low-level stromatoporoid taxonomy in a much more loosely-defined way. This approach aims to move beyond the historically persistent practice of repeatedly redefining taxa and reassigning them among families or orders [that stromatoporoid taxonomists have delighted in doing over previous decades]. This approach may help assemblage-level analyses and ultimately prove more productive and biologically meaningful.

FINAL COMMENT

The authors of this atlas hope you have benefitted from the information presented here, and we also hope you have enjoyed reading this as much as we have enjoyed writing it (which, after decades of thinking about it, is quite a lot of enjoyment).

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