BRITISH SILURIAN STROMATOPOROIDS.
FAUNAS, PALAEOBIOLOGY, AND
PALAEOGEOGRAPHICAL SIGNIFICANCE

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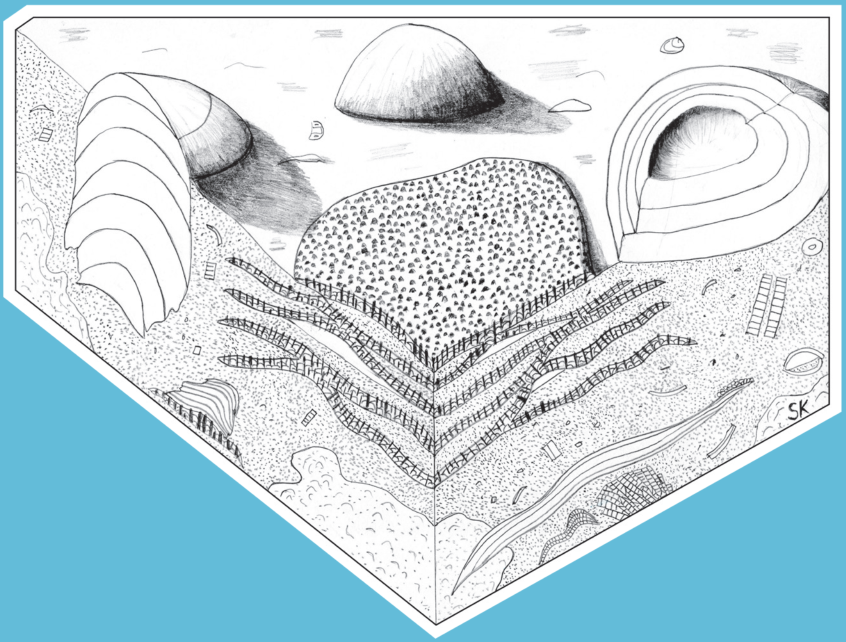

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MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

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## ABSTRACT

British Silurian stromatoporoids occur in carbonate rocks, mostly in the Wenlock Series, together with a small number in the Llandovery Series and very few in the Ludlow Series. Using field and museum material (408 samples) and literature, this study identifies 15 stromatoporoid genera, doubling the previously known generic diversity, so the British Isles holds the third highest genera-diversity Wenlock assemblage after Gotland/Estonia (23 genera) and the Siberian Platform (20 genera). Remarkably, nearly all samples come from the small (100 × 100 km) Much Wenlock Limestone Formation (MWLF) (Homerian Stage, uppermost Wenlock Series) in the Midland Platform of central England (Avalonia), surrounded, underlain, and overlain by siliciclastics. On the Midland Platform one sample is Llandovery age; 11 samples are Ludlow age (Aymestry Limestone). Other samples from the Isle of Man (Wenlock age, six samples) and south-west Scotland (Llandovery age, three samples) are in transported material, with associated corals and they indicate unpreserved carbonate platforms in northern Britain. A few Llandovery Series stromatoporoids are also reported from Ireland, both north and south of the Iapetus Suture; published reports of Wenlock stromatoporoids from Ireland are shown to be misidentified trace fossils. In the MWLF stromatoporoids (together with the more abundant rugose corals, tabulates, heliolitids, and some microbial carbonates) occur in small patch reefs and in bedded bioclastic grainstones, packstones, and nodular wackestones; stromatoporoids are more common in and near patch reefs. The MWLF stromatoporoid fauna has 15 confirmed low-level taxa: *Labechia conferta (Lc), Lophiostroma schmidti (Ls), Ecclimadictyon macrotuberculatum (Em)* and *E. astrolaxum (Ea), Petridiostroma simplex (Ps) and P. linnarssoni (Pl), Actinostromella vaiverensis (Av), Araneosustroma fistulosum (Af), Densastroma pexisum (Dp), Plectostroma intertextum (Pi), Simplexodictyon yavorskyi (Sy), Eostromatopora impexa (Ei), ‘Stromatopora’ venukovi (‘S’v), Syringostromella borealis (Sb)* and *Parallelostroma typicum (Pt)*. No new taxa were found. The five most abundant taxa (*Lc, Av, Dp, Px,* and *Sb*) total 230 specimens, 64.2% of the MWLF assemblage, consistent with taxa proportions in other Palaeozoic stromatoporoid assemblages. The stromatoporoids have limited growth forms: *Lc* grew laminar frames, mostly in patch reefs; the other taxa range from laminar to high domical, maximum sizes around 40 cm basal diameter. They almost completely lack the complexities and diversities of form of their contemporaries in nearby large carbonate platforms of Baltica (Gotland/Estonia) and Laurentia (eastern USA and Canada); only two samples contain intergrown corals. Overall, British Silurian stromatoporoids may be viewed as a relatively limited shallow marine assemblage that took advantage of suitable conditions in a short time-and-space window in an episode of raised sea level with low siliciclastic input. The MWLF has the largest assemblage in the Avalonia microcontinent at the end of the Wenlock Epoch. Palaeogeographically, the Avalonia assemblage of stromatoporoids lay in an important location between Laurentia, Baltica and other Silurian continents and may have aided distribution pathways of stromatoporoids that presumably had planktonic forms for migration. Stromatoporoids were likely not affected by the mid-Silurian extinction event, but data are insufficient to be certain.

Les stromatoporoïdes de Silurien de Grande-Bretagne. Faunes, paléobiologie et signification paléogéographique

## RÉSUMÉ

Les stromatoporoïdes du Silurien de Grande-Bretagne sont présents dans les roches carbonatées, principalement dans la série Wenlock, ainsi qu’un petit nombre dans la série Llandovery et très peu dans la série Ludlow. En utilisant du matériel de terrain et de musée (408 échantillons) et la littérature, cette étude identifie 15 genres de stromatoporoïdes, doublant la diversité générique connue auparavant. Les Îles Britanniques détiennent donc le troisième plus grand assemblage de Wenlock en termes de diversité des genres après Gotland/Estonie (23 genres) et la Plate-forme sibérienne (20 genres). Fait remarquable, presque tous les échantillons proviennent de la petite (100 × 100 km) Formation calcaire de Much Wenlock (MWLF) (Stage Homérien, dernière série du Wenlock) de la plate-forme du Midland du centre de l’Angleterre (Avalonia), entourée de sédiments siliciclastique sus- et sous-jacents. Sur la plate-forme du Midland, un échantillon est d’âge Llandovery ; 11 échantillons sont d’âge Ludlow (calcaire Aymestry). D’autres échantillons provenant de l’île de Man (âge Wenlock, six échantillons) et du sud-ouest de l’Écosse (âge Llandovery, trois échantillons) se trouvent dans des matériaux transportés, avec des coraux associés et ils indiquent des plates-formes carbonatées non préservées dans le nord de la Grande-Bretagne. Quelques stromatoporoïdes de la série Llandovery sont également signalés en Irlande, tant au nord qu’au sud de la suture de Iapetus ; les stromatoporoïdes metionnés dans des publications concernant le Wenlock d’Irlande se révèlent en fait être des bioturbations fossiles mal identifiées. Dans le MWLF, les stromatoporoïdes (ainsi que les coraux rugueux, les tabulés, les héliolitides et certains carbonates microbiens plus abondants) sont présents dans les petits “patch reefs” et également dans les grainstones bioclastiques lités, les packstones et les wackestones nodulaires ; les stromatoporoïdes sont plus fréquents dans et près des récifs isolés ou “patch reefs”. La faune de stromatoporoïdes du MWLF compte 15 taxons de faible niveau confirmés : *Labechia conferta (Lc), Lophiostroma schmidti (Ls), Ecclimadictyon macrotuberculatum (Em)* et *E. astrolaxum (Ea), Petridiostroma simplex (Ps)* et *P. linnarssoni (Pl), Actinostromella vaiverensis (Av), Araneosustroma fistulosum (Af), Densastroma pexisum (Dp), Plectostroma intertextum (Pi), Simplexodictyon yavorskyi (Sy), Eostromatopora impexa (Ei), ‘Stromatopora’ venukovi (‘S’v), Syringostromella borealis (Sb)* et *Parallelostroma typicum (Pt)*. Aucun nouveau taxon n’a été trouvé. Les cinq taxons les plus abondants (*Lc, Av, Dp, Px* et *Sb*) totalisent 230 spécimens, soit 64,2 % de l’assemblage MWLF, ce qui correspond aux proportions des taxons des autres assemblages de stromatoporoïdes du Paléozoïque. Les stromatoporoïdes ont des formes de croissance limitées : *Lc* a développé des formes laminaires, principalement dans les “patch reefs” ; les autres taxons vont du laminaire à la forme en dôme haute, avec des tailles maximales d’environ 40 cm de diamètre basal. Ils n’ont pas la complexité et la diversité de formes de leurs contemporains des grandes plates-formes carbonatées voisines de Baltica (Gotland/Estonie) et Laurentia (est des États-Unis et du Canada) ; seuls deux échantillons contiennent des intercroissances avec des coraux. Dans l’ensemble, les stromatoporoïdes du Silurien britannique peuvent être considérés comme un assemblage marin peu profond et relativement limité qui a profité de conditions favorables durant une courte fenêtre spatio-temporelle lors d’un épisode d’élévation du niveau de la mer avec un faible apport silicico-clastique. Le MWLF possède le plus grand assemblage du microcontinent Avalonia à la fin de l’ère Wenlock. Sur le plan paléogéographique, l’assemblage de stromatoporoïdes d’Avalonia se trouvait à un endroit important entre les Laurentides, la Baltique et d’autres continents du Silurien, ce qui pourrait avoir favorisé les voies de distribution des stromatoporoïdes qui avaient vraisemblablement des formes planctoniques pour la migration. Les stromatoporoïdes n’ont probablement pas été affectés par l’extinction du milieu du Silurien, mais les données sont insuffisantes pour être totalement concluantes.

## Britische Silurian Stromatoporen. Fauna, Paläobiologie und paläogeographische Bedeutung

## KURZFASSUNG

Britische silurische Stromatoporen kommen in Karbonatgesteinen vor, überwiegend in der Wenlock-Serie, vereinzelt auch in der Llandovery-Serie und selten in der Ludlow-Serie. Aus eigenen Aufsammlungen und Museumsmaterial (408 Proben), sowie aus der Literatur wurden 15 Stromatoporen-Gattungen identifiziert, wodurch sich die zuvor bekannte Gattungs-Diversität verdoppelt. Damit hat die Wenlock-Vergesellschaftung Britische Inselne die dritthöchste Diversität auf Gattungsebene, nach Gotland/Estland (24 Gattungen) und der Sibirischen Plattform (20 Gattungen). Bemerkenswerterweise kommen fast alle Stücke aus der eng begrenzten (100 × 100 km) Much Wenlock Limestone Formation (MWLF) (Homerium, oberste Wenlock-Serie) auf der Midland-Plattform in Mittel-England (Avalonia), die von Siliziklastika umgeben, unterlagert und überlagert ist. Ein Exemplar von der Midland-Platform hat ein Llandovery-Alter, 11 Proben haben ein Ludlow-Alter (Aymestry-Kalk). Weitere Stücke von der Isle of Man (Wenlock-Alter, sechs Proben) und aus dem Südwesten Schottlands (Llandovery-Alter, drei Proben) stammen aus transportiertem Material, wo sie zusammen mit Korallen vorkommen, und weisen auf die Existenz nicht überlieferter Karbonat-Plattformen im Norden Grossbritanniens hin. Auch aus der Llandovery-Serie Irlands sind einige Stromatoporen nachgewiesen, sowohl nördlich als auch südlich der Iapetus-Sutur. Bei publizierten Nachweisen von Wenlock-Stromatoporen aus Irland handelt es sich um fehlbestimmte Spurenfossilien. In der MWLF kommen Stromatoporen (zusammen mit den häufigeren rugosen Korallen, Tabulaten, Heliolitiden und mikrobiellen Karbonaten) sowohl in kleinen Fleckenriffen als auch in geschichteten bioklastischen grainstones, packstones und wackestones vor. Am häufigsten sind Stromatoporen in und in der Nähe von Fleckenriffen. Auf Artebene sind 15 Taxa aus der MLWF belegt: *Labechia conferta (Lc), Lophiostroma schmidti (Ls), Ecclimadictyon macrotuberculatum (Em)* and *E. astrolaxum (Ea), Petridiostroma simplex (Ps)* und *P. linnarssoni (Pl), Actinostromella vaiverensis (Av), Araneosustroma fistulosum (Af), Densastroma pexisum (Dp), Plectostroma intertextum (Pi), Simplexodictyon yavorskyi (Sy), Eostromatopora impexa (Ei), ‚Stromatopora‘ venukovi (‚S‘v), Syringostromella borealis (Sb)* und *Parallelostroma typicum (Pt)*. Neue Arten wurden nicht gefunden. Die fünf häufigsten Taxa (*Lc, Av, Dp, Px* und *Sb*) umfassen insgesamt 230 Exemplare, 64.2% der MWLF Vergesellschaftung, was ihren Anteilen an anderen paläozoischen Stromtoporen-Vergesellschaftungen entspricht. Die Variabilität der Stromatporen-Wuchsformen ist begrenzt. *Lc* bildete laminare Gerüste, überwiegend in Fleckenriffen. Die anderen Arten variieren von laminar bis hoch-kuppelförmig, mit maximalen Durchmessern von 40 cm an der Basis. Die Komplexizität und Formenvielfalt zeitgleicher Vorkommen auf benachbarten Karbonatplattformen Balticas (Gotland/Estland) und Laurentias (östliche USA und Kanada) fehlt fast vollständig. Nur zwei Exemplare sind mit Korallen verwachsen. Zusammenfassend sind britische silurische Stromatoporen als eine relativ limitierte flachmarine Vergesellschaftung zu betrachten, die die günstigen Bedingungen auf kleiner Fläche in einem kurzen Zeitfenster ausnutzte, die sich während einer Episode mit erhöhtem Meeresspiegel und niedrigem Eintrag von Siliziklastika boten. Die MWLF beherbergt die größte Vergesellschaftung auf dem Avalonia Mikrokontinent gegen Ende der Wenlock-Epoche. Paläogeografisch gesehen befand sich die Stromatoporen-Vergesellschaftung Avalonias an einem wichtigen Punkt zwischen Laurentia, Baltica und anderen silurischen Kontinenten, und trug dadurch wohl zur Expansion der Stromatoporen bei, die vermutlich planktonische Verbreitungsstadien hatten. Wahrscheinlich wurden die Stromatoporen nicht vom Mittel-Silurischen Aussterbeereignis beeinträchtigt. Die Datenlage dazu ist jedoch nicht ausreichend um das abzusichern. [Translation by Simon Schneider.]

# Британские силурианские строматопороиды. Фауна, палеобиология и палеогеографическое значение

## АБСТРАКТ

Британские силурийские строматопороиды встречаются в карбонатных породах, в основном в венлокском отделе, а так же в небольших количествах в лландоверийском отделе и в очень малых количествах в лудловском отделе. Используя полевые и музейные материалы (408 образцов) и литературные данные, в настоящей работе определяются 15 родов строматопороидов, удваивая ранее известное родовое разнообразие. Таким образом, Британские острова занимают третье место по родовому разнообразию венлокских групп после Готланда/Эстония (24 родов) и Сибирской платформы (20 родов). Примечательно, что почти все образцы взяты из небольшой (100 × 100 км) Мач Венлоксой Известняковой формации (MWLF) (гомерский ярус, поздний венлок) с платформы Мидленд в центральной Англии (Авалония), окруженной, подстилаемой и перекрытой силикокластическими породами. На платформе Мидленд, один образец имеет лландоверийский возраст; 11 образцов лудловский возраст (Айместры известняк). Другие образцы с острова Мэн (венлоксий возраст, шесть образцов) и юго-запада Шотландии (лландоверийский возраст, три образца) найденные из переотложенного матерала в ассоциациях с кораллами, указывают на несохранившиеся карбонатные платформы на севере Британии. Несколько лландоверийских строматопороид были найдены в Ирландии, к северу и к югу от Япетской сутуры. Опубликованные отчеты по венлокским строматопороидам Ирландии указывают на неверное определение последних, как ихнофоссилий. В MWLF, строматопороиды (вместе с более многочисленными ругозовыми кораллами, табулятами, гелиолитидами и некоторыми микробиальными карбонатами) встречаются в малых изолированных рифах, а также в слоистых биокластических грейнстоунах, пакстоунах и гнездовых вакстоунах; строматопороиды наиболее часто встречаются, как в самих изолированных рифах, так и неподалеку от них. В MWLF, фауна строматопороидов имеет 15 подтвержденных таксонов низкого порядка: *Labechia conferta (Lc), Lophiostroma schmidti (Ls), Ecclimadictyon macrotuberculatum (Em)* и *E. astrolaxum (Ea), Petridiostroma simplex (Ps)* и *P. linnarssoni (Pl), Actinostromella vaiverensis (Av), Araneosustroma fistulosum (Af), Densastroma pexisum (Dp), Plectostroma intertextum (Pi), Simplexodictyon yavorskyi (Sy), Eostromatopora impexa (Ei)*, ‘*Stromatopora’ venukovi (‘S’v), Syringostromella borealis (Sb)*, и *Parallelostroma typicum (Pt)*. Новые таксоны не найдены. Пять наиболее распространенных таксонов (*Lc, Av, Dp, Px* и *Sb*) насчитывают 230 особей или 64,2% фауны MWLF, что соответствует пропорциям таксонов в других палеозойских строматопоридных группах. Строматопороиды имеют ограниченные формы роста: *Lc* формировал ламинарные каркасы, в основном на небольших изолированных рифах. У других таксонов каркасы варьируются от ламинарных до высоких куполообразных с максимальным диаметром до 40 см. По сравнению с одновозрастнами фаунами из карбонатных платформы Балтики (Готланд, Эстония) и Лаврентии (восточный США и Канада), строматопороиды из MWLF не обладают разнообразием и сложностью форм. Только в двух образцах найдены сросшиеся кораллы. В целом, британские силурийские строматопороиды можно рассматривать, как относительно ограниченную мелководную морскую группу, которая, воспользовавшись коротким интервалом роста уровня моря, развилась на ограниченной территории с обедненным привносом силикокластики. MWLF предславляет самую большую фауну Авалония микроконтинента конца венлокского отдела. В палеогеографическом отношении, авалонская фауна строматопороидов имела важное геогафическое расположение между Лаврентийским, Балтийским и другими силурийскими континентами и могла содействовать распространанию строматопороидов, предположительно мигрировавших планктонным путем. Строматопороиды, вероятно, не были затронуты средне-силурийским вымиранием, однако из-за недостаточности данных, этот вопрос остается открытым. [Translation by Davit Vasilyan and Sergei Lazarev.]

Edited by Y. Candela, B. Moon and P. Crowther

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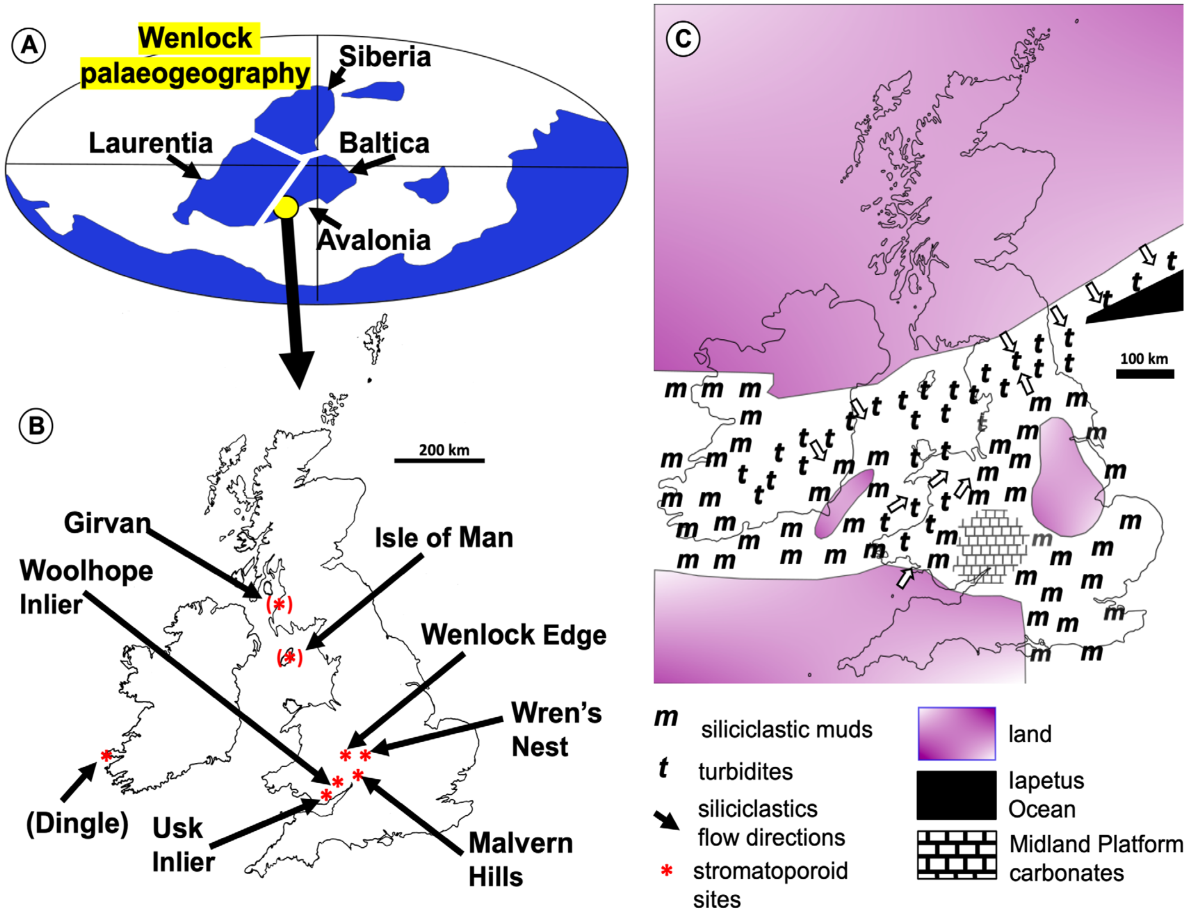
# BRITISH SILURIAN STROMATOPOROIDS. FAUNAS, PALAEOBIOLOGY, AND PALAEOGEOGRAPHICAL SIGNIFICANCE

## CONTENTS

# INTRODUCTION

Stromatoporoids were major components of shallow-marine carbonate systems during 100 million years between the Middle Ordovician and end-Devonian periods (Wilson 1975, chapter 4). There were two peaks of reef development in the Palaeozoic Era: mid-Silurian (Wenlock) and mid-late Devonian (Copper 2002) when stromatoporoids played a key role in reef development; the British geological sequence contains evidence of both peaks. The Silurian Period was a time of major development of stromatoporoid faunas (Nestor 1994) after their recovery from the Late Ordovician extinction (Nestor & Stock 2001). This study focuses on the mid-Silurian stromatoporoids of Britain and Ireland. Most sites lie south of the Iapetus Suture, in the microcontinent of Avalonia, that was by that time merged with Baltica (Text-fig. 1). Some sites are north of the Iapetus Suture and are therefore on the easternmost side of Laurentia. Thus, the British deposits occur in an important region for understanding the pattern of stromatoporoids during the Silurian because of their palaeogeographical position between the stable intracontinental carbonate platforms in Laurentia and Baltica (Text-fig. 1).



Text-fig. 1. **A**, map showing location of British Isles during the Silurian as part of the combined Avalonia-Baltica plate prior to the Caledonian collision with Laurentia. **B**, localities for stromatoporoids used in this study. The five southern localities (Wenlock Edge, Wren's Nest, Malvern area, Woolhope and Usk) expose stromatoporoid-bearing Silurian limestones in the Midland Platform. The Isle of Man contains pebbles of Wenlock-age limestone-bearing stromatoporoids and corals, within the Devonian Peel Sandstone (Crowley *et al*. 2009), of uncertain source. The Girvan area records three stromatoporoid samples incompletely described by Nicholson (NHMUK collections) of unconfirmed Silurian age. The Dingle area has no confirmed stromatoporoids; NMING and CAMSM collections contain misidentified trace fossils in clastic sediments from the 19th century Griffiths collection and the Dingle area is highlighted here to emphasize that point. **C**, palaeogeography of British Isles during Wenlock time, showing the carbonate-rich Midland Platform surrounded by siliciclastics, close to the developing collision zone of the Caledonian orogenic belt.

Stromatoporoid taxa developed through the Silurian Period with changes in the Llandovery and Wenlock epochs (Stock *et al.* 2015, pp. 671–677). Most of the taxa classified as genera, present in this study, are first found in the Llandovery Series and some appeared in the Wenlock Series. Significantly, environmental conditions in the late Wenlock of the Midland Platform in central England allowed a short period of development of a stromatoporoid fauna together with corals and other taxa in reefs and related carbonates. The only available prior comprehensive source is the seminal monograph of British Palaeozoic stromatoporoids published in four parts by Nicholson (1886, 1889, 1891, 1892). Nicholson's work is now significantly out of date; his taxonomy is superseded by specific chapters in the 2015 *Treatise on Invertebrate Paleontology* volume (Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a); also, descriptions of palaeobiological aspects of British stromatoporoids were somewhat limited in Nicholson's work. Therefore, this study aims to fill the gap in knowledge by providing the first modern synthesis of Silurian stromatoporoids from Britain, together with a small number from the Isle of Man (IoM), and some from Ireland documented in literature. For geographical clarity for the purposes of this study, Britain is defined as England, Wales, and Scotland; Ireland includes Northern Ireland and Eire. The IoM is politically separate from the UK and considered in this text where applicable. We draw together all the samples we have been able to obtain from a combination of new field sampling collected since 1975, with appropriate permissions, together with historical museum collections supported by some literature. Throughout this monograph, most of the work applies to the Much Wenlock Limestone Formation. Evidence from other sites including Irish material is less abundant, so in many places reference is made to British and IoM stromatoporoids alone; consideration of other sites is included where appropriate.

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### ABBREVIATIONS

*Museum abbreviations.* BGS, British Geological Survey, Keyworth; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge; NHMUK, Natural History Museum, London; NMING, National Museum of Ireland, Dublin; NMW, National Museum of Wales, Cardiff.

*Stratigraphical abbreviations.* LQLM, Lower Quarried Limestone Member of the Much Wenlock Limestone Formation; MWLF, Much Wenlock Limestone Formation; UQLM, Upper Quarried Limestone Member of the Much Wenlock Limestone Formation.

*Thin section abbreviations.* TS, transverse section; VS, vertical section.

## HISTORY OF RESEARCH OF BRITISH SILURIAN STROMATOPOROIDS

### Occurrence of stromatoporoids

British Silurian stromatoporoids are found in carbonate-rich deposits, but are rare in clay-rich facies, and not known from sandstones. Stromatoporoids are benthic sessile sponges that grew, in the British Silurian, in small build-ups called patch reefs, as well as biostromes and associated bedded bioclastic grainstones and wackestones (Riding 1981). Following the first published description of stromatoporoids by Goldfuss (1826) of *Stromatopora concentrica* Goldfuss (a Devonian sample from Germany), the first reference to British Silurian stromatoporoids seems to be three samples collected from Wenlock Edge, Shropshire, by Lonsdale in 1839, reported by Nicholson (1886, p. 6) in his historic review of stromatoporoids. Nicholson discussed one of Lonsdale's samples, that Lonsdale called *S. concentrica* Goldf. (Nicholson called it *Clathrodictyon striatellum*; in this study it is recognized as *Petridiostroma simplex*) and this is likely the earliest-named British Silurian stromatoporoid. Another of Lonsdale's specimens was noted by Nicholson to be a pisolitic limestone and the third a recrystallized stromatoporoid. Nicholson (1886, p. 12) referred to several other stromatoporoid taxa from Wenlock Edge, including *Stromatopora typica*, *Stromatopora astroites*, *Stromatopora elegans*, *Stromatopora schmidti*, *Stromatopora dentata* (which Nicholson called *Labechia*); apart from *Labechia* the names of all of these were subsequently changed in publications discussed later; the new names are used in this monograph.

Following Nicholson's (1886, 1889, 1891, 1892) seminal work, the succeeding 129 years have yielded limited information on British Silurian stromatoporoids; the same is true for British Devonian System stromatoporoids that are not part of the present study. For the Silurian System, publications generally describe the reefs and associated bedded limestones and commonly note the presence of corals and stromatoporoids with some details. Although coral taxa are sometimes described, stromatoporoids are normally reported as only stromatoporoids, without taxonomic discrimination. Scoffin (1971, 1972) considered the Wenlock reefs in Shropshire, but did not identify stromatoporoids. Other studies of reefs mention stromatoporoids from a sedimentological viewpoint, for example Pässler *et al.* (2014), Ratcliffe (1988), Ratcliffe & Thomas (1999, p. 200), Ray & Butcher (2010), Ray *et al.* (2010). Abbott (1975, 1976) considered growth forms of stromatoporoids, but no taxa were identified. However, Crosfield & Johnston (1914) noted some stromatoporoid taxa from Wenlock Edge reefs (Crosfield & Johnston 1914, p. 200: *Stromatopora carteri* and *Actinostroma*; p. 207: *Stromatopora typica* and *Stromatopora discoidea*; pp. 209–210: *Labechia*, *Stromatopora typica*, *Stromatopora discoidea*, *Clathrodictyon striatellum*, *Clathrodictyon fastigiatum*, *Actinostroma intertextum* of older taxonomy). It is not clear from their paper whether these were found as new samples or were repeated from Nicholson's (1886, 1889, 1891, 1892) work because, although the NHMUK collections include samples collected by Crosfield & Johnston (1914), they have not been formally identified in thin sections. Crosfield & Johnston (1914, p. 201) also noted that a greater number of fossils were found in life orientation in the reefs compared to nearby bedded limestones. Thin sections of new taxa reported (*Labechia rotunda* by Johnston [1915] and *Labechia scabiosa* by Nicholson [1891, pp. 160, 161]) are in the NHMUK; both are reconsidered in this monograph. Caldwell (1936, p. 107) recorded *Actinostroma astroites* and *Hermatostroma* from the Aymestry Limestone south of Wenlock Edge (Elizabeth Alexander, née Caldwell, wrote her PhD on the Aymestry Limestone, then later played a major part in application of radar in the Pacific theatre during the Second World War, see Orchiston 2005). The most comprehensive description of British stromatoporoids since Nicholson's (1886, 1889, 1891, 1892) work is by Colter (1957) in an unpublished PhD thesis on palaeoecology of the Wenlock Limestone, which identified numerous stromatoporoids (held by the Sedgwick Museum, Cambridge) and used Nicholson's taxon names. A second unpublished PhD thesis, by Powell (1980), that focused on rugose corals, tabulates and heliolitids, included valuable information on stromatoporoids. Both PhD theses described stromatoporoid taxonomic and palaeobiological information, which are highlighted in this study. Riding (1981) reviewed the history and geological setting of European Silurian reefs, with a valuable summary of the British exposures. Powell (1991) described an association between a stromatoporoid and an alga from

Wenlock Edge. Generally, the Much Wenlock Limestone Formation (MWLF) in the area south of Hill Top, approximately halfway along Wenlock Edge, Shropshire, was in deeper water and has rare stromatoporoids. Holland *et al.* (1963, pp. 105, 136) noted the presence of *Stromatopora carteri* in the MWLF of the Ludlow area and recorded *Stromatopora* sp. in limestones in the Upper Bringewood Beds, Ludlow Series (Holland *et al.* 1963, pp. 101, 103, 134).

The result of the prior descriptions is that the compilation of stromatoporoid taxa globally, by Stock *et al.* (2015) in the *Treatise on Invertebrate Paleontology*, Part E, reported only eight genera for the Wenlock of England, and that information comes from only Nicholson's (1886, 1889, 1891, 1892) work. Colter's (1957) and Powell's (1980) studies are additional references but the taxa they described are within the total reported by Stock *et al.* (2015).

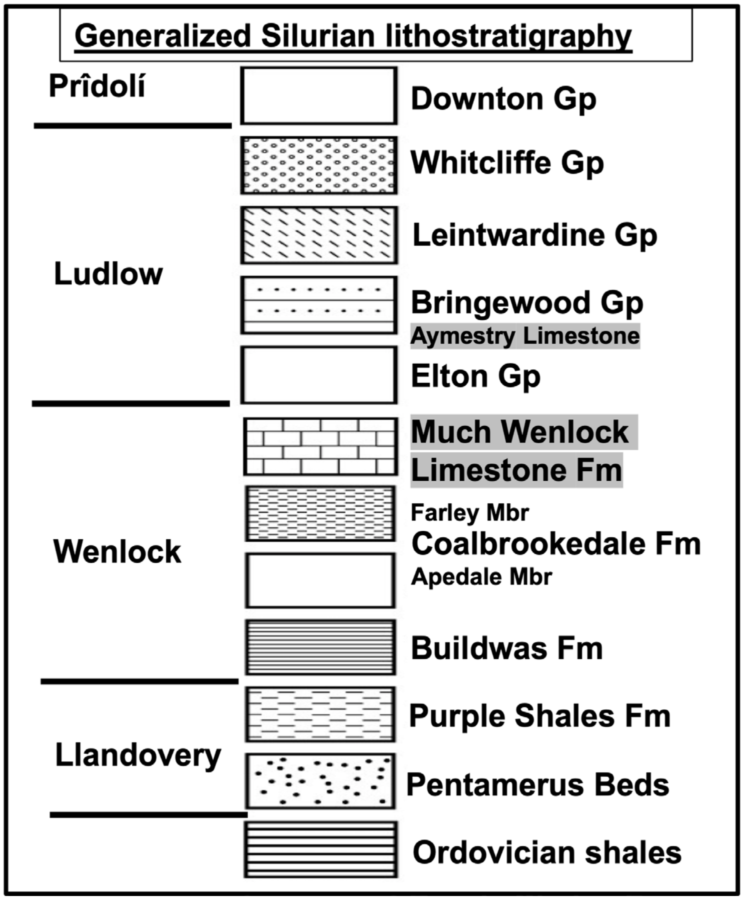
### Stromatoporoid affinity

Regarding the taxonomic position of stromatoporoids, Nicholson (1886, pp. 16, 17) concluded his discussion by reporting on his own earlier work (Nicholson & Murie 1878), with the view that stromatoporoids are calcareous sponges, in accord with modern views confirmed by reports of coralline sponges by Hartman & Goreau (1970); thus from 1970 onwards the living calcified sponges were grouped as Sclerospongiae. For the fossils, the name Stromatoporoidea dates from Nicholson & Murie (1878), and the prevailing view through most of the 20th century is that the stromatoporoids formed their own taxonomic group, Stromatoporoidea. However, discovery by modern sponge workers that spicules of different sponge groups occur in modern calcified sponges (Reitner *et al.* 2001; Vacelet 1985; see also review by Debrenne 1999) led to the view that Sclerospongiae, and thus stromatoporoids, are not a unified group but represented taxa from different sponge groups that had sporadically undergone high degrees of calcification (hypercalcified, hence the title of the 2015 *Treatise on Invertebrate Paleontology*) irrespective of their taxonomic status (see succinct summary by Reitner *et al.* 1999). Stromatoporoids are regarded by modern sponge workers as belonging to the poriferan class Demospongiae because of the presence of astrorhizae, that are evidence of an exhalent canal system (Reitner & Wörheide 2002), despite their lack of spicules. Thus, Sclerospongiae is effectively abandoned as a phyletic group. The discovery of multiphyletic positioning of calcified sponges led to differences of view as to how to classify stromatoporoids. Researchers on modern sponges do not group stromatoporoids together, but authors of the 2015 *Treatise on Invertebrate Paleontology* consider them as a single group and classify stromatoporoids using the established calcareous-skeleton-based groupings that are not consistent with spicule-based groupings (see Nestor 2015; Stearn 2015a; Stock *et al.* 2015; Webby 2015a). Complexities of species identifications and relationships between modern sponge spicule-based taxonomy and fossil stromatoporoid calcareous-skeleton-based taxonomy (e.g. Wörheide *et al.* 1997, 2000) leads to great uncertainty of the phylogenetic value of the calcareous skeleton. Because of these differences of views, the present work adopts a taxonomic approach that aims to maximize on the information obtainable from the stromatoporoids for applications in palaeobiology and palaeogeography by dealing with them at only the lowest level of taxonomy. Thus, mostly, we avoid being hampered by issues regarding higher taxonomic groupings that are largely not needed for this study. This aspect is explored later in this text.

## GEOLOGICAL SETTING, STRATIGRAPHY AND LOCALITIES

### Geological setting and stratigraphy

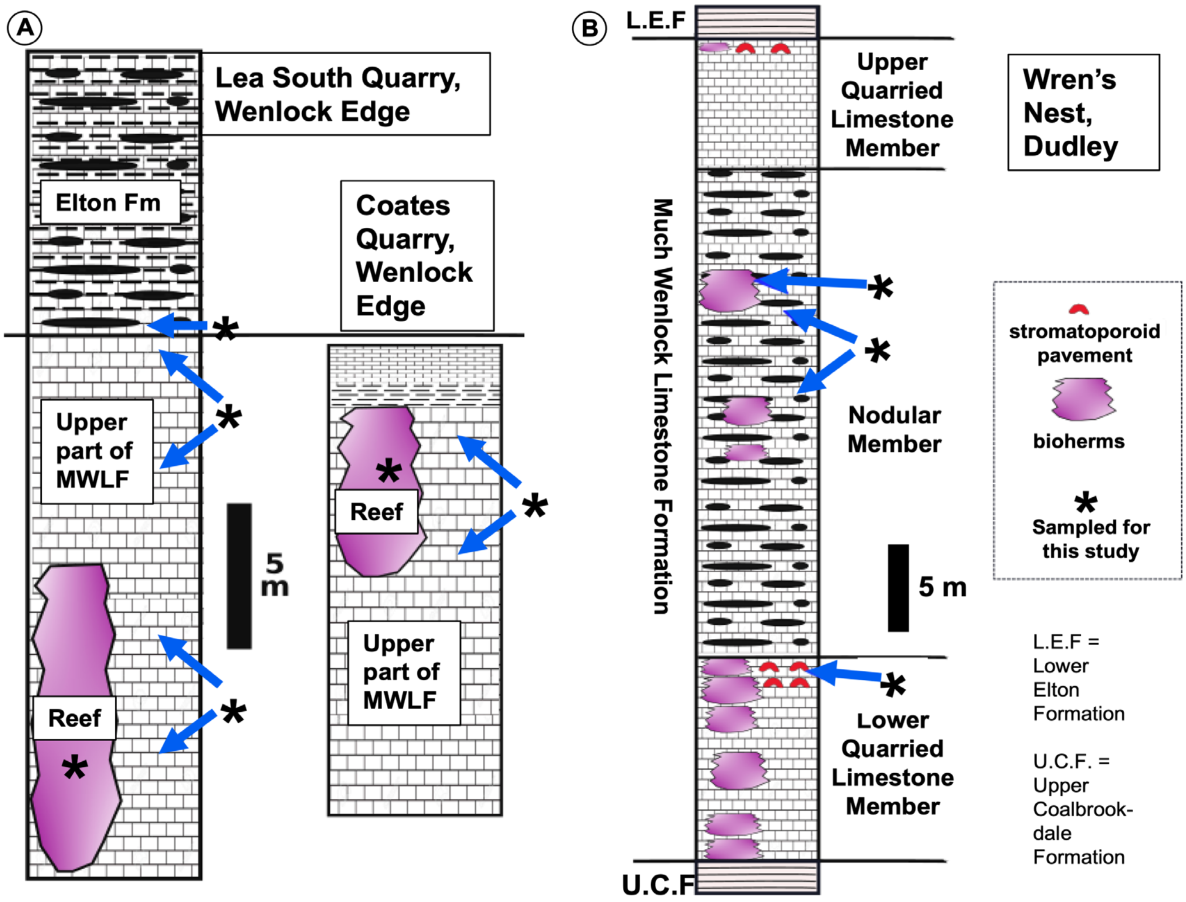
The traditionally named Wenlock Limestone was deposited in the upper Homerian Stage of the upper Wenlock Series (Cocks *et al.* 1992; Zalasiewicz *et al.* 2009). The Wenlock Limestone was formalized as the Much Wenlock Limestone Formation by Bassett *et al.* (1975) (Text-fig. 2) and was divided into three units by Butler (1939). Butler's units were updated according to modern stratigraphic practice by Dorning (1983) to: the Lower Quarried Limestone Member, Nodular Member and Upper Quarried Limestone Member (Text-fig. 3). The MWLF lies largely in the *Colonograptus ludensis* Graptolite Zone (the last zone of the Wenlock Series) in the Wenlock Edge and Ludlow area of Shropshire, and the inliers of May Hill, Usk, and Woolhope, but shows diachroneity of facies because the MWLF in its easternmost outcrops in the Dudley area of West



TEXT-FIG. 2. General stratigraphy of Silurian System sedimentary formations in the Midlands region of England. Textures used in the boxes of the sequence are symbolic to discriminate the successive formations, which comprise a mixture of lithologies. The two highlighted in grey (Much Wenlock Limestone Formation [MWLF] and the thin Aymestry Limestone) contain limestones with low siliciclastic component that allowed stromatoporoid development; all the others are siliciclastic-dominated. However, note that in the Dudley and Malvern areas, the diachronism affecting the MWLF means that the limestones extend down to become age-equivalent to the Farley Member muds of Wenlock Edge area. Silurian chronostratigraphy is complex and variable in the British Isles because of proximity to the Caledonian Orogen; even within the area containing stromatoporoids there are notable regional differences in stratigraphy. For full details of the variation see Ray (2011).

Midlands is within the underlying *Cyrtograptus lundgreni* Graptolite Zone (Bassett 1974, fig. 2). The MWLF of the Malverns and Abberley Hills area is also within the *lundgreni* Zone (see Pässler *et al.* 2014). More recent work by Fry *et al.* (2017) allowed a higher resolution stratigraphy that divided the *ludensis* Zone into two and showed the base of the MWLF is diachronous between the Ludlow anticline and Wenlock Edge. Because the museum collections studied here are poorly stratigraphically constrained within the MWLF, there is limited evidence from the taxonomy of in-place samples of stratigraphic change of stromatoporoid taxa, discussed later in relation to extinctions of other organisms in the late Wenlock Epoch.

The carbonate Midland Platform of central England, the key focus of this study, developed during gentle subsidence allowing the reef system to build its thickness (Woodcock *et al.* 1996), and was outside the main impact of clastic sediments from the south. In south Wales, marginal marine clastics developed (Hillier 2000) and presumably supplied clastics to the Midland Platform. Overall, the contemporaneous tectonic setting of the location of southern Britain close to the closing ocean margin means that Silurian sequences are dominated by siliciclastic sediments, with brief intervals of carbonates during episodes of reduced siliciclastic supply, when stromatoporoids and corals were able to develop. The stromatoporoids occur in shallow-marine carbonates, in both patch reefs and their associated limestones in an area *c.* 100 × 100 km of the Midland Platform, almost all in the MWLF together with rare occurrence in the



TEXT-FIG. 3. Simplified logs of the two major areas of stromatoporoid-bearing limestones, Wenlock Edge (**A**) and Wren's Nest, Dudley (**B**). Most stromatoporoids examined in this study, both from field-based and museum material were collected in these two sites, from the Much Wenlock Limestone Formation (MWLF) in the uppermost part of the Wenlock Series. 'Stromatoporoid pavement' in the Wren's Nest is an informal term used in some references, and represent two thin biostromes rich in stromatoporoids discussed in the text. Brickwork symbol is limestone and black ovoidal shapes represent nodules; horizontal dashed lines are shales. See Ray *et al*. (2010) for detailed logs.

Llandovery and Ludlow series (Text-figs 1–3). Stromatoporoids in Ireland occur in sediments of the Llandovery Series (Nestor 1999).

British Silurian stromatoporoids are not as abundant as in the widespread intracontinental carbonate platforms in neighbouring cratonic areas of Baltica and Laurentia because of the rapidly changing sedimentary regime in proximity to the developing Caledonian Orogen during closing of the Iapetus Ocean (see Stock *et al.* 2015 for comparison of stromatoporoids in different regions in the Silurian). Woodcock (2000) gave an overview of the Silurian stratigraphy and history, and Woodcock & Strachan (2012) described a summary geological history of the Caledonian orogenesis; the stable Midland Platform provided a location for stromatoporoid development, but was under the influence of subsidence (Woodcock *et al.* 1996) and extensional tectonics especially in its western part, particularly during the Llandovery Epoch (Butler *et al.* 1997), that limited carbonate platform development. A broad review by Cocks *et al.* (2003) of the Silurian System of Avalonia explained that because Avalonia was subject to continuous tectonic activity, lithologies tend to be limited vertically and only locally distributed in contrast to the broader areas on larger continents. Within the Midland Platform, Hughes & Ray (2015) presented evidence of a continuous carbonate deposit across the platform.

Riding (1981) made a valuable overview of the carbonates and reefs in the Midland Platform region, demonstrating the small sizes of the reefs in contrast to those of Gotland. Frykman (1989) showed that the Klinteberg Formation on Gotland, approximately equivalent in age to the MWLF in the Wenlock Edge and Ludlow areas (Calner *et al.* 2004), formed a broad carbonate platform with numerous biostromal and biohermal structures; later in this text comparisons are made between the British Isles and Gotland stromatoporoids. In the Dudley and Malvern areas, due to diachronism, the slightly older age of the MWLF approximately coincides with the Halla Formation (underlies Klinteberg Formation) on Gotland and are thus approximately the same age as the Farley Member clastics in Wenlock Edge. Calner *et al.* (2004, fig. 3) summarized the relationship between the Gotland carbonate sequences and climatic episodes, where the Klinteberg Formation lay within one of the episodes of warm climates named Secundo episodes ('S episodes' of Jeppsson 1990), in this case it is the Klinte S episode. Underlying the Klinte S episode are sediments containing the mid-Homerian Mulde Event (Eriksson & Calner 2005, fig. 10) that records extinctions, particularly amongst graptolites. Coinciding with the Mulde Event and Klinte Secundo episode is a double-peaked carbon isotope excursion (the Homerian isotope excursion) that came to an end at approximately the upper limit of the Klinteberg Formation, equivalent to the top of the MWLF described in detail in several papers from Britain (Blain *et al.* 2016; Fry *et al.* 2017; Marshall *et al.* 2012; Ray *et al.* 2010). Stromatoporoids in the lower part of the MWLF thus grew at the time of the Mulde Event extinction and continued to the last part of the Homerian carbon isotope excursion. Evidence of any effect on the stromatoporoids by that extinction and the isotope excursion is discussed later.

British Silurian reefs of the MWLF are small, only up to 30 m diameter and 10–20 m thick. Text–figures 4–7 and 9 illustrate the range of reef structures and their relationship with surrounding bedded clay-rich limestones, strongly contrasting those on Gotland, which can be several kilometres across in the case of middle Silurian biostromes of the Klinteberg Formation (Frykman 1989). A further profound illustration of the small size of MWLF Silurian reefs is the contrast with those of the Canadian Arctic, where De Freitas *et al.* (1993, p. 175) recorded pinnacle reefs that are 300–400 m to as much as 700 m thick, through the Llandovery to Ludlow series on the stable Laurentian Craton; see also the general study of pinnacle reefs by McLaughlin *et al.* (2019). Nevertheless, the concept of pinnacle reefs has been questioned by Brunton *et al.* (2012) in the subsurface of the Michigan Basin, where pinnacle reefs are interpreted as erosional karst towers. Furthermore, even in locations where reefs can be viewed on cliff faces in the Arctic (De Freitas *et al.* 1993, fig. 5), there remains the issue of verification of single reef bodies that would have been several million years old if they are valid; nevertheless, these reefs are certainly much larger than those in Britain. Also lacking in the British reef deposits are: (1) large bioherms such as the giant Thornton reef, up to 2.7 km diameter, in the middle Silurian of Illinois (McGovney 1989) and other reefs in eastern USA (Bourque 1989), and (2) large flat-shaped biostromal structures preserved in extensive carbonate platforms distant from clastic supply, such as eastern Canada (Desrochers & Bourque 1989) and the Ludlow Series of Gotland (Kershaw & Keeling 1994; Sandström & Kershaw 2002). Philcox (1970) described upper Llandovery to lower Wenlock series coral-stromatoporoid bioherms (10 m thick and up to 30 m apart) in the Hopkinton Formation of Ohio. Although some metazoan frames are visible in these beds, no stromatoporoid taxa were recorded.

Narbonne & Dixon (1984, 1989), working in platform interior reefs of the upper Silurian System of Canada, found that such reefs are dominated by noncalcified sponges of the type called lithistids, which are demosponges with siliceous spicules; lithistid is now considered an informal term because lithistids are polyphyletic (Kelly 2007). Stromatoporoids are rare in those reefs, which were also defined by sharp margins (described further below). In Britain, in contrast, there is insufficient preservation of outcrop to know if sponge reefs were present in the platform interior, that is, to the east of the MWLF outcrops. Nevertheless, Scoffin's (1971) interpretation that the exposed Wenlock reefs on the Midland Platform grew close to the platform margin is an appropriate overall environmental interpretation for the Wenlock reefs. Thus, along Wenlock Edge, in the western part of the platform, outcrops reveal a reef tract passing to an off-reef tract within the carbonate platform. Water deepening towards the west prevented reef growth, yet non-reef limestone accumulation continued to the carbonate platform margin further west. Nevertheless, some of the MWLF reefs may be better classified as mounds rather than frame-built structures because of their low content of skeletal metazoans, considered later.

In the Wenlock Series of Ellesmere Island, northern Canada, De Freitas & Dixon (1995, p. 155) recorded uncommon stromatoporoid taxa in mud mounds, including tentatively identified (but not illustrated) *Clathrodictyon*, *Densastroma*, and *Actinostroma*. In the taxonomic work of the revised *Treatise on Invertebrate Palaeontology*, part E (Nestor 2015; Stearn 2015a; Stock *et al.* 2015 Webby 2015a) many of the names are redefined, and we speculate about the possibility that De Freitas & Dixon's (1995) *Clathrodictyon* may be *Petridiostroma*, and their *Actinostroma* may be *Plectostroma*. If so, then all three (*Densastroma*, *Petridiostroma*, and *Plectostroma*) may be the same genera present in the MWLF, considered in the Discussion section of this study.

The sequence stratigraphy approach applied by Ray & Thomas (2007) for Wren's Nest, Ray *et al.* (2010) for Wenlock Edge and Wren's Nest and Ray *et al.* (2013) for the Malvern area, provided evidence that the stromatoporoid-bearing limestones occur in the upper portion of parasequences where water shallowed. That approach is consistent with reports by Riding (1981), citing Crosfield & Johnston (1914), who regarded reef termination as being due to extreme shallowing. Nevertheless, the sequence stratigraphical work of Ray and colleagues cited above shows that some reefs terminate at parasequence boundaries where the sea level deepened abruptly, whereas others terminate below the parasequence boundaries, expressing the individuality of reef development under local controls, presumably variations of clastic sediment supply and water depth. Bentonites present in the MWLF indicate volcanic activity in the region but the impact of this on reef growth is not determined. Certainly, the shallow water nature of the reefs is not in doubt, with occurrence of such cyanobacterial calcimicrobes as *Girvanella* (Green 1959; Johnson 1966) in the reefs (Colter 1957, p. 33). Reefs grew with sharp margins where, in many cases, the abundance of skeletal reef-builders is very low; these margins appear to have been constructed by microbial carbonates (Colter 1957; Kershaw *et al.* 2007), emphasizing the complex mixture of skeletal metazoans and microbial carbonates of which the reefs are composed (see also Riding 1981; Scoffin 1971). Text-figure 7A, B show the general character of the sharp margins, and detailed views are provided by Kershaw *et al.* (2007).

### Localities – general points

Localities that provided new samples for this study are limestone quarries with exposed rocks from: Wenlock Edge in Shropshire; Wren's Nest at Dudley, West Midlands; and the Malvern and Abberley Hills in Worcestershire. Stromatoporoids are mentioned and described in early publications from these sites: Murchison (1839, p. 214) for Wenlock Edge; Butler (1939) for Wren's Nest; Phillips (1848) for the Malverns area. Museum collections include material from all three areas and also: Benthall Edge and Lincoln Hill near Ironbridge (these are northern extensions of Wenlock Edge); Walsall in the West Midlands (Colter 1957); the Woolhope Inlier in Herefordshire (Squirrel & Tucker 1960, p. 173), where there are several stromatoporoid taxa in the Wenlock Limestone; and the Usk Inlier in Monmouthshire, from which Walmsley (1958, p. 512) listed tabulates but no stromatoporoids, yet there are some from Usk in museum collections. In the May Hill inlier, west of the Malvern Hills, Lawson (1955, p. 90) mentioned tabulates and stromatoporoids, commonly in growth position, in patch reefs in Hobbs Quarry, but no further details are provided; although tabulates are mentioned in Lawson's (1955) fossil list of Ludlow fossils in the area, stromatoporoids are not. Gardiner's (1920) list of fossils from May Hill includes some tabulates but not stromatoporoids. However, Nicholson (1889, p. 149) noted at least one stromatoporoid taxon at May Hill, but there are no samples from May Hill in the Natural History Museum Silurian stromatoporoid collections (where all Nicholson's material is stored); however, one sample from May Hill, unidentified, is in the British Geological Survey collections in Keyworth. In Text-figure 1 the approximate locations of the sites are illustrated; detailed descriptions of locations, stratigraphy, and correlation of sites are provided by Ray & Thomas (2007) and Ray *et al.* (2010, 2013), to which the reader is directed for further information. Although not part of the UK, the southwestern Ireland Dingle Peninsula has reports of Wenlock-age stromatoporoids with older names for taxa, as part of the Avalonian microcontinent, and thus approximately age-equivalent to the MWLF (Griffiths & McCoy 1846). However, two specimens from the collections of Griffiths & McCoy (1846), one in CAMSM, the other in NMING, examined during this study, were revealed as *Zoophycos*-like trace fossils in fine-grained argillaceous sandstones, possessing concentric patterns resembling the basal surfaces of many stromatoporoids, but they were not the real McCoy. Given that Griffiths & McCoy (1846) described them only 20 years after stromatoporoids were first described by Goldfuss (1826), such a mistake is understandable and posthumously forgivable! This error means that there are no current records of Wenlock stromatoporoids in western Ireland, but the location is included in Text-fig. 1 to highlight this misidentification.

Llandovery-age stromatoporoids are rare in the British Silurian, with one sample included for the southern part of Britain, south of the Iapetus Suture line and therefore part of Avalonia. There are some in the northern part of Ireland that was north of the Iapetus Suture and thus part of the Laurentian area (Nestor 1999). These are briefly considered in the context of this study.

Two other occurrences of Silurian stromatoporoids are recorded in the British Isles, both as pebbles in conglomerates: (1) pebbles of likely Llandovery age from two localities near Girvan in southern Scotland, studied by Nicholson (NHMUK collections) discussed later; and (2) Wenlock-age pebbles in the Lower Devonian Peel Sandstone in the Isle of Man (Crowley *et al.* 2009). These two deposits have a sparse stromatoporoid fauna and are briefly considered in the context of British Silurian palaeogeography. The Isle of Man was located very close to the northern edge of Avalonia during the Silurian (Cope *et al.* 1992) but the Wenlock-age pebbles in the Peel Sandstone are presumably derived from an unknown location, no longer preserved. The Girvan area lay on the northern margin of Iapetus (Cope *et al.* 1992) also representing unknown source areas.

### Localities of new samples

Coordinates of localities that sourced stromatoporoids are accurate in our new sampling; estimates are made for museum materials, listed below.

*Wenlock Edge, Shropshire.* Coates Quarry (MWLF): SO 605 993; Lea Quarry South (MWLF including a few specimens from the very base of the overlying Elton Formation at the top of the quarry): SO 594 982.

*Dudley, West Midlands.* Wren's Nest Hill (MWLF): SO 937 920.

*Malvern Hills, Worcestershire.* Parkwood Quarry [main] (MWLF): SO 7644 4440; Crews Hill Quarry (MWLF): SO 733 529.

*Abberley Hills, Worcestershire.* Whitman's Hill Quarry (MWLF): SO 7490 4830; Penny Hill Quarry (MWLF): SO 7517 6132.

*May Hill, Herefordshire.* Hobbs Quarry, near Longhope (MWLF): SO 695 195.

*Isle of Man.* Peel Bay (Peel Sandstone): between 4.6819° W 54.2288° N (SC 2527 8478) and 4.6812° W 54.2298° N (SC 2527 8481); Whitestrand beach (Peel Sandstone): between 4.6582° W, 54.2382° N (SC 2684 8577) and 4.6578° W 54.2388° N (SC 2686 8588).

### Additional sites to include museum samples

*Walsall, Midland Platform.* Daw End railway cutting (MWLF): SK 034 009.

*Girvan area, South Ayrshire.* Woodland Point and Balcletchie (Lower Silurian): NX 169 952.

*Craven Arms, Shropshire.* View Edge Quarry (Aymestry Limestone, lower Ludlow Series): SO 425 808.

*Woolhope Inlier, Herefordshire.* Unspecified localities of MWLF near Dormington and Stoke Edith, central Herefordshire; these are sites labelled on thin sections in NHMUK and CAMSM.

*Usk Inlier, Monmouthshire.* Cilwrgi Quarry (MWLF): ST 3394 9836.

*Southwestern Ireland.* Dunquin, Dingle Peninsula (upper Wenlock Series): 10.4517° E; 52.1237° N.

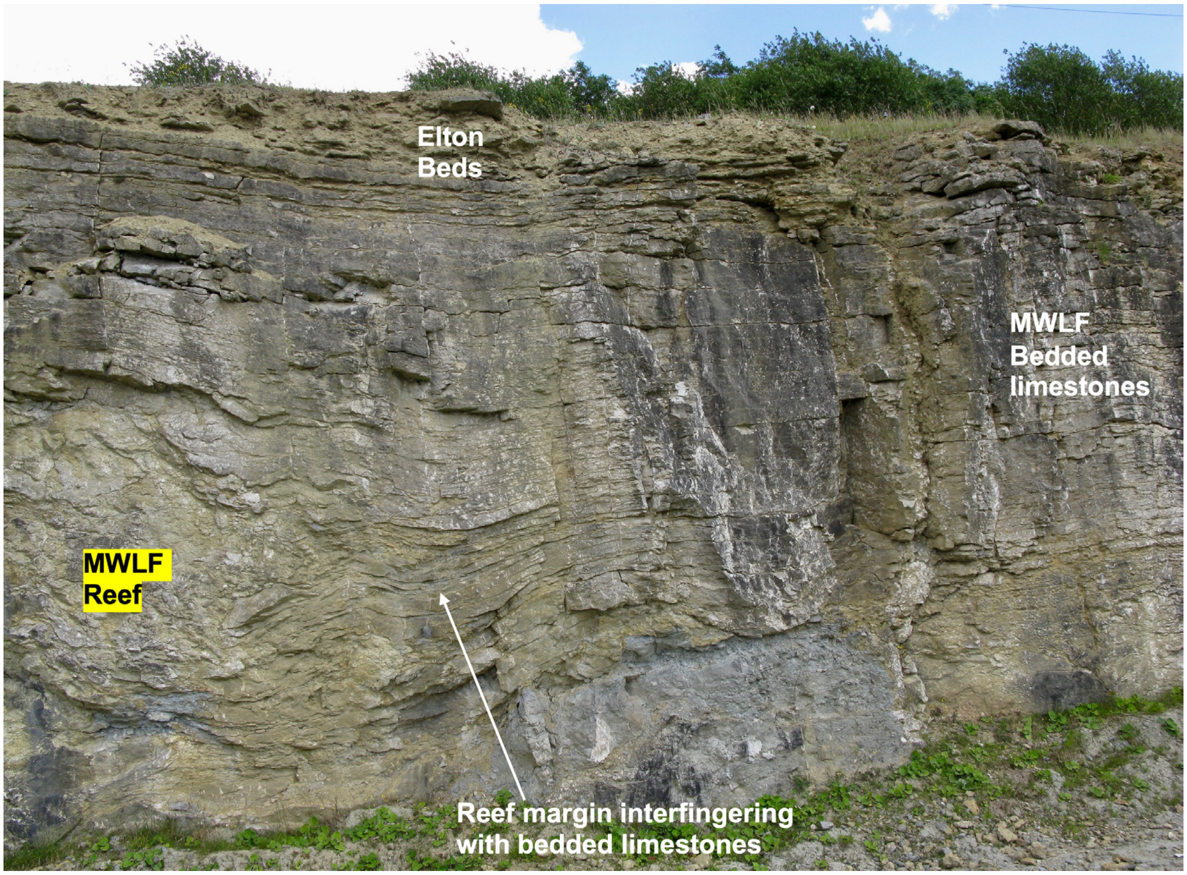
## MATERIALS AND METHODS

### Nature of the sample set and approach to analysis

Because of extensive historical industrial quarrying for limestone in the Midlands of England, there are numerous exposures in old quarries, but unfortunately the reef limestones were major targets for extraction and little now remains. Furthermore, geoconservation of outcrops is an important aspect of our approach to obtaining samples, resulting in a strategy of careful collecting with appropriate permissions, causing as little damage to in-place samples as could be achieved. Samples were assembled from: Coates and Lea Quarries on Wenlock Edge; Wren's Nest in Dudley, and the Malverns and Abberley Hills area; they are a mixture of in-place and loose samples. Text-figures 4–10 illustrate the nature of outcrops of key sites and examples of in-place stromatoporoids used in this study. Text-figure 11 provides a schematic reconstruction of MWLF reefs and their principal features, explained in detail in the Results section.

Text-fig. 4. Field photographs of small reefs and associated bedded limestones that contain stromatoporoids in the Much Wenlock Limestone Formation (MWLF) of the Midland Platform in central England. **A**, Whitman's Hill Quarry, Abberley Hills, Worcestershire at SO 7490 4830, showing very small patch reef (centre, arrow) in bedded limestones dipping gently to the left. **B**, patch reef (arrow) and bedded limestones, Harley Road section, Wenlock Edge, 1 km west of Much Wenlock, Shropshire at SJ 609 004.

Museum collections provided an important source of information on taxa, with thin sections and some hand specimens examined in the Natural History Museum, London; Sedgwick Museum, Cambridge; National Museum of Ireland; and National Museum of Wales, Cardiff. Most museum samples studied are labelled "Wenlock Limestone" from times before definition of the MWLF by Bassett *et al.* (1975). Therefore, we assume that all samples labelled Wenlock Limestone are from the MWLF, but mostly without knowledge of which of the three members (Dorning 1983) they came from. Several samples listed at the Oxford University Museum of Natural History as Llandovery-age stromatoporoids were unfortunately mislabelled and are

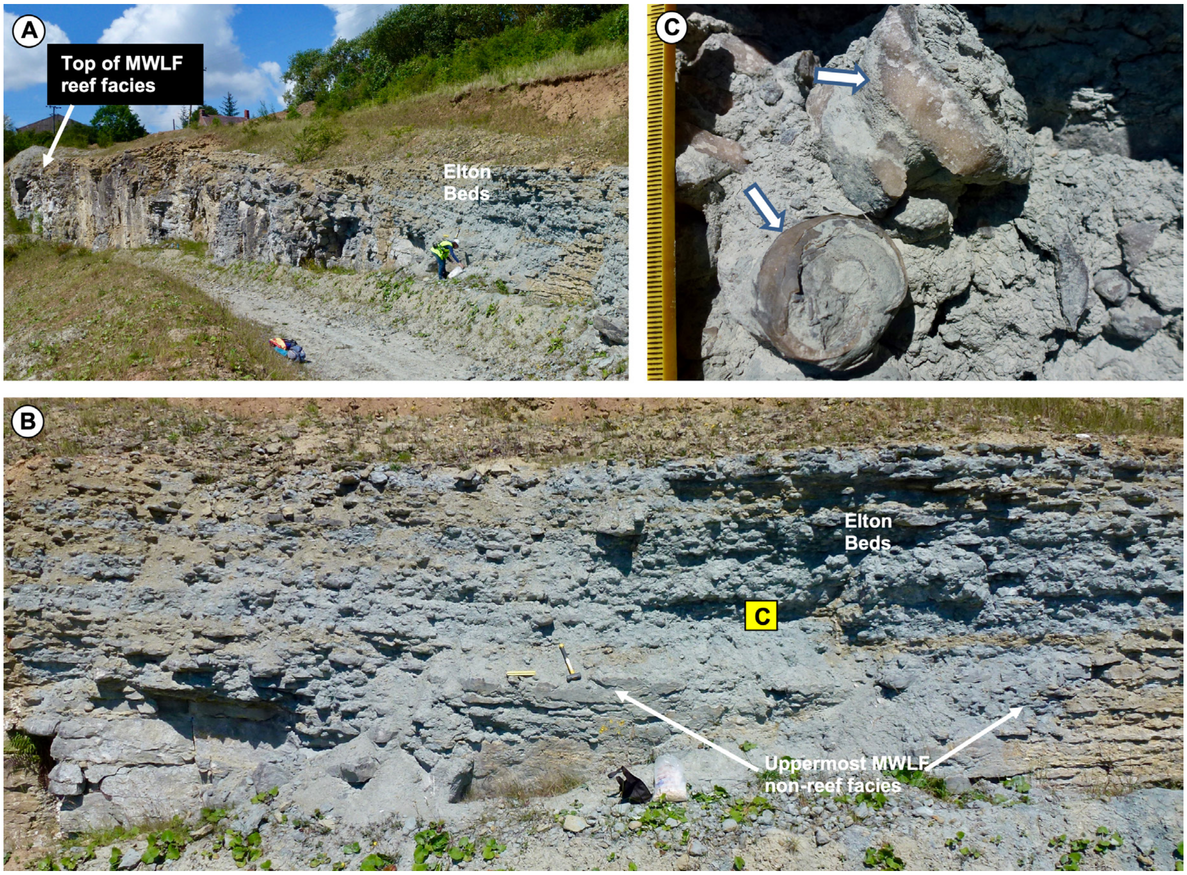


TEXT-FIG. 5. Field photograph of vertical section through part of a large patch reef (left quarter of photo) in the uppermost part of the Much Wenlock Limestone Formation (MWLF), showing interfingering of its margins with bedded limestones (packstones to wackestones), together with overlying Elton Beds of the lower Ludlow Series, north end of Lea South Quarry, Wenlock Edge, SO 594 982. The top of the MWLF is defined as the upper surface of the thick crinoidal limestone beds (Ray *et al*. 2010; Blain *et al*. 2016), shown near the top of the photo. This is one of the few remaining large patch reefs preserved in the MWLF.

sandstones lacking stromatoporoids. The British Geological Survey has nine Silurian specimens from old collections, three were not identifiable and the remaining six contain the same taxa as found in other sources, but most are not well linked to localities; they are not included in the data array and are mentioned only briefly in this study. Finally, some very helpful private collectors donated some samples.

Thus, we have assembled the largest collection of British Silurian stromatoporoids so far achieved, and, together with literature including Irish material, present an integrated study of their taxonomy, growth forms, and environmental settings. During this work we also encountered tabulates and heliolitids that grew along with stromatoporoids and in many cases have similar growth forms. Comparison is therefore made where appropriate.

We considered the possibility that museum collections comprise samples selected for their visual appearance in the field, so that the overall sample set may be biased and not representative of the proportional occurrence of stromatoporoid taxa in nature. It is possibly important that some stromatoporoids are more noticeable than others, in particular *Labechia conferta* (Lonsdale) has a distinctive papillate upper surface and may thus be noticeable to collectors; it is also a rare example of a Silurian stromatoporoid that can be reasonably reliably identified from hand specimens. Attractive features of other taxa include the banding formed by successive growth layers, the upper surface astrorhizae (not present in all taxa) and concentric basal rings caused by growth on soft substrates from which the mud was weathered in outcrop. Kershaw *et al.* (2006, 2018) drew attention to the ability of stromatoporoids to grow on soft substrates, which to a large extent applies to all stromatoporoids, so that basal rings

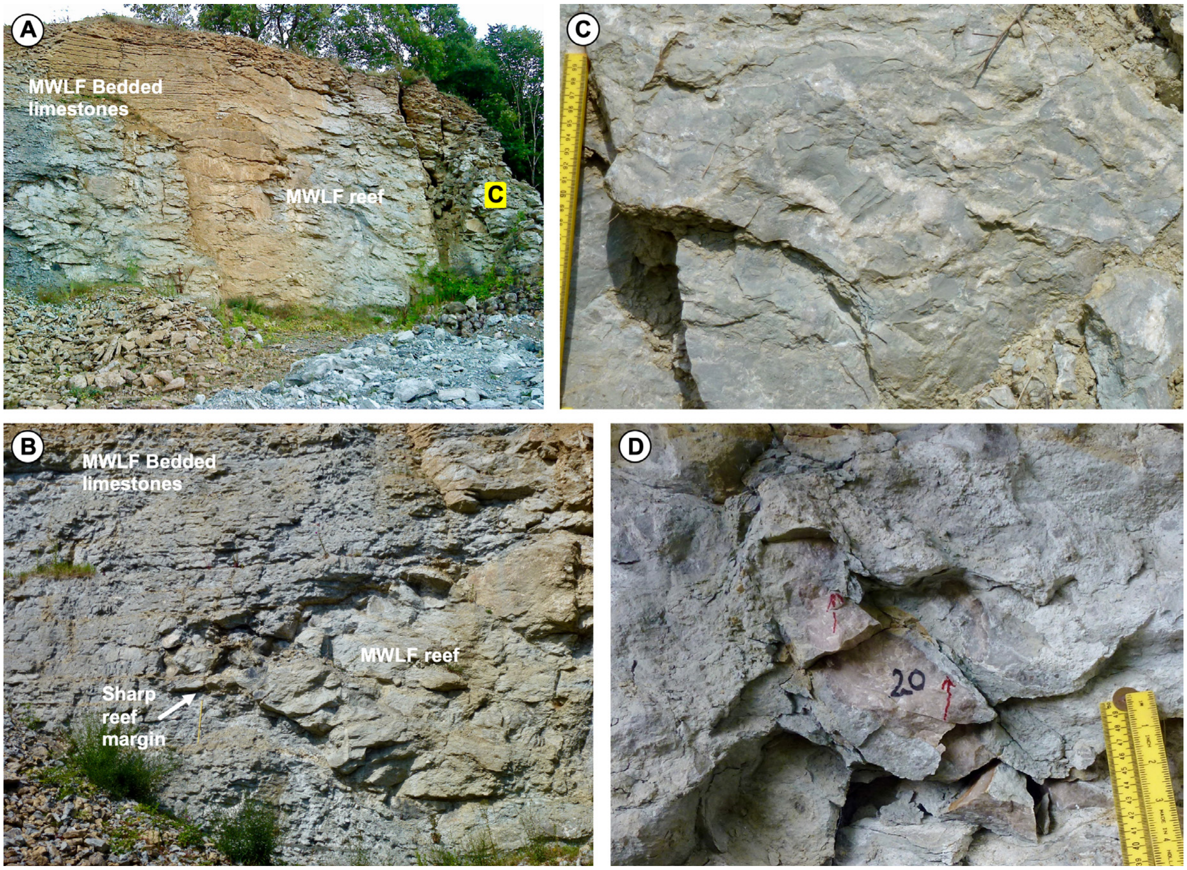


TEXT-FIG. 6. Field views of top part of Much Wenlock Limestone Formation (MWLF), with overlying Elton Beds, Lea South Quarry, Wenlock Edge, Shropshire SO 594 982. **A**, general view; the reef shown in Text-fig. 5 is on the left. **B**, closer view of carbonate-rich MWLF overlain by muddy Elton Beds sediments; location of C shown in centre. **C**, detail of fossils in boundary area between the MWLF and Elton Beds. Lower arrow shows a stromatoporoid (*Araneosustroma fistulosum*) encrusted a gastropod then rolled over onto its side; upper arrow shows a tabulate coral.

are common. Stromatoporoids cemented into the limestone in rock faces are not as visually attractive and are more difficult to sample. Nevertheless, despite these concerns, there is no noticeable difference in the distribution of stromatoporoid taxa in our own samples compared to museum collections. Furthermore, there is no noticeable difference in the taxonomic distribution of loose stromatoporoids sampled, from those collected in-place. Consequently, we have no evidence of collecting bias in the distribution of taxa in our overall dataset, so we are confident that the suite of stromatoporoid taxa found in this study is as representative of the living assemblage as we could expect. Museum material was studied mostly as thin sections of stromatoporoids; together with loose samples from our own collecting, much of the dataset lacks exact locality positioning, growth form, and sedimentary facies data. Thus, we have opted for simple statistical representation of the data, in histograms and graphs, and base our interpretations on these basic forms of analysis.

### STROMATOPOROID GROWTH FORMS

Quarry faces and loose blocks commonly reveal stromatoporoid growth form cut in vertical section (e.g. Text-figs 7, 8, 10 for in-place samples), where the stromatoporoids are mostly orientated upright in the outcrop, noted also in historical documentation (e.g. Colter 1957; Scoffin 1971). Complete loose samples weathered out of soft argillaceous carbonates are common on the quarry floors; in many cases they are small enough to be displayed in their entirety in large thin sections. Such samples provide valuable information on growth forms, the nature of the substrate upon which the stromatoporoids grew, and the response of stromatoporoids to



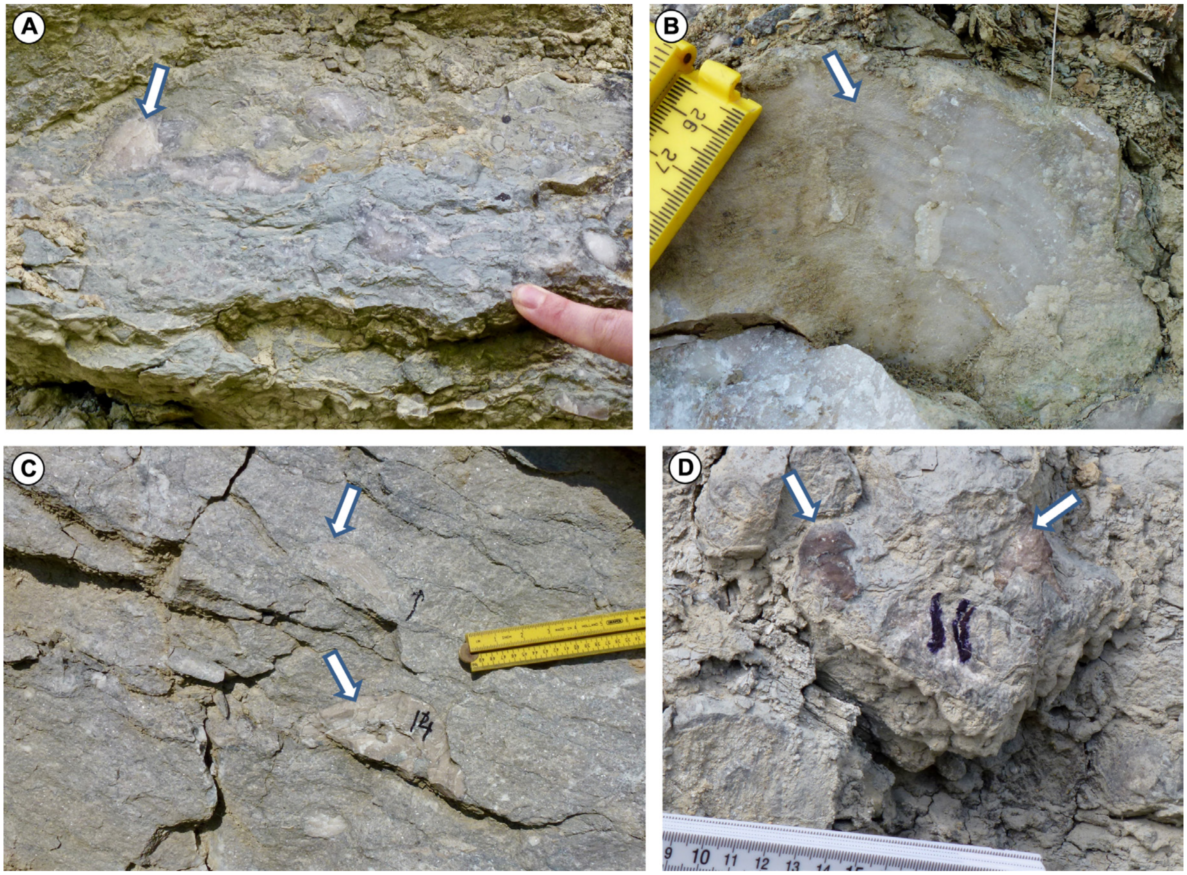
TEXT-FIG. 7. Field photographs comparing appearance of patch reef and non-reef facies in the Much Wenlock Limestone Formation (MWLF), Coates Quarry, Wenlock Edge, Shropshire, SO 605 993. **A, B**, general views of patch reef, showing its unbedded structure and its sharp margin with adjacent bedded limestones. Location of C is shown in A. **C, D**, comparison between reef framework (**C**) of laminar-form stromatoporoid *Labechia conferta* (one of few stromatoporoid taxa identifiable in the field) with green-grey micrite infill and inter-reef wackestone (**D**) showing one stromatoporoid (*Plectostroma intertextum,* number 20 [CAMSM X.50347.148] in centre), typical of isolated specimens in inter-reef beds.

growth interruption events. Growth form may be related to taxa in some cases, although in the British Silurian stromatoporoids growth forms are mostly simple and range from laminar to high domical and are rarely larger than 20 cm in basal diameter. Overall, stromatoporoid growth form is most usefully studied by a combination of observations and measurements from field sites, polished surfaces of cut samples and details in thin sections.

## ISSUES OF IDENTIFYING STROMATOPOROIDS

In his Victorian-era monograph on British stromatoporoids, Nicholson (1886, Introductory remarks) highlighted two critical aspects of stromatoporoids that are barriers to simple taxonomy; we add a third issue below:

1. There is a variable effect of diagenetic alteration on stromatoporoid skeletal structure that may obscure clear view of the skeletal elements required to identify taxa. Nicholson (1886) drew attention to the need to assess well preserved specimens in an assemblage that can then be used to identify altered specimens. With due care, it is normally possible to identify all samples as long as both vertical (VS) and transverse (TS) thin sections are available, unless the stromatoporoids are severely altered. Note that the 2015 *Treatise on Invertebrate Paleontology* volume uses the alternative terminology of longitudinal for vertical and tangential for transverse.
2. There is considerable variability of skeletal structure, so that one sample may be easily identified from the ideal combination of VS and TS thin sections, but another sample

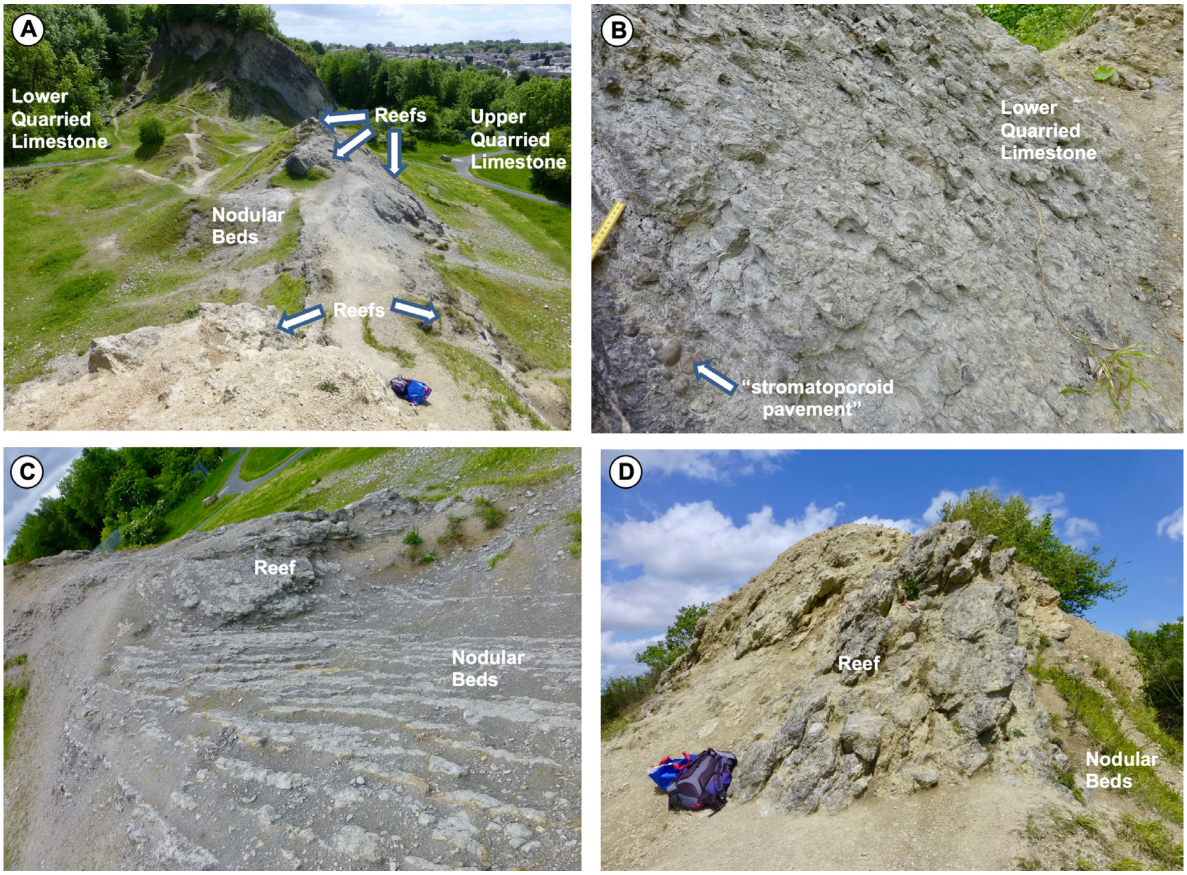


TEXT-FIG. 8. Field photographs of typical appearance of stromatoporoids and tabulates (arrows) in the Much Wenlock Limestone Formation, Wenlock Edge, Shropshire. **A, B**, reef stromatoporoids in Coates Quarry; **A**, low domical form (CAMSM X.50347.163, *Plectostroma intertextum*). **B**, high domical form (CAMSM X.50347.143, *Ecclimadictyon macrotuberculatum*) shows growth banding. **C**, non-reef stromatoporoids in Lea South Quarry; number 14 is a domical form (CAMSM X.50347.72, *Actinostromella vaiverensis*). **D**, high domical form of tabulate, illustrating difficulty of distinguishing stromatoporoids and corals in the field.

of the same taxon may be more difficult because its growth history, or perhaps precise environmental conditions, resulted in sufficient variation of structure that requires careful study to recognize both samples as one taxon. It is also common for one part of a large thin section to be readily identifiable, but another part of the same thin section, where the structure varies, to be not clearly recognizable. Stearn (1989) in a very short but insightful discussion, analysed the problem of variability of stromatoporoid structure in taxonomy, raising awareness of the need for understanding of variability and the danger of taxonomic over-splitting.

3. Following on from the previous point: historically, publications on stromatoporoids present only limited areas of thin sections at large scale in small photographs that prevent the reader from appreciating variability across the sample and can lead to problems of identification and comparisons between taxa.

In order to address these problems, our approach, where samples are large enough, is to use large thin sections and illustrate them at different scales, so that large areas of a thin section may be imaged, together with selected smaller areas at higher magnification. Plates 1–22 were assembled on this basis. We also advocate the addition of scale bars directly onto the photographs, instead of the common practice of stating the magnification of the photograph in the caption, critical in these days of electronic files. Thus, the text-figures and plates of this study present a comprehensive illustration of British Silurian stromatoporoid taxa, in order to



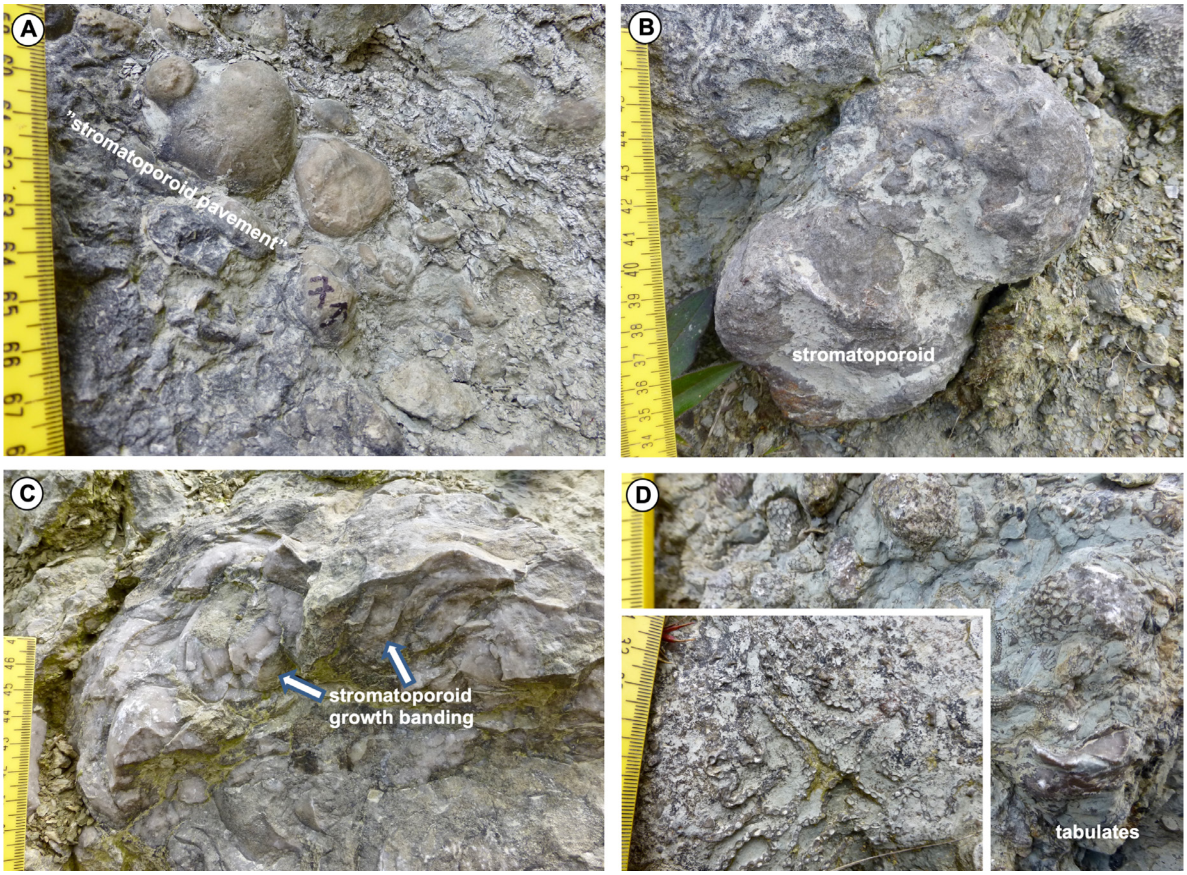
Text-fig. 9. Field views of reefs and bedded nodular limestones of the Much Wenlock Limestone Formation, Wren's Nest, Dudley, West Midlands, SO 937 920. **A**, general views with small patch reefs (arrows) in the Nodular Member. **B**, bedded mud-rich limestones of the top of the Lower Quarried Limestone, showing a 50 cm thick stromatoporoid biostrome, lower left, informally termed 'stromatoporoid pavement' in Ray & Thomas (2010). **C, D**, vertical section views of the Nodular Member showing patch reefs and adjacent nodular bedded limestones (**C** is re-orientated so the beds are horizontal; **D** is the largest patch reef).

demonstrate their appearance in as full detail as possible, but also to provide future researchers with a tool set of images to assist identification of new samples and their growth features. We have also found that good photographs of stromatoporoid thin sections are at least as good as, and often better than, the thin sections themselves, because optical features of photographs can be compared more readily with those in publications.

Apart from *Labechia*, the names are all changed in the modern taxonomy presented in this paper, but it was interesting to discover during research for this study in the NHMUK collections that the names of stromatoporoids in Nicholson's collection are not always consistent. Thus, it was not possible to simply translate each of Nicholson's taxa names into a modern name without first carefully checking each Silurian-age specimen in thin sections held in NHMUK. The same caveat applies to the NMW and CAMSM collections by other researchers.

### Approach to taxonomic classification of stromatoporoids

As with many fossil groups, stromatoporoid taxonomy is easy for some taxa and ranges from easy to very difficult for others. As mentioned above stromatoporoids lack the spicules used in modern sponge taxonomy (except in a single Devonian specimen: Da Silva *et al.* 2014). Thus, taxonomy relies on the calcified skeleton, which is a secondary skeleton formed by calcification of the primary spongin framework (Vacelet 1985). As in all palaeontological taxonomy, we accept as low-level taxa those specimens that are clearly and consistently distinguishable from other taxa. Skeletal variation within and between specimens considered to be the same taxon can be



Text-fig. 10. Field views of stromatoporoids (**A–C**) and tabulates & heliolitids (**D**) in patch reefs of Upper Quarried Limestone, Much Wenlock Limestone Formation, Wren's Nest, Dudley, West Midlands, SO 937 920. **A**, stromatoporoid biostrome ('pavement' of Ray & Thomas 2010) level in the upper part of the Lower Quarried Limestone (Text-fig. 3B) is the upper of two thin biostromes described in the text; this biostrome contains a stromatoporoid fauna dominated by *Syringostromella borealis*. **B, C**, small domical stromatoporoids from patch reefs in the Nodular Member. **D**, heliolitid and halysitid tabulates near to B and C, included as reminders that the patch reefs are dominated by heliolitids and tabulates, and that stromatoporoids are much less abundant.

significant and has led to significant over-splitting, not helped by use of photographs of only small areas of thin sections in publications as explained in the previous section. We agree with Stearn (1989) that it is much more realistic to view stromatoporoids as having far fewer low-level taxa than recorded across stromatoporoid literature. Genera defined in several chapters of the *Treatise on Invertebrate Paleontology*, Part E (Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a) have stabilized stromatoporoids of the traditional genus level. However, within modern hypercalcified sponges the recognition that the calcified skeleton is phyletically convergent, and that calcified sponges occur across different sponge groups (summarized in a discussion paper by Vacelet 1985), reduces confidence in the value of traditional higher-level taxonomic groupings in fossil stromatoporoids. Furthermore, Reitner & Engeser (1987) recognized, using spicules, three different species of the living chaetetid-form calcified sponge *Acanthochaetetes* within an identical calcareous skeleton. More recent sponge work has taken the taxonomy a stage further: Wörheide *et al.* (2000), noting that the modern stromatoporoid-like calcified sponge *Astrosclera willeyani* has great variability in spicule morphology, tested the sponge for variations in DNA, and discovered sufficient variation to warrant division into three species. None of these distinctions are possible in fossil stromatoporoids so the possibility remains that the lowest-level taxa we use in this study contain more than one biological species. Therefore, reliability of distinction of *biological species* in fossil stromatoporoids is not supported by evidence. Da Silva *et al.* (2011a, b) approached this problem in Devonian stromatoporoids of Belgium by accepting genus-level of stromatoporoid taxonomy as being taxonomically robust, but in this monograph we have considered the problem further. For example, in two taxa common in the MWLF, *Ecclimadictyon macrotuberculatum* is distinctly different from *Ecclimadictyon astrolaxum* (compare Pls 8 and 9), such that there is no doubt that they can be separated in the same deposits, but, based on the argument regarding modern sponges above, there is no certainty that these two traditionally recognized stromatoporoid species represent only two biological species. A logical extension of this argument is that there is no proof that these two taxa even lie within the same genus. The consequence of this approach is that comparisons in literature are somewhat compromised. The recognition that the *Ecclimadictyon* genus is cosmopolitan in the Wenlock (Stock *et al.* 2015) does not discriminate whether the traditional *species* within *Ecclimadictyon* are cosmopolitan. If the two lowest-level taxa identified as *E. macrotuberculatum* and *E. astrolaxum* were indeed from different biological genera (which is unknown of course), then the summary tables of genera distribution in Stock *et al.* (2015) would not give an accurate account of the true distribution of the taxa. Thus, because there is no guarantee of phyletic relationship between taxa that have similar architecture of calcareous skeleton, grouping stromatoporoid taxa into families, orders, and even classes is highly uncertain. Stearn (2015c, pp. 566, 567) expressed the view that the calcareous skeleton is the only available material in Palaeozoic stromatoporoids for phyletic groupings, but the problem continues that because those skeletons are not phyletically useful in modern hypercalcified sponges, then there is no certainty that phylogeny based on calcareous skeletons in the fossils has any value. However, for the purposes of this study, phylogeny has minimal impact in applications of stromatoporoids in palaeobiology, palaeoecology, and sedimentology and so our focus on lowest-level taxa without consideration of higher groupings is appropriate to our aims. Consequently, in the systematic descriptions of Silurian stromatoporoids presented in this monograph, we have provided, for reference purposes only, the classification of traditionally used families, orders and classes adopted by most publications (e.g. Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a). However, we have not used this classification in the stromatoporoid fauna analysis because, as outlined above, the relationship between the low-level taxa is unknown. Nevertheless, our work has required careful decisions about the identity of each sample. As a result, we regard each taxon as having equal status, so the difference between *E. macrotuberculatum* and *E. astrolaxum* mentioned above, and the difference between either of these and any of the other taxa are considered equal. Some problematic samples were partly identified, because their preservation was poor and so these are not included in the systematics section included at the end of this monograph. Nevertheless, poorly preserved material was included in the overall count in order to maintain the largest assemblage we can provide. No new taxa were found, and so we follow the formal descriptions of the updated versions of genera in the *Treatise on Invertebrate Paleontology*, Part E of 2015 (Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a), they are repeated in the systematic descriptions section.

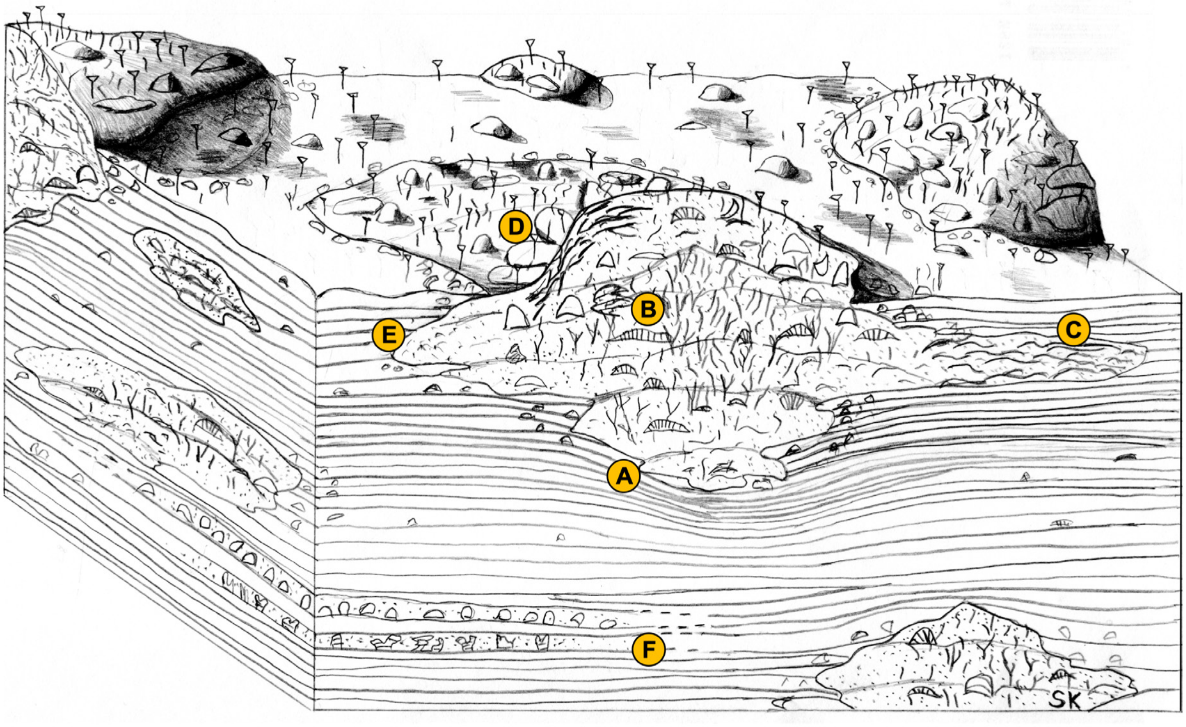
A curious addendum to the discussion of stromatoporoid taxonomy is the debate in the literature regarding the phyletic position of tabulates and heliolitids, which are much more abundant than stromatoporoids in the Silurian System deposits studied here. Flügel (1976) considered that favositids may have been sponges. Copper (1985) interpreted calcified structures in the calyces of *Favosites* tabulates, from Llandovery Series Jupiter Formation on Anticosti Island, Quebec, Canada, as proof of the coral affinity of those corals. Chatterton *et al.* (2008) found spicules in *Favosites* from the Llandovery Series of Anticosti Island, yet regarded these as allied to the Alcyonacea family of Octocorallia. Dixon (2010) interpreted rare soft tissue preservation in heliolitids from Ludlow Series of Devon Island, Arctic Canada, as corals. Kazmierczak (1994) regarded spicules in Silurian samples from Gotland as being proof of a sponge affinity, but Scrutton's (1997a) review maintained the opinion that favositids are corals. Curiously, Reitner & Wörheide (2002, p. 52) noted that Calcarea sponges have affinities with Cnidaria; they also (Reitner & Wörheide 2002, p. 59) viewed chaetetids as belonging to the tabulates, in contrast to the 2015 *Treatise on Invertebrate Paleontology*, where they are classed as sponges, noting that they contain astrorhizae (e.g. West 2011). Khabibulina & Sennikov (2021) described spicules and microspheres in Silurian heliolitids as structures comparable to octocorals. Although the evidence is more strongly weighted towards tabulates and heliolitids as being corals, if they are sponges then that would bias the MWLF reef builders to a greater proportion of calcified sponges.

Finally, although stromatoporoids are calcified sponges, lessons may apply from the modern genus *Merlia*, which has four species but only two are calcified (West 2011, p. 37). If that situation applied to ancient stromatoporoid reefs, then there may be an answer to the question of why the taxonomic richness of stromatoporoid assemblages is always relatively low compared to the number of sponges that live in modern environments. It remains possible that the Wenlock reefs may have contained many more taxa of sponges that were not calcified and not preserved, given that modern sponge spicules break down very quickly after sponge death (Vacelet *et al.* 2010; Wulff 2016). Noncalcified sponges do occur in the Wenlock reefs (Colter 1957, pp. 27, 28) but are uncommon. Thus, although the stromatoporoid taxa present in the outcrop may give a representative collection of those taxa that calcified, the unknown question is whether there were a lot more sponges, or not, in these facies in the Silurian.

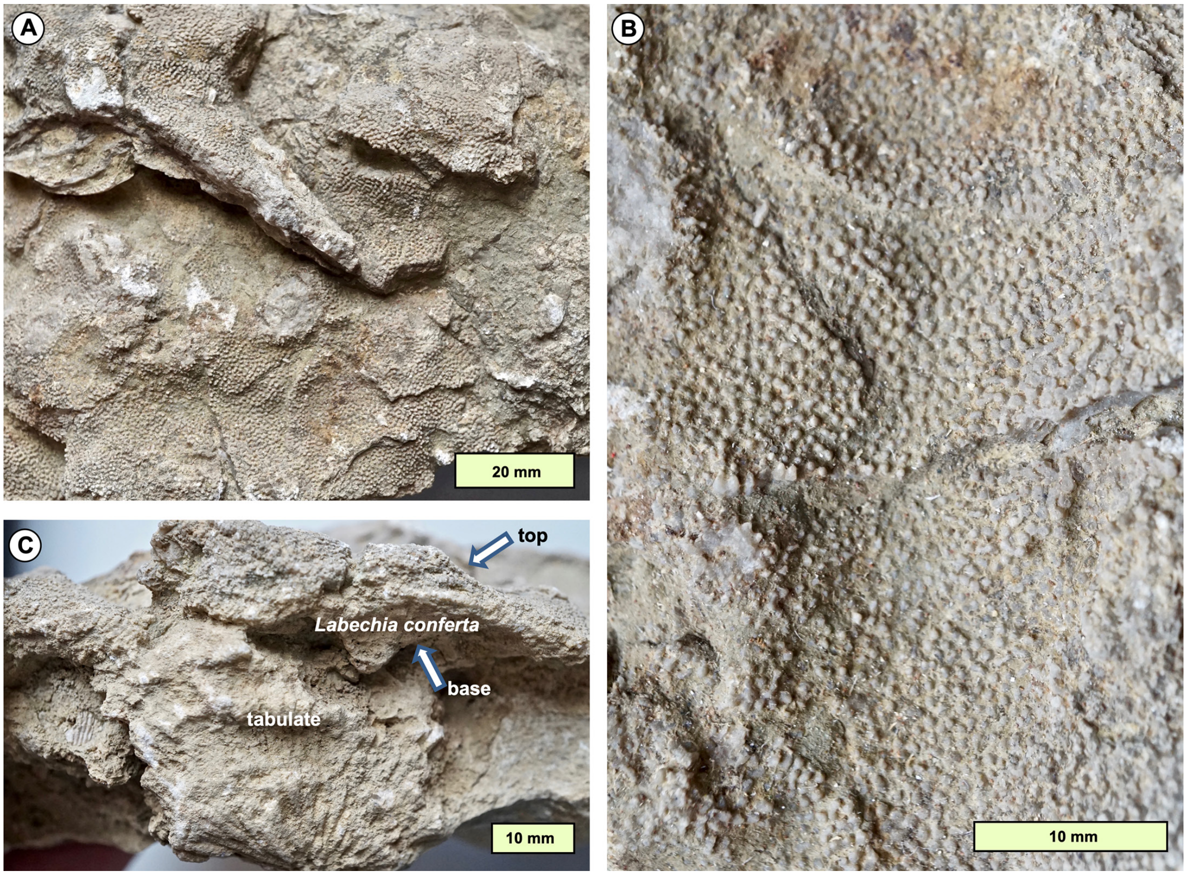
## RESULTS

### Growth characteristics of British Silurian stromatoporoids

Kershaw *et al.* (2018) recognized four major features of Palaeozoic stromatoporoids applicable to understanding controls on their growth: (1) relationship to substrate, (2) growth history and importance of growth interruption events, (3) nature of their relationship with associated organisms, and (4) relationship between growth form and taxonomy. Evidence of the impacts of these four on development of British Silurian stromatoporoids is recognizable in the dataset studied here for most of the taxa found. Thus, this subsection contains a description



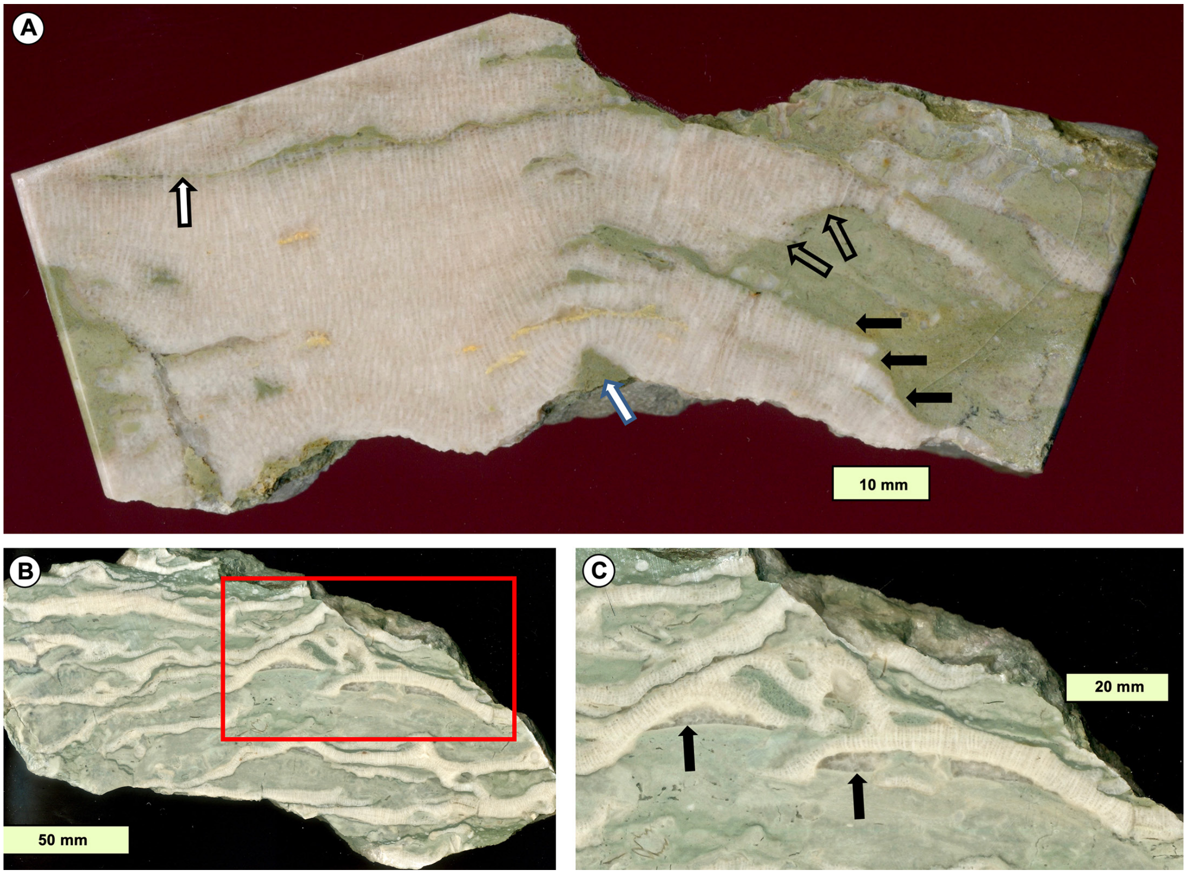
Text-fig. 11. Schematic reconstruction of general features of reefs and associated bedded limestones in the Much Wenlock Limestone Formation (MWLF), central England; the large central patch reef is approximately 30 m wide. **A**, reefs commonly grew on crinoidal limestone lens. **B**, reefs composed of tabulates and heliolitids (radial line symbol), with fewer stromatoporoids (white symbol). Clay seams show approximate time planes. **C**, laminar-shaped reef builders at the margins, including coral *Thecia* and stromatoporoid *Labechia conferta*. **D**, reef margin laminar fossils (*Thecia*, *L. conferta*) commonly lie at angles up to about 20° from horizontal, demonstrating reefs had some topography. **E**, reef margins commonly sharply defined due to microbial fabrics that were important components of reef growth. **F**, two thin stromatoporoid-rich biostromes, 50 cm thick, found only at Dudley, West Midlands, within the Lower Quarried Limestone in the lower MWLF.



Text-fig. 12. **A, B**, plan views of two specimens of *Labechia conferta*, a stromatoporoid with a laminar growth form. B shows the prominent upper surface papillae that represent the tops of the robust pillars characteristic of this taxon (Text-fig. 13). In A, the stromatoporoid skeleton is fractured by compaction in the muddy carbonates in which this sample developed. **C**, side view showing the lower and upper surfaces (marked by arrows) of the laminar stromatoporoid, that grew partly on a favositid, bottom centre. Much Wenlock Limestone Formation, Lilleshall Quarry, Wenlock Edge. Sample CAMSM A7720 collected by Dorothy Hill during a field excursion in 1935, reported by Hill (1936).

of growth features of British Silurian stromatoporoids within reef and reef-related settings, beginning with an overall description of the reef facies (Text-fig. 11).

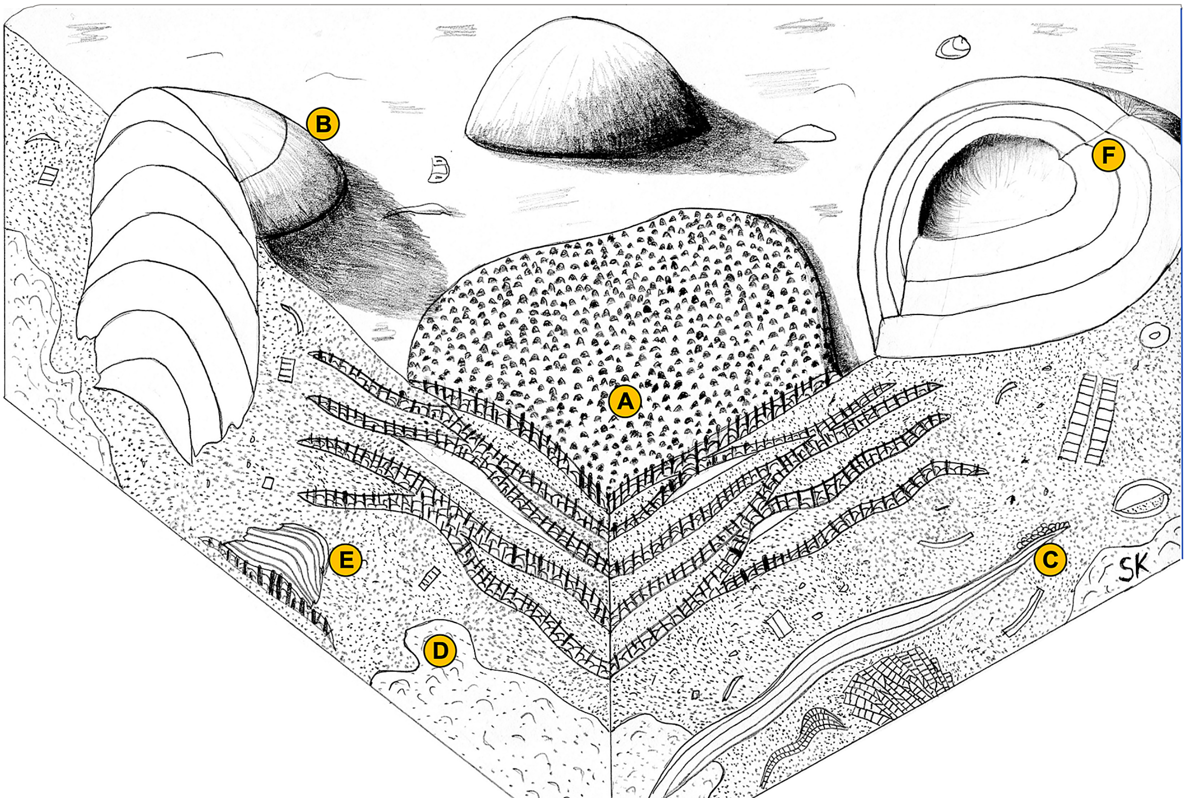
Reefs did not form at particular horizons within the MWLF but developed wherever and whenever conditions of sedimentation rate and water depth promoted growth of tabulates, heliolitids, rugose corals, and stromatoporoids (Colter 1957; Riding 1981; Scoffin 1971). Reef bases developed commonly on crinoidal limestone lenses (Text-fig. 11) but in some cases formed directly on clay-bearing calcareous mudstones-packstones. Subreef limestones sag below reefs due to higher reef density and greater compaction in the bedded limestones relative to cemented reefs (Butler 1939; Colter 1957; Scoffin 1971) and were named as Philip structures after a Swedish architect (Arne Philip) who discovered them from aerial photography on Gotland (Eriksson & Laufeld 1978). Reefs are constructed from mostly tabulates and heliolitids, of which one heliolitid taxon, *Stelliporella parvistella*, is most abundant, and commonly has a branching form. Stromatoporoids are much less common than rugose corals, tabulates, and heliolitids. Reefs developed with only a small profile above the surrounding sea floor, based on evidence from clay seams that pass through the reef indicating sedimentation events as reefs grew. Clay seams also help to identify successive approximate time planes through reefs. Reef margins are commonly characterized by higher proportions of laminar-shaped reef builders, in particular the tabulate coral genus *Thecia*, and stromatoporoid taxon *Labechia conferta*. In some places *L. conferta* forms anastomosing masses that extend laterally from the reef to form biostromal extensions of the biohermal reef margins (Colter 1957), see Text-fig. 11. Reef margins also sometimes show places where reef-building laminar fossils (*Thecia*, *L. conferta*) lie at angles up to about 20° from horizontal, associated with geopetals that prove they grew on slopes (Colter 1957; Scoffin 1971) and thus demonstrate that the upper surfaces of reefs had topography, but the reefs did not protrude much above the sea floor. Low profile reef builders were common in the reef margins, their morphology interpreted by Colter (1957) and Scoffin (1971) to indicate response to raised water energy at reef margins. Reef margins are generally sharply defined, abutting the bedded sediment, such that it is commonly possible to identify the reef edge to within 1 cm. Some areas of reef margins comprise sediment without reef-building metazoan frameworks; in some cases, microbial fabrics are present and are evidence that the reefs formed cemented masses on the sea floor, against which bedded sediments were deposited (Colter 1957; Kershaw *et al.* 2007; Scoffin 1971). In outcrops at Dudley, West Midlands, within the Lower Quarried Limestone unit of the lower part of the MWLF, are two thin beds, approximately 50 cm thick, of biostromes comprising almost only stromatoporoids (Text-fig. 11), together with some corals and other minor shelly faunas (Butler 1939; Colter 1957). These two stromatoporoid biostromes occur in only this limited area and represent horizons interpreted as low energy and low sedimentation rate ideal for stromatoporoid growth. Kershaw (1998) showed that stromatoporoids developed



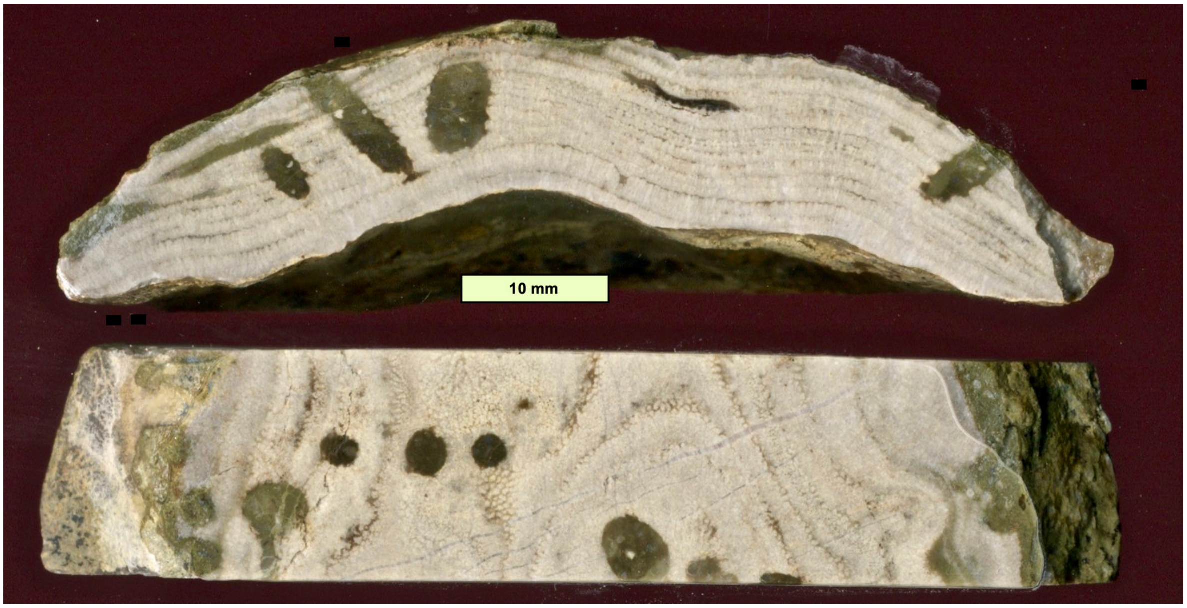
Text-fig. 13. *Labechia conferta* (Lonsdale), vertical sections of polished blocks. **A**, bottom arrow shows growth over a topographic high, with skeletal structure fanning out over the sediment, common in stromatoporoids. Three solid arrows on lower right show three small growth interruption events that partly affected the stromatoporoid growth. Two open arrows, centre-right, show skeleton abutting sediment, possibly due to growth in a period of gradual sediment accumulation, noting the presence of small amounts of sediment encased in the centre of the stromatoporoid in this portion of its growth. Upper left arrow shows a prominent growth interruption event and sedimentation, over which the stromatoporoid grew; the skeleton directly below the interruption is indurated with sediment, evidence that the interruption was caused by sedimentation. Also a final interruption event near the top centre of the photograph. Much Wenlock Limestone Formation (MWLF), Wenlock Edge, NMW 99.35G.2845. **B**, reef framework of *L. conferta* typical of reef cores of Wenlock reefs from the MWLF, Coates Quarry, Wenlock Edge; see Text-fig. 7C for field appearance. **C**, enlargement of box in B showing geopetal cavities beneath parts of the convex-up curved laminar skeleton, evidence of primary cavities. B and C from MWLF, Wenlock Edge, CAMSM X.50347.162.

their most successful constructions as biostromes and these two thin beds may be minor indications of that character for short periods of stability during the Wenlock Epoch in the Midland Platform.

From their low-profile shape, laminar stromatoporoids are evidence of a low sedimentation rate and stable substrate for development (Kershaw 1990). Text-figures 12 and 13 show the obligate laminar taxon *Labechia conferta* that forms a framework in MWLF reefs. Its characteristic upper surface shows protruding pillars as papillae, and because of its thin laminar form it may be fractured by burial compression (Text-fig. 12) indicative of growth on poorly consolidated substrates rich in mud. In other cases, morphology of the basal portion is evidence of growth on substrate that may been partly lithified (Text-fig. 13A), see Kershaw *et al.* (2018) for discussion. Determining the degree to which sediment was solidified before stromatoporoid growth lacks clear criteria in these cases, but the commonly irregular shapes of topographic highs and lack of geopetal cement is evidence of partial, potentially full, seafloor lithification and erosion before stromatoporoid growth (see also Kershaw *et al.* 2021). In some cases, the frame contains geopetal cements below upwardly arched portions of skeleton (Text-fig. 13B, C) that are evidence of growth on unconsolidated substrates; but mostly these arched portions of skeleton are filled completely with sediment, leaving a question as to whether they were primary cavities that were backfilled or the stromatoporoid grew directly on the sediment surface. Some have downward-pointing basal encrusters that prove either an original growth cavity or sediment



Text-fig. 14. Reconstruction of stromatoporoids in reef core of the Much Wenlock Limestone Formation at Coates Quarry, Wenlock Edge. This schematic drawing was constructed from fieldwork; the reef core is partly exposed (Text-fig. 7) and comprises the following features. **A**, anastomosing framework of *Labechia conferta*, with geopetal cavities under some upward-arched portions of the skeleton (see Text-Fig. 13B, C). **B**, large domical *Ecclimadictyon macrotuberculatum*, that grew on the reef surface. **C**, smaller laminar stromatoporoid (not a specific taxon) grew directly on sediment surface. **D**, patch of microbially cemented sediment. **E**, small stromatoporoid grew on upper surface of small *L. conferta*. **F**, overturned broken domical stromatoporoid representing occasional storm energy across the reef. Scale: total width of the *L. conferta* laminar frame is *c.* 50 cm.

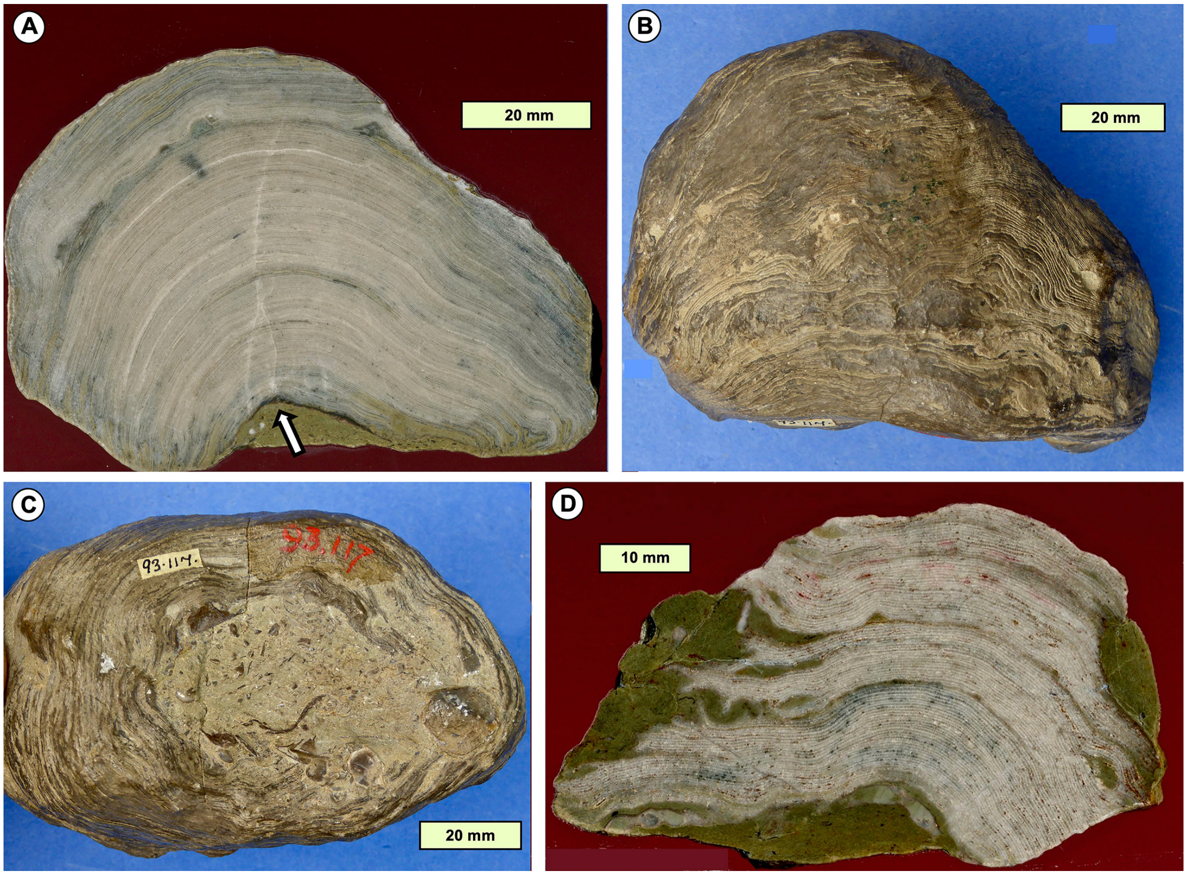


Text-fig. 15. *Lophiostroma schmidti* (Nicholson), vertical and transverse sections of polished blocks (NMW 99.35G.2582). The stromatoporoid contains borings that are presumably post-mortem because the stromatoporoid laminations do not show any reaction to the boring. Thus, the stromatoporoid may have been used as a hard substrate for boring organisms after its death before final burial. Much Wenlock Limestone Formation, Haugh Wood, Woolhope Inlier.

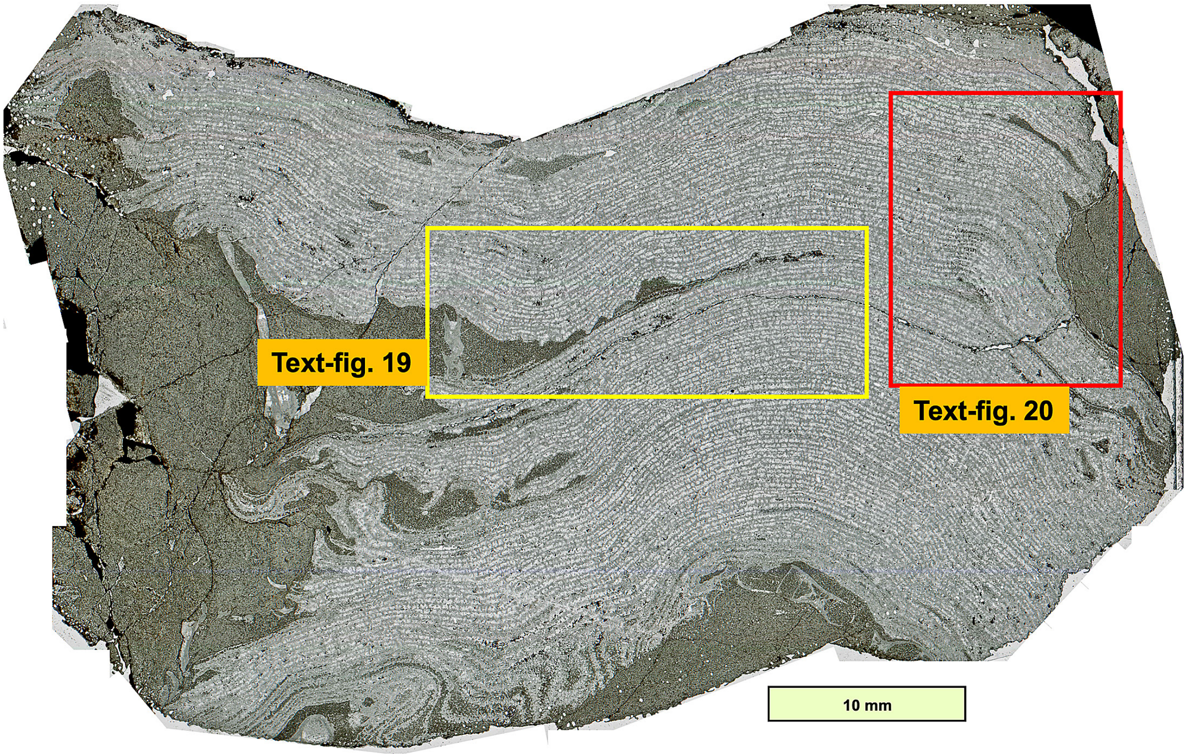
Text-fig. 16. *Ecclimadictyon macrotuberculatum* (Riabinin), vertical section of whole specimen (except for minor loss at margins). Note the complex interdigitation of skeletal structure and sediment, with no geopetal cavities, interpreted here as evidence of growth on a sediment surface that was actively changing, with repeated small-scale depositional events followed by growth. Brachiopods, tabulates, bryozoans and crinoids are also involved in the growth of this sample. Much Wenlock Limestone Formation, Wren's Nest, CAMSM X.50347.225.

removal on the sea floor (see Text-figs 30C, 51B), described further below. Text-figure 14 shows a reconstruction of part of the reef core at Coates Quarry, Wenlock Edge, emphasizing the laminar frame of *Labechia conferta* together with large domical stromatoporoids of other taxa (in this case they are *Ecclimadictyon macrotuberculatum*). Another laminar-form stromatoporoid *Lophiostroma schmidti* (Text-fig. 15) also grew on sediment substrates directly, known also from the Ludlow (Kershaw 1990); this seems to be also an obligate laminar form.

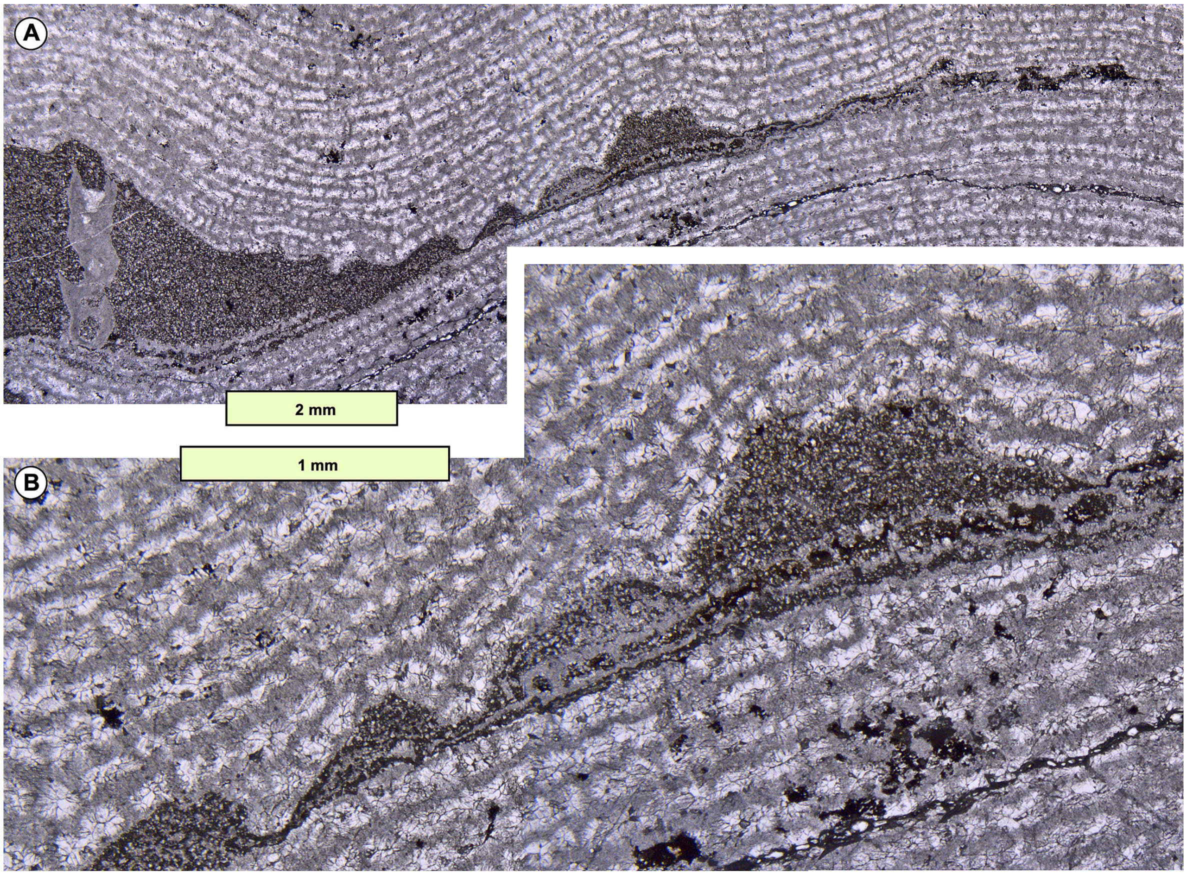
Domical stromatoporoids in the British Silurian are generally more complex than laminar forms, although as for laminar forms many domical ones show interdigitation with sediment during growth (Text-figs 16, 17D), others have smooth margins that are normally non-enveloping (Text-figs 17A–C, 18, 20) (that is, successive growth layers do not completely overlap earlier laminae, but result in a smooth margin; terminology of Kershaw & Riding 1978). In detail the interdigitations may be highly complex (Text-figs 18–21). Geopetal infills (e.g. Text-fig. 21) may have been caused either by growth to form primary cavities, sediment removal by currents after growth recovery, sediment settling below stromatoporoid skeletons, or later partial recrystallization in the sediment during diagenesis, described by Scoffin (1972). Geopetals are common in stromatoporoids, with many cases of uncertainty as to which of those explanations is valid. Minor interruption surfaces where sediment lies on the surface (Text-fig. 21) are evidence



TEXT-FIG. 17. *Petridiostroma simplex* (Nestor), hand specimens. **A, B**, vertical section and side view of a whole specimen showing its smooth-surfaced non-enveloping laminations that clearly terminate at successively higher levels on the side of the sponge as it grew (**B**). It is possible that slow sedimentation as it grew was the reason for the non-enveloping form. Note the steep smooth concave base in A (arrow), likely due to growth on a curved prior shell. **C**, basal view of the same specimen in A and B before it was cut, to show its concave base and the outer part of the growth layers terminating on the sediment surface. Presumably the sediment below the outer part of the stromatoporoid was unconsolidated, explaining why much of the base is visible. The ovoidal central concavity may represent the former presence of an oncocerid orthoconic nautiloid, that have ovoidal shapes and are common as stromatoporoid substrates in the Silurian (see Kershaw *et al.* 2018). **D**, cut vertical section through specimen with growth interruption, likely to have been caused by sedimentation. Much Wenlock Limestone Formation. A–C: Wren's Nest, NMW 93-117; D: Wenlock Edge, NMW 99.35G.2840-2.

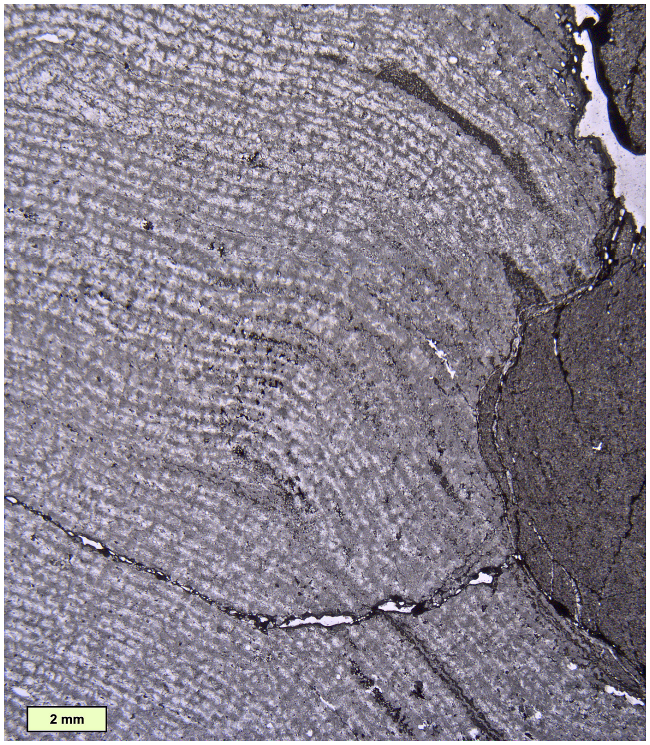


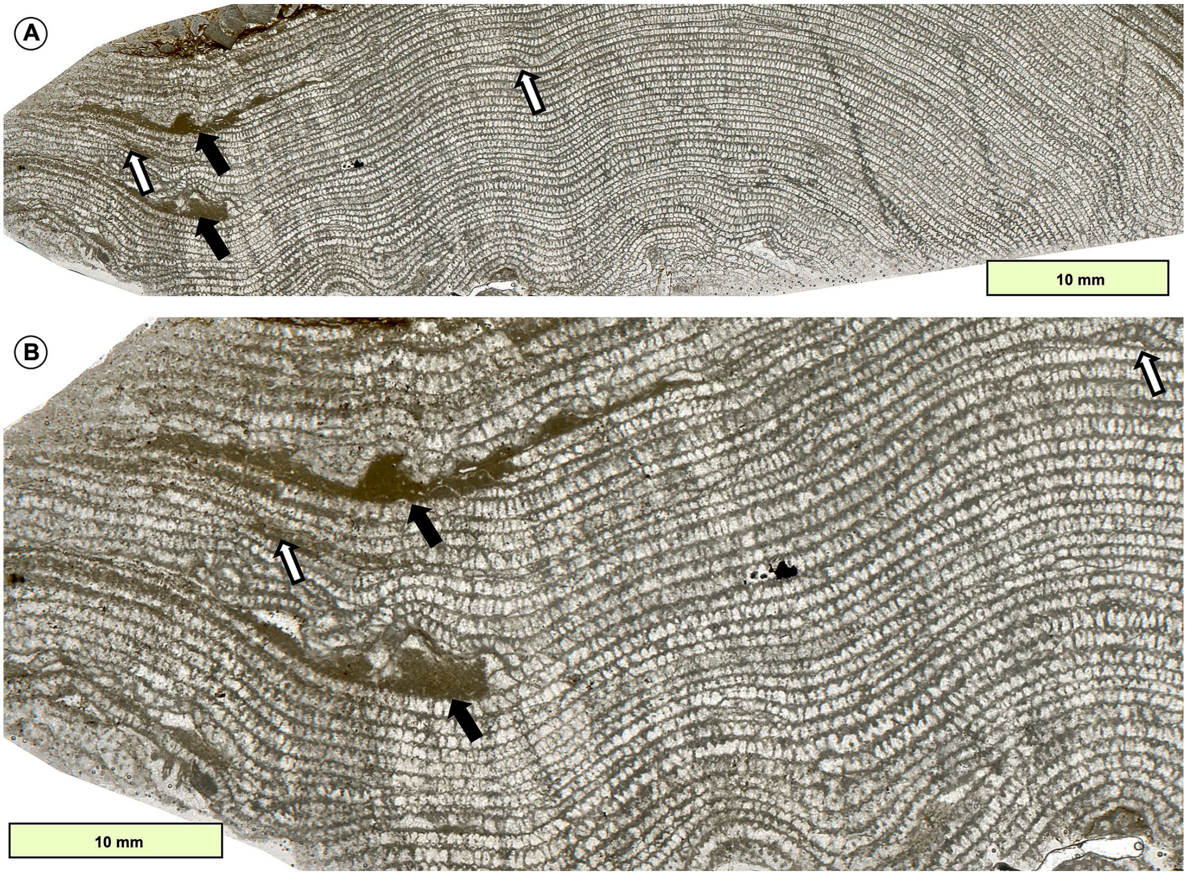
Text-fig. 18. *Petridiostroma simplex* (Nestor). Vertical section, acetate peel, of counterpart of same specimen as Text-fig. 17D, showing concave base (possibly grew on a prior curved shell not preserved, or a partially-lithified sediment surface) and repeated growth interruptions, likely caused by episodic sediment deposition. Left-hand box: enlargement shown in Text-fig. 19. Right-hand box: enlargement shown in Text-fig. 20. Much Wenlock Limestone Formation, Wenlock Edge, NMW 99.35G.EDG-3.23.



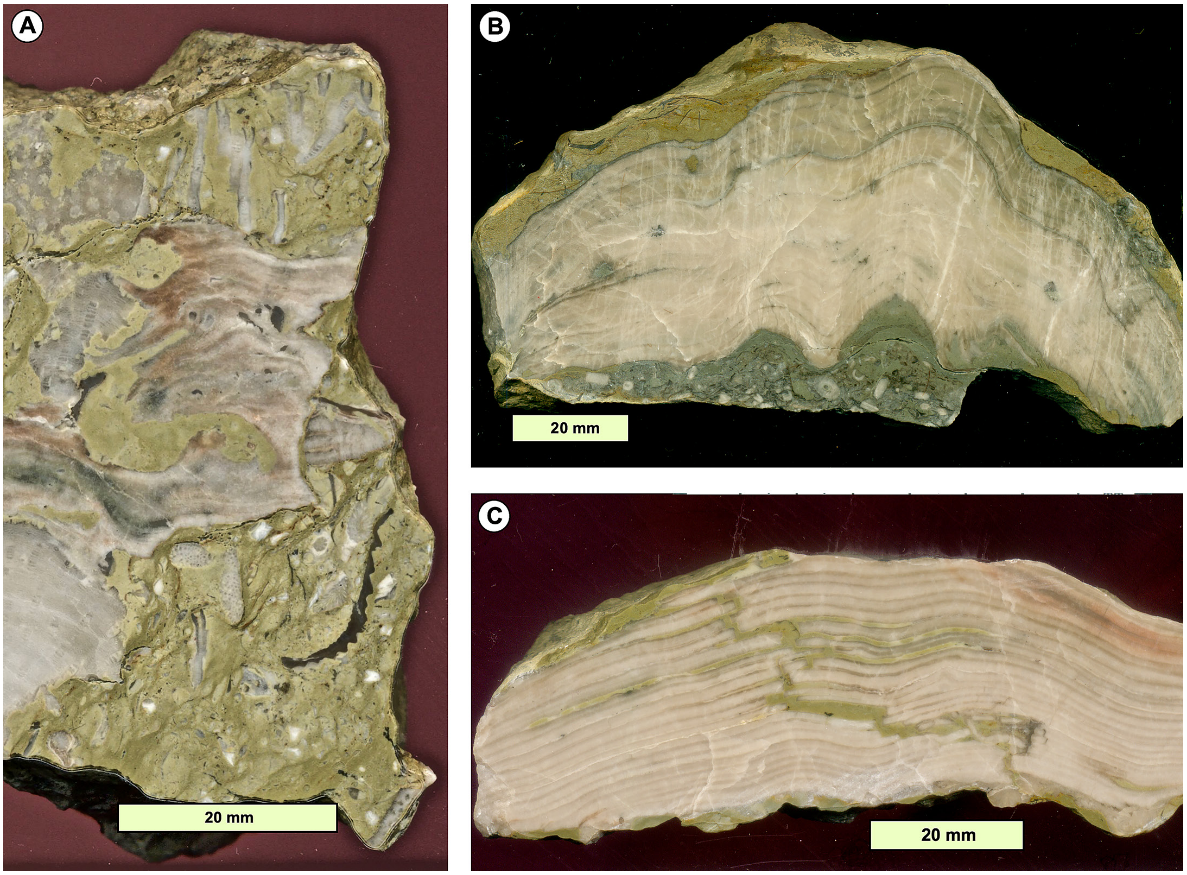
Text-fig. 19. *Petridiostroma simplex* (Nestor). Vertical section, acetate peel, enlargement of left-hand box in Text-fig. 18, showing details of upper growth interruption, which seems to have caused death of stromatoporoid surface (skeleton indurated with sediment), followed by deposition of sediment which formed an undulose surface, possibly by erosion of a partly lithified micrite, prior to regrowth. **B** is an enlargement of the central part of **A**. Much Wenlock Limestone Formation, Wenlock Edge, NMW 99.35G.EDG-3.23.

Text-fig. 20. *Petridostroma simplex* (Nestor). Vertical section, acetate peel, enlargement of right-hand box in Text-fig. 18, showing details of termination of laminae to form a smooth margin, and the side of the stromatoporoid was then buried in sediment which formed a small growth interruption (upper part of photo). Much Wenlock Limestone Formation, Wenlock Edge, NMW 99.35G.EDG-3.23.





Text-fig. 21. *Petridiostroma simplex* (Nestor). **A**, vertical thin section of large area, showing several small concavities at the base, likely it grew across an uneven substrate. Subsequent growth shows less undulation, as the stromatoporoid developed into a coherent dome form. Two major (black arrows) and one minor (white arrows) growth interruptions are preserved on the left side. The lower interruption (lower black arrow) has geopetal infills, caused either by sediment that was removed prior to growth recovery or by partial recrystallization in the sediment, described by Scoffin (1972). **B**, enlargement of A showing the details of growth interruption surfaces. Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.47.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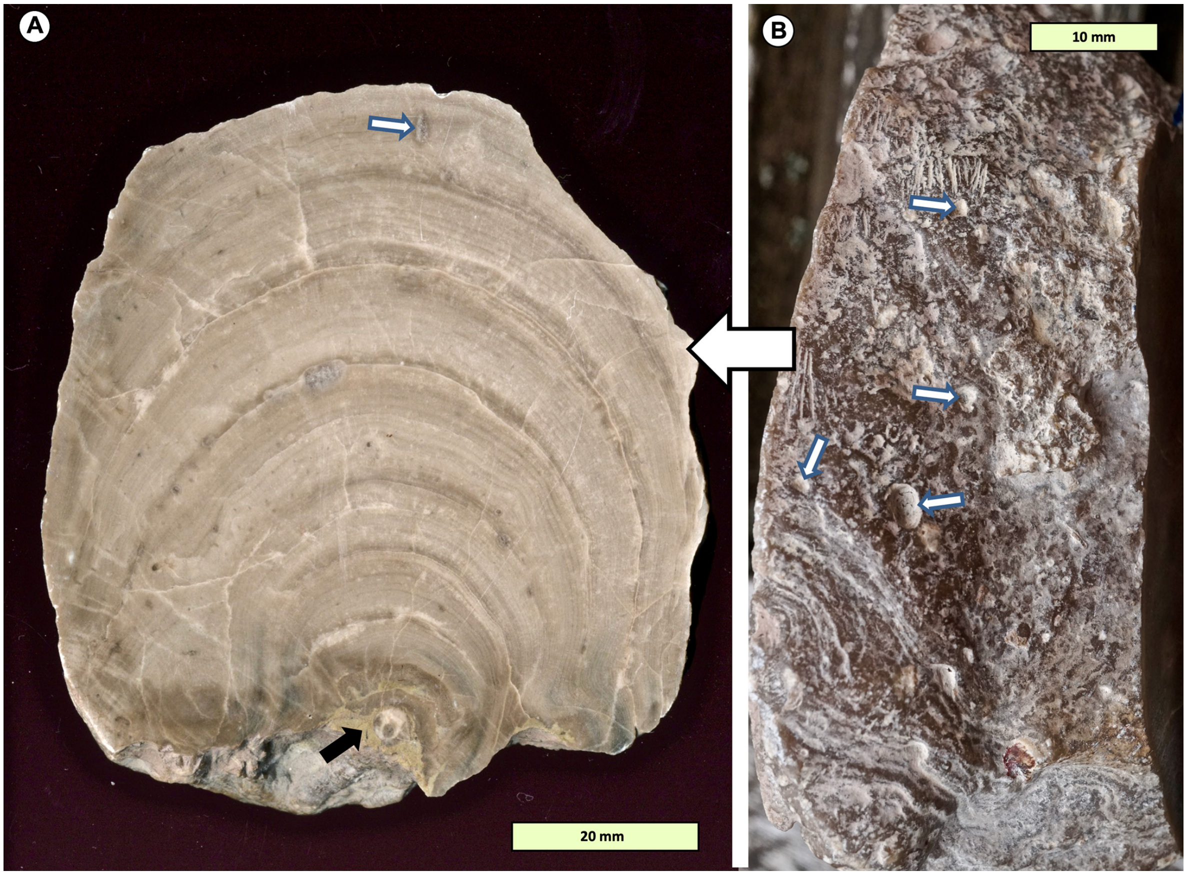
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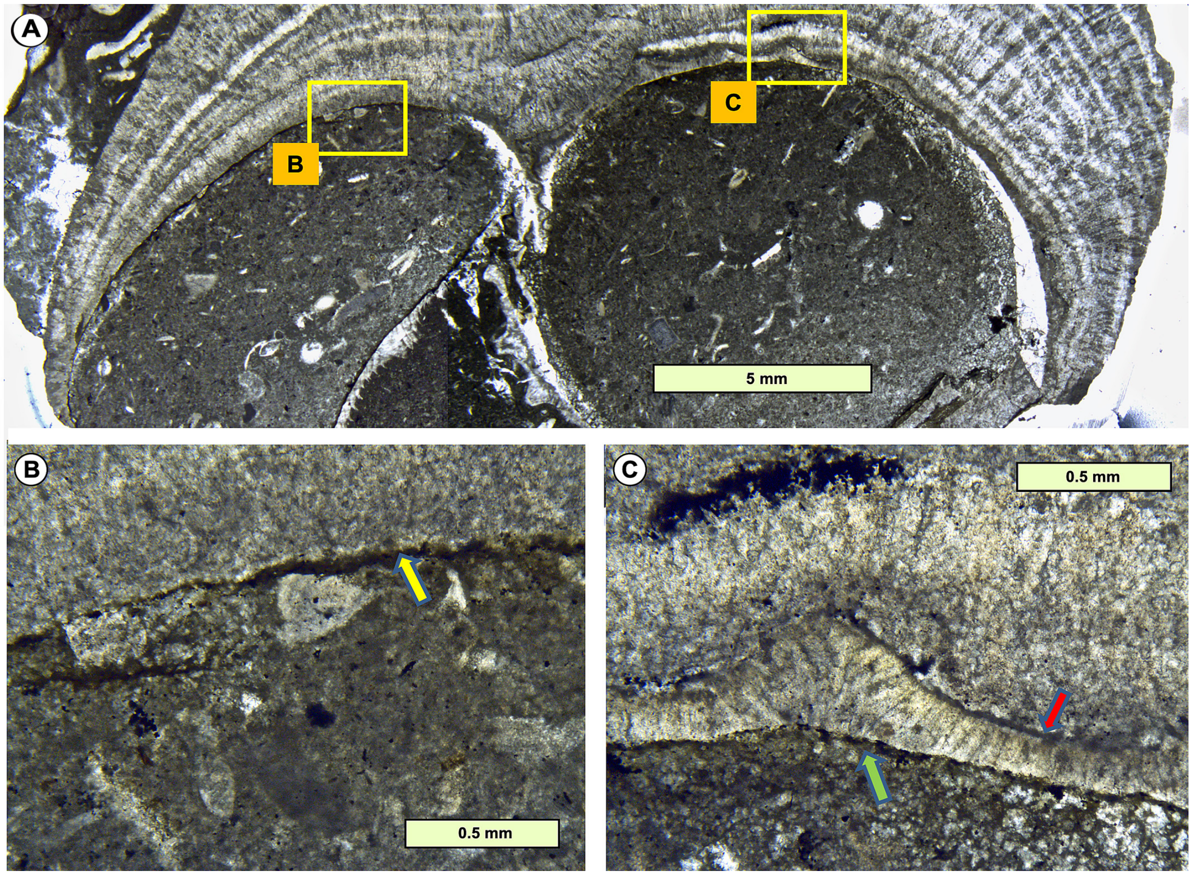
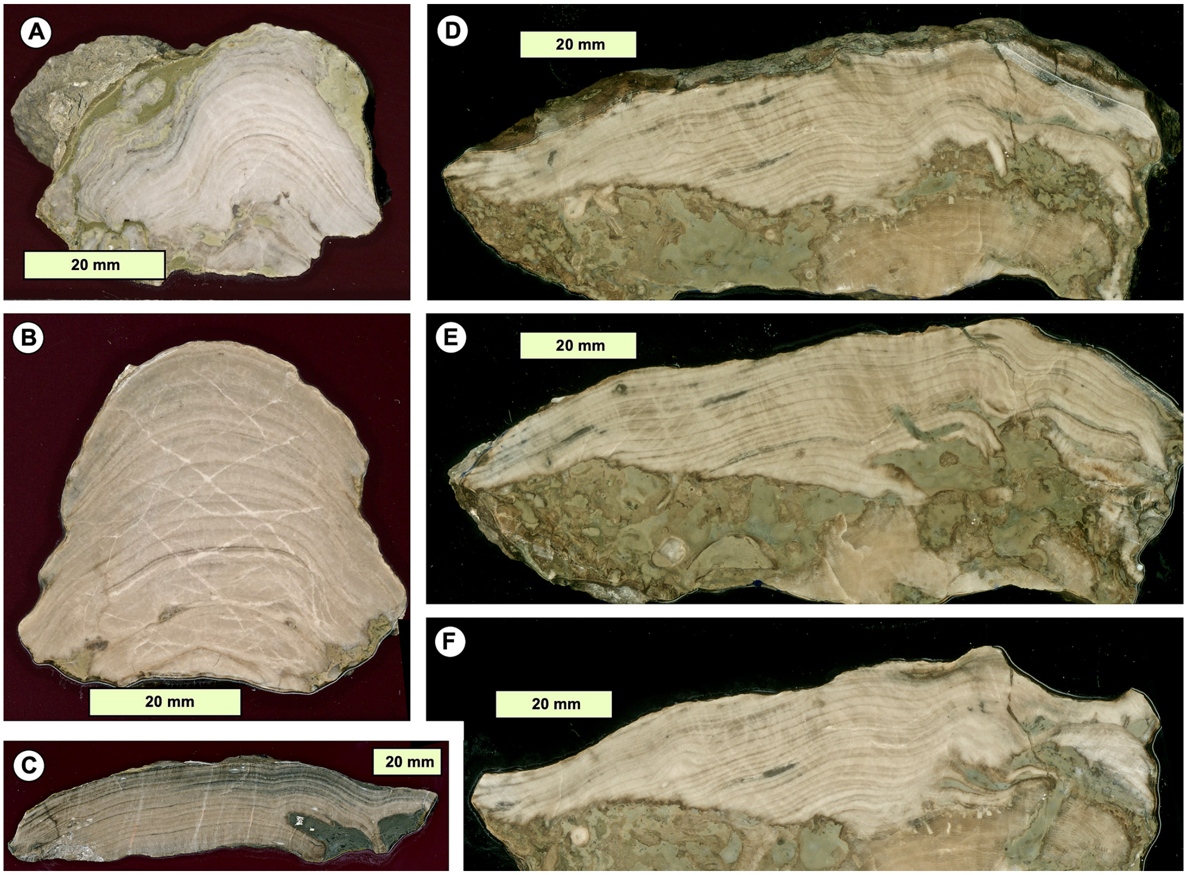
Text-fig. 22. *Actinostromella vaiverensis* Nestor, vertical sections of polished blocks, showing variations of form, likely influenced by substrate consistency and sedimentation rate. **A**, domical ragged form. **B**, domical form with growth on irregular substrate of prior shells. **C**, loose sample of part of a domical form, showing contemporaneous fractures likely due to folding in the Caledonian event. A: Wenlock Edge, NMW 99.35G.1384-1; B, C: Much Wenlock Limestone Formation, Wren's Nest, CAMSM X.50347.188 & CAMSM X.50347.243 respectively.

Text-fig. 23. *Actinostromella vaiverensis* Nestor. **A**, vertical section through centre of stromatoporoid, showing growth on a mixture of bioclasts and micrite (black arrow at base); the stromatoporoid likely began initial growth on a crinoid stem fragment and then spread to surrounding micrite. The specimen shows prominent regular banding that may or may not be annual; and it grew during a period of no or little sediment deposition. *Trypanites* boring (highly likely to be post-death) visible at top of sample (upper arrow). **B**, surface view from the right-hand side of the polished section in A, as indicated by large arrow, showing the edges of laminae terminate on the nearly smooth surface with very little sediment interruption at the base. Several *Trypanites* borings visible (white arrows). Much Wenlock Limestone Formation, Major's Leap site, Wenlock Edge, CAMSM X.50347.165, donated by David Walker.



Text-fig. 24. *Araneosustroma fistulosum* Lessovaya. **A**, growth directly on gastropod, sample shown in field photograph in Text-figure 6C; locations of B and C shown by the two labelled boxes. **B**, dissolution of gastropod on left side, with minor pressure solution (arrow). **C**, well-preserved gastropod shell on right side, with sediment infill (lower arrow) and direct growth of stromatoporoid on gastropod (upper arrow). Basal Elton Formation, just above top of the Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.61.

TEXT-FIG. 25. Bedding surface view of hand specimen with corals and stromatoporoids. *Densastroma pexisum* (Yavorsky) domical specimen (arrow). Much Wenlock Limestone Formation, Wenlock Edge, NMW 99.35G.690.



TEXT-FIG. 27. *Araneosustroma fistulosum* Lessovaya, hand specimen, 3D view of broken surface of domical specimen showing prominent banding in growth layers enhanced by weathering. The apparent regular banding superficially resembles regular growth banding, but the problem of determining whether it is due to some regular forcing process or is just an artefact of the weathering process, is not determinable in this sample because its margins are missing. Marginal information, where the stromatoporoid interacts with the sediment, is essential to develop understanding of the nature of the banding. Much Wenlock Limestone Formation at Crews Hill Quarry, Malvern Hills, CAMSM X.50347.258.

TEXT-FIG. 26. *Densastroma pexisum* (Yavorsky), vertical sections of cut samples of small domical specimens, showing layers that illustrate the difficulty in determining the nature of banding in stromatoporoids. **A–C**: Wenlock Edge, NMW 24-587-G10(FJNMW33), 99.35G.847-1, 99.35G.3029 respectively; **D–F**: Much Wenlock Limestone Formation, Penny Hill Quarry, Malvern Hills area, CAMSM X.50347.272 from upper to lower of those three photographs.

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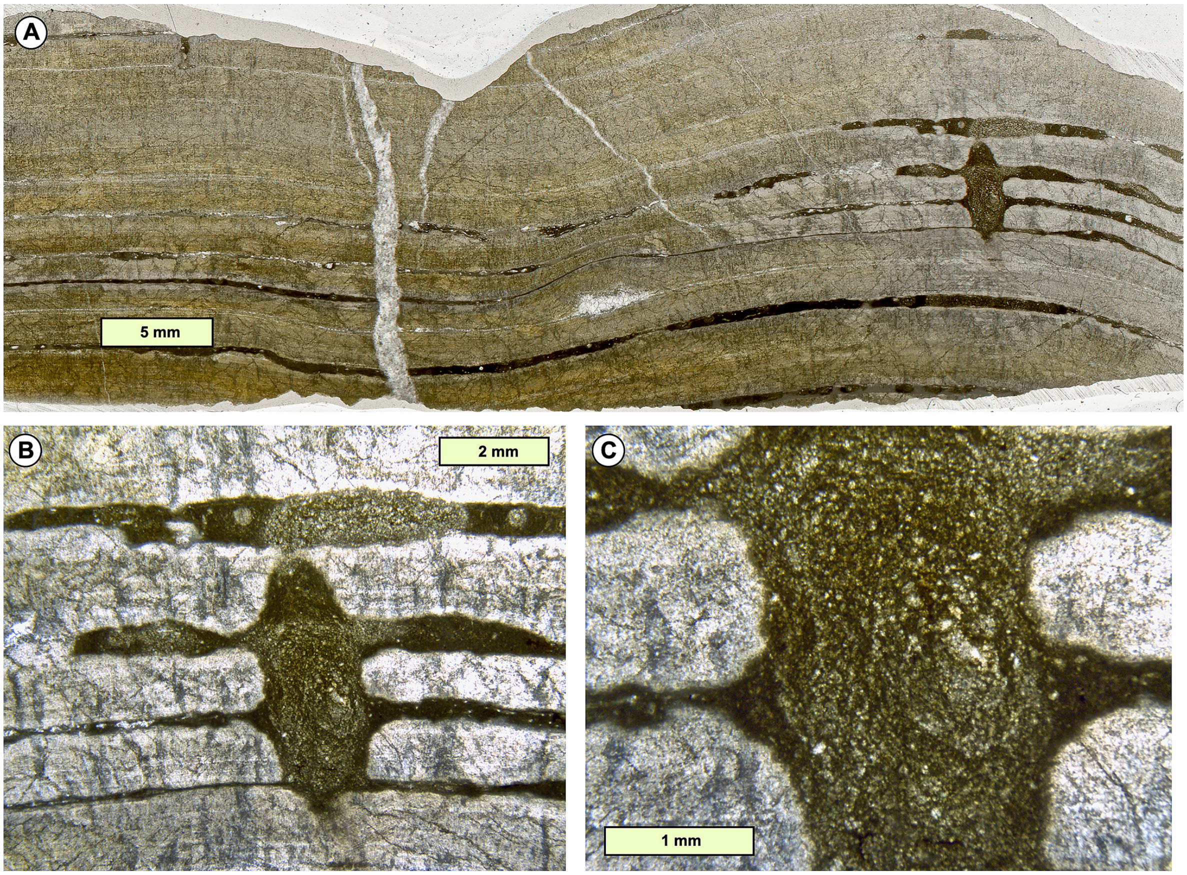
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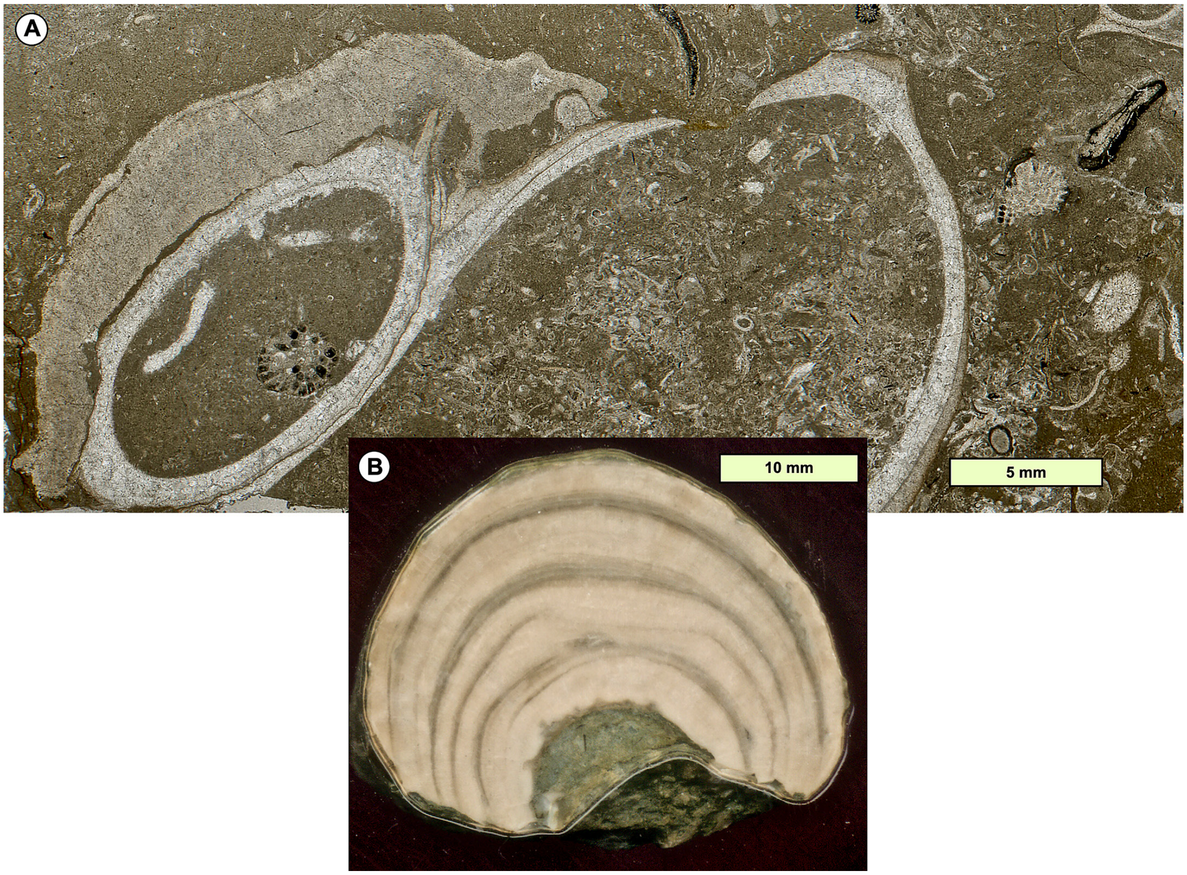
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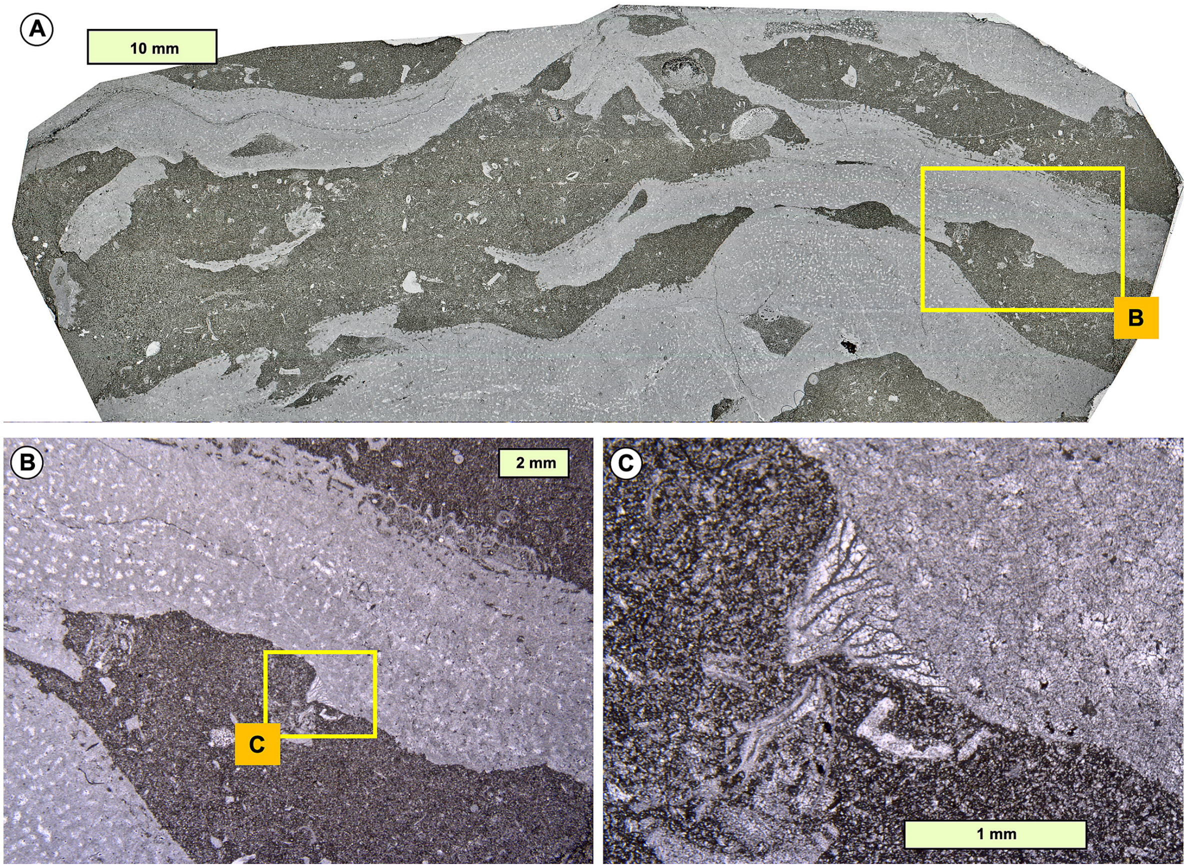
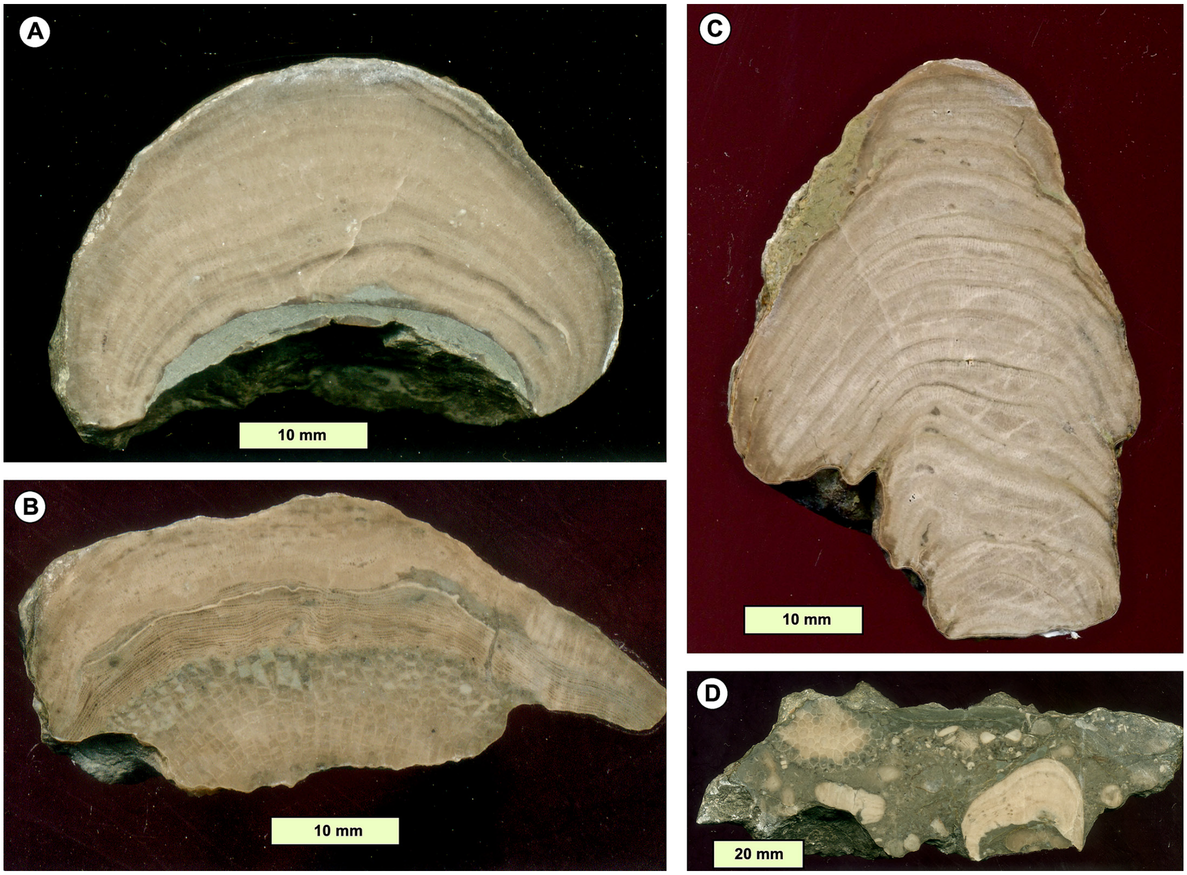
Text-fig. 28. *Densastroma pexisum* (Yavorsky). Vertical thin section of stromatoporoid skeleton showing details of growth interruption sediment layers that show sharp boundaries. **A**, within the large sediment-filled area centre right are patches of coarser sediment that are cross sections through borings. Approximately regular banding is partly related to growth interruption. **B, C**, enlargement of boring, that is filled with vague concentric sediment layers, evidence they were backfilled as the borer cut through the sediment. The sharp contact between the boring's sediment and the sediment layers is evidence that the sediment layers were at least partly lithified before the borer drilled into the stromatoporoid. There is no mixing between the boring's sediment and the sediment layers. This is one example of many cases that suggest early partial lithification was common in the Palaeozoic stromatoporoids. Much Wenlock Limestone Formation at Crews Hill Quarry, Malvern Hills, CAMSM X.50347.257.

Text-fig. 29. *Densastroma pexisum* (Yavorsky). **A**, vertical thin section of early growth of stromatoporoid on a recrystallized gastropod. Note that the right-hand part of the stromatoporoid is partly on sediment, raising the question about whether the sediment was deposited before the stromatoporoid grew or whether the stromatoporoid created a small growth cavity that was later backfilled (see Kershaw *et al.* 2018 for discussion of substrate relationships in stromatoporoids). Much Wenlock Limestone Formation (MWLF), Parkwood Quarry, Malvern Hills, CAMSM X.50347.267. **B**, vertical section of stromatoporoid that grew on an orthoconic nautiloid, the ornamentation of which is visible as tiny irregularities in the basal surface of the stromatoporoid. This specimen shows colour variation in layering (represented in black and white as different shades of grey), that may or may not reflect growth controls on banding. Note that this photograph was made using a document scanner, with water on the glass, hence the rim of water around the edge of the sample on this photo. From the 'stromatoporoid pavement', Lower Quarried Limestone, MWLF, Wren's Nest, Dudley, CAMSM X.50347.208.



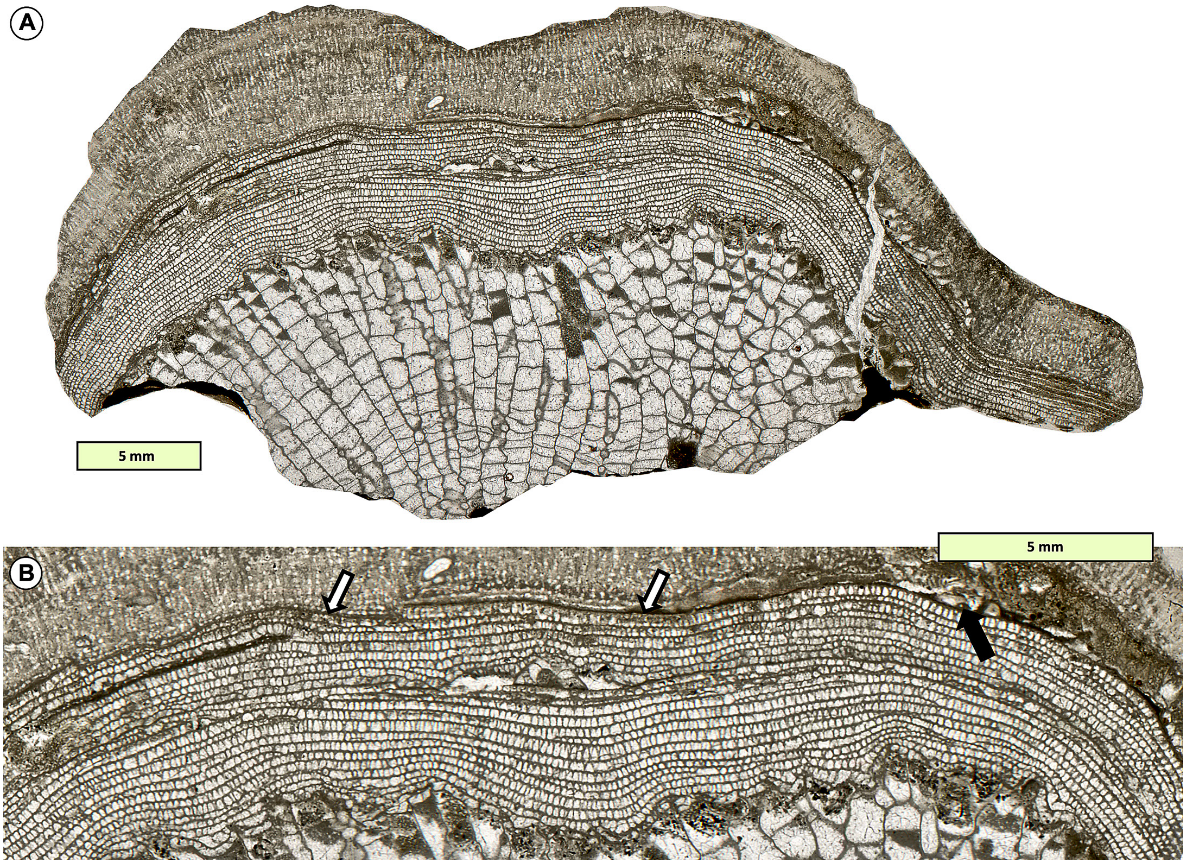
Text-fig. 30. *Eostromatopora impexa* (Nestor). **A**, vertical section acetate peel of ragged laminar form, composed of repeated laminar sheets presumably controlled by episodic sedimentation. However, on the base of the second growth phase (**B, C**, locations of which are shown by labelled boxes), is a downward-pointing encruster on the base of the stromatoporoid, evidence of growth on the roof of a cavity that may have been a primary cavity backfilled with sediment. Nevertheless, there is no geopetal cement that would be proof of a geopetal, and this is a very common case in stromatoporoids regardless of taxon (see Kershaw *et al.* 2018 for discussion), leaving an uncertainty regarding conditions of development of the stromatoporoid. Much Wenlock Limestone Formation, Wenlock Edge, NMW 99.35G.ED6-3-27.



Text-fig. 31. *Syringostromella borealis* (Nicholson). Vertical cut sections of samples. **A**, stromatoporoid grew on an orthoconic nautiloid and formed a smooth non-enveloping dome. **B**, multiple growth consisting of *Petridiostroma simplex* on a favositid coral, then *S. borealis* grew on the *P. simplex*. A thin section view of this sample is given in Text-fig. 32. **C**, small-size tall domical example, likely grew upwards because of gradual sedimentation during its life. **D**, section through fossil-rich bed containing small sample of *S. borealis*, centre right, that grew on bioclastic material with micrite, that may have been partially lithified and eroded before the stromatoporoid grew (see discussion in Kershaw *et al.* 2018). A, B, D, Much Wenlock Limestone Formation, Wren's Nest, Dudley A: CAMSM X.50347.193; B: CAMSM X.50347.204; D: CAMSM X.50347.186; C: MWLF, Farley Dingle, Wenlock Edge, NMW 99.35G.851.

that the interruption was caused by sedimentation; commonly areas of surface covered by sediment can be traced laterally within the sample into areas where no sediment is present but there is indication of a break in growth (Text-fig. 21). Modern sponges have efficient sediment-clearing mechanisms (discussed in Kershaw *et al.* 2018) and recover well from sedimentation events. It is therefore possible that minor growth interruptions lacking sediment (Text-fig. 21, surface indicated by white arrow) may reflect efficient sediment-clearing mechanisms. Minor variations in laminae spacing through the thickness of some stromatoporoids (e.g. Text-fig. 21; Pl. 8, figs 1–3; Pl. 21, figs 1, 2) may be evidence of variation in growth rate of the stromatoporoid, but whether such variations are due to cyclic forcing agents remains unclear. Broadhurst (1966) commenting on the asymmetry of sediment interdigitations, such as those shown in Text-fig. 18, theorized that stromatoporoids responded to currents so that sediment wedges formed in the downstream margins of a specimen in a current. Verification of this idea requires evidence and at the very least needs numerous samples in-place with the same orientation of asymmetry, not observed in the current samples.

Stromatoporoids commonly show variations of growth form within taxa. A typical example is *Actinostromella vaiverensis* in Text-figs 22 and 23; sediment depositional events and varying rates may be the reasons for wide variations in growth forms within this taxon; non-enveloping growth in Text-fig. 23 indicates minimal influence of sedimentation on the growth. Stromatoporoids commonly grew on solid substrates, proven where they grew on bioclasts (Text-figs 23, 24), but



Text-fig. 32. *Syringostromella borealis* (Nicholson) and *Petridiostroma simplex* (Nestor). Vertical thin section of sample in Text-fig. 31B. Vertical whole thin section (**A**, enlargement in **B**) showing *P. simplex* grew on a favositid, with a small layer of sediment between them, that presumably killed the favositid. The protruding calyx walls of the favositid became part of the highly irregular substrate on which *P. simplex* grew; the *P. simplex* suffered two growth interruption events before dying and then was encrusted by small tubes (black arrow, right-hand side). *S. borealis* grew partly on micrite and partly on the surface of *P. simplex* (two white arrows). A single spiral symbiotic tube grew in *S. borealis*, but occurs in only the lower part of *S. borealis*, a very common situation, discussed by Kershaw *et al.* (2018) to indicate chance settling of the tube on the stromatoporoid surface but the stromatoporoid soon overwhelmed its visitor. From 'stromatoporoid pavement' biostrome in Lower Quarried Limestone, Much Wenlock Limestone Formation, Wren's Nest, CAMSM X.50347.204.2.

cases where shells were dissolved in diagenesis may leave the stromatoporoid directly in contact with the sediment surface, yet the shape of the basal surface indicates the stromatoporoid grew originally on a shell (Text-fig. 24B). *Densastroma pexisum* is another typical example having variations in growth and is commonly found upright on bedding planes in the MWLF (Text-fig. 25); when sectioned it too illustrates more variation in growth form within one taxon (Text-fig. 26).

The largest stromatoporoids in the British suite studied here mostly do not exceed 20 cm in basal diameter, and many are *Densastroma pexisum*, and another taxon with fine skeletal structure, *Araneosustroma fistulosum* (Text-fig. 27), from reefs and reef-related facies. Internal complexities not always recognizable in small-scale vertical sections (such as in Text-fig. 27) are shown in the larger scale in Text-fig. 28, where growth interruption events, sedimentation and burrowing organisms are involved in the complex history of this sample. Text-figure 23 illustrates banding in a stromatoporoid, but more pronounced banding is shown in Text-fig. 29B in a taxon (here a small specimen of *Densastroma pexisum*) that also commonly occurs on shelly debris.

Although stromatoporoids commonly grew on sediment surfaces, some have downward-pointing basal encrusters (Text-fig. 30C; see also Text-fig. 51B) that can be interpreted as growing into cavities unless stromatoporoids have been moved on the substrate. However, in stromatoporoids that are strongly interdigitated with sediment, as in Text-fig. 30, it is reasonable to interpret them as growth to form primary cavities that were completely filled so that no

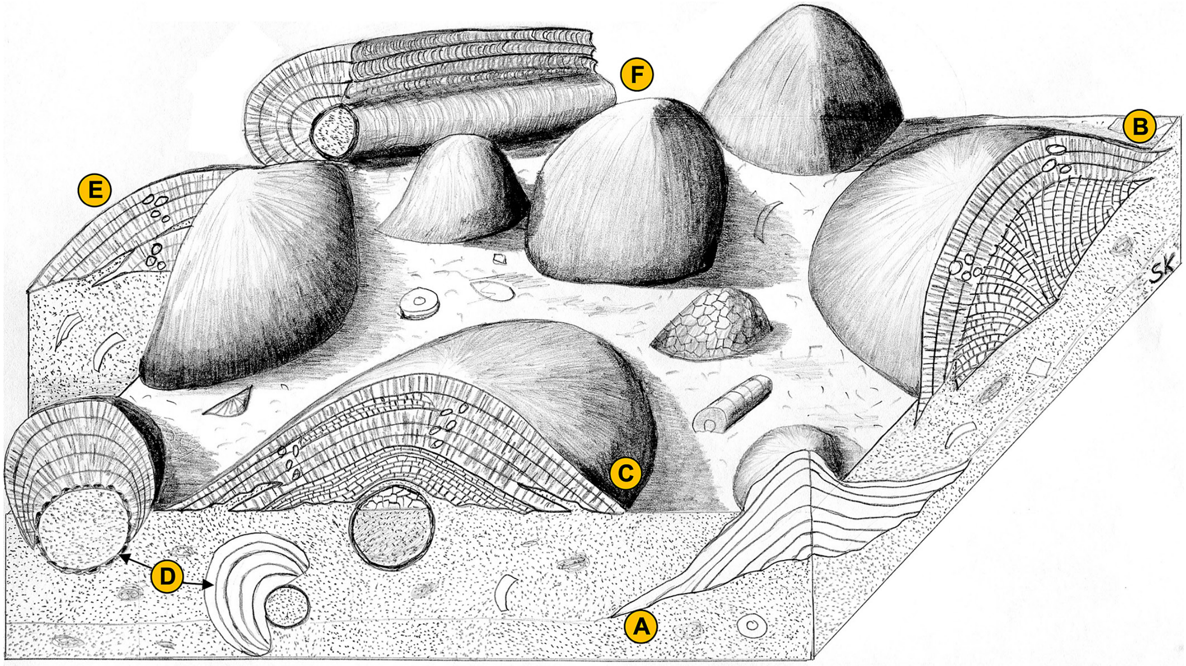
Text-fig. 33. *Syringostromella borealis* (Nicholson) and *Petridiostroma simplex* (Nestor). Vertical thin section showing initial growth of both stromatoporoid taxa on a broken stick of bryozoan. The two stromatoporoids seemed to compete with each other, each successively having advantage. Small spiral symbiotic tubes also grew within *S. borealis*, but not in *P. simplex*; this may be an example of taxon-selection by the tubes in stromatoporoids, noting that stromatoporoid symbionts tend to occur in only some species and not in others (Kershaw *et al.* 2018), see also Text-fig. 46. From 'stromatoporoid pavement' biostrome in Lower Quarried Limestone, Much Wenlock Limestone Formation, Wren's Nest, CAMSM X.50347.198.

geopetal sediment remains. Backfilled cavities contrast examples where the stromatoporoid may have moved on the sediment surface resulting in a secondary cavity in which cryptic basal encrusters could have developed (Kershaw 1980; Segars & Liddell 1988). Apart from the minor evidence of cavities beneath some reef builders (see also Scoffin 1972), there is no evidence of large cavities in the MWLF reefs, and nothing as large as those described by Berkowski *et al.* (2019) in Devonian mounds in Morocco.

Text-figure 31A, B, D shows growth on solid objects of prior shells but Text-fig. 31C is a case where a solid object is not confirmed. Text-figure 32 shows details of growth of two stromatoporoids, the lower on a favositid, and the upper on the surface of the lower stromatoporoid, but with encrusters between. This and Text-fig. 33, with intergrowth of two stromatoporoid taxa, demonstrates the dynamic growth habits of these sponges. The sample in Text-fig. 31B (same sample as Text-fig. 32) is from the upper of the two stromatoporoid biostromes at the Wren's Nest, Dudley, a level in the upper part of the LQLM that is unique to the Dudley area (Colter 1957). Text-figure 34 shows a schematic reconstruction of the sea floor during the formation of that biostrome.

## Taxonomic synonyms in British Silurian stromatoporoids

As described earlier, small-area photographs commonly used to illustrate taxa in published stromatoporoid taxonomy studies do not in all cases allow skeletal variation of stromatoporoid structure to be fully assessed by readers. Examination of publications during this study made



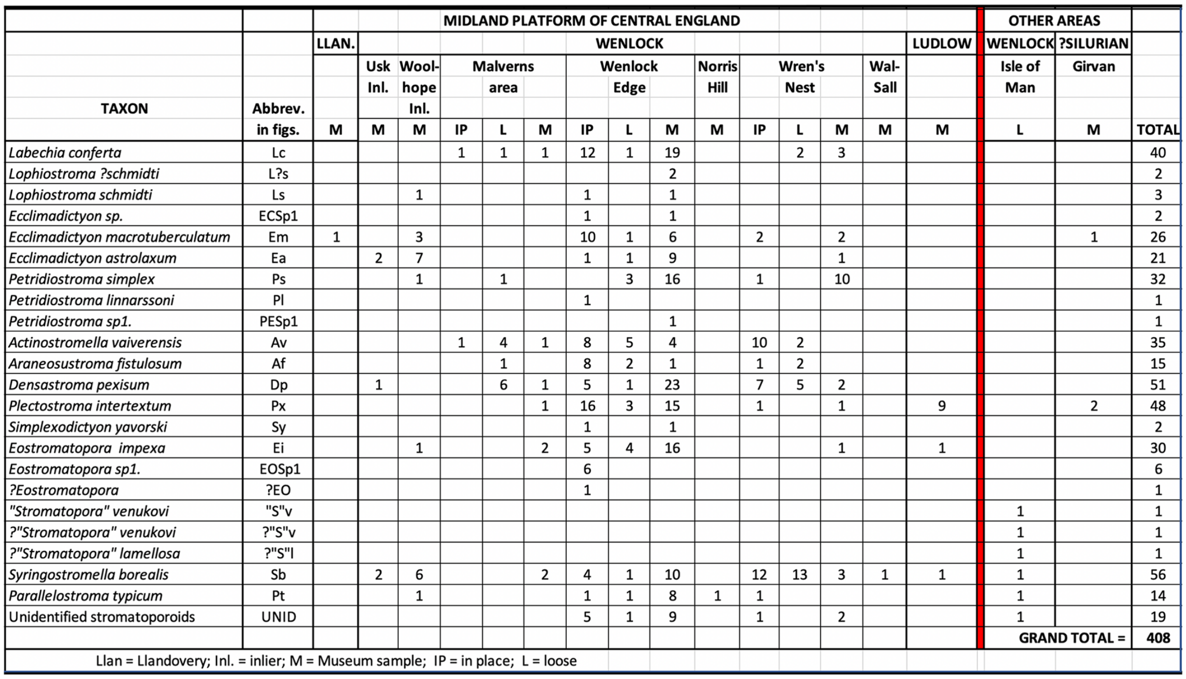
TEXT-FIG. 34. Reconstruction of stromatoporoids in the upper of two stromatoporoid biostromes ('stromatoporoid pavement'), in the upper part of the Lower Quarried Limestone unit at Wren's Nest, Dudley. The lower biostrome is recorded as containing branching stromatoporoids (Butler 1939) of the same taxa that form domical stromatoporoids elsewhere (Colter 1957). In the upper biostrome illustrated here, the globose and domical growth forms noted by Butler (1939) and Colter (1957) are represented, demonstrating the following features: **A**, stromatoporoid growth directly on mudstone-wackestone substrate, which may or may not have been partly lithified before stromatoporoid growth (see Kershaw *et al.* 2018 for discussion). **B**, stromatoporoid growth on a favositid tabulate, that itself grew directly on the sediment surface. **C**, growth of one stromatoporoid taxon (representing *Petridiostroma simplex*) on an orthoconic nautiloid that has a geopetal infill; the *P. simplex* was overgrown by a second stromatoporoid taxon (representing *Syringostromella borealis*), with no sediment between the two stromatoporoids. A small growth interruption led to a minor sediment wedge that partly affected the *S. borealis* but it recovered and expanded across the substrate. However, this later growth is complicated by a second growth of *P. simplex* and further *S. borealis*. This and other examples of *S. borealis* (features B and E) also have spiral intergrown tubes that are interpreted as settlement on the living stromatoporoid surface, grew along with it, but ultimately overgrown by the stromatoporoid so that the tubes do not appear on the stromatoporoid surface. **D**, growth of two stromatoporoids on orthoconic nautiloids; on the right (representing a third taxon, *Densastroma pexisum*) the combined growth was moved on the substrate and buried; on the left (representing *S. borealis*) a stromatoporoid in-place on the orthocone. **E**, another example of *S. borealis* that grew directly on the sediment surface in the visible part of the sample. **F**, surface views of several stromatoporoids, including an overturned *S. borealis* on an orthocone (left). Scale: width of the front cut face of the diagram is *c.* 20 cm.

us aware of the overlap of structure in taxa that have been treated by other authors as different traditional species. Here we describe the British taxa affected by this problem. Five published stromatoporoid taxa are involved in this taxonomic issue, treated in turn below, arising from publications by Mori (1969a, 1970), Nicholson (1886, 1889, 1891, 1892) and Johnston (1915). The last two of these problematic taxa are considered together:

1. Mori (1969a, pl. IV, figs 6, 7) illustrated *Clathrodictyon simplex* (now called *Petridiostroma simplex*), and Mori (1970, pl. III, figs 1–4) illustrated *Clathrodictyon striatellum* (now *Petridiostroma striatellum*). Comparison of photographs in these two plates, described by Mori as different traditional species, leads to our conclusion that they are essentially identical, thus the same taxon, based on the limited-area photographs presented in Mori's work. Here we have combined *C. striatellum* and *C. simplex* and refer to them as *Petridiostroma simplex* because they resemble *Petridiostroma*; their laminae are planar contrasting the wrinkled laminae of *Clathrodictyon* (Nestor 2015). *Petridiostroma* is illustrated in Pls 10 and 12 of this monograph.

2. Mori (1970, pl. XII, figs 5–6) illustrated *Stromatopora carteri*, and Mori (1970, pl. XV, figs 1–6) illustrated *Syringostromella borealis*. The similarity between the photographs of these two taxa, nominally placed even in different traditional genera, is profound and it is not at all clear that they are different. The problem is exacerbated by illustration in Mori's (1970) paper of *S. carteri* in two small-area photographs (one VS, one TS) while *S. borealis* is shown in six photographs (three VS and three TS); thus variation in *S. borealis* is shown in these several photographs but not in *S. carteri*. The overlap in structure is significant in these pictures, which cannot be relied upon for taxonomic distinctness. Nicholson (1891, pp. 175, 176) also noted the similarity between *S. carteri* and *S. borealis* but made a brief comparison to discriminate them. He wrote that the growth form of *S. carteri* is laminar, implying that this is a taxonomic feature, but Kershaw (1990) found that both these taxa are laminar-shaped fossils in the Ludlow of Gotland, although in the MWLF, *S. borealis* is a domical form. Nevertheless, growth form cannot be relied upon for taxonomic distinction. Nicholson also stated that the skeletal architecture of *S. borealis* contained more tabulae in vertical spaces and that they are commonly aligned horizontally to give the impression of "continuous concentric lines" (Nicholson 1891, p. 176). This distinction is rather weak, and the problem is compounded by the images presented in Stearn's (2015a, p. 811) photographs defining *Syringostromella*, which clearly overlaps in appearance with Mori's (1970) illustrations of the two taxa. An additional point is the work by Stearn (2015b) in a chapter illustrating different microstructures in stromatoporoids. In Stearn (2015b, figs 3.38, 3.40) are pictured microstructures of one sample from the NHMUK (PI P5678) that Stearn called *Syringostromella carteri*! Our study of all Silurian stromatoporoids from museum and new material (including NHMUK PI P5678) recognizes these as a single taxon identified as *S. borealis*. We have discounted *Stromatopora carteri* and thus *Syringostromella carteri* as valid taxa and refer to all these samples as *Syringostromella borealis*, because the structure is very different from *Stromatopora* but matches *Syringostromella* (Stearn 2015a). Thus, we illustrate a taxon called only *S. borealis* in Pl. 21 of this monograph.
3. Mori (1970, pl. XII, figs 1–2) figured *Stromatopora antiqua* and *Actinostromella vaiverensis* (Mori, 1970, pl. IX, figs 3–6). Apart from small variations in the contrast of the photos due to preservation differences, these two taxa are identical, and so we have named these as *A. vaiverensis*, discarding *S. antiqua* not least because its structure is not compatible with *Stromatopora* as defined by Stearn (2015a) in the *Treatise on Invertebrate Paleontology*. We illustrate *A. vaiverensis* in Pl. 15 of this monograph.
4. *Labechia rotunda* of Johnston (1915) and *Labechia scabiosa* of Nicholson (1891) were both defined by those authors from hand specimens, but thin sections were not made for their publications. Only one specimen of each taxon exists in the NHMUK collections, so it is clear that these holotypes were introduced but no further work was done. Thin sections of both samples of these proposed taxa were subsequently made and are stored in the NHMUK. Plates 3–7 provide the first photographs of these thin sections, presented at various scales, and it is clear that neither taxon is *Labechia*. Both holotypes are somewhat diagenetically altered, but study using cross-polarized light reveals their structure is most similar to *Lophiostroma schmidti*, which is an unusual stromatoporoid with a unique solid skeletal architecture comprising stout vertical pillar-like components that are actually made of thin plates. Therefore, in this monograph we reject both *L. rotunda* and *L. scabiosa* and they are excluded from the compilation of British Silurian taxa, recording them instead as *Lophiostroma ?schmidti*, illustrated in Pls 3–7 of this study, including *L. schmidti* for comparison. Nevertheless, we have not included them as confirmed taxa in the compilation of stromatoporoid taxa in Text-fig. 35, they are included as *Lophiostroma ?schmidti*.

We conclude that the problem of *Labechia rotunda* and *Labechia scabiosa* is resolved, even though the precise taxon within the *Lophiostroma* form is not fully identified. However, for those taxa that are also described by Mori (1969a, 1970) from Gotland, the way forward to address those taxonomic problems is to re-examine all of Mori's (1969a, 1970) Gotland stromatoporoid



| | | MIDLAND PLATFORM OF CENTRAL ENGLAND | | | | | | | | | | | | | | | OTHER AREAS | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LLAN. | WENLOCK | | | | | | | | | | | | | LUDLOW | WENLOCK | ?SILURIAN | |
| | | | Usk Inl. | Wool-hope Inl. | Malverns area | | | Wenlock Edge | | | Norris Hill | Wren's Nest | | | Wal-Sall | | Isle of Man | Girvan | |
| TAXON | Abbrev. in figs. | M | M | M | IP | L | M | IP | L | M | M | IP | L | M | M | M | L | M | TOTAL |
| *Labechia conferta* | Lc | | | | 1 | 1 | 1 | 12 | 1 | 19 | | | 2 | 3 | | | | | 40 |
| *Lophiostroma ?schmidti* | L?s | | | | | | | | | 2 | | | | | | | | | 2 |
| *Lophiostroma schmidti* | Ls | | | 1 | | | | 1 | | 1 | | | | | | | | | 3 |
| *Ecclimadictyon sp.* | ECSp1 | | | | | | | 1 | | 1 | | | | | | | | | 2 |
| *Ecclimadictyon macrotuberculatum* | Em | 1 | | 3 | | | | 10 | 1 | 6 | | 2 | | 2 | | | | 1 | 26 |
| *Ecclimadictyon astrolaxum* | Ea | | 2 | 7 | | | | 1 | 1 | 9 | | | | 1 | | | | | 21 |
| *Petridiostroma simplex* | Ps | | | 1 | | 1 | | | 3 | 16 | | 1 | | 10 | | | | | 32 |
| *Petridiostroma linnarssoni* | Pl | | | | | | | 1 | | | | | | | | | | | 1 |
| *Petridiostroma sp1.* | PESp1 | | | | | | | | | 1 | | | | | | | | | 1 |
| *Actinostromella vaiverensis* | Av | | | | 1 | 4 | 1 | 8 | 5 | 4 | | 10 | 2 | | | | | | 35 |
| *Araneosustroma fistulosum* | Af | | | | | 1 | | 8 | 2 | 1 | | 1 | 2 | | | | | | 15 |
| *Densastroma pexisum* | Dp | | 1 | | | 6 | 1 | 5 | 1 | 23 | | 7 | 5 | 2 | | | | | 51 |
| *Plectostroma intertextum* | Px | | | | | | 1 | 16 | 3 | 15 | | 1 | | 1 | | 9 | | 2 | 48 |
| *Simplexodictyon yavorski* | Sy | | | | | | | 1 | | 1 | | | | | | | | | 2 |
| *Eostromatopora impexa* | Ei | | | 1 | | | 2 | 5 | 4 | 16 | | | | 1 | | 1 | | | 30 |
| *Eostromatopora sp1.* | EOSp1 | | | | | | | 6 | | | | | | | | | | | 6 |
| *?Eostromatopora* | ?EO | | | | | | | 1 | | | | | | | | | | | 1 |
| *"Stromatopora" venukovi* | "S"v | | | | | | | | | | | | | | | | 1 | | 1 |
| *?"Stromatopora" venukovi* | ?"S"v | | | | | | | | | | | | | | | | 1 | | 1 |
| *?"Stromatopora" lamellosa* | ?"S"l | | | | | | | | | | | | | | | | 1 | | 1 |
| *Syringostromella borealis* | Sb | | 2 | 6 | | | 2 | 4 | 1 | 10 | | 12 | 13 | 3 | 1 | 1 | 1 | | 56 |
| *Parallelostroma typicum* | Pt | | | 1 | | | | 1 | 1 | 8 | 1 | 1 | | | | | 1 | | 14 |
| Unidentified stromatoporoids | UNID | | | | | | | 5 | 1 | 9 | | 1 | | 2 | | | 1 | | 19 |
| | | | | | | | | | | | | | | | | | | GRAND TOTAL = | 408 |

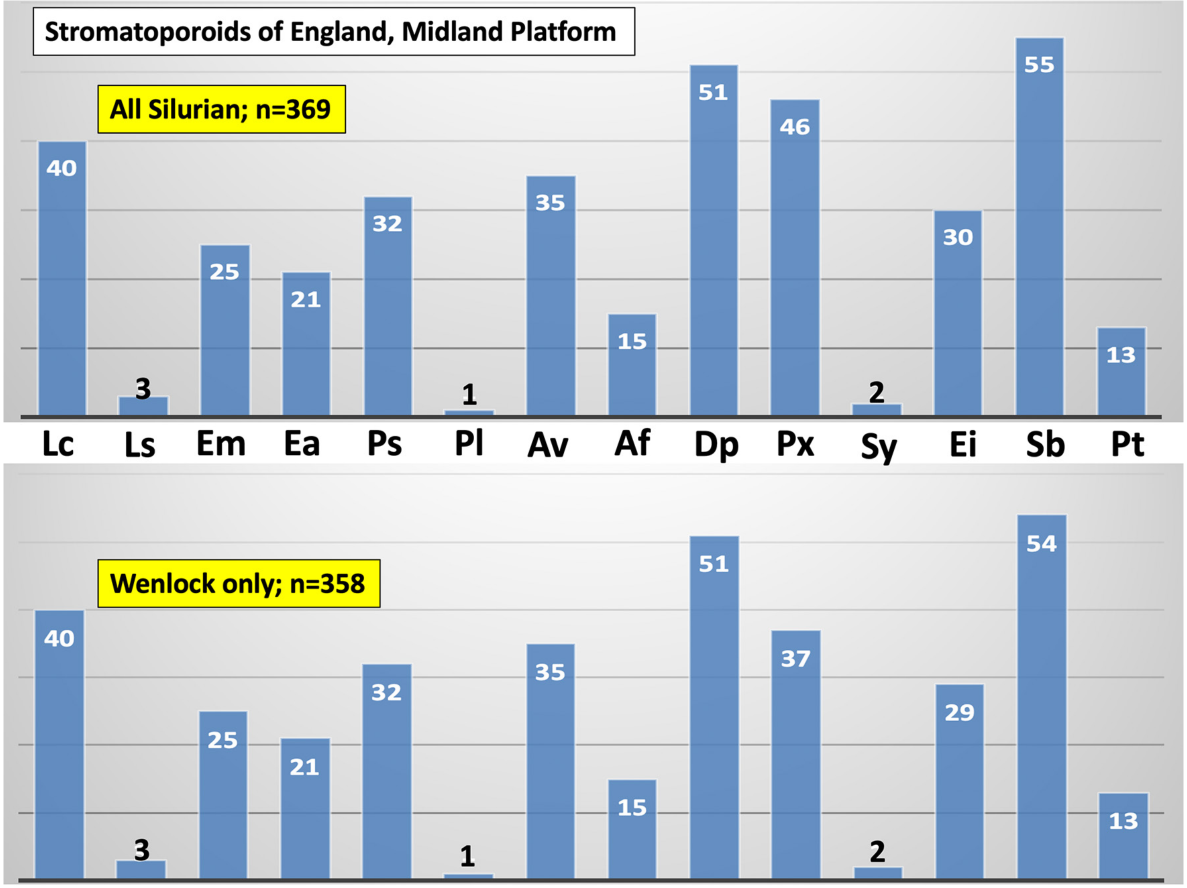
Llan = Llandovery; Inl. = inlier; M = Museum sample; IP = in place; L = loose

Text-fig. 35. Distribution table showing all the stromatoporoid taxa examined in this study. Of the 408 total, 189 were assembled from fieldwork plus a few donated samples from private collectors; 219 are in museum collections. Of 189 field samples, 128 were collected in-place and the other 61 were loose. 15 taxa were fully identified (375 specimens), 7 partly identified (14 specimens) taxa and 19 samples identified only as stromatoporoids. Thus, 88% of the assemblage was fully identified. The five most abundant taxa are *Labechia conferta* (40 specimens, 10.6%), *Actinostromella vaiverensis* (35 specimens, 9.3%), *Densastroma pexisum* (51 specimens, 13.6%), *Plectostroma intertextum* (48 specimens, 12.8%) and *Syringostromella borealis* (56 specimens, 14.9%), and totalling 230 specimens, 64.2% of the assemblage, which is a typical proportion for stromatoporoid assemblages (see Kershaw *et al.* 2018).

taxa and assess their viability of discrimination of low-level taxa. All six of these traditional taxa (*C. simplex* and *C. striatellum*, *S. borealis* and *S. carteri*, *A. vaiverensis* and *S. antiqua*) are named in the British Silurian stromatoporoid compilations in published works, but we view them as only three taxa (*Petridiostroma simplex* [combines *C. simplex* and *C. striatellum*], *Syringostromella borealis*, and *A. vaiverensis*). These cases emphasize the point that stromatoporoid low-level taxonomy still has a long way to go before determination of taxa can be considered complete. Extending this argument across stromatoporoids as a whole leads to the logical step of a need to revisit thin sections of all published studies to document all the variations, a task outside this study but one which may lead to a more comprehensive understanding of the diversity and distribution of stromatoporoid taxa.

## Stromatoporoid distributions

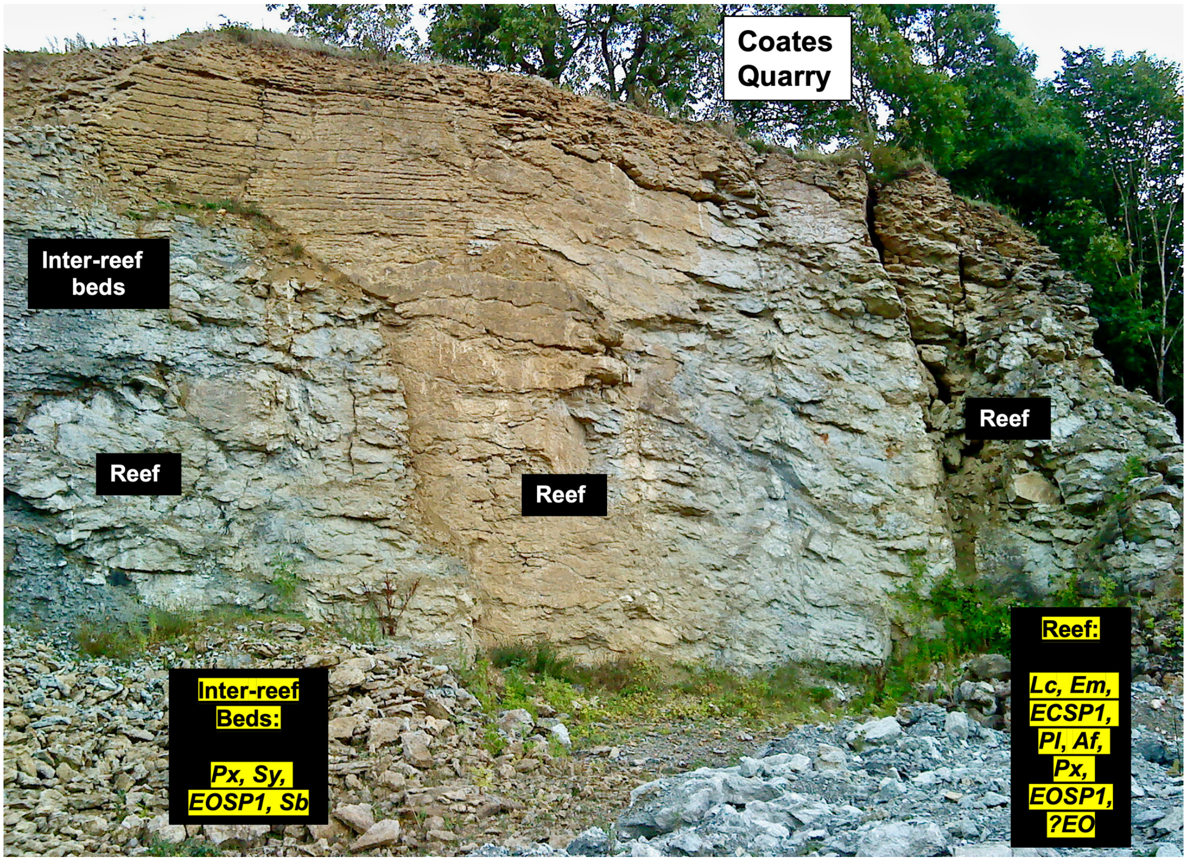
*General points.* A summary table of all taxa found in this study is provided in Text-fig. 35, arranged in the same sequence as normally presented in traditional stromatoporoid classifications. This is how they are shown in Stock *et al.* (2015, table 37) for Wenlock-age stromatoporoids, to keep compatibility with the *Treatise on Invertebrate Paleontology*, but without the grouping into orders, as explained earlier. Text-figure 36 visualizes the relative abundance of fully identified taxa for all the Silurian and for only the MWLF, including all material (field-collected in-place, loose, complete, broken; and museum samples). Text-figures 37–39 indicate the locations of in-place taxa collected during this study, most taxa occur in both reef and non-reef positions. Text-figure 40 shows shape and size data from the relatively small number of samples that could be measured fully, given that loose material is commonly broken, and museum thin sections have these data for only a few specimens in those collections. Most stromatoporoids are of low to high domical shape, using the shape classification of Kershaw & Riding (1978), and rarely exceeded 20 cm in basal diameter. Thus, British Silurian stromatoporoids are notably

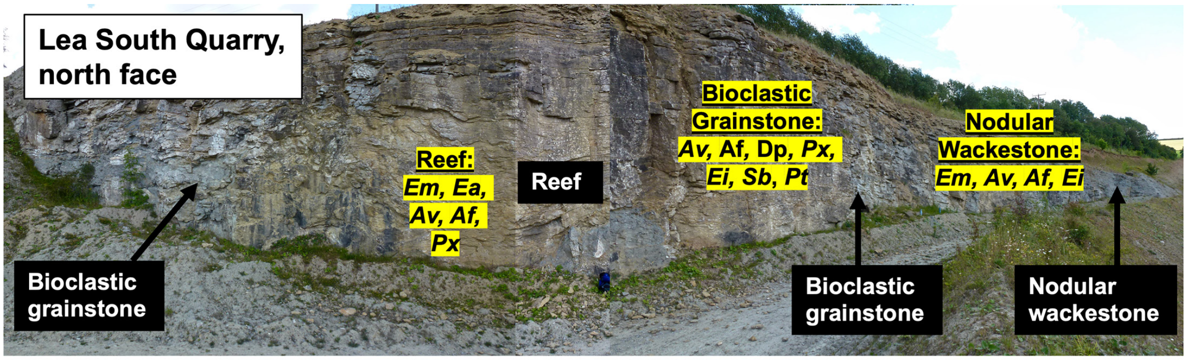


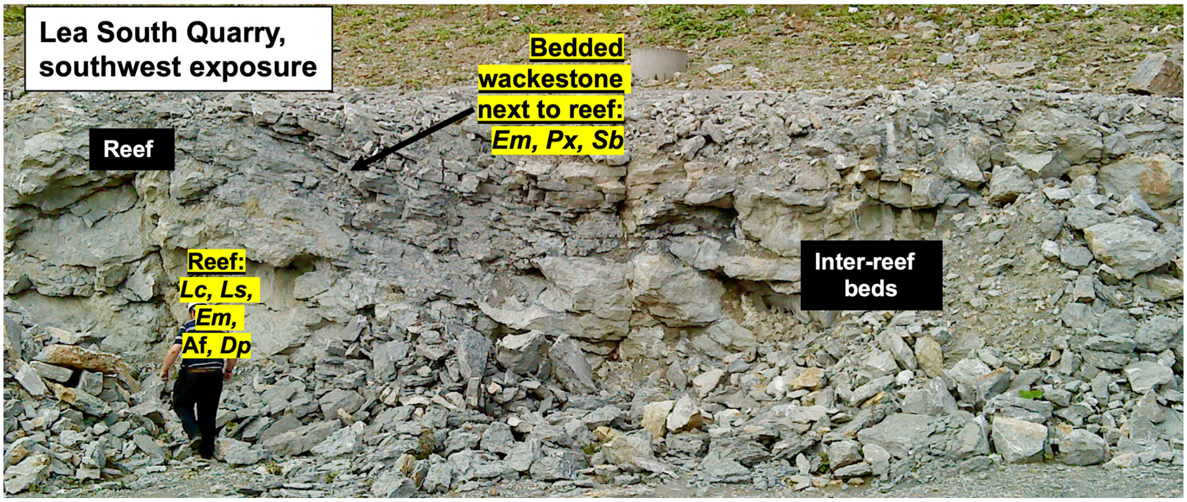
TEXT-FIG. 36. Histograms of the fully identified taxa from the Silurian of the Midland Platform, to emphasize the portion of the stromatoporoid assemblage across the carbonate facies. Upper diagram shows all the Silurian; lower diagram shows only the Wenlock stromatoporoids, the great majority of which are from the relatively small area occupied by the Much Wenlock Limestone Formation (MWLF) (see Text-fig. 1C), a narrow time window during which Silurian stromatoporoids thrived in England. Although these histograms are similar, both are provided to illustrate the high abundance of stromatoporoids in the MWLF, most of the British Silurian stromatoporoids. Abbreviations of the taxa are given in Text-fig. 35.

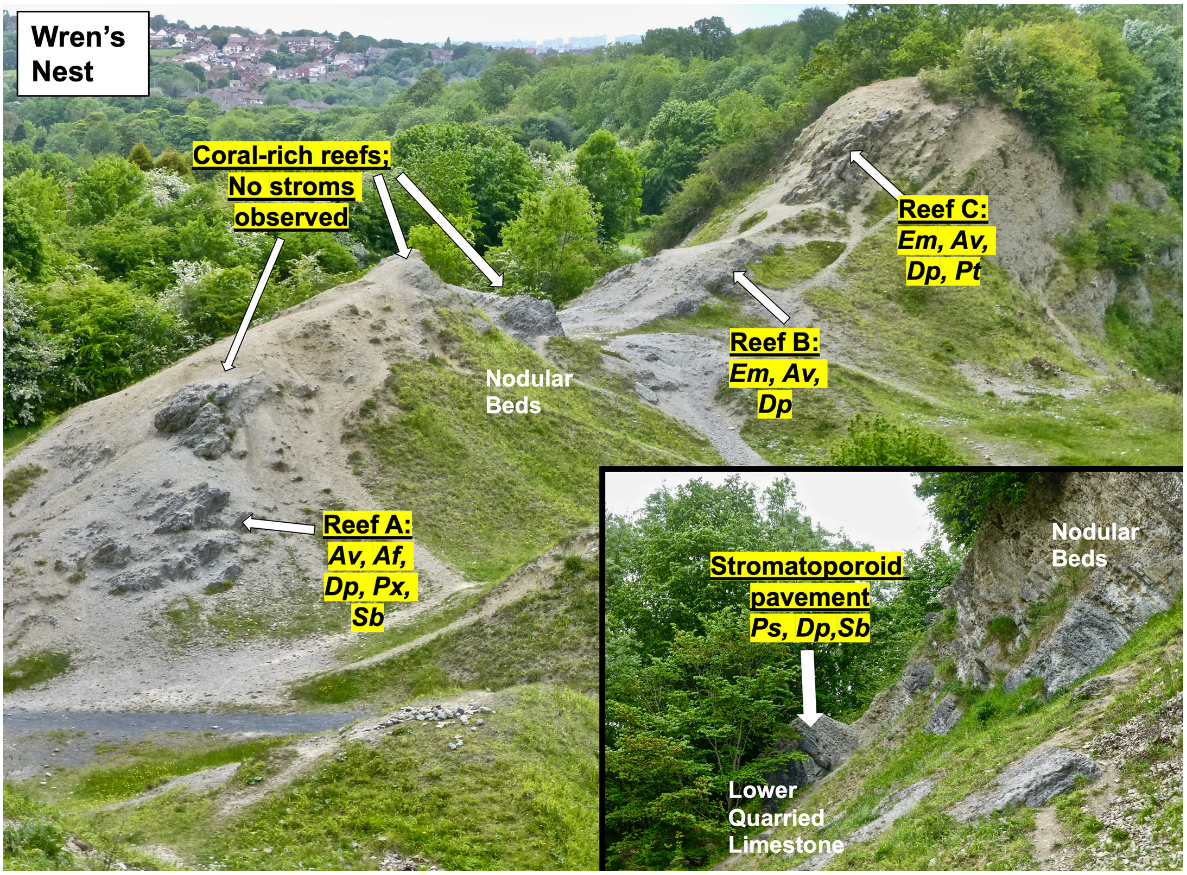
TEXT-FIG. 37. Patch reef showing both reef and inter-reef facies, from which stromatoporoids were collected in-place. The abbreviations of stromatoporoid taxa are given in Text-fig. 35. The Coates Quarry reef core on the right-hand side of the photograph is the best site now remaining of the limited Wenlock Edge reefs preserved, that shows a laminar reef frame of *Labechia conferta* shown in Text-fig. 7C, and large domical specimens of reef-constructing stromatoporoids, in this case *Ecclimadictyon macrotuberculatum* shown in Text-fig. 8B. Much Wenlock Limestone Formation, Coates Quarry, Wenlock Edge.

TEXT-FIG. 38. Two accessible rock faces in Lea South Quarry, Wenlock Edge, showing both reef and inter-reef facies, from which stromatoporoids were collected in-place. The abbreviations of stromatoporoid taxa are given in Text-fig. 35. In the upper photograph, the reef was difficult to access because of its sheer face, and sampling was also avoided in locations that would damage the appearance of the face, given that this is a rare example of a Wenlock reef site now clearly visible, remaining after quarrying ended; in the lower photograph only the top of the reef was exposed. Thus, the taxa list gives only a general impression of the stromatoporoid taxa present. Although laminar frames of *Labechia conferta* are a feature of Wenlock reefs in Britain, other taxa occur in reef and inter-reef beds, indicating that there was no essential difference between reef and non-reef facies for stromatoporoid growth. Much Wenlock Limestone Formation.


Coates Quarry
Inter-reef beds
Reef
Reef
Reef
Reef: Lc, Em, ECSP1, Pl, Af, Px, EOSP1, ?EO
Inter-reef Beds: Px, Sy, EOSP1, Sb


Lea South Quarry, north face
Reef: Em, Ea, Av, Af, Px
Reef
Bioclastic Grainstone: Av, Af, Dp, Px, Ei, Sb, Pt
Nodular Wackestone: Em, Av, Af, Ei
Bioclastic grainstone
Bioclastic grainstone
Nodular wackestone


Lea South Quarry, southwest exposure
Bedded wackestone next to reef: Em, Px, Sb
Reef
Reef: Lc, Ls, Em, Af, Dp
Inter-reef beds

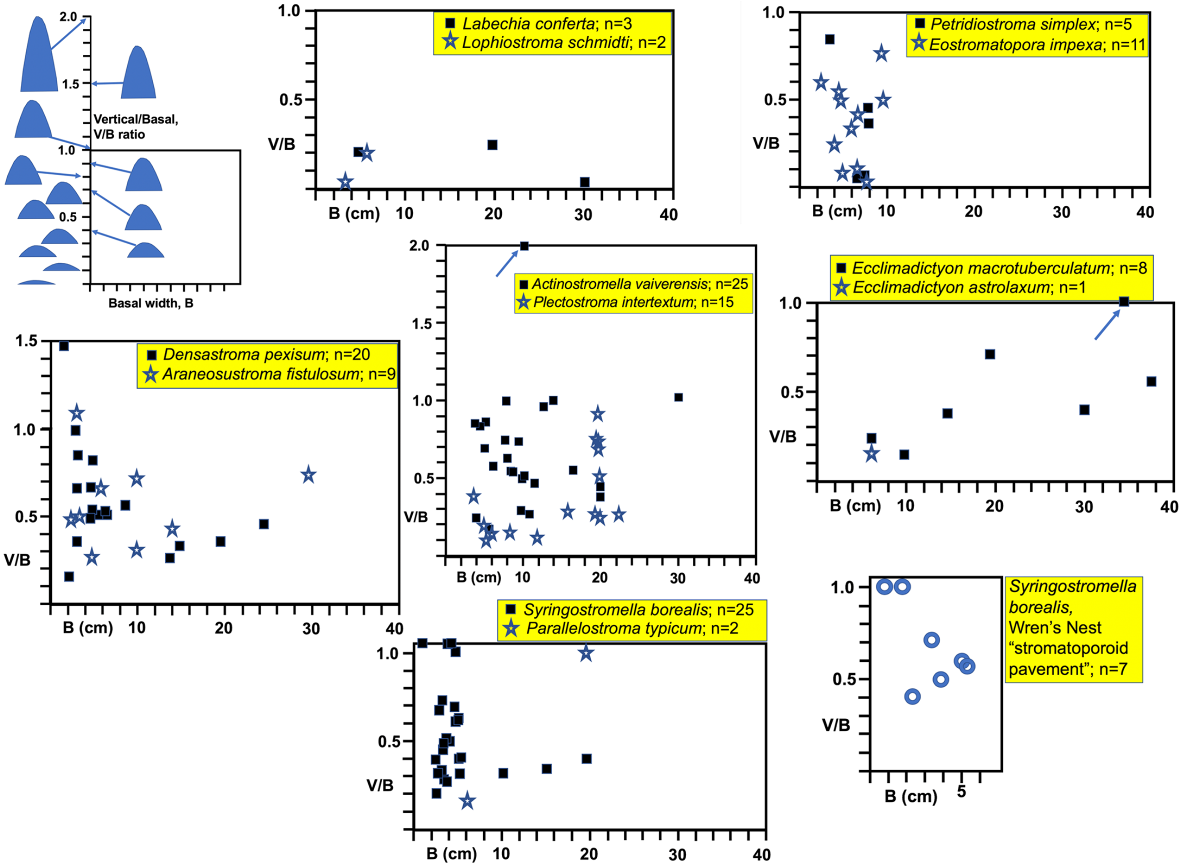


TEXT-FIG. 39. Stromatoporoid assemblages in accessible sites in Wren's Nest, in the Lower Quarried Limestone and Nodular members. The abbreviations of stromatoporoid taxa are given in Text-figure 35. The 'stromatoporoid pavement' of the Lower Quarried Limestone is the upper of two stromatoporoid-rich biostromes (Butler 1939). *Syringostromella borealis* is most abundant in this biostrome, concentrated on one horizon. This is interpreted as a level of settlement of this taxon during a phase of lowered sedimentation. No stromatoporoids were confirmed in-place in the bedded limestones of the Nodular Beds, but several occur in the small patch reefs, where the stromatoporoid assemblage was more limited in numbers of taxa than in Wenlock Edge. Much Wenlock Limestone Formation, Wren's Nest, Dudley.

smaller than those in the large carbonate platforms on stable cratonic areas, such as in Baltica and Laurentia. In the British Silurian, larger samples grew in reefs.

*Midland Platform, southern Britain.* Text-figure 36 displays those stromatoporoids that were completely identified from the English Midland Platform MWLF; these are the most reliable samples to characterize the stromatoporoid assemblage in the upper Homerian Stage of the Wenlock Series in Britain. Note that a few samples in Lea South Quarry on Wenlock Edge were collected from the very base of the overlying Elton Formation calcareous mudstones but are included with the MWLF taxa for simplicity. Two taxa, *Densastroma pexisum* and *Syringostromella borealis* together make up 29.6% of the MWLF stromatoporoid suite, and the five most abundant taxa total 64.2% of the MWLF. This bias towards a small number of taxa making up a significant portion of the assemblage is a feature found in other stromatoporoid deposits, and is characteristic of the Silurian of Gotland, for example (Kershaw *et al.* 2018).

Of the total sample of 358 MWLF identified stromatoporoids distributed in Text-fig. 36 (primary samples plus museum collections), 118 (= 33%) are from in-place sampling (from Malverns, Wenlock Edge, and Wren's Nest), giving a good impression of the facies distribution of the stromatoporoids. Although Text-figures 37–39 show the taxa found in all three facies where the stromatoporoids occur (patch reefs, bioclastic grainstones and wackestones), the limited availability of reef exposures prevents full assessment of stromatoporoid distribution.



TEXT-FIG. 40. Graphs of stromatoporoid shapes and sizes using plots of vertical height / basal diameter, against basal diameter on *x*-axis, hence they are V/B : B plots. These graphs are based on a limited subset of the new samples data for which growth form measurements were obtainable. The graphs show the low-profile form of *Labechia conferta*, contrasting the domical form of most taxa, which show considerable variation in size and shape within the limitations of small size of stromatoporoids in the British Silurian.

However, *Labechia conferta* was found mostly in reefs, while the other taxa tend to occur in both reefs and bedded limestones. The most accessible reef in current exposures is in Coates Quarry (Wenlock Edge), where the reef core shows a large laminar frame mass of *L. conferta* plus numerous large domical *E. macrotuberculatum*, together with small specimens of *P. intertextum* and *D. pexisum*. Colter (1957) in a PhD thesis written in the mid-1950s, had access to the sites before the modern infilling and reported that the MWLF reefs were primarily constructed by tabulates and particularly heliolitids, with one taxon he called *Heliolites parvistella* (now is *Stelliporella parvistella* [Young & Scrutton 1991]), showing variations of growth form from branching to domical (Scrutton 1997b; Young & Scrutton 1991). Colter (1957) regarded the prevalence of low-profile stromatoporoids at the reef margins as an indication that they responded to higher wave energy, although there is general agreement that these reefs grew in conditions of relatively low energy (Colter 1957; Scoffin 1971; see also Riding 1981). Note, however, that *L. conferta* always grew low-profile growth forms and most likely is taxonomically controlled so its abundance on reef margins may be due to its morphological advantage. In reef margins, an interesting possibility is that some stromatoporoids and tabulates may have slipped and rotated during life on the slopes, a feature recognized in Devonian mounds by Krol *et al.* (2016). However, although there are numerous cases of stromatoporoids and tabulates that have been reorientated by disturbance (presumably currents), no cases that could be attributed to slipping on a slope have been found in the material studied here, consistent with the high percentage of reef builders recorded in-place by Crosfield & Johnston (1914). The possibility that growth occurred on partly lithified substrates, known to be common in stromatoporoids

(Kershaw *et al.* 2018), may have played a part in stabilizing their growth in the MWLF. Finally, all authors note that the reefs and their stromatoporoid faunas occur in the northern part of Wenlock Edge, while to the south-west, the off-reef tract lacks reefs because of deeper water, although some stromatoporoids were recorded by Colter (1957). Note that the line of the outcrop of Wenlock Edge is oblique to the shelf margin, so that southern parts of Wenlock Edge represent deeper water than the northern parts.

In the Malvern Hills, Penn (1971) recorded stromatoporoid taxa (*Actinostroma* and *Stromatopora* of older taxonomic names, and *Labechia*) in the Parkwood Quarry bioherms on the western slopes of the Malvern Hills, where the stromatoporoids grew laminar to low-domical growth forms as part of the reef frameworks. However, at nearby Whitman's Hill Quarry, the reef structure was recorded by Penn (1971) as lacking a reef framework, confirmed by Pässler *et al.* (2014). Penn noted presence of small stromatoporoids at Whitman's Hill Quarry, and in this study, we found two specimens of *Labechia conferta* and one of *Petridiostroma simplex*. A small number of samples from the Woolhope and Usk inliers are in the NHMUK and CAMSM collections (Text-fig. 35).

*Isle of Man.* The Lower Devonian Peel Sandstone on the Isle of Man contains Wenlock-age pebbles as described earlier. Of the six stromatoporoid specimens found in the study by Crowley *et al.* (2009), only three were fully identifiable as *Parallelostroma typicum, Syringostromella borealis* and *'Stromatopora' venukovi*. The latter is not compatible with the structure of the traditional genus *Stromatopora* (see Stearn 2015a), but is a distinct taxon, being common in the Wenlock and Ludlow series on Gotland (Mori 1970). However, *'S.' venukovi* is not found in the Midland Platform. *'Stromatopora' venukovi* contains intergrown syringoporid tabulate tubes (Pl. 18). One of the three unidentified stromatoporoids is a single thin section in TS, and also contains abundant symbiotic syringoporid tabulates, a feature common in the large carbonate platforms such as Gotland (Kershaw 1987; Mori 1970) but symbiotic tabulates are absent from the Midland Platform sites. Of all the samples studied in this project, only two contained intergrown tabulates, both in the Peel Sandstone.

*Northern Britain.* In northern Britain, in sites which were on the north side of the closing Iapetus Ocean area in the middle Silurian (Cope *et al.* 1992; Woodcock & Strachan 2012), three stromatoporoid specimens were described by Nicholson (1889, pp. 140, 149), but the samples were given to him by a famous Victorian Scottish fossil collector, Mrs Robert [Elizabeth] Gray (see Clarkson, 1985, p. 393), in the Girvan area of southwest Scotland, in two sites:

1. Labelled "Balcletchie" (now spelled Balclatchie), noted by Nicholson (1889, p. 140) as from a unit described as the Balcletchie Conglomerate of Silurian age. However, the Balcletchie Conglomerate was renamed Burn Side Conglomerate, as part of the Ardwell Farm Formation and is Sandbian age (earlier Caradoc Series in UK stratigraphy), Late Ordovician (Fortey *et al.* 2000; Williams & Floyd 2000; also named in the BGS Lexicon of Named Rock Units, https://www.bgs.ac.uk/lexicon/lexicon.cfm?pub=BUN, accessed on 3 September 2019). The problem here is that two samples contain a stromatoporoid known from only the Silurian, *Plectostroma intertextum*. We presume that, despite the efforts of the Gray family in assembling fossils from Girvan, these particular samples are mislabelled, and are Silurian stromatoporoids.
2. Nearby at Woodland Point, one stromatoporoid specimen, *Ecclimadictyon macrotuberculatum*, was found in the "Woodland Beds" (Nicholson, 1889 p. 149, see also Nicholson & Etheridge 1880, pp. 238–240 and pl. XIX), also described as Silurian by Nicholson (1889). Woodland Point contains rocks of Llandovery age (upper Rhuddanian–lower Aeronian, see Floyd & Williams 2003), consistent with the known range of that stromatoporoid taxon. The Woodland Point sample was most likely collected from pebbles in the Woodland Point Formation or from the Haven Conglomerate, noting that halysitid tabulates were also found (Ward 1989); these coarse-grained clastics are polymictic, contain dolomite and formed part of downslope gravelly flows.

The provenance of the Isle of Man Wenlock-age material and the Girvan Llandovery material are unknown but are evidence of other former carbonate platforms of both Llandovery and Wenlock age in the British Silurian. The Midland Platform is the only one preserved. These few specimens from areas north of the Midland Platform are evidence of a more widespread distribution of carbonates containing stromatoporoids and tabulates in early to middle Silurian times in the British Isles.

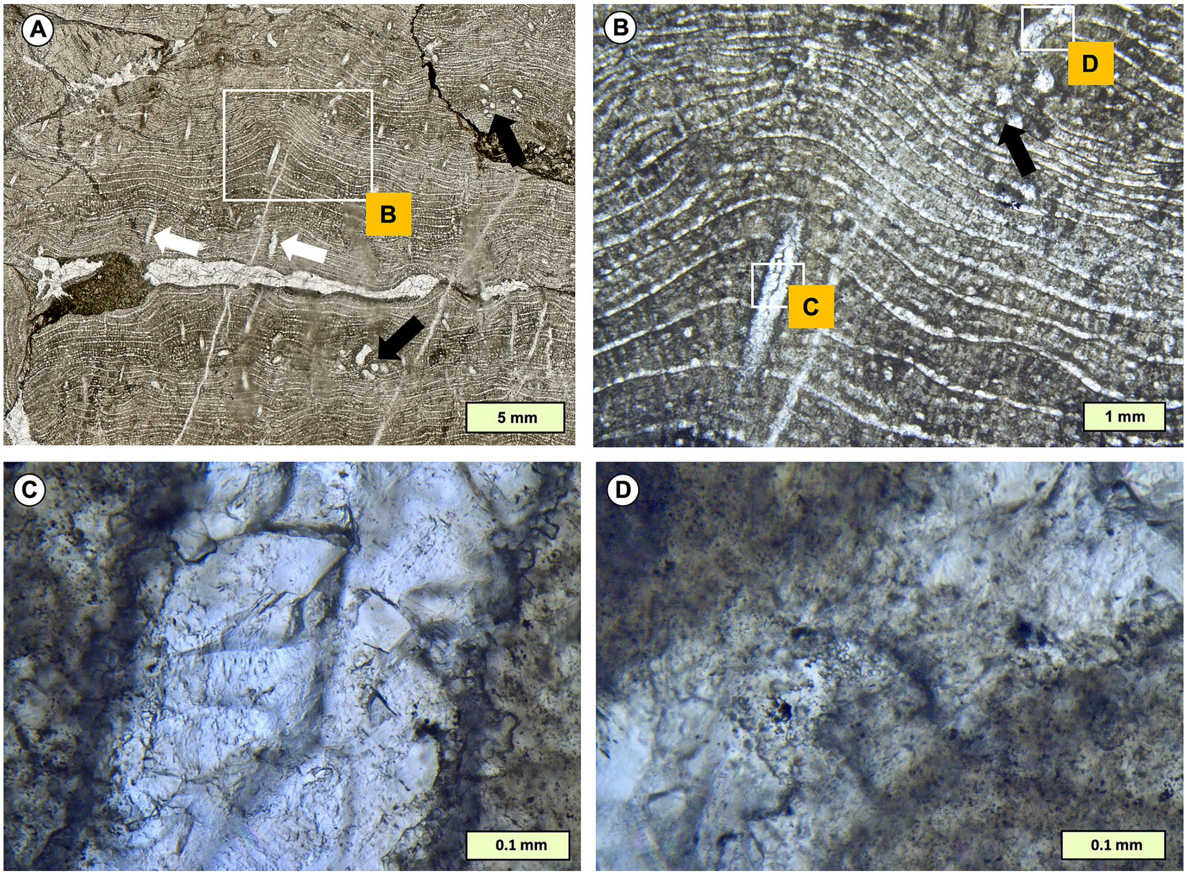
*Northern part of island of Ireland.* Scrutton & Parkes (1992) and Nestor (1998) described Telychian (lower Silurian, therefore somewhat below the MWLF) stromatoporoids from the Charlestown Inlier, County Mayo, west Ireland, north of the Iapetus Suture and therefore part of Laurentia during the Silurian. Petryk (1965) recorded a range of Silurian stromatoporoids from Baffin Island. Nestor (1998, p. 116) compared stromatoporoid faunas between Baffin Island, Canada, the Oslo area, Norway, and the Charlestown Inlier. He concluded that the assemblages are so similar that they may be considered part of the same general fauna. Given that Baffin Island and NE Ireland were effectively on the same continental margin that conclusion is not surprising, but Oslo area is part of Baltica, so the similarity is part of the evidence of faunal migration abilities in stromatoporoids considered in the Discussion.

*Western part of Ireland.* The Dingle area of County Kerry, southwest Ireland, is part of the Avalonia microcontinent south of the Iapetus Suture line. This area has a shallow marine Wenlock carbonate deposit in the Dunquin Group, dated as late Wenlock (Benton & Underwood 1994; Holland 1988; Mac Niocaill 2000; Todd 2015), approximately equivalent to the Midland Platform. Brachiopod communities containing corals were reported by Bassett *et al.* (1976) and Watkins (1978). A general summary of all fossils across Ireland was provided by Griffiths & McCoy (1846), using what is now older taxonomy. Amongst their descriptions, Griffiths & McCoy (1846, p. 64) recorded one Silurian stromatoporoid taxon listed as *Stromatopora concentrica* Goldfuss, commonly occurring at "Doonquin" (now Dunquin), presumed to be from the Wenlock Dunquin Group rocks. One specimen from 'Doonquin' was deposited by Sir Richard Griffiths in the Sedgwick Museum (CAMSM A39258); another is in the National Museum of Ireland (NMING:F7097). Both samples are labelled as *Stromatopora concentrica*, but neither was cut, and no thin sections had been made. These two samples were examined by the authors and revealed as a trace fossil similar to *Zoophycos*, thus there is no current confirmation of the occurrence of stromatoporoids in western Ireland. Griffiths & McCoy (1846, p. 64) also mentioned rare occurrence of another taxon, *Stromatopora polymorpha* Goldfuss, from the "limestone of the Chair of Kildare, Kildare County" in eastern Ireland, also south of the Iapetus Suture (NMING:7096 is the only recorded sample). However, the Chair of Kildare limestones are dated as Late Ordovician (Dean 1977), but overall, the Kildare Inlier ranges from Ordovician to middle Silurian (Parkes & Palmer 1994), so it is possible that Griffiths & McCoy (1846, p. 64) have correctly located Wenlock stromatoporoids there, but this deduction is tenuous and needs further work.

The Dingle sites in this marginal area of the Avalonia microcontinent were interpreted by Watkins (1978) as a volcanic island area separated from the mainland of Avalonia. The presence of corals there reflects the ability of these faunas to take advantage of shallow marine carbonate environments, and the deposits may represent a fragment of larger carbonate platforms no longer preserved. Further investigation beyond the scope of this study is required to determine whether stromatoporoids are present or not.

### Associated organisms

Kershaw *et al.* (2018) divided organisms associated with stromatoporoids into two broad groups: epibionts (organisms that grew on stromatoporoid surfaces) and endobionts (organisms found within the skeletal structure, and in most cases grew symbiotically with the stromatoporoid host). In the British Silurian, epibionts on stromatoporoids are not recorded in detail but we have observed bryozoans as common encrusters on stromatoporoid bases in the material examined for this study. Borings on the upper surfaces of specimens are not commonly found,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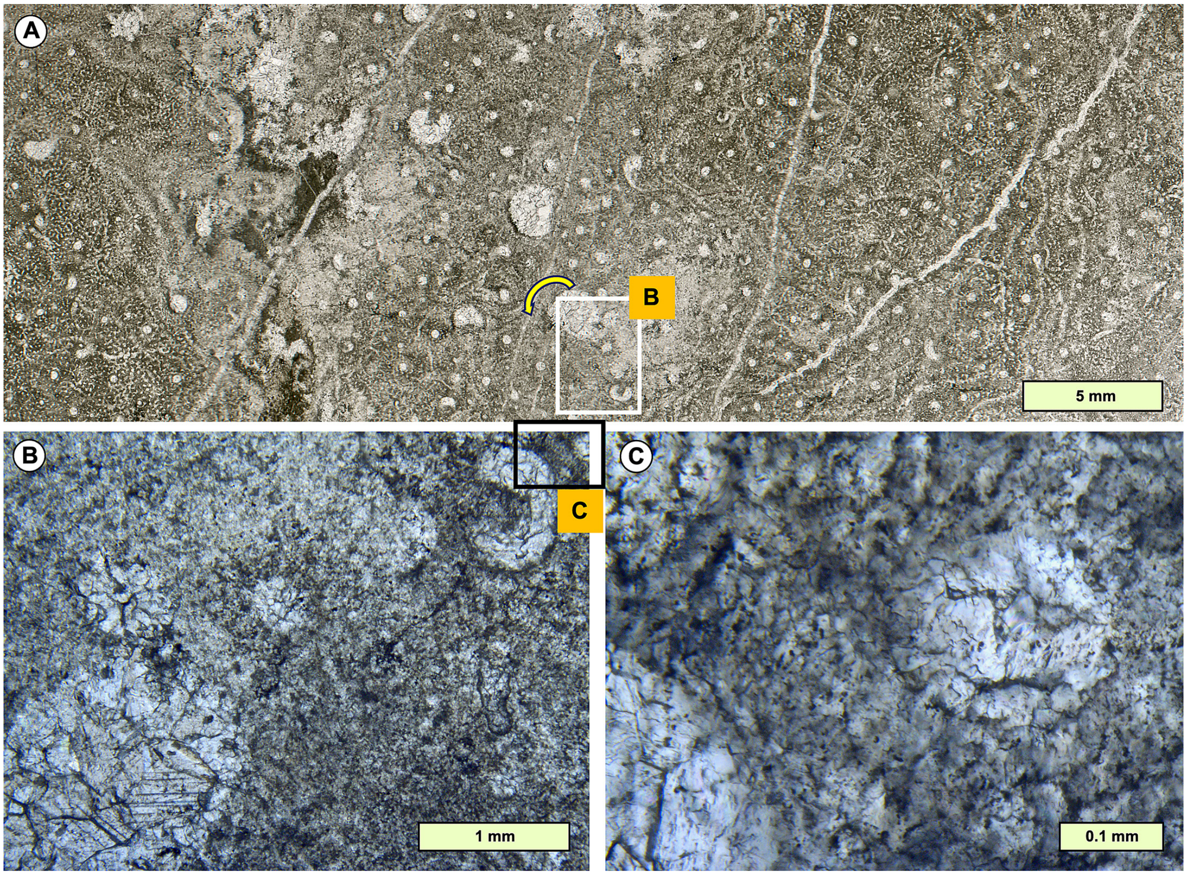
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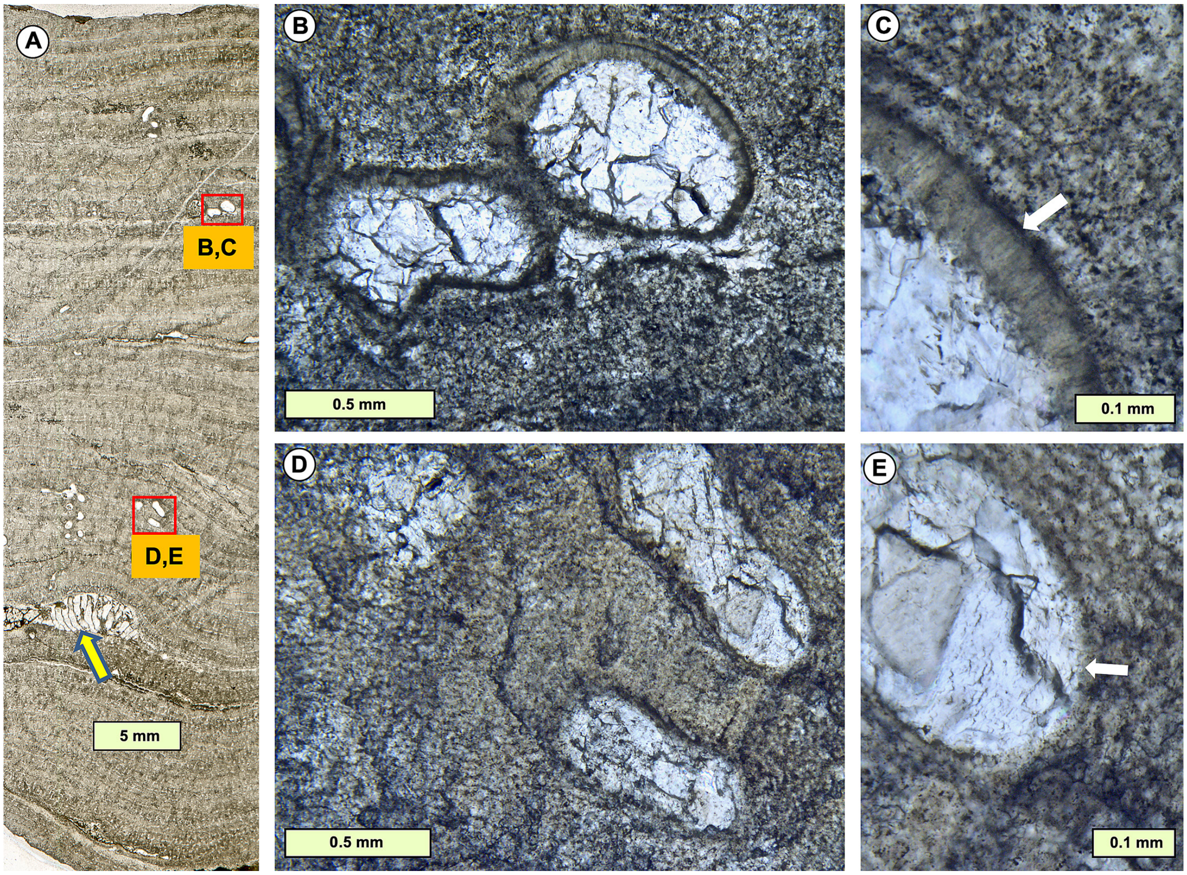


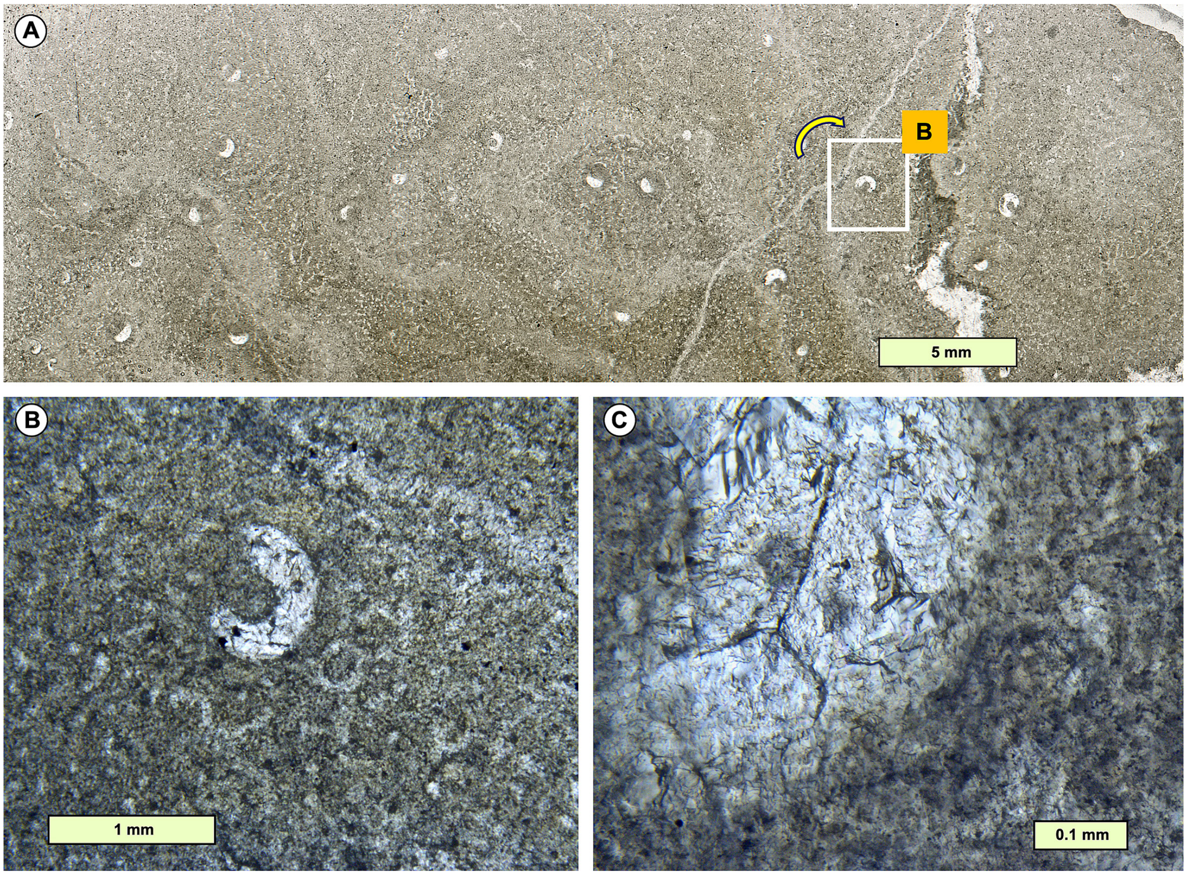
TEXT-FIG. 43. *Actinostromella vaiverensis* (Nestor). **A**, vertical section showing spiral symbiotic tubes that grew upwards for short distances within the stromatoporoid. A bryozoan colony (arrow) grew on an interruption surface. The spiral tubes all seem to have been overwhelmed by the stromatoporoid host, evidence of the ability of stromatoporoids to defeat unwelcome guests during their lives. **B–E**, show the difference between a lined tube (**B, C**) and an unlined tube (**D, E**). The difference may be explained if there was a mineral tube in B, C compared to a possible soft-tissue tube in D, E (also may be a bioclaustration; i.e. an endosymbiont lacking a shell, see Tapanila 2005, Vinn 2016). Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.65.

in contrast to some facies in the large carbonate platforms in Baltica and North America, but we note that boring organisms are uncommon in the Palaeozoic relative to later reefs and reef-associated facies.

Endobionts are more common than epibionts in the MWLF stromatoporoids studied here and occur in some taxa as both lined and unlined tubes (Text-figs 41–44). In contrast, some cases of apparently endobiotic tubes are actually encrusters on a stromatoporoid surface but the stromatoporoid recovered and overgrew the encruster, an example is shown in Text-fig. 45. Text-figure 46 summarizes the occurrence of endobionts in the MWLF and shows their bias towards association with certain stromatoporoid taxa, that may be interpreted as indicating an active biological relationship between the two organisms. However, in the case of spiral tubes illustrated in Text-figs 32, 33, and 41–44, in all cases the stromatoporoid overgrew the tubes, reconstructed in Text-fig. 34. We interpret the relationship between stromatoporoid hosts and

TEXT-FIG. 41. *Parallelostroma typicum* (Rosen). Vertical thin section, showing details of symbiotic straight tubes (white arrows in A). **B**, enlargement of box in **A**, showing the tubes and locations of C and D. **C, D**, enlargements illustrating the tube details, showing they are unlined in this sample and may therefore be bioclaustrations (endosymbionts lacking a shell: Taylor 1990; Tapanila 2005; Vinn 2016). Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.77.

TEXT-FIG. 42. *Parallelostroma typicum* (Rosen). Transverse thin section, same specimen as Text-fig. 41, showing details of symbiotic straight tubes, which are unlined in this sample and may therefore be bioclaustrations. Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.77.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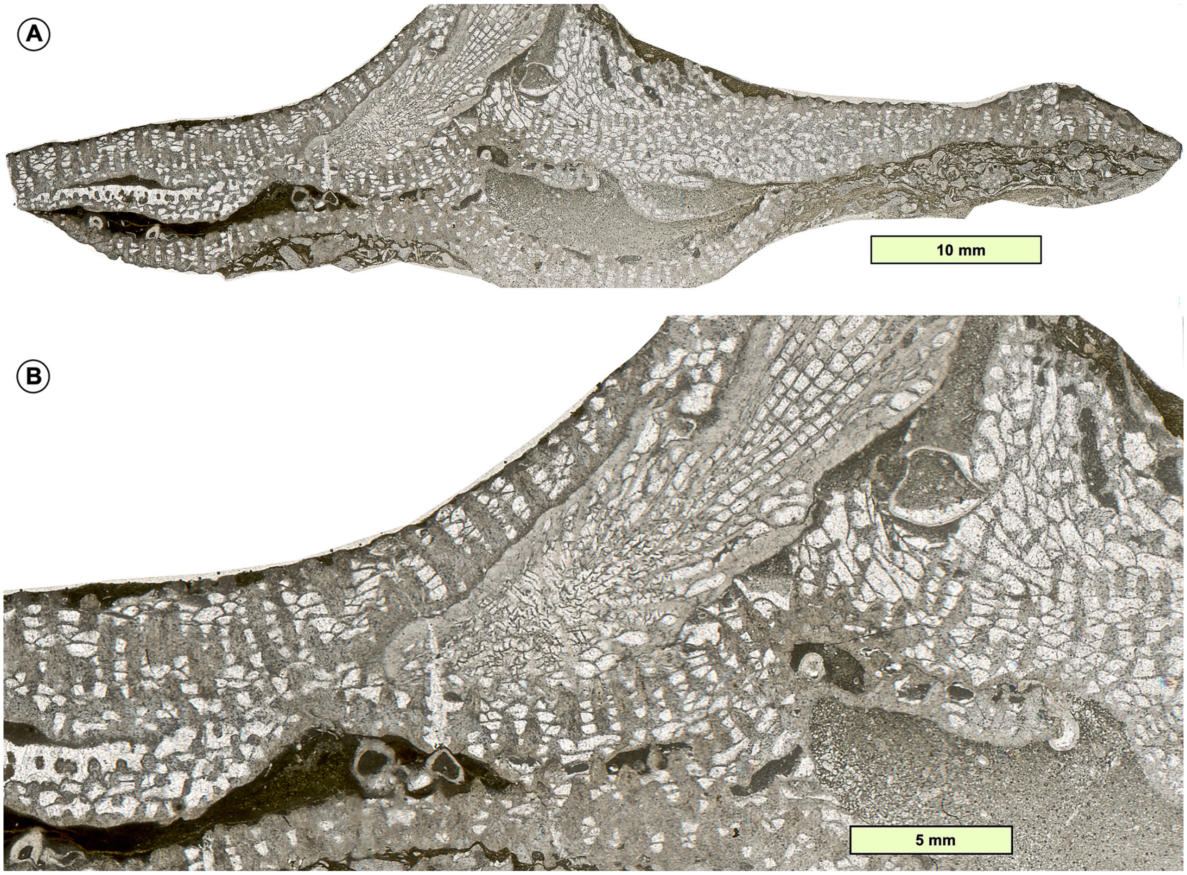
A
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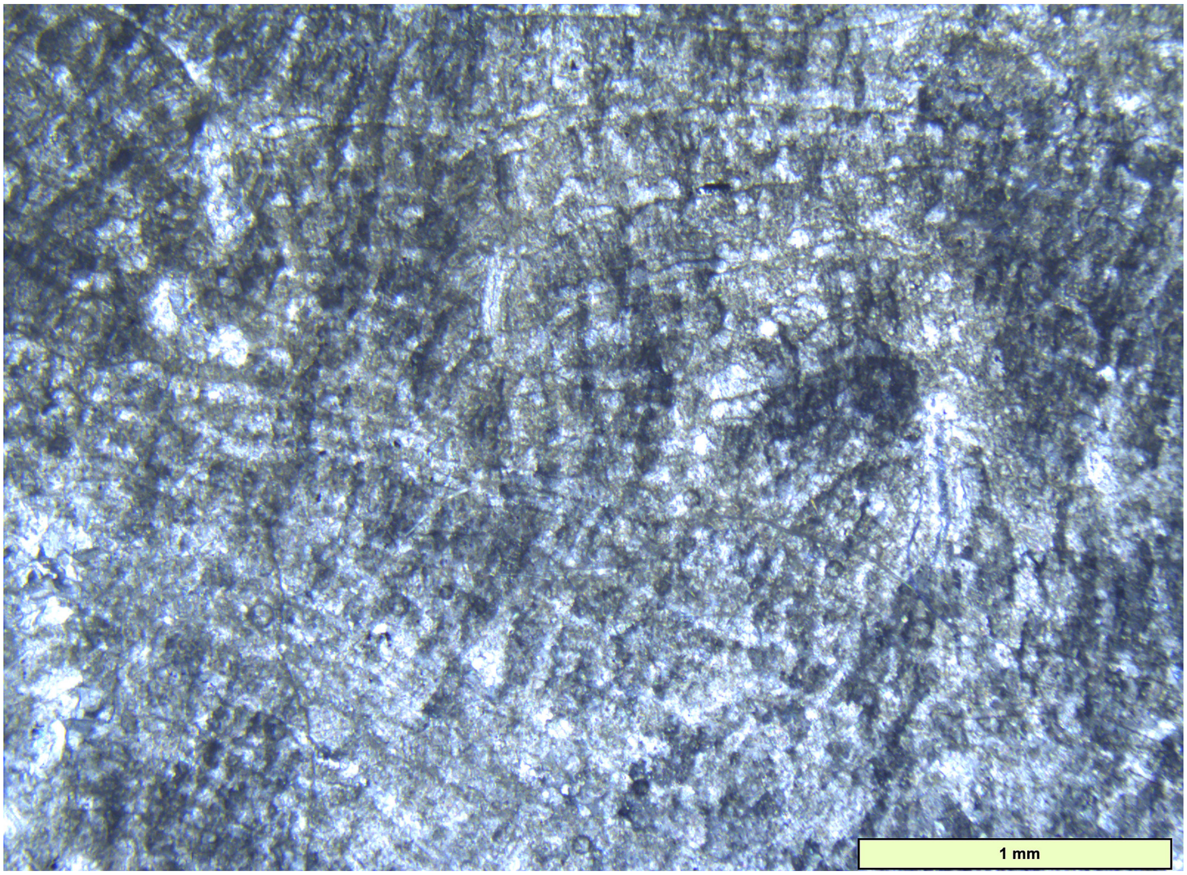
Text-fig. 44. *Actinostromella vaiverensis* (Nestor). **A**, transverse section (TS) of same sample in Text-fig. 43 showing unlined spiral symbiotic tubes in TS, enlargements in **B, C**. Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.65.

Text-fig. 45. *Labechia conferta* (Lonsdale). Vertical whole thin section showing its characteristic laminar form, with growth interruptions. The uppermost growth interruption left sediment deposited on the top of the stromatoporoid (left-hand side) and a rugose coral is present in the centre. The close fit of the lower side of the coral to the top of the stromatoporoid is evidence that the coral settled and grew on the dead surface of the stromatoporoid in that part of its surface. The stromatoporoid recovered from the interruption and grew over the coral but the top of the coral is missing from this sample so it cannot be confirmed whether the coral was ultimately overwhelmed by the stromatoporoid or not. This sample is an example of a case where a foreign organism lies within the structure of a stromatoporoid, but in this case it is not a symbiotic relationship, contrasting the examples in Text-figs 41–44. Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.119.

intergrown tubes as evidence that the spiral-tube organisms settled on living stromatoporoid surfaces and were unwanted by the stromatoporoid, which overgrew the intruding organism. Such a situation contrasts with the syringoporid tabulates (previously called caunopore tubes; see Nicholson 1886, pp. 110–130) and rugose corals commonly found in reef stromatoporoids in Gotland, for example, where there is evidence of a live-live symbiotic interaction, because the symbionts maintained their tubes just above the stromatoporoid surface in almost all cases (Kershaw 1987). Symbionts in stromatoporoids are common in the large carbonate platforms of Laurentia (e.g. De Freitas & Dixon 1995; Young & Noble 1989) and Baltica (e.g. Mori 1970). In contrast, there are no syringoporid tabulates in stromatoporoids in the MWLF of the Midland Platform and only two samples in the Isle of Man (Pl. 18; Text-fig. 46), thus two specimens in the British and Irish suite of 408 specimens.

| | | **NUMBERS OF STROMATOPOROID SPECIMENS WITH INTERGROWN ORGANISMS** | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **TAXON** | **Number of Specimens of this taxon** | **Straight narrow lined tubes** | **Spiral narrow lined tubes** | **Spiral wide lined tubes** | **Specimens with 2 types of lined tube*** | **"Caunopores" (syringoporid tabulates)** | **Bioclaustrations and borings** | **% specimens of this taxon with intergrown organisms** |
| *Labechia conferta* | **40** | | | | | | | **0** |
| *Lophiostroma ?schmidti* | **2** | | | | | | | **0** |
| *Lophiostroma schmidti* | **3** | | | | | | | **0** |
| *Ecclimadictyon sp.* | **2** | | **1** | | | | | **50** |
| *Ecclimadictyon macrotuberculatum* | **26** | | | | | | | **0** |
| *Ecclimadictyon astrolaxum* | **21** | | | | | | | **0** |
| *Petridiostroma simplex* | **32** | | **1** | | | | | **3** |
| *Petridiostroma linnarssoni* | **1** | | | | | | | **0** |
| *Petridiostroma sp1.* | **1** | | | | | | | **0** |
| *Actinostromella vaiverensis* | **35** | **6** | **18** | **6** | **[7**]** | | **1** | **85** |
| *Araneosustroma fistulosum* | **15** | | **7** | **4** | **[2]** | | | **73** |
| *Densastroma pexisum* | **51** | **2** | **12** | **3** | **[2]** | | **1** | **35** |
| *Plectostroma intertextum* | **48** | **1** | **10** | | | | | **23** |
| *Simplexodictyon yavorski* | **2** | | | | | | | **0** |
| *Eostromatopora impexa* | **30** | **1** | **5** | **2** | | | | **27** |
| *Eostromatopora sp1* | **6** | | | | | | | **0** |
| *?Eostromatopora* | **1** | | | | | | | **0** |
| *"Stromatopora" venukovi* | **1** | | | | | **1 (IoM)** | | **100** |
| *?"Stromatopora" venukovi* | **1** | | | | | | | **0** |
| *?"Stromatopora" lamellosa* | **1** | | | | | | | **0** |
| *Syringostromella borealis* | **56** | **1** | **16** | **8** | **[6]** | | | **45** |
| *Parallelostroma typicum* | **14** | **1** | **1** | **1** | **[1]** | | | **28** |
| Unidentified stromatoporoids | **19** | | | | | **1 (IoM)** | | **-** |
| **Total** | **408** | | | | | | | |

Text-fig. 46. Table of taxa with different kinds and abundances of symbiotically intergrown organisms. These data show that only some taxa contain intergrown organisms. It is possible there was a biological relationship between the symbiotic organisms in these interactions (see Kershaw *et al.* 2018 for discussion). * Entries in this column are duplicates from the other columns and are not included in the percentage calculation in the right-hand column. ** One of the 7 samples has all three types of lined tubes. IoM, Isle of Man sample.



Text-fig. 47. *Parallelostroma typicum* (Rosen). Vertical thin section view of the skeletal architecture of this taxon in cross-polarized light, demonstrating the bladed calcite crystal structure that overprinted the skeletal structure, a characteristic of the majority of stromatoporoids. Much Wenlock Limestone Formation, Lea South Quarry, Wenlock Edge, CAMSM X.50347.77.

## Diagenesis of stromatoporoids

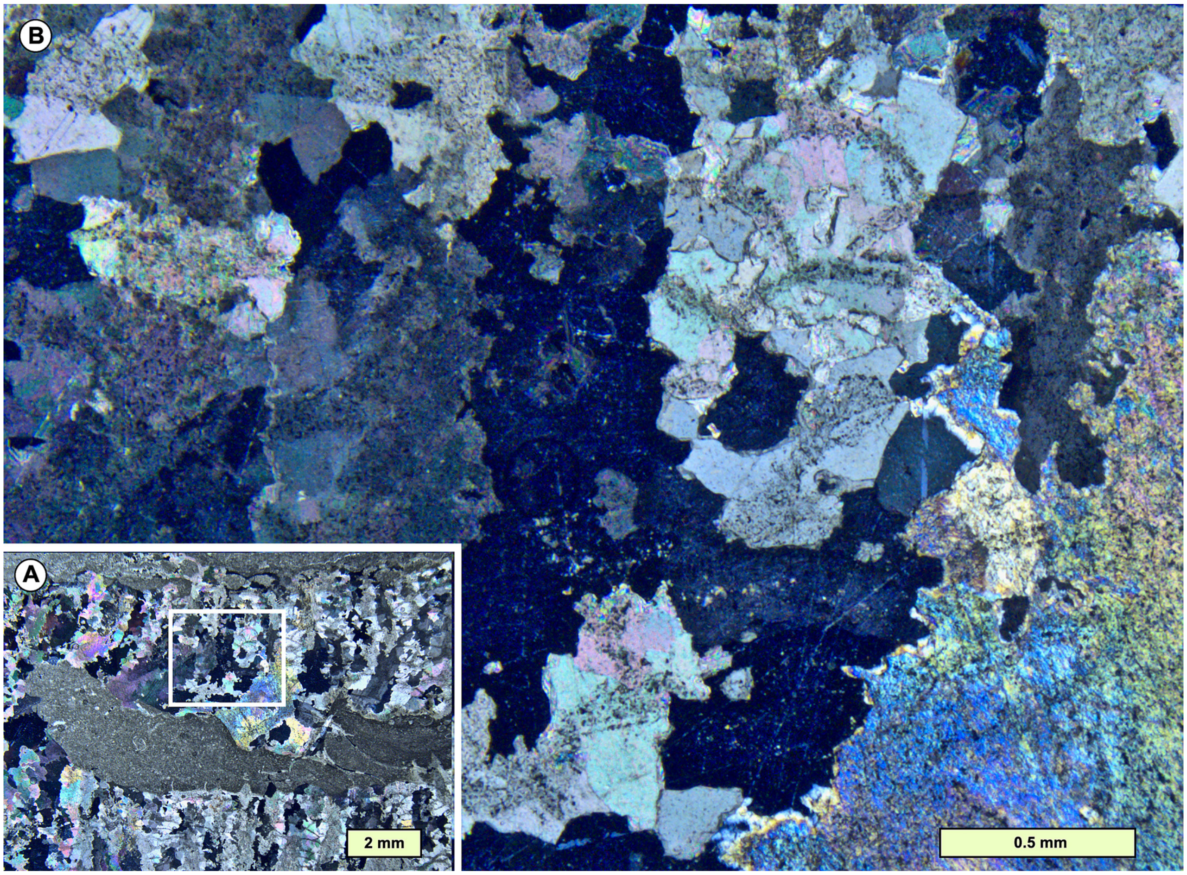
Stromatoporoids are preserved as sparitic calcite with remnant skeletal structure. Their sparitic nature is revealed in very thin sections of approximately 15 microns (not illustrated here), in which the stromatoporoid skeleton is visible as a faint speckle on sparite crystals (see Kershaw 2013; Kershaw *et al.* 2021); their ubiquitous poor preservation makes it difficult to illustrate the structure, because thin sections of 50–80 microns thickness are needed to securely identify and illustrate taxa and inevitably lead to photographs that lack sharpness of focus of thinner sections.

Text-fig. 48. *Labechia conferta* (Lonsdale). **A**, vertical thin section in cross-polarized light through a laminar sheet of the stromatoporoid showing its heavily recrystallized structure, but the skeletal elements are visible. The recrystallization stops abruptly at the margin of the stromatoporoid and does not continue into the overlying and underlying sediment. See Text-figure 51 for location of this photograph on a larger specimen. **B**, enlargement of box in A in which the dissepiments and thick pillars characteristic of this taxon are clearly seen in the recrystallized fabric. The overprinting of recrystallization onto the skeletal structure in stromatoporoids is present in almost all taxa in all facies and geological ages of stromatoporoid history. Nevertheless, the tripartite structure of cyst plates recorded by Mori (1970, p. 79) is visible in some of the cyst plates in B. Much Wenlock Limestone Formation, Coates Quarry, Wenlock Edge, CAMSM X.50347.162.

↑

Text-fig. 49. *Araneosustroma fistulosum* (Lessovaya). **A**, plane-polarized light view of vertical section of a portion from a complete sample, on micritic substrate with small shelter cavity. **B, C**, cross-polarized light views of cement infilling the cavity shows optical continuity with the bladed calcite overprint within the stromatoporoid. This is presented here as evidence that the diagenetic cement which overprinted the stromatoporoid grew early in the diagenetic history of the stromatoporoid. These illustrations are presented as evidence of the unstable nature of the original mineralogy of the stromatoporoid, a feature of all stromatoporoids. Much Wenlock Limestone Formation, Lea Quarry, Wenlock Edge, CAMSM X.50347.30.

→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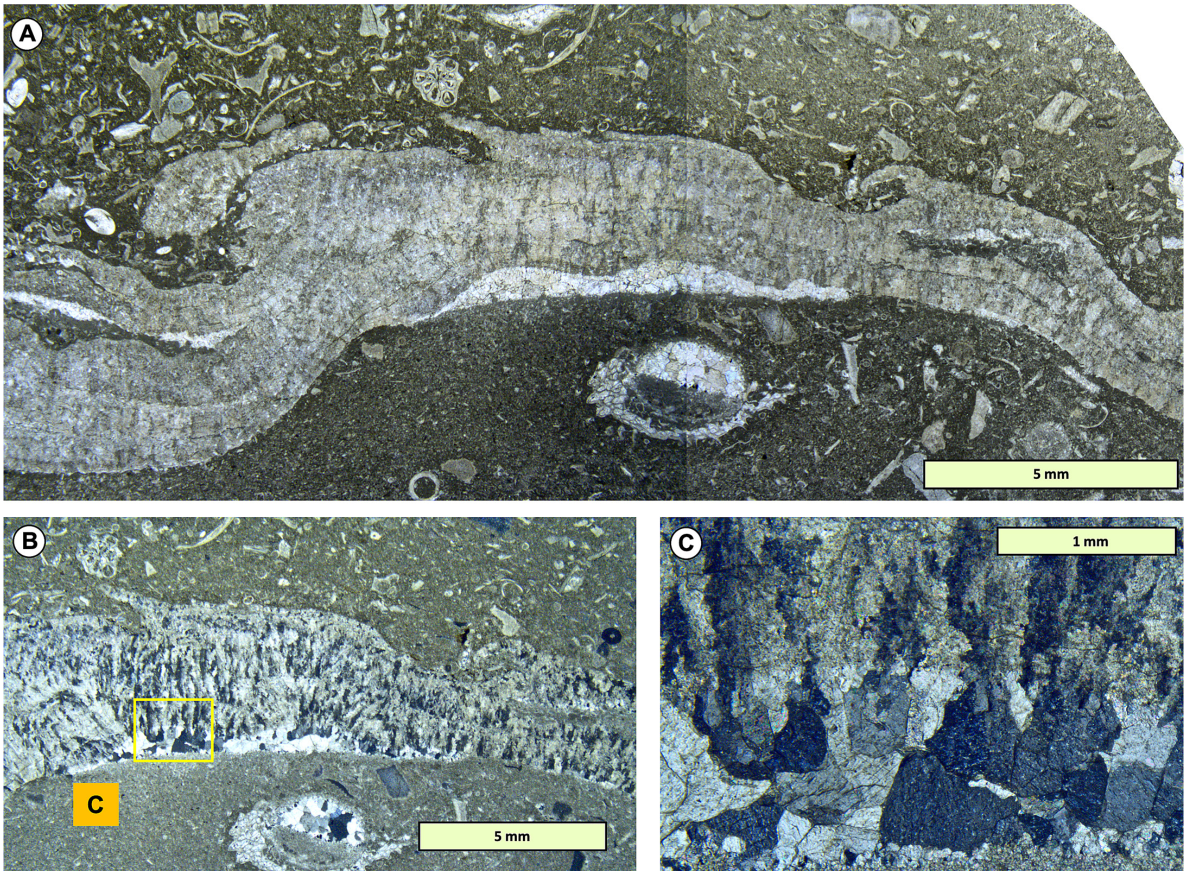
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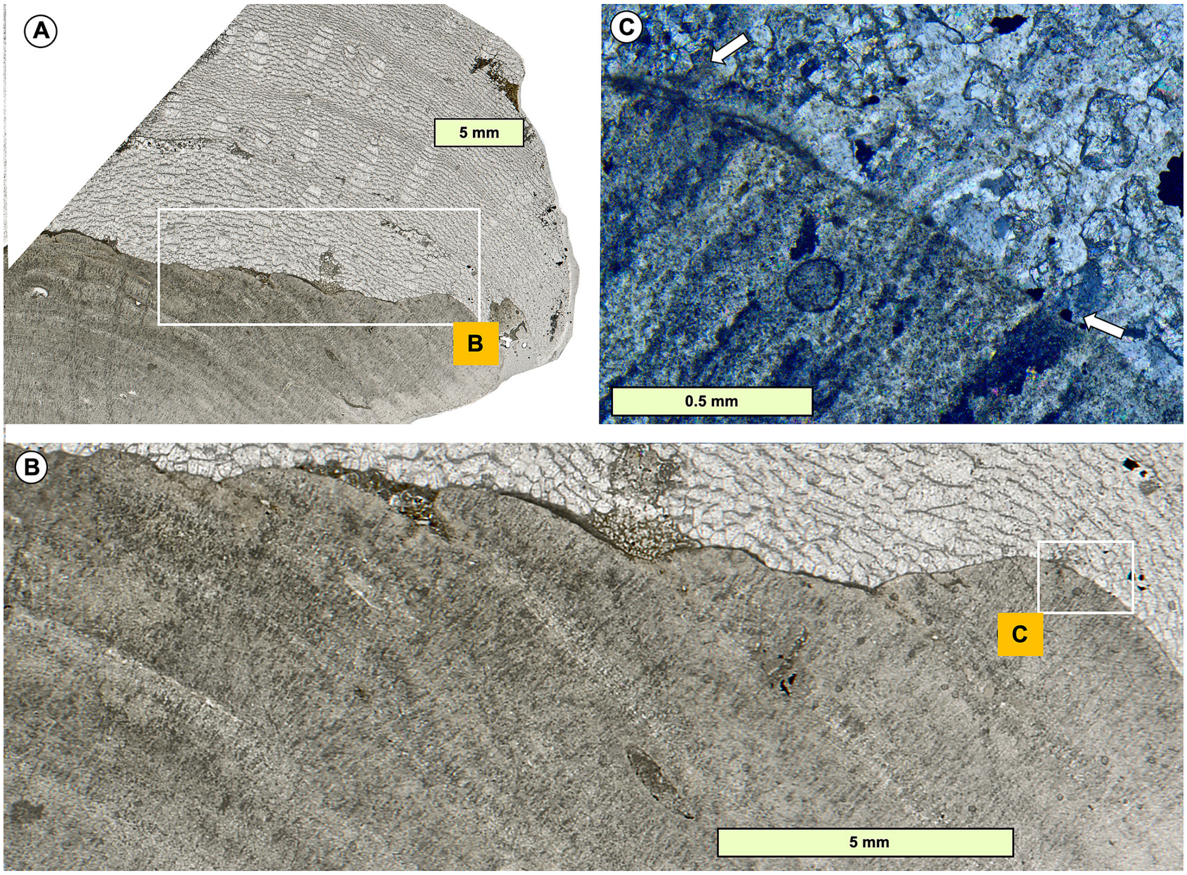
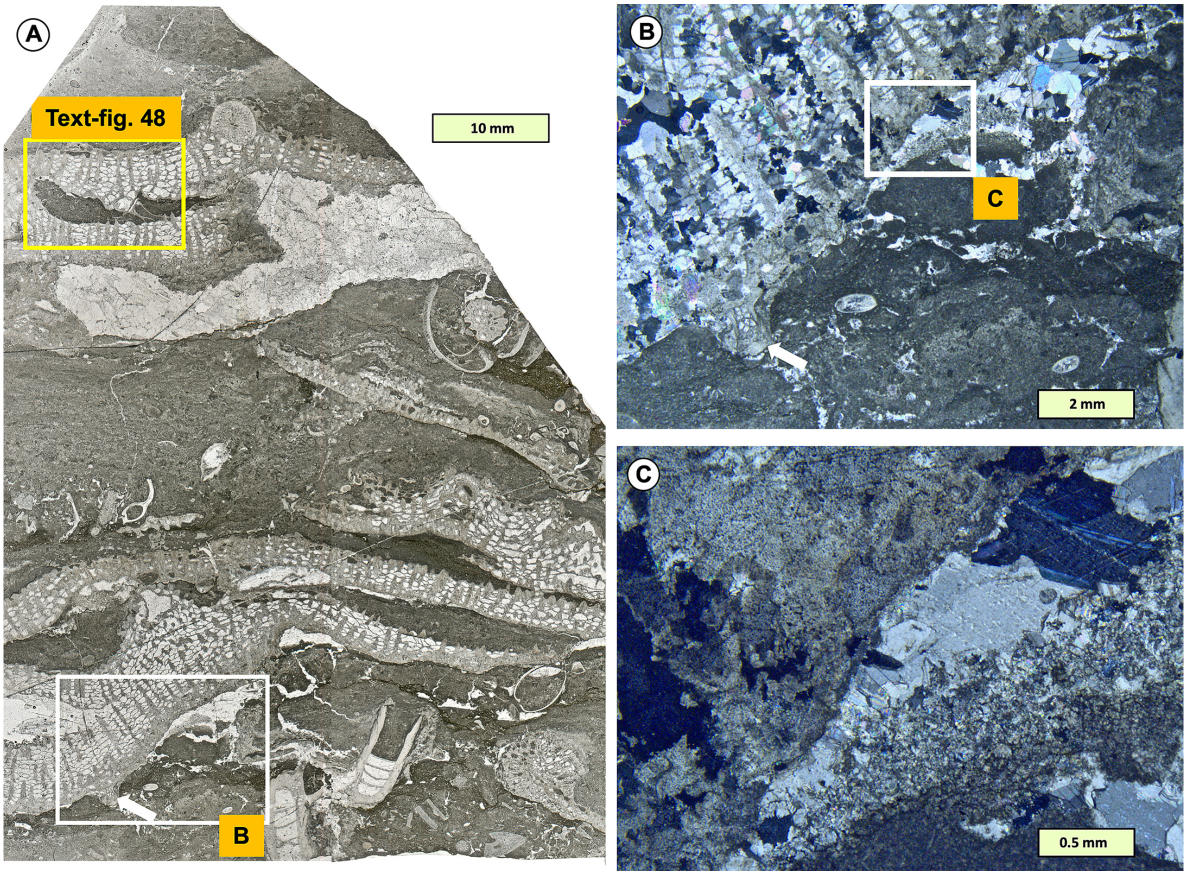


TEXT-FIG. 50. *Araneosustroma fistulosum* (Lessovaya). **A, B**, plane-polarized light view of vertical section of eroded skeleton overgrown by a heliolitid. **C**, cross-polarized light view of enlargement of vertical section in box in B, showing optical continuity of the bladed overprint cement of the stromatoporoid up into the cement infilling of the heliolitid (arrows). The optical continuity is despite the stromatoporoid surface being eroded before growth of the heliolitid, and is presented here as evidence that the overprinting cement grew during diagenesis after burial had occurred, so that although Text-fig. 49 indicates the bladed overprint cement formed early, it was during burial (likely shallow burial and early in diagenetic history) rather than on the sea floor. Much Wenlock Limestone Formation, Lea Quarry South, Wenlock Edge, CAMSM X.50347.52.

Stromatoporoids are composed of low-magnesium calcite and their original mineralogy is debated because of recrystallization of the skeleton (Rush & Chafetz 1991; Smosna 1984) and overprinting by irregular bladed calcite cements (Text-figs 47, 48; Kershaw 2013). Although stromatoporoid skeletons are always at least partly recrystallized, in almost all cases they are better preserved than molluscan shells, yet always more poorly preserved than brachiopods, bryozoans, tabulates, and heliolitids with which they occur. That pattern is evidence that stromatoporoid mineralogy was neither aragonite nor low-magnesium calcite originally. Rush & Chafetz (1991) reported microdolomite inclusions in stromatoporoids, pointing to an original high-magnesium calcite mineralogy, yet the irregular recrystallization structure is very different from the appearance of crinoids, for example, in the same rocks. Thus, the determination of stromatoporoid original mineralogy remains unresolved.

Observations showed that overprinting by irregular diagenetic calcite crystals terminates at the margins of the stromatoporoid, where the stromatoporoid abuts the surrounding sediment (Text-fig. 48A), the overprinted calcite crystals do not pass into the sediment. However, in this study we have new information that shows features which advance knowledge of this issue. Text-figure 49 shows geopetal cement in a cavity directly below a stromatoporoid skeleton, wherein the bladed irregular crystal replacement in the stromatoporoid passes in optical continuity into the cement infill. Text-figure 50 shows a variation of this feature, where the bladed cement passes between the top of a stromatoporoid and the base of the heliolitid tabulate coral that



TEXT-FIG. 51. Vertical section through laminar frame of *Labechia conferta* (Lonsdale) collected in-place. **A**, whole thin section view of the frame with parts of the skeleton in contact with sediment and parts associated with sparitic calcite. Arrow shows a downward-pointing basal encruster demonstrating presence of a primary cavity, partly backfilled. Position of Text-fig. 48 is labelled. **B**, enlargement of lower box in A, in cross-polarized light, showing details of partly recrystallized micrite in the geopetal infill of a primary cavity. Arrow shows the downward-pointing basal encruster shown in A. **C**, enlargement of box in B detailing the recrystallized micrite; sparite in the cavity passes with optical continuity into the base of the stromatoporoid, as in Text-fig. 50. Much Wenlock Limestone Formation, Coates Quarry, Wenlock Edge, CAMSM X.50347.162.

the stromatoporoid grew on. Note that the stromatoporoid upper surface was eroded prior to heliolitid encrustation. These samples show the bladed irregular cement was able to pass out of the stromatoporoid.

Scoffin (1972), describing cavities in the Wenlock reef of Wenlock Edge, drew attention to some cavities formed by recrystallization of the sediment and observed that geopetal sediment below reef builders was modified by recrystallization in some cases. Text-figure 51 shows an example of this feature, where a primary cavity is partly infilled, then the upper part of the infill is interpreted here as recrystallized, with parts of the primary cavity cement being in optical continuity with the recrystallized stromatoporoid that roofs the cavity. The implications of these features are discussed below.

## DISCUSSION

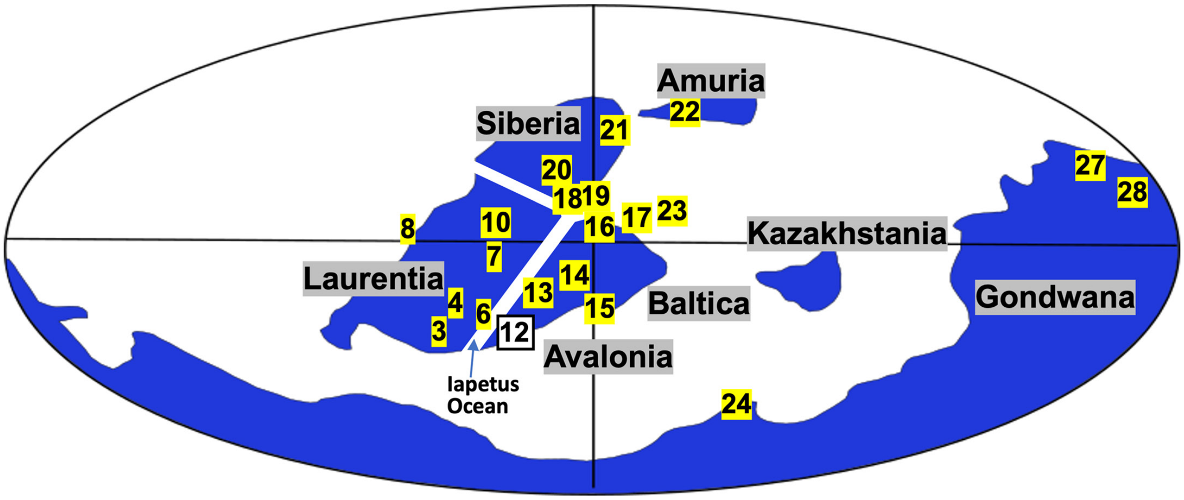
To develop a modern understanding of British Silurian stromatoporoids several aspects need consideration. Much of the following text develops a greater level of detail not appropriate in shorter works and is presented here as a lengthy discussion in order to provide as comprehensive a current view as possible of British and Irish Silurian stromatoporoids. We draw attention to the perspective that limited information was published since Nicholson's (1886, 1889, 1891, 1892) work that warrants a detailed approach now. Some key points are repeated from the Results section, in order to maintain clarity of discussion. In the following subsections we address key aspects of the stromatoporoids: (1) palaeogeographical location of Avalonia between the stable continental platforms of Baltica and Laurentia, (2) stromatoporoid roles in reef facies, (3) stromatoporoid diversity and palaeobiology (including associated organisms), (4) stromatoporoid mineralogy and diagenesis, and (5) potential impacts of middle Silurian extinctions on stromatoporoids.

## Palaeogeographical significance of British and Irish Silurian stromatoporoids

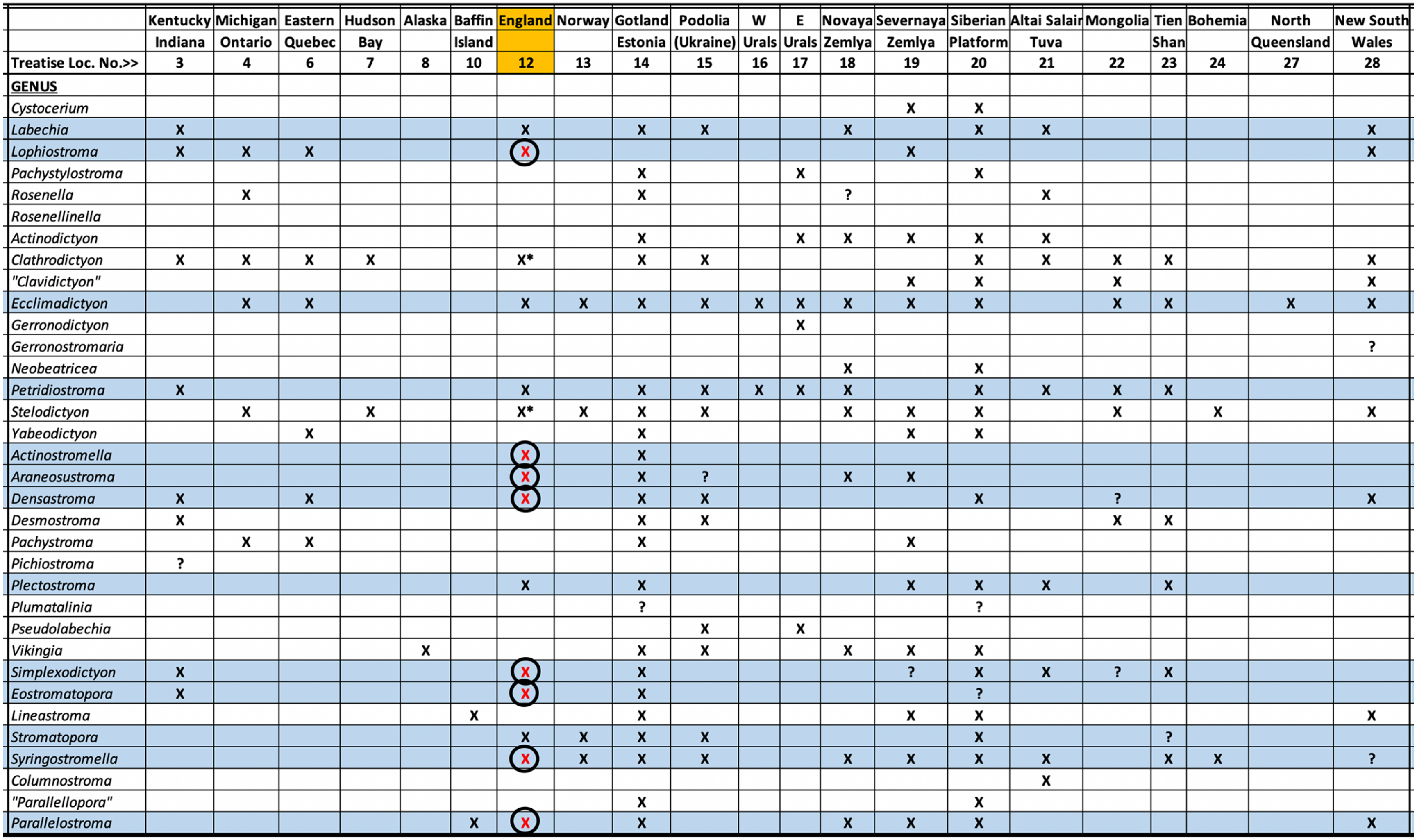
*General aspects.* During the Silurian Period, the British and Irish land masses were divided into two parts, with implications for stromatoporoid-bearing sites. Southern Britain and southern Ireland were part of the combined Avalonia and Baltica continents (Text-figs 1, 52) and included the English Midland Platform and southern Ireland sites of rare Llandovery-age stromatoporoid deposits. In contrast, northern British and Irish sites with rare Llandovery stromatoporoids were part of the Laurentian margin. Palaeogeographical reconstruction (Text-fig. 52) shows the intervening Iapetus Ocean was small (and was closing), so the British and Irish stromatoporoid-bearing sites lay in an important location between the major part of Laurentia on one side and Baltica and other Silurian continents on the other side. Thus, the British and Irish shallow marine carbonate-rich areas may have aided distribution pathways of stromatoporoids that presumably had planktonic forms for migration. Therefore, comparison of taxa between the continental masses neighbouring Britain and Ireland during the Silurian has potential value for understanding the palaeobiology of stromatoporoids.

Text-figures 52 and 53 summarize the global pattern of Silurian stromatoporoids. The presence in Britain and Ireland of taxa that occur also in the larger continental platforms on either side is potential evidence that the stromatoporoid larvae were widespread and abundant in the oceans, and needed only the appropriate conditions, likely the key aspects of reduced sedimentation rate and shallow marine waters, to develop reefs and individuals in non-reef bedded limestones. The largest preserved area is the upper Wenlock Series Midland Platform, but there is evidence of former carbonate platforms of Llandovery (Girvan area) and Wenlock (Isle of Man and southwestern Ireland) ages.

*Stromatoporoid taxonomic details and palaeogeography.* As explained earlier, the taxonomic approach used in this study is that low-level stromatoporoid taxa are considered as having equal taxonomic status, that may or may not be related to other taxa if a hierarchy of groupings was applied. It may appear obvious to state that one taxon described in one region is the same



Text-fig. 52. Palaeogeographical map for the Wenlock Epoch (continental positions derived from Stock *et al.* (2015, p. 670, fig. 382), with locations of stromatoporoid sites in numbered boxes. Numbers are explained in Text-fig. 53, and match those used by Stock *et al.* (2015) to maintain continuity with the source. Number 12 is Britain and Ireland.



| | Kentucky | Michigan | Eastern | Hudson | Alaska | Baffin | England | Norway | Gotland | Podolia | W | E | Novaya | Severnaya | Siberian | Altai Salair | Mongolia | Tien | Bohemia | North | New South |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Indiana | Ontario | Quebec | Bay | | Island | | | Estonia | (Ukraine) | Urals | Urals | Zemlya | Zemlya | Platform | Tuva | | Shan | | Queensland | Wales |
| **Treatise Loc. No.>>** | **3** | **4** | **6** | **7** | **8** | **10** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **27** | **28** |
| **GENUS** | | | | | | | | | | | | | | | | | | | | | |
| *Cystocerium* | | | | | | | | | | | | | | X | X | | | | | | |
| *Labechia* | X | | | | | | X | | X | X | | | X | | X | X | | | | | X |
| *Lophiostroma* | X | X | X | | | | Ⓧ | | | | | | | X | | | | | | | X |
| *Pachystylostroma* | | | | | | | | | X | | | X | | | X | | | | | | |
| *Rosenella* | | X | | | | | | | X | | | | ? | | | X | | | | | |
| *Rosenellinella* | | | | | | | | | | | | | | | | | | | | | |
| *Actinodictyon* | | | | | | | | | X | | | X | X | X | X | X | | | | | |
| *Clathrodictyon* | X | X | X | X | | | X* | | X | X | | | | | X | X | X | X | | | X |
| *"Clavidictyon"* | | | | | | | | | | | | | | X | X | | X | | | | X |
| *Ecclimadictyon* | | X | X | | | | X | X | X | X | X | X | X | X | X | | X | X | | X | X |
| *Gerronodictyon* | | | | | | | | | | | | X | | | | | | | | | |
| *Gerronostromaria* | | | | | | | | | | | | | | | | | | | | | ? |
| *Neobeatricea* | | | | | | | | | | | | | X | | X | | | | | | |
| *Petridiostroma* | X | | | | | | X | | X | X | X | X | X | | X | X | X | X | | | |
| *Stelodictyon* | | X | | X | | | X* | X | X | X | | | X | X | X | | X | | X | | X |
| *Yabeodictyon* | | | X | | | | | | X | | | | | X | X | | | | | | |
| *Actinostromella* | | | | | | | Ⓧ | | X | | | | | | | | | | | | |
| *Araneosustroma* | | | | | | | Ⓧ | | X | ? | | | X | X | | | | | | | |
| *Densastroma* | X | | X | | | | Ⓧ | | X | X | | | | | X | | ? | | | | X |
| *Desmostroma* | X | | | | | | | | X | X | | | | | | | X | X | | | |
| *Pachystroma* | | X | X | | | | | | X | | | | | X | | | | | | | |
| *Pichiostroma* | ? | | | | | | | | | | | | | | | | | | | | |
| *Plectostroma* | | | | | | | X | | X | | | | | X | X | X | | X | | | |
| *Plumatalinia* | | | | | | | | | ? | | | | | | ? | | | | | | |
| *Pseudolabechia* | | | | | | | | | | X | | X | | | | | | | | | |
| *Vikingia* | | | | | X | | | | X | X | | | X | X | X | | | | | | |
| *Simplexodictyon* | X | | | | | | Ⓧ | | X | | | | | ? | X | X | ? | X | | | |
| *Eostromatopora* | X | | | | | | Ⓧ | | X | | | | | | ? | | | | | | |
| *Lineastroma* | | | | | | X | | | X | | | | | X | X | | | | | | X |
| *Stromatopora* | | | | | | | X | X | X | X | | | | | X | | | ? | | | |
| *Syringostromella* | | | | | | | Ⓧ | X | X | X | | | X | X | X | X | | X | X | | ? |
| *Columnostroma* | | | | | | | | | | | | | | | | X | | | | | |
| *"Parallellopora"* | | | | | | | | | X | | | | | | X | | | | | | |
| *Parallelostroma* | | | | | | X | Ⓧ | | X | | | | X | X | X | | | | | | X |

Text-fig. 53. Table of global distribution of Wenlock stromatoporoids derived from Stock *et al.* (2015, fig. 37), with genera from this study highlighted in darker shade, and those not previously recorded are added and circled. Sites are numbered across the top row, with England (12) highlighted. The British taxa ranges are comparable with other stromatoporoid-rich deposits, for the narrow time period of the Much Wenlock Limestone Formation in which the majority of Wenlock-age stromatoporoids are found. This table, and the palaeogeographical map in Text-fig. 52, show the important position of the British Isles in the Laurentia-Avalonia-Baltica distribution of Wenlock stromatoporoids. The two asterisked taxa, *Stelodictyon* and *Clathrodictyon*, are regarded as important cosmopolitan genera in the Wenlock according to Stock *et al.* (2015), but it is notable that neither genera were found in the dataset assembled for this study, discussed in the text.

taxon as the same-named taxon in another region, as would be applied in other fossil groups. Thus, for example, *Ecclimadictyon macrotuberculatum* in the MWLF is most reasonably interpreted as the same taxon as a stromatoporoid with the same structure in the Klinteberg Formation on Gotland. Unfortunately, because of the issues regarding the phyletic value of the calcareous skeleton of stromatoporoids, described earlier, we must regard as suspect the presumption that they are the same biological species. There is also the uncertain problem that one biological species, producing a particular calcareous structure in one region might, due to geographical separation, have a slightly different calcareous structure in another region, where it would be called another name. Such issues are impossible to resolve, but recognition of their possibility should not be ignored for stromatoporoids because such ideas keep alive the questions about their taxonomy.

Nevertheless, some comparisons are worthwhile in the context of understanding British Silurian stromatoporoids, to further discussion of stromatoporoid biology. However, preservation makes comparisons difficult in many cases. For example, Watkins (1993) included stromatoporoids in a study of Wenlock-age reef faunas in Wisconsin, but unfortunately dolomitization and dissolution led to poor stromatoporoid preservation, precluding full comparison with other areas. In those Wisconsin deposits, stromatoporoids of laminar, domical, and bulbous shapes, with sizes generally 10–50 cm diameter, rarely 100 cm, were reef constructors, comparable to Wenlock reefs in Britain.

In places where stromatoporoid taxa are well-preserved, there is the possibility of comparing taxa that may be important to understand geographical dispersal (notwithstanding the above caveat), shown below in some records particularly relevant to this study:

1. Mori (1978, table 1) described a small sample of Silurian stromatoporoids from the Oslo area, probably near to the Midland Platform during the Wenlock Epoch (the intervening North Sea extension zone developed later, during the Mesozoic Era). In this suite, Llandovery-age rocks contain *'Clathrodictyon'* (now *Petridiostroma*) *simplex* and *P. linnarssoni* that are both present in the MWLF. However, in the Wenlock Series of the Oslo area, Mori (1978, table 1) found three taxa that are not recorded in the MWLF; two of them (*Plectostroma norvegicum* and *Clathrodictyon crickmayi*) certainly appear different from taxa in the MWLF (see Mori's 1978 illustrations), but the third (*Stromatopora discoidea*) is very similar to *Syringostromella borealis* (= *'Stromatopora' carteri* discussed earlier), in both Gotland and MWLF of England. There may be transport of *S. borealis*, but *P. norvegicum* and *C. crickmayi* may be regionally controlled. Thus, there is some overlap of taxa between Sweden and England in the late Wenlock time of the MWLF, yet some taxa in Sweden are missing from England.
2. Stromatoporoids from the upper Silurian of Scania (southern Sweden) described by Mori (1969b), are of Ludlow age including some taxa that also occur in the Ludlow of Gotland. Pope (1986) in a Master's thesis, described upper Silurian stromatoporoids from the Gaspé Peninsula in eastern Canada (eastern Laurentian margin), containing taxa that also occur in the Ludlow of Gotland. Both Mori (1970) and Pope (1986) include *Ecclimadictyon macrotuberculatum*, which is common in the (earlier) MWLF in England. Pope (1986) also illustrated a taxon she called *Syringostromella simplex* that looks identical to *Syringostromella borealis*, which occurs in both the MWLF and the Wenlock Klinteberg Formation on Gotland (equivalent to much of the MWLF) as well as the Ludlow Series of Gotland. Parks (1933) described upper Silurian stromatoporoids from the Baie des Chaleurs region of Quebec, including several taxa, one of which resembles *Petridiostroma simplex*. Unfortunately, the quality of Parks' (1933) illustrations is too poor to assess the taxa in his work, in relation to the current suite studied here; recourse to the original thin sections is needed, not possible in this study. In the Llandovery-age limestones of Anticosti Island, Nestor *et al.* (2010) illustrated *E. macrotuberculatum* and a taxon identical to *Petridiostroma simplex*. Stock (1979) and Stock & Holmes (1986) described *Parallelostroma typicum* and *Densastroma pexisum* from, respectively, upper Silurian (Pridoli) of New York State, and upper Silurian/Lower Devonian of Virginia, which both occur in slightly older beds (Ludlow) on Gotland and also occur in the even older (Wenlock) limestones of the MWLF. Nevertheless, Carl Stock (personal

communication, 5 July 2020) noted that the identification of *P. typicum* in these beds is under reconsideration. Overall, the similarity of the taxa noted here indicates a pathway between Laurentia and Baltica likely existed through Avalonia, open during the Wenlock and Ludlow epochs, even though during the Ludlow Epoch there was nowhere in Avalonia (dominated by siliciclastic facies) for them to settle and leave fossils.

3. Scrutton (1975) recorded a small assemblage of upper Llandovery stromatoporoids from northern Greenland, including two taxa incompletely identified by Scrutton (1975). However, his photographs are sufficiently good to allow recognition of *Petridiostroma simplex* and *Syringostromella borealis* (Scrutton 1975, pl. 1, figs 2, 4, and 6–8, respectively). A third taxon most closely resembles *Petridiostroma linnarssoni* (Scrutton 1975, pl. 1, figs 1, 3). All three taxa are components of the MWLF, and *S. borealis* also occurs in the Wenlock of the Isle of Man.
4. Looking further afield to Gondwana, Hill *et al.* (1969, pl. S1) illustrated some Silurian stromatoporoids from Queensland, Australia, including taxa that have much similarity to MWLF taxa and have stratigraphical ranges that cross late Wenlock time. Following are the taxa named by Hill *et al.* (1969) with comment on their relationship with the British equivalents: (1) *Clathrodictyon*: this resembles *Petridiostroma simplex* of the British samples; (2) *Stromatopora*: this resembles *Syringostromella borealis* of the British samples; (3) *Tienodictyon*: but this does not resemble that in the *Treatise on Invertebrate Paleontology* (Nestor 2015, p. 274), although it does look exactly like *Simplexodictyon yavorskyi* in the *Treatise on Invertebrate Paleontology* (Stearn 2015a, p. 786), which is also a taxon in the MWLF; (4) *Plectostroma* cf. *intertextum*, which has a slightly oblique VS (Hill *et al.* 1969, pl. S1, fig. 6a) and is considered here as *Plectostroma intertextum*, present in the MWLF; (5) *Actinostroma* sp. aff. *stellatum*, which does not resemble *Actinostroma* or any similar taxon, but is more similar to *Petridiostroma*, although the photograph (Hill *et al.* 1969, pl. S1, fig. 7, showing both VS and TS in one picture) does not show enough of the skeleton to be certain of its identity; and (6) *Ecclimadictyon* sp.: this is only a VS and is not very clear, it is an *Ecclimadictyon* structure but not clear enough to identify a low-level taxon. Another study by Ripper (1933, 1937) illustrated stromatoporoids from the Silurian Lilydale Limestone, in Victoria, South Australia. None of the drawings in Ripper (1933) sufficiently resemble stromatoporoid taxa in the MWLF, but Ripper (1937, pl. VIII, figs 7, 8) photographed a taxon that looks very similar to *Syringostromella borealis* of the MWLF.
5. The South China craton, positioned close to Gondwana in low latitudes during the Silurian, has a stromatoporoid fauna in the Llandovery (Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a), but lacks any stromatoporoids in the Wenlock due to uplift. Llandovery taxa have similarity with the other areas described above (taxa of traditional Orders Labechiida, Clathrodictyida, Actinostromatida and Stromatoporida), but are currently under revision, so details are not provided here.

Following from the examples above, there are limitations to the application of palaeogeographical reconstructions in understanding stromatoporoid dispersal behaviour, but there are enough cases to convince us of the ability of some stromatoporoid taxa to travel, but others had to stay at home. Otherwise, although there is a poor British stromatoporoid record outside the Midland Platform, there is evidence from the Isle of Man and Girvan area described earlier that tectonic reconfiguration has likely destroyed other evidence, discussed here:

1. On the Isle of Man (IoM), north of the Midland Platform, indication of presence of carbonates with stromatoporoids in neighbouring areas is shown by the six samples (Crowley *et al.* 2009) in limestone clasts in the Devonian-age Peel Sandstone. These clasts were part of a Wenlock coral-stromatoporoid fauna, approximately the same age as the MWLF of the Midland Platform, but must have originated elsewhere. The IoM fauna includes *Syringostromella borealis* and *Parallelostroma typicum* found also in the MWLF, but also contains another taxon, '*Stromatopora*' *venukovi*, that does not occur in MWLF. During the Devonian, after Iapetus Ocean closure, these faunas represent transported material on land in the Old Red Continent. Crowley *et al.* (2009) stated that the Peel Sandstone represents Old Red

Sandstone facies located at the former northern margin of the southern Britain area during the Early Devonian (Cope *et al.* 1992). Hartley & Leleu (2015) presented a model for the Lower Old Red Sandstone, indicating erosion from the Scandian Orogen that lies on the western margin of the Baltica palaeocontinent; their reconstruction (Hartley & Leleu 2015, fig. 3) interpreted a broad fluvial system flowing WSW from what is now the Scandinavian landmass. The possibility is open that the origin of Wenlock-age pebbles bearing corals and stromatoporoids in the Isle of Man is from the east.

2. For the northern Britain area, three specimens (one *Ecclimadictyon macrotuberculatum* [*Em*] and two *Plectostroma intertextum* [*Px*]) from Girvan in southern Scotland are present in Nicholson's collections at the NHMUK. One (*Em*) is certainly lower Silurian, the other two (*Px*) are interpreted here as lower Silurian, but mislabelled as Ordovician, as noted earlier. These are scant but essential pieces of evidence of a northern stromatoporoid fauna, that requires further investigation. In northern Ireland, Nestor (1999) described lower Silurian stromatoporoids from north of the Iapetus Suture, as further indication of a wider distribution of lower Silurian stromatoporoid-bearing platform deposits that are no longer adequately represented in the sedimentary sequences. Crosfield & Johnston (1914, p. 222) recognized this problem and in a remarkably foreseeing comment stated the following (quoted): "Although at each end of the 'broad thoroughfare' which joined Wisconsin and Iowa to Gotland and Wenlock there is evidence of a reef-phase, information on the Silurian bed round the present Arctic Ocean is too imperfect to determine if scattered reef colonies dwelt between."

The notion of transport of faunas with pelagic larval stages is of course present in other organisms. Relevant to the current study is recognition that even in the Late Ordovician there is evidence in the Girvan area of similar ostracod faunas present in both Laurentia and Baltica (Williams & Floyd 2000 for the Caradoc; Floyd *et al.* 1999 for the Ashgill). In the early Silurian, there is evidence from crinoids of dispersal between New Brunswick in Laurentia and Shropshire in Avalonia (Donovan & Keighley 2015). Thus, it is perhaps not surprising to find in the northern parts of the British area elements of Silurian stromatoporoids common to Baltica, Avalonia, and Laurentia, although a topic of continuing research is to explain why some stromatoporoid taxa were able to disperse, whereas others were not. A parallel situation was reported for Wenlock Series bryozoans, which show similarities between the Niagara area of Laurentia and the MWLF in Dudley (Avalonia) but differences from Gotland, for which Owen (1969) proposed climatic differences based on modern bryozoan patterns in the oceans. Brood (1974, p. 403), however, recorded similarities between Wenlock bryozoans of Gotland and England, but differences in the Ludlow, evidence of either closure of a marine connection in the Ludlow, or changes in the habits of those bryozoan taxa. Phytoplanktonic biotas, in contrast, show widespread distributions through much of the Palaeozoic, including pronounced cosmopolitan occurrence in the middle Palaeozoic, and thus in the Silurian (Molyneux *et al.* 2013). This interesting area of investigation continued for other Silurian material, with evidence of differences in benthic components even over short distances within Baltica, discussed by Kershaw & Motus (2016) for Ludlow stromatoporoids in Gotland and Estonia.

Overall, British Silurian stromatoporoids may be viewed as a relatively limited assemblage that took advantage of suitable conditions in some places in the Llandovery and Wenlock epochs. The largest deposit in the English Midlands developed in a short time-and-space window of shallow conditions in an episode of raised sea level, with little siliciclastic sediment at the end of the Wenlock Epoch. The presence of debris from Silurian carbonate platforms in or near southern Scotland are fragments in the prevailing siliciclastic deposits in the area north of the Midland Platform where Silurian turbidites are abundant (see King 1994 for excellent illustrations).

## Stromatoporoids in reef building

*General features.* There is little evidence of environmental gradients in the stromatoporoid occurrence in the MWLF. Colter (1957) and Scoffin (1971) highlighted the occurrence of the laminar-form stromatoporoid *Labechia conferta* (and the laminar-form tabulate *Thecia swinderniana*) in reef margins, explained as reflecting higher energy conditions on the margins. Nevertheless, Powell (1980) noted the occurrence of masses of *L. conferta* laminar frames in the cores of some reefs, an example of which survives in the preserved reef exposure in Coates Quarry, Wenlock Edge (Text-fig. 7C). Elsewhere there is also little evidence of environmental gradients affecting stromatoporoid taxa distributions in the late Wenlock. One case was noted by Brood (1974) in the Halla and Mulde Beds on Gotland (now both included within the Halla Formation of which the Mulde is a part, see Calner *et al.* 2004). Brood (1974, fig. 4) recorded an association between *Stromatopora antiqua* (regarded in this study as a synonym of *Actinostromella vaiverensis*) and possible algal taxon *Solenopora gothlandicus* (reinterpreted as a chaetetid by Riding 2004), in very shallow marine waters, compared to a slightly deeper water association of heliolitid *Heliolites interstinctus* and tabulate *Halysites catenularius*. In the MWLF, these low-level stromatoporoid, tabulate, and heliolitid taxa occur together.

Schumacher & Plewka (1981) presented evidence that the modern calcified sponge *Ceratoporella nicholsoni* has a mechanically strong skeleton in contrast to the weaker skeletons of modern scleractinian corals; their interpretation was that Palaeozoic stromatoporoids may have had greater mechanical resistance to damage than do modern corals, and this contributed to their abundance in the Palaeozoic. In numerous studies of stromatoporoid assemblages, stromatoporoids are commonly found as complete specimens in both reef and non-reef environments (Da Silva *et al.* 2011a, b, 2012; Kershaw *et al.* 2018). In our studies of British Silurian stromatoporoids, most in-place specimens were found complete, a feature also seen in tabulates and heliolitids. It may be too simplistic to attribute stromatoporoid success to mechanical strength, but may be part of the reason for their abundance in middle Palaeozoic strata.

The small patch reefs in the Nodular Member in Wren's Nest are rich in rugose corals, tabulates and heliolitids; only a small percentage of skeletons are stromatoporoids, as small laminar to domical forms. It is certainly true that tabulates and heliolitids are more abundant than stromatoporoids in the MWLF reefs and bedded limestones, but there is considerable variation of abundance of these groups of skeletal metazoans. We return to the very good example of a reef frame in Coates Quarry, Wenlock, where part of the patch reef contains a frame of *Labechia conferta* (Text-figs 7C, 14) and several large domical forms of *Ecclimadictyon macrotuberculatum* (Text-figs 8B, 14). Text-figures 7, 8, and 10, of Coates and Lea Quarries on Wenlock Edge, and Wren's Nest, show stromatoporoids that were collected from reefs and non-reef facies, and demonstrate variability of occurrence, with *L. conferta* frames occurring mostly in the reefs, and other taxa occurring in both reef and non-reef facies. Crosfield & Johnston (1914, pp. 203, 204) reported *L. conferta* frames from nodular limestones associated with reefs on Wenlock Edge. Consequently, the stromatoporoid content of the MWLF varies locally and presumably was controlled by availability of larvae for settlement and development of stromatoporoid skeletons. Colter (1957, p. 94) offered the view that if stromatoporoids and tabulates did not have symbiotic algae to assist their growth like modern corals do, then the fossil organisms when alive must have been more efficient than modern corals.

*Reef variations and reef margins.* Brunton *et al.* (1997) and Copper (2002) recorded that MWLF reefs were part of a global reef-building event in the late Wenlock. Abbott (1975, 1976) presented evidence that Wenlock reefs on Wenlock Edge were not frame-constructed, and regarded them as banks composed largely of sediment, by comparison with modern coral banks in south Florida. This view contrasted the work of Scoffin (1971) who described the reefs as having a framework of skeletal metazoans (principally corals, stromatoporoids, and bryozoans), with binding action by stromatolites and laminar forms of metazoans. Nevertheless, both authors viewed the MWLF reefs as shallow water structures; Scoffin (1971) recorded one reef with an eroded top (Blakeway Hollow Quarry, now infilled), evidence of sea level fall and exposure. Ratcliffe & Thomas (1999, p. 197) described two types of reefs in the MWLF, matching the contrasting descriptions of Abbott (1976) and Scoffin (1971), and explained the difference by interpreting the frame-built reefs to have formed in shallow conditions while mud-dominated reefs (considered to be microbially constructed) developed in a mid-shelf setting. Ratcliffe & Thomas (1999, p. 197) also noted that both reef types contain stromatoporoids, rugosans, tabulates, and heliolitids, but the microbial reefs have only a small number of the metazoans. Thus, the conclusion by Baarli *et al.* (1992, p. 281) that, in general, stromatoporoids were common between storm wave-base and fair-weather wave base is consistent with these interpretations of the formation of MWLF reefs. Hodges & Roth (1986) measured orientations of fossil Silurian and Devonian stromatoporoids and Pleistocene corals and showed that reefs have higher percentages in-place, compared to bedded limestones, comparable to the outline results of Crosfield & Johnston (1914) for Wenlock Edge corals and stromatoporoids.

Colter (1957) and Victor Colter (personal communication with SK, July 2019 [at age 88 years, 62 years after his PhD thesis was written!]) recognized the sharp margins of Wenlock reefs in Britain, and Kershaw *et al.* (2007) documented these in Britain and Gotland. The sharp margins of patch reefs show leiolitic fabrics; leiolites are structureless micrites forming solid masses that lead to conviction they must have been microbial (Riding 2000). Leiolites thus indicate lithification of the sediment on the sea floor where, in some cases, the number of reef building metazoans were limited (Colter 1957; Kershaw *et al.* 2007; Scoffin 1971). Such early lithification may have been a component of reef strengthening that aided stromatoporoid survival. The currently preserved reef in Coates Quarry, Wenlock Edge, has metazoan frames in its core and has sharp margins lacking obvious metazoans, evidence that microbial action was common in both frame-built and mound types of MWLF reefs.

Other examples of Silurian reefs are relevant to this discussion. Narbonne & Dixon (1984, p. 30) noted that upper Silurian sponge reefs in Arctic Canada have sharp margins. Soja (1991) noted stromatoporoids (unnamed) along with corals and red algae are reef builders during the Silurian in the Alexander Terrane, likely located NW of Laurentia during the Silurian and accreted to a location that is now modern-day Alaska. The reefs formed on the seaward edge of the marine shelf, somewhat similar to the MWLF. Other Silurian reefs described from the Alexander Terrane platform margin (Soja *et al.* 2000) were stromatolite reefs lacking stromatoporoids, demonstrating the diversity of reef forms in that region, which was likely within the tropical belt during that time (Soja 1991, fig. 16).

Thus, in the MWLF, the reefs generally represent denser accumulations of the fossils than in inter-reef beds and that stromatoporoid taxa were able to survive well in both reefs and level sea floors. These observations are evidence that stromatoporoids required only low sedimentation rates and shallow marine conditions, together with synsedimentary lithification, to develop substantial growth, as an explanation of why reefs form in the MWLF.

## Stromatoporoid diversity and palaeobiology

*Issues of stromatoporoid taxonomy and diversity.* It is clear from the new samples and museum material examined that this study doubles the number of traditional genera (alpha diversity, i.e. genus numbers) in the Avalonia stromatoporoid assemblages of the middle Silurian, from the previous seven to the current 15 taxa (Text-fig. 51). It is possible there are more in the unidentified samples. Even without unconfirmed additional taxa in the unidentified specimens, 15 traditional genera make the British and Irish Silurian assemblages the third most diverse Silurian group globally, after Gotland (Baltica) and Siberia at the level of traditional genera. Nevertheless, there are problems with that total of 15 because two of the previous seven listed in the *Treatise on Invertebrate Paleontology* (Stock *et al.* 2015, table 37) are not consistent with the samples studied here. The traditional genera called *Clathrodictyon* and *Stelodictyon* are not present in the British Silurian samples, from any new or museum material, yet are noted as key taxa for the British Silurian in Stock *et al.* (2015, table 37). The only source for British Silurian stromatoporoids used in that table is Nicholson's (1886, 1889, 1891, 1892) monograph (taxa described by Colter [1957] are not included in the 2015 *Treatise on Invertebrate Paleontology,* but Colter's identifications were taken from Nicholson's work, so it is Nicholson's monograph that is the key). Nicholson (1886, 1889, 1891, 1892) described British Silurian taxa and although *Clathrodictyon* is included, all the samples in Nicholson's NHMUK collections and new samples are *Petridiostroma*; *Clathrodictyon* as currently defined is not present. Furthermore, no specimens resembling *Stelodictyon* (Nestor 2015, pp. 757, 758) are present in the British Silurian samples of Nicholson's or any of the other collections. We have not been able to resolve the reason for this discrepancy, but it means that although 15 British and Irish Silurian genera are tabulated in the literature, only 13 are confirmed in this study. However, some have subdivisions as traditional species, so there is a total of 15 low-level taxa (= traditional species) in the assemblage.

In Gotland and Siberia, within the traditional genera listed in Stock *et al.* (2015, table 37) and Text-fig. 51 there are numerous traditional species (e.g. Mori 1970 for Gotland; Nestor 1966 for Estonia), so there is not a full comparison between these areas and Avalonia. Also, in the British material there are five partly identified taxa (Text-fig. 35). Thus, the number of traditional species (= low-level taxa of this study) in the stable large platforms of Baltica and Siberia are somewhat higher than in the Avalonia region, which is expected from stable large platforms. Despite these points, the total for Britain and Ireland, fitted into a short time window and a small geographical area, is of importance palaeogeographically, described later.

Nestor (1984, pp. 278, 279) noted that diversity of traditional stromatoporoid taxa is rather low in the Silurian, with highest diversity of about 15 species, and commonly only 5–6 species occur together. This pattern is consistent throughout stromatoporoid assemblages, of all ages and environments (Kershaw *et al.* 2018); commonly only two or three taxa are very abundant and all the others are less so. Nestor (1984, p. 279) also commented that stromatoporoids possessing fine skeletal structure are common in facies he called "extreme conditions", the margins of stromatoporoid survival. Certainly, in places where fine-grained sediment was abundant, stromatoporoids commonly are fine-structured. Nestor (1984, p. 279) viewed stromatoporoids with more "irregular and very variable inner structure" tend to be more common in shallow waters; and stromatoporoids with regular forms were typical of open shelf settings. In general, Nestor's (1984) summary is appropriate for the British Silurian stromatoporoids, but what environmental relationship may exist between skeletal architecture and stromatoporoid success remains to be determined. For example, *Labechia conferta*, one of the most open-structured skeletons of all stromatoporoids, is a prominent feature of the MWLF reefs, but so is *Densastroma pexisum*, which has a very fine skeletal structure.

Nestor (1999) also attempted to develop the concept of community structure in early Palaeozoic stromatoporoids and proposed a series of named communities for the Ordovician and Silurian of the Baltoscandian region. Of these communities, the late Wenlock (middle Homerian) "*Labechia conferta* community" (Nestor 1999, pp. 131, 132) is closest in age to the MWLF and is composed of *L. conferta*, *Ecclimadictyon macrotuberculatum*, *'Clathrodictyon vesiculosum'*, *'Stromatopora antiqua'*, and *Stelodictyon striatellum*. In the MWLF, *L. conferta* is common and *E. macrotuberculatum* is present. *'Stromatopora antiqua'* is considered here to be a synonym of *Actinostromella vaiverensis* but *'Clathrodictyon vesiculosum'* and *Stelodictyon striatellum* listed by Nestor (1999) were not found in our new samples or museum collections of the MWLF. Instead, *L. conferta*, *Petridiostroma simplex*, *Actinostromella vaiverensis*, *Densastroma pexisum*, *Plectostroma intertextum*, and *Syringostromella borealis* are common components of the MWLF. The difference between Nestor's (1999) late Wenlock community and our taxonomic assemblage from the MWLF might be explained if certain taxa (*L. conferta* and *E. macrotuberculatum*) had a dispersal mechanism that more preferentially allowed their migration between southern Britain and Baltica during the time of the MWLF, noting that *D. pexisum* is also common in Gotland and Estonia during the early Wenlock. Thus, the community approach proposed by Nestor (1999), whereby certain stromatoporoid taxa occur together, might be appropriate in limited regions, but there is no clear cause for co-occurrence of particular stromatoporoid lowest-level taxa.

The presence of only 15 fully identified taxa in the British sample set is typical of stromatoporoid assemblages, but this is a low diversity in comparison with the distribution of modern sponge taxa assemblages and raises a question as to why the alpha diversity (i.e. a simple count of taxa) of Palaeozoic stromatoporoids is not higher. The answer might lie in the process of calcification itself, because in modern sponges, only a few taxa are calcified; most are not. As stated earlier, in the case of *Merlia*, only two of the four species calcify (West

2011). Furthermore, in *Acanthochaetetes*, Reitner & Engeser (1987) found that three species defined on spicules formed an identical calcified skeleton. If these situations were true of Palaeozoic stromatoporoids, then it follows that the biodiversity (compared to fossil diversity) of the live stromatoporoid assemblages may well have been much higher in the MWLF, thus more consistent with modern sponge-rich shallow marine communities. Therefore, in the stromatoporoid suites we may be seeing only a small portion of what was originally present in the assemblages. Nevertheless, it remains true that stromatoporoid fossils did not easily recrystallize to the point of being unrecognizable, noting that all stromatoporoids are recrystallized to some extent. Therefore, of the calcified taxa represented by the British stromatoporoid assemblage, it is very likely that the preserved fossils are representative of the taxa of these calcified sponges when they were alive (Kershaw 2013), but likely not representative of the total sponge assemblage alive in the Wenlock Epoch.

Finally, Kershaw (1998, p. 517) incorrectly reported Willenz & Hartman (1989) that calcified sponges do not contain bacteria. Willenz & Hartman (1989, p. 395) in fact made clear that modern calcified sponges can contain up to 20% of their mass as bacteria. Later work (e.g. López *et al.* 1999; Santavy & Colwell 1990) showed the widespread occurrence of bacteria in calcifying and noncalcifying sponges. As much as 60% of the biomass of some sponges is bacterial (Lee *et al.* 2001). The degree to which the bacterial communities played a part in sponge growth is not fully determined, but the ubiquity of microbes opens the possibility of symbiosis in ancient stromatoporoids, for which there is no physical evidence (discussed by Kershaw *et al.* 2018).

*Stromatoporoid substrates and growth aspects.* The idea that stromatoporoids were able to deal with a range of different types of substrates was explored by Kershaw (1998) and Kershaw *et al.* (2018). Evidence was presented that stromatoporoids were capable of growing directly on partly lithified and unconsolidated substrates composed of a mixture of carbonate and clay mud, although they are rare on pure clay mud substrates. A similar conclusion was previously drawn by Narbonne & Dixon (1984, p. 47) for Silurian lithistids (Demospongiae) in reefs on Somerset Island, Arctic Canada, drawing on a discussion by Heckel (1972, pp. 248, 249). Problematically, Heckel's own text (Heckel 1972, p. 249) and his fig. 8 are contradictory; the text states that sponges need a firm substrate to settle, yet his fig. 8 classifies sponges as being able to grow on soft, firm, and hard substrates. Unfortunately, none of Heckel's (1972, p. 249) statement is supported by observations or any verifiable reference. Nevertheless, these former views that sponges in general were able to grow on soft substrates is consistent with the repeated observation that Ordovician, Silurian, and Devonian stromatoporoids were able to do that (Kershaw *et al.* 2018). In some cases, stromatoporoids are found in abundance close to regions of siliciclastic input, such as the inner shelf extensive biostromes of Middle Devonian Fanning Group, Queensland, Australia, which occur close to siliciclastic deltaic facies (Cook 1995, fig. 8). Stromatoporoids also encrusted hard substrates. Wright & Cherns (2016) proposed that lithification of sediments from late Precambrian to Early Ordovician times was progressively deepened from the sediment surface down into the sediment. Overall, stromatoporoids from the British and Irish deposits studied here are consistent with the patterns of growth in stromatoporoids generally, showing an ability to grow on a range of substrates. However, Silurian stromatoporoids examined here, as noted elsewhere in this study, are generally rather small and have limited growth form range. They are also subject to growth interruption, as is universal in stromatoporoids (Kershaw *et al.* 2018) and also true of other calcified sponges such as chaetetids (Miller & West 1997), and our observations of tabulates in this study. Powell (1991, p. 296), based on Powell (1980), regarding stromatoporoid taxon *Stromatopora carteri* (here called *Syringostromella borealis*) from the MWLF, showed this taxon has regular interruptions of sediment in its growth that might indicate annual growth. Stearn (2015c, p. 563) explored the idea of a growth module in stromatoporoids that have prominent laminae, with focus on *Simplexodictyon yavorskyi* (see Powell 1991). In stromatoporoids with such laminae it may be possible to define their growth on the behaviour of successive laminae, but this approach would not work for stromatoporoids that lack laminae. An alternative is to develop a growth model using growth interruption events to define episodes of growth within a single stromatoporoid, an idea that may be explored in future work.

*Associated organisms (epibionts and endobionts).* Because the museum stromatoporoid collections examined for this study are largely thin sections (that show only a small part of a sample) it was not possible to collect comprehensive data on the organisms associated with stromatoporoids. Kershaw *et al.* (2018) recognized two major groups of organisms associated with stromatoporoids: epibionts as surface encrusters and borers after death of stromatoporoids, and endobionts as various tubes that grew inside stromatoporoids during their lives. Epibiont data are too scarce in the sample set to warrant documentation; unfortunately overall, the new samples collected for this study, and the museum material examined, lacked much exposed upper and lower surfaces of stromatoporoids, so studies of the types presented by Nield (1984, 1986), Segars & Liddell (1988), Lebold (2000), and Tapanila *et al.* (2004) were not possible. However, endobionts are sufficiently abundant in thin sections from new and museum material to provide an overall view of their types and distribution. Five categories of intergrown tubes are documented in the British Silurian stromatoporoids (Text-fig. 46) with a notable bias towards certain stromatoporoid taxa. Seven of the 15 fully identified stromatoporoid taxa contain intergrown tubes, evidence of biological selection between the stromatoporoid and associated taxa. Thus, British Silurian stromatoporoids exhibit the same type of pattern as other assemblages, with selective presence of intergrown organisms in certain stromatoporoid taxa, and reflect complex biological associations that leave little evidence of their nature. However, the stromatoporoids were able to overgrow the symbionts in almost all cases observed, as is the case for other assemblages (see Kershaw *et al.* 2018 for more discussion). It is possible that the symbiont taxa encountered the stromatoporoids by chance, but given that certain stromatoporoid taxa more commonly have intergrown organisms, there may have been a biological reason for settling of symbionts on the stromatoporoid surfaces. Nevertheless, if so, then it was a bad choice for the symbionts, which were overwhelmed by the (stromatoporoid) host's growth.

Darrell & Taylor (1993), in a valuable review, noted that most symbiotic relationships associated with corals involve soft tissue interactions that are unlikely to be preserved. In stromatoporoids, intergrown organisms leave either a lined tube, or an unlined tube. It is obvious that the occurrence of intergrown organisms in the British Silurian stromatoporoids is likely to be a true reflection of the extent of intergrowth that stromatoporoids experienced. Although Text-figure 46 shows that several taxa contain intergrown tubes (likely of worms and gastropods), no samples from the Midland Platform contain the well-known intergrown syringoporid tabulates formerly called 'caunopores' (Nicholson 1886, pp. 110–130). Kershaw *et al.* (2018, table 1) compiled data from Mori (1970) of the occurrence of intergrown corals and tabulates in stromatoporoids from the Wenlock and Ludlow series of Gotland. This compilation showed that some stromatoporoid taxa that contain intergrown corals and tabulates on Gotland also occur in the Midland Platform but lack those intergrown symbionts. Those taxa, from Mori (1970) are: *Simplexodictyon yavorskyi* (4 of 8 samples on Gotland) and *Parallelostroma typicum* (2 of 97 samples in Gotland). In the Midland Platform, *S. yavorskyi* is rare (2 samples) and *P. typicum* is uncommon (13 samples) so it is possible that the British stromatoporoid sample size is statistically so low that there was a negligible chance of finding intergrown corals in our assemblage. Mori (1970) also recorded common occurrence of *Stromatopora venukovi* (which in modern classification is not *Stromatopora* and therefore needs to be stated as '*Stromatopora*' pending revision of its taxonomy) on Gotland, and 13 of the 22 specimens contain intergrown syringoporids. In the Peel Sandstone on the Isle of Man included in this monograph, pebbles of Wenlock-age stromatoporoids of unknown provenance contain one specimen of '*Stromatopora*' *venukovi* (Text-fig. 35 and Pl. 18) and this one sample has intergrown syringoporids (Text-fig. 46). One possibility is that the lack of stromatoporoids with intergrown syringoporids in the Midland Platform may be an indicator that those stromatoporoids were more restricted in their environmental tolerance so were unable to develop symbiotic intergrowths in the Midland Platform. This aspect of stromatoporoids requires further work to investigate the possible interpretations, one of which is that the stromatoporoids of the British Silurian were under stress and lived towards the margins of their physiological capability.

Powell (1991) described the stromatoporoid taxon *Diplostroma* (now called *Simplexodictyon) yavorskyi* in the MWLF from Farley Quarry near Much Wenlock, which showed an association with four calcimicrobes (*Girvanella*, *Rothpletzella*, *Wetheredella*, and *Rhabdoporella*). *Simplexodictyon* *yavorskyi* has paired laminae that have a central light-toned region, creating a tripartite lamina, separated by substantial pillars. There seems to be a basic unit of this taxon's growth style that consists of two laminae joined by vertical pillars, which may or may not be separated from similar units above and below in the skeleton. Powell's (1991) sample shows calcimicrobial growth along the contact between paired laminae, so that the stromatoporoid grew as a series of thin sheets separated in places by calcimicrobes. The stromatoporoid apparently episodically rolled on the substrate, and Powell's (1991) interpretation is that the calcimicrobes grew in areas where the stromatoporoid soft tissue was missing. Thus, it seems that the calcimicrobes used the stromatoporoid as a substrate when it was available rather than any kind of symbiotic behaviour.

### Mineralogy and diagenesis

A review of stromatoporoid mineralogy (Kershaw 2013) emphasized that stromatoporoids are always recrystallized to some extent, but are rarely completely altered, in contrast to molluscs, and never as well-preserved as brachiopods and bryozoans in the same beds. These observations were presented as evidence that stromatoporoid original mineralogy may not have been aragonite or low-magnesium calcite, so the default is that they may have grown high-magnesium calcite skeletons. Nevertheless, confirmation is not currently available, but new evidence in this study, noted in the Results section (see Text-figs 49–51) extends the knowledge a little. Text-figure 49 shows calcite crystals that are part of stromatoporoid recrystallized skeleton pass with optical continuity into the underlying geopetal cement and may be an indication that the recrystallization process in the stromatoporoid occurred at the same time as the cement infilling the geopetal cavity. If that is true then it indicates a very early diagenetic recrystallization of the stromatoporoid, which may have occurred a short distance below the sea floor, in early burial. Smosna (1984, p. 1004) proposed that stromatoporoid recrystallization took place in the meteoric phreatic environment. Meteoric phreatic diagenesis is not confirmed in the MWLF, but the shallow marine nature of the deposits opens the possibility that stromatoporoids may have been recrystallized during phases of sea level fall as the MWLF developed. However, evidence from stained thin sections (e.g. Pl. 14) shows that some stromatoporoids contain ferroan calcite and underwent alteration below the redox boundary, noting that this could have occurred early in shallow burial.

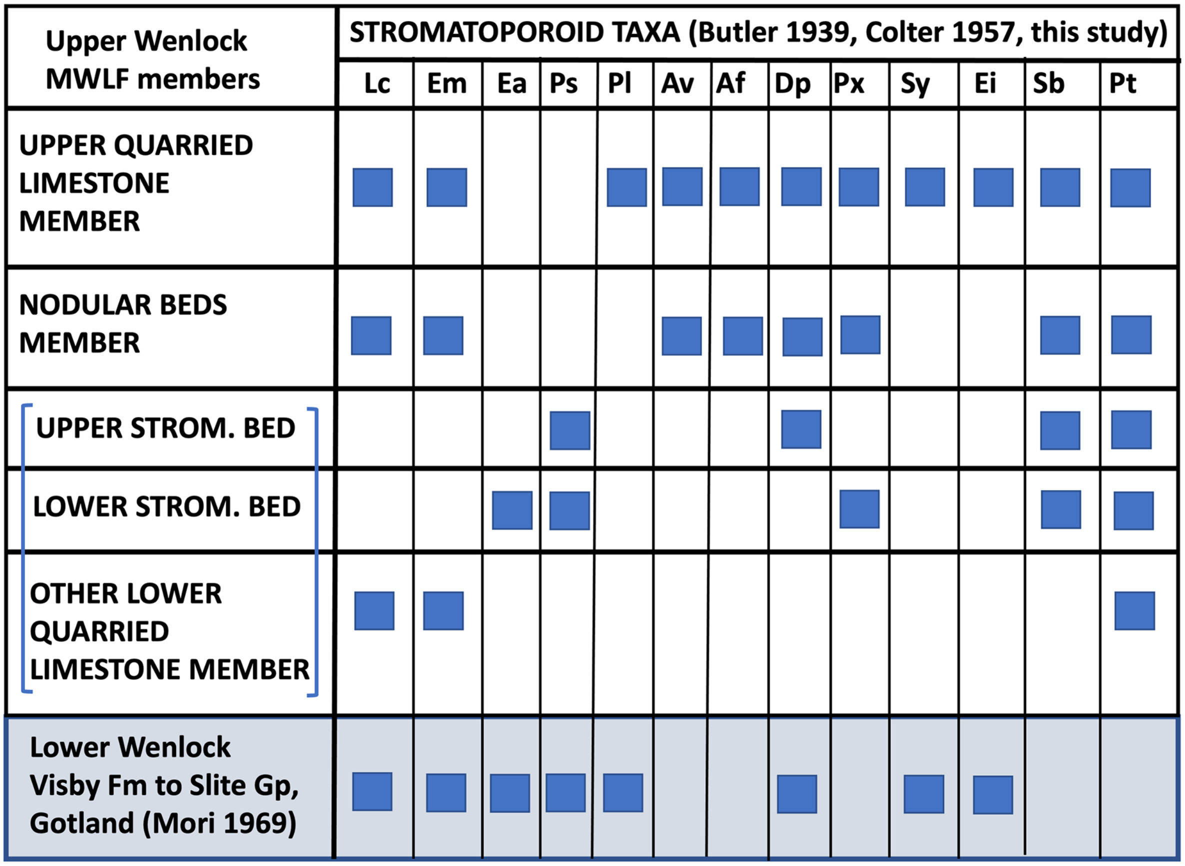
Further support for the idea of early recrystallization is shown in Text-fig. 50, in a case where a heliolitid encrusted an eroded pebble of a stromatoporoid, with optical continuity of sparite across the contact between stromatoporoid and tabulate. Here, recrystallization of the stromatoporoid may have taken place prior to cement infilling the heliolitid intraskeletal space, thus may also be simply a continuation of the cement into the coral's empty corallite space. Features illustrated in Text-fig. 51 build on the work of Scoffin (1972) regarding cavities in the MWLF reefs. Scoffin (1972) recognized cases of primary cavities below reef builders were sites not only of cement infilling but were locations where sediment was recrystallized to calcite in some cases.

Finally, Reitner & Wörheide (2002, figs 12, 13) proposed that the granular microstructure of a Middle Devonian stromatoporoid *Syringostroma* cf. *borealis* is a remnant of microscleres (constructional elements) of a hadromerid sponge skeleton. In Plate 21, figs 7, 8 of this study, a very similar cellular structure is visible at high magnification. Noting that Reitner & Wörheide (2002) make clear their comparison of taxonomy is an assumption, we draw attention to the fact, stated above, that when stromatoporoid thin sections are ground very thin, the skeletal structure is so poorly visible against the sparite cement background the stromatoporoid is composed of, that we contend no firm deductions regarding stromatoporoid affinity can be made about this comparison. The topic of stromatoporoid diagenesis throughout the Palaeozoic Erathem is addressed further by Kershaw *et al.* (2021).

## Relationship between stromatoporoids and middle Silurian extinctions

*Middle Silurian extinctions, major features.* In recent years, an extinction amongst graptolites, associated with changes in conodonts, in the middle of the Homerian Age, was discovered in the lower part of the Homerian carbon isotope excursion (e.g. Cramer *et al.* 2006, 2012) in Baltica, Avalonia, and Laurentia. This extinction is also called the Mulde Event (Calner *et al.* 2004). The impact on conodonts is less clearly defined (Jarochowska & Munnecke 2015), but there is no question that the graptolite extinction was a major event. The extinction overlaps the earliest part of stromatoporoid-bearing MWLF rocks in the Dudley and Malvern areas that formed in the *lundgreni* Zone, contrasting the other areas of MWLF deposition that was slightly later, in the overlying *ludensis* Zone, the last zone of the Wenlock Series (Bassett 1974; Ray *et al.* 2013). There is an interesting possibility that the stromatoporoid assemblages of the British sequences were affected by the mid-Homerian extinction, considered below.

*Stromatoporoid taxa and the mid-Homerian extinction.* The British Silurian stromatoporoid fauna is most easily compared with that of Gotland in Baltica (Mori 1970). Most of the MWLF (except in Dudley and Malvern Hills) is approximately equivalent to the Klinteberg Formation on Gotland, for which Mori (1970) identified 11 species of approximately equal abundance, contrasting the unequal abundance of taxa (Text-fig. 36) shown in the present study for Avalonia. In Mori's (1970) compendium, *Actinostromella vaiverensis*, *Densastroma pexisum* (as *Pycnodictyon densum*, a junior



| Upper Wenlock MWLF members | STROMATOPOROID TAXA (Butler 1939, Colter 1957, this study) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Lc | Em | Ea | Ps | Pl | Av | Af | Dp | Px | Sy | Ei | Sb | Pt |
| UPPER QUARRIED LIMESTONE MEMBER | ■ | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| NODULAR BEDS MEMBER | ■ | ■ | | | | ■ | ■ | ■ | ■ | | | ■ | ■ |
| UPPER STROM. BED | | | | ■ | | | | ■ | | | | ■ | ■ |
| LOWER STROM. BED | | | ■ | ■ | | | | | ■ | | | ■ | ■ |
| OTHER LOWER QUARRIED LIMESTONE MEMBER | ■ | ■ | | | | | | | | | | | ■ |
| Lower Wenlock Visby Fm to Slite Gp, Gotland (Mori 1969) | ■ | ■ | ■ | ■ | ■ | | | ■ | | ■ | ■ | | |

Text-fig. 54. Compilation of data from literature sources and this study, in an attempt to display the stratigraphic occurrence of stromatoporoid taxa in the Much Wenlock Limestone Formation (MWLF). The data are somewhat limited, because numbers of in-place samples are low, so only presence/absence of taxa are shown as blue squares. The MWLF was deposited in only the upper Homerian Stage, and so data are added from Mori's (1969a) taxonomic treatment of lower Wenlock stromatoporoids from Gotland (gray box). The Mulde extinction event occurred during the deposition of the Lower Quarried Limestone Member of the MWLF, where only three stromatoporoid taxa are recorded, compared to higher numbers below and above. Whether the extinction had any effect on the stromatoporoid assemblages or not is unclear, see text for discussion.

synonym of *D. pexisum*), *Syringostromella borealis*, and *Parallelostroma typicum* are also all present in the MWLF. Note that one taxon included by Mori (1970) is *Stromatopora carteri*, which as discussed earlier is considered here as a synonym of *Syringostromella borealis*. Another taxon from Mori (1970), also noted by Powell (1980), is *Stromatopora antiqua*, considered here a synonym of *Actinostromella vaiverensis*. However, several of the taxa recorded by Mori (1970) in the Klinteberg Formation are not present in British stromatoporoids. Nevertheless, for the upper Wenlock localities of the MWLF, equivalent to the Klinteberg Formation on Gotland and somewhat after the extinction, there is a healthy assemblage of stromatoporoids.

Directly underlying the Klinteberg Formation on Gotland are units called the Halla Beds and Mulde Beds in the older stratigraphy used by Mori (1969a, 1970). The lithostratigraphy was later amended in line with more accurate biostratigraphic data (see Calner *et al.* 2004; Cramer *et al.* 2012) so that the Halla and Mulde beds were redefined as the Halla Formation, which has facies variations. Thus, the Halla and Mulde of older terminology are now considered to be partly overlapping in age, so that the Mulde Beds are included as a marly facies within the redefined Halla Formation. Mori (1970) found *Labechia conferta* was abundant in the Halla Beds. In the Mulde Beds, two abundant taxa are *A. vaiverensis* and *D. pexisum* (misnamed *P. densum* by Mori 1970, stated above). In the Dudley and Malverns areas, the MWLF is equivalent to the Halla Formation and all three stromatoporoid taxa (*Labechia conferta*, *A. vaiverensis*, and *D. pexisum*) are present (Text-fig. 35), see also Text-fig. 54 that gives partial information on their stratigraphic distribution in the Dudley MWLF sequence at Wren's Nest. Indeed, all three taxa are abundant in the MWLF, which, except for the Dudley and Malverns areas, is a slightly younger deposit than these on Gotland.

In the Malverns area, Pässler *et al.* (2014) detailed a reef at Whitman's Hill Quarry, in the upper part of the LQLM of the MWLF, where the reef is rich in micrite and has few metazoan reef-building components. Whitman's Hill Quarry is stratigraphically located in the Mulde Event, associated with sea level rise in the part of the MWLF that passes from the LQLM to the Nodular Member (Text-fig. 3). Only three stromatoporoids were collected during this study from Whitman's Hill Quarry: two samples of *Labechia conferta* from the reef and one *Petridiostroma simplex* sample as a loose specimen. Ratcliffe (1988, fig. 2) described a micritic facies in reefs of the LQLM from several sites and Pässler *et al.* (2014) interpreted Whitman's Hill reef as related to the water deepening, with accommodation space for sediment accumulation, to explain why its reef has mostly micritic sediment and fewer metazoan fossils. There are parallels here with the small reefs in the lower part of Hobb's Quarry, May Hill, a small inlier containing MWLF, located west of the Malvern Hills near the Woolhope Inlier (Text-fig. 1). These reefs are also composed largely of micrite and have sharp margins against the bedded sediment, with bedded sediments deformed over the reef tops, indicating early cementation of the reef mass (Colter 1957; Kershaw *et al.* 2007). The Hobb's Quarry reefs are overlain by nodular limestones and are presumed to be at the level of the upper part of the LQLM, likely similar to Whitman's Reef in the nearby Malvern area and the lower part of the Dudley sequence at Wren's Nest.

The dominance of muddy carbonate sediment in these LQLM reef masses, with few corals and a poor stromatoporoid fauna, at the time of the Mulde Event when graptolites underwent extinction (the 'Big Crisis' of Cramer *et al.* 2012), raises the question of whether the stromatoporoids (and tabulates) were affected by the Mulde Event extinction. Answering this question is hampered by the relatively low numbers of stromatoporoids described from the British Silurian and from the fact that the MWLF is the only shallow margin carbonate unit in Britain where stromatoporoids could develop in abundance in a tight time window of the upper part of the Wenlock Series. However, the question may be addressed by examining stromatoporoid assemblages elsewhere, particularly Gotland. On Gotland, the Mulde Event occurs within a succession of the Fröjel Formation, Bara Oolite, and the Halla Formation (Calner *et al.* 2004, fig. 3), a series of sediments in which stromatoporoids are uncommon. Calner *et al.* (2000) did not find stromatoporoids in a tabulate-constructed biostrome that grew on the shelf margin in the Halla Formation (the part containing the Mulde Beds of older terminology) shortly after the Mulde Event on Gotland. However, Mori (1969a, table 1, 1970, table 1) listed different stromatoporoid taxa between the Slite Beds (Slite Group of modern stratigraphy) and overlying Halla Beds and Mulde Beds (Bara Oolite and Halla formations of modern stratigraphy). Brood

(1974) noted three stromatoporoid taxa in his work on bryozoans and showed environmental preference of the stromatoporoids for shallower waters. In Brood's (1974) study, the Klinteberg Formation overlying the Halla Formation contains some taxa continuing upwards from the Mulde Beds (Halla Formation), although largely the Klinteberg Formation stromatoporoids are different taxa from the underlying units.

From the information of the previous paragraphs, it appears there was a faunal turnover in the stromatoporoids of Gotland through the time of the Mulde Event. Castagner *et al.* (2015) cited Kershaw & Da Silva (2013) who indicated a somewhat low diversity of stromatoporoids in the MWLF in Britain, in a preliminary report that contained only part of the dataset. However, the full results reported here show that the MWLF stromatoporoid assemblages are one of the more diverse of the Wenlock Series globally. Stearn (2015d, fig. 360) compiled alpha diversity of traditional Palaeozoic stromatoporoid genera and showed expansion in the Wenlock compared to the Llandovery, and further expansion in the Ludlow. However, these data are illustrated as broad boxes based on complete stratigraphic series and do not reveal changes within a series. Stearn (2015d, fig. 361) showed the diversity variation of traditional stromatoporoid orders do not collectively indicate a decline in the Wenlock that might be attributed to the Mulde Event, but because of the broad scale illustration by Stearn (2015d, fig. 361), any effects of the Mulde Event are not detectable in the stromatoporoid fauna.

*Comparisons with other Silurian extinctions.* In order to further explore the possible effect of Silurian extinctions on stromatoporoids, we briefly consider two other Silurian isotope excursions that are linked to extinctions of planktonic faunas, in relation to stromatoporoid occurrence on Gotland, where stromatoporoid faunas are very rich. Both cases show the problems of linking Silurian stromatoporoids to these extinctions. First, the Ireviken isotope excursion, which is associated with faunal changes in the early Wenlock (Sheinwoodian) Ireviken Event and is related to carbon and sulphur changes in the oceans at that time (e.g. Munnecke *et al.* 2003; Rose *et al.* 2019). In the early Wenlock sequence on Gotland, significantly earlier than deposition of the MWLF, extinctions in conodonts are associated with the Ireviken Event carbon isotope excursion that began around the Llandovery–Wenlock series boundary. That boundary on Gotland approximates to the junction between the Lower and Upper Visby formations, where the facies are mud-dominated with low carbonate content (Calner *et al.* 2004). Stromatoporoids do not occur until after the extinction event in this sequence. However, the facies sequence above the Llandovery–Wenlock boundary shows shallowing water depth through the lower Wenlock Series Upper Visby and Högklint formations (Munnecke *et al.* 2003) and stromatoporoids become abundant as the environment became suitable for their growth. Although it is not possible to link the Ireviken extinctions with stromatoporoids, this case is an illustration of the impact of local facies control on stromatoporoid development. Second, the globally recognized Lau Event in the Ludlow Series on Gotland records a large positive carbon isotope excursion at the same time as conodont extinctions (Younes *et al.* 2017). Ludlow-age stromatoporoids on Gotland occur from below to above the strata containing evidence of the Lau Event. Hemse Group limestones that underlie the Lau Event beds have a rich stromatoporoid fauna of 23 taxa (Mori 1970), falling to five taxa within facies that record the Lau Event (Eke Formation). The succeeding Burgsvik Formation is a deltaic sandstone with no stromatoporoids, but the overlying beds (Hamra and Sundre formations, containing reefs) have a total of six stromatoporoid taxa. Thus, a fall from 23 to 5–6 taxa through the extinction and its aftermath makes the Lau Event a possible candidate to have driven loss of stromatoporoids in this sequence. It is interesting that the Hamra and Sundre formations have abundant stromatoporoids, albeit with reduced diversity compared with the Hemse Group below the Lau Event (Mori 1970, table 1). However, in nearby Estonia, Kershaw & Motus (2016) studied in depth a stromatoporoid-rich deposit at Katri on Saaremaa Island that is dated as equivalent to the Eke Formation on Gotland. Thus, it is clear that the changes in stromatoporoid faunas on Gotland through the Lau Event strata are facies-driven and not due to extinction. Comparisons with stromatoporoid-bearing strata elsewhere might shed light on the issue of recognizing stromatoporoid extinction in the Lau Event, but unfortunately no other stromatoporoid assemblages in the late Ludlow have been analysed in the detail available for Gotland and Estonia, so it is not currently possible to correlate the changes on Gotland with other areas, noting also that in most places the late Ludlow was a time of regression and stromatoporoid assemblages do not occur (e.g. South China Block) or less common (eastern USA). A candidate for detailed study is the late Ludlow–Pridoli age West Point Formation, Gaspé Peninsula, eastern Canada that has abundant stromatoporoids, examined in an unpublished Master's thesis by Pope (1986); Pope's careful stratigraphic tabulation showed those taxa too were facies-related, and lacked evidence of faunal loss at particular horizons.

The foregoing discussion demonstrates the difficulty of linking stromatoporoids to extinctions in the Silurian because of the significant effect of facies control, which applies to the Mulde extinction episode in the British Silurian System. Although stromatoporoids occur in clay-rich deposits and high energy very shallow settings of oolites, they are not common in either of these facies, noting also that the base of the Halla Formation on Gotland has the mid-Homerian unconformity when the rocks were exposed above sea level (Calner *et al.* 2004, fig. 5) and erosion occurred. Thus, it is currently unclear as to whether MWLF stromatoporoids were affected by the Mulde Event, but certainly they responded to ideal growth conditions in shallow marine waters with lower levels of clays in the Klinteberg Formation on Gotland, equivalent of the upper parts of the MWLF in the British sequence. Regarding the Wenlock Epoch extinction of graptolites and turnover of conodonts, Bassett (1974) noted that the Wenlock shelf facies have relatively few graptolites, a likely reflection of the Mulde Event. Discussion by Stearn (2015e), regarding the loss of Palaeozoic stromatoporoids in the Late Devonian extinctions, explored the possibility that stromatoporoids lost their ability to calcify at that time. In contrast, Kershaw & Sendino (2020) pointed out that the Carboniferous calcified sponge faunas contain abundant chaetetid sponges, so that if loss of calcification occurred, then it selectively affected calcified sponges that had a stromatoporoid architecture. Whether loss of calcification could apply to the Wenlock-age stromatoporoids studied here would require verification criteria that are currently unavailable. A more likely reason why stromatoporoids and corals show little evidence of effect of extinction as a result of the Mulde Event was because they were shallow marine benthos in contrast to the pelagic nature of graptolites and conodonts, and is an area for future research.

## CONCLUSIONS

This first synthesis of British Silurian stromatoporoids reveals the following outcomes:

1. In a total sample of 408 stromatoporoids from a combination of field and museum collections, 15 taxa are described, all exist in the Silurian global stromatoporoid literature from other areas; none are unique to Britain and Ireland and no new taxa have been found. The five most abundant taxa make up 59% of the total assemblage; such bias towards a small number of taxa is consistent with the pattern of other stromatoporoid assemblages throughout the Palaeozoic. This study adds eight new taxa at the traditional genus level to the seven in the compendium in Stock *et al.* (2015), increasing the importance of British Silurian stromatoporoids in their global distribution.
2. Nearly all Silurian stromatoporoids in the Avalonia microcontinent grew on the English Midland Platform, associated with carbonates of the MWLF, in shallow marine tropical conditions in a small area surrounded by siliciclastics associated with the nearby Caledonian orogenic system. Underlying and overlying facies are siliciclastic-dominated, demonstrating that the stromatoporoids grew in a limited time-and-space window, taking advantage of the appropriate conditions of carbonate-rich sediments in shallow warm waters. Two other confirmed occurrences are: (1) small number of Wenlock-age stromatoporoids in an Early Devonian conglomerate on the Isle of Man, evidence of a fauna that existed in the north of Britain, possibly derived from Scandinavia; and (2) one stromatoporoid of certain early Silurian age, and two of likely early Silurian age from Girvan (southwest Scotland), preserved in gravity flows and indicating input from shallow marine carbonates containing stromatoporoids. These cases are evidence of other shallow marine carbonate platform areas in or near the Britain and Ireland region, no longer preserved, containing stromatoporoids. However, reported Wenlock-age stromatoporoids from the Dingle Peninsula of western

Ireland are misidentified trace fossils.

3. British Silurian stromatoporoids have a limited range of laminar to high domical growth forms and maximum sizes of individual stromatoporoids rarely exceed 20 cm in basal diameter (maximum 40 cm). This limited range forms a stark contrast to the abundance and larger sizes of stromatoporoids, often with complex and diverse growth form, in assemblages in larger intracratonic carbonate platforms such as the upper Wenlock Series Klinteberg Formation on Gotland, the same age as the MWLF.
4. Taxa described are found in nearby shallow marine areas of Laurentia and Baltica. Thus, it is surmised that stromatoporoids were distributed through the oceans as planktonic forms, carried by currents, and that their occurrence in the British Midland Platform is evidence of the ease with which stromatoporoids were able to develop if the conditions were right. Nevertheless, there is some evidence of variability of geographical occurrence that may be due to differences in dispersal mechanisms but could be an artefact of sampling.

## SYSTEMATIC DESCRIPTIONS

### Introduction

Fifteen taxa were found in this sample of British Silurian stromatoporoids. As explained in the main body of this monograph, the approach towards systematics adopted here is to accept that the taxa are Phylum Porifera, and are hypercalcified sponges, noting that there is not proof of a sponge affinity in one taxon, *Lophiostroma schmidti*, included in this systematic account. Below the phylum level, however, the absence of spicules makes classification of stromatoporoids a problem that lacks evidence to resolve it, giving a dilemma about how to present the taxa in this section.

In order to conform with the traditional stromatoporoid systematics as presented in publications, below we give the traditional classification scheme, for reference. However, after that the taxa are described as lowest-level taxa without any formal interrelationship, to emphasize the approach in this study of regarding the lowest-level taxa as equal-status taxonomic objects without assuming any relationship between them, other than knowing that they are calcified sponges.

### Traditional taxonomic scheme of Palaeozoic stromatoporoids

The classification presented below uses the scheme presented by Stearn (2015f) who provided full details of division into orders and families. It is interesting to note that Stearn (2015f, p. 700), referring to the classification as presented in the *Treatise on Invertebrate Paleontology*, duplicated below, noted that “the authors assume and hope that the major groups are monophyletic, but monophyly is difficult to prove”. Thus, we contend that although this scheme provides a valuable form-grouping classification for descriptive purposes, its application in interpretations of stromatoporoid palaeobiology, palaeoenvironment, and palaeogeography, where comparisons are of taxa above the lowest (= traditional species) level, has no secure scientific basis. Because of the problems of the biological classification of stromatoporoids discussed earlier in this study, the arrangement of this section departs from the traditional pattern of defining taxa into increasing levels of species, genera, families, orders, and classes. However, the stromatoporoids are presented in the same order as commonly used in stromatoporoid work, and in this case the same order as in Stock *et al.* (2015, table 37). Thus, we stress that although the traditional classification is presented here for information, we are not applying it in the analysis of the material studied in this project. For clarity we also record which of the traditional orders and families do not have representatives in the British Silurian suite and we include the list of taxa found in this study. Page numbers indicate the start of descriptions.

Phylum PORIFERA Grant, 1836
  Class STROMATOPOROIDEA Nicholson & Murie, 1878
    Order *LABECHIIDA* Kühn, 1927

        Family Rosenellidae: no taxa
        Family Labechiidae: *Labechia conferta* (p. 69)
        Family Stromatoceriidae: no taxa
        Family Platiferostromatidae: no taxa
        Family Stylostromatidae: no taxa
        Family Aulaceratidae: no taxa
        Family Lophiostromatidae: *Lophiostroma schmidti* (p. 70), *Labechia rotunda* (p. 71), *Labechia scabiosa* (p. 71)
    Order *CLATHRODICTYIDA* Bogoyavlenskaya, 1969
        Family Clathrodictyidae: no taxa
        Family Actinodictyidae: *Ecclimadictyon macrotuberculatum* (p. 72), *E. astrolaxum* (p. 72)
        Family Gerronostromatidae: *Petridiostroma simplex* (p. 73), *P. linnarssoni* (p. 74)
        Family Tienodictyidae: no taxa
        Family Anostylostromatidae: no taxa
        Family Atelodictyidae: no taxa
    Order *ACTINOSTROMATIDA* Bogoyavlenskaya, 1969
        Family Actinostromatidae: *Plectostroma intertextum* (p. 76)
        Family Pseudolabechiidae: no taxa
        Family Actinostromellidae: *Actinostromella vaiverensis* (p. 75)
        Family Densastromatidae: *Densastroma pexisum* (p. 76), *Araneosustroma fistulosum* (p. 75)
    Order *STROMATOPORELLIDA* Stearn, 1980
        Family Stromatoporellidae: *Simplexodictyon yavorskyi* (p. 78)
        Family Trupetostromatidae: no taxa
        Family Idiostromatidae; no taxa
    Order *STROMATOPORIDA* Stearn, 1980
        Family Stromatoporidae: *Eostromatopora impexa* (p. 79); also see below this list
        Family Ferestromatoporidae: no taxa
        Family Syringostromellidae: *Syringostromella borealis* (p. 80)
    Order *SYRINGOSTROMATIDA* Bogoyavlenskaya, 1969
        Family Coenostromatidae: no taxa
        Family Parallelostromatidae: *Parallelostroma typicum* (p. 80)
        Family Stachyoditidae: no taxa
    Order *AMPHIPORIDA* Rukhin, 1938
        Family Amphiporidae: no taxa
    Order and Family Uncertain: no taxa
Class Uncertain
    Order *PULCHRILAMINIDA* Webby, 2012
        Family Pulchrilaminidae: no taxa

No new taxa, at either traditional genus or species levels were discovered in the sample set of new material and museum samples. We surmise that the range of taxa of British and Irish Silurian stromatoporoids is stable and discovery of new taxa considered unlikely. Illustrations of taxonomic features is provided here together with notes on each taxon. For formal taxonomic descriptions at genus level, reference is made to published work in relevant chapters of the *Treatise on Invertebrate Paleontology*, Part E (Nestor 2015; Stearn 2015a; Stock 2015; Webby 2015a). We draw on a combination of information from new samples, and accounts from Nicholson (1886, 1889, 1891, 1892) and Mori (1969a, 1970) which include all the taxa found in this study.

One discrete lowest-level taxon that occurs in the British Silurian suite that is misnamed, but its taxonomic name is not established, is *'Stromatopora' venukovi*. Another, incompletely identified, is *'?Stromatopora' lamellosa*. It is clear that these do not match the criteria for inclusion in the form-family Stromatoporidae, but formal identification awaits further study.

Two taxa incompletely described in the British Silurian stromatoporoid literature are included in this systematic list. They are *Labechia rotunda* Johnston (1915) and *Labechia scabiosa*

Nicholson (1891), the holotypes of which are in the NHMUK and are indeed the only samples of these taxa available to us. Both taxa were presented by these authors using only hand specimens, without thin section study, surprising considering the high research calibre of both Mary Johnston and Alleyne Nicholson in their era. Both taxa were considered by Mori (1970) to be invalid, a conclusion we agree with, but these taxa are illustrated here for the first time.

Definitions of terminology of stromatoporoid architecture may be found in Webby (2015b).

### Taxonomic descriptions

**Labechia conferta** (Lonsdale, 1839) Pl. 1; Text-figs 12, 13, 14A, 40, 45, 48, 51

1839 *Monticularia conferta* Lonsdale; p. 686, pl. 16, figs 5, 5a.

*Material.* CAMSM X.50347.187 (Pl. 1), CAMSM A7720 (Text-fig. 12), CAMSM X.50347.162 (Text-fig. 13), parts of laminar frame from patch reefs. Other examples observed throughout Wenlock Edge and in Malverns area. Overall, 40 separate specimens, noting that this taxon occurs commonly as anastomosing frameworks, of which most samples are pieces, so the sample number underestimates its abundance.

*Locality and horizon.* CAMSM X.50347.187, Wren's Nest, Dudley, West Midlands; CAMSM X.50347.162, Coates Quarry, Wenlock Edge, Shropshire; CAMSM A7720, Lilleshall Quarry, Wenlock Edge, Shropshire. Much Wenlock Limestone Formation, Wenlock Series, Silurian.

*Diagnosis of* Labechia *(Milne-Edwards & Haime, 1851).* From Webby (2015a, pp. 719, 720):

> Simple, upwardly curving convex to flattened cyst plates of variable size and rounded pillars exhibiting a range of morphologies from somewhat sporadically developed small pillars and denticles to, more commonly, more continuous, large, solid pillars, and occasionally where closely spaced, forming chainlike rows. […] Skeleton composed of long, stout, rounded pillars to more sporadically developed, less continuous, small pillars, and an intricate mesh of cyst plates with moderately upward convexity; pillars may terminate as papillae on upper surface and may show upwardly converging cone-in-cone banding in longitudinal section (concentric rings in tangential section). The genus includes a wide range of longitudinal structural elements, from those with a patchy development of small, short pillars that are grouped in the *Labechia prima* species group to those with long and stout, rounded pillars of the *L. conferta* species group.

*Description of* Labechia conferta *(Lonsdale).* It occurs throughout the MWLF, mainly in reefs where it commonly forms anastomosing laminar frameworks. Its distinctive thick pillars and cyst plates separate it from all other taxa and it can be identified in the field, unlike all other stromatoporoids in the British suite. Frame diameters can be up to 1 m and patches of frames contain variable numbers of connected sheets *of L. conferta*, the maximum number observed being approximately 20 sheets. Thickness of laminar sheets within a patch of frame ranges from 5–50 mm, commonly *c.* 10 mm. Individual sheets taper to their margins (Text-fig. 13). Mori (1970, p. 79) noted that samples from Gotland have a surface that is distinctly papillate, consistent with all the specimens observed in Britain. The skeleton is composed of long continuous pillars 0.1–0.2 mm thick, although Mori (1970, p. 79) recorded them as ranging from 0.2–0.95 mm thick. Pillar lengths are difficult to determine precisely because thin sections do not cut perfectly down their long axes. Measured pillars are maximum of 10 mm but are likely to extend through the entire thickness of an individual laminar sheet, potentially up to 50 mm long. The pillars are circular or slightly oval in tangential sections, generally well separated from each other. Pillars begin at the base of the specimen; the papillate surface structure of specimens forms because pillars protrude slightly from the stromatoporoid surface. In VS the pillars have zigzag edges, which join the cyst plates. Some pillars preserve a cone-in-cone structure (Pl. 1, fig. 4; Webby 2015a, p. 720, fig. 392). Between pillars are thin cyst plates, which in most cases arch upwards, but some are flat. Each cyst plate overlaps the adjacent one. Mori (1970, p. 79) recorded in specimens from the Silurian of Gotland that cyst plates are tripartite, consisting of a median, thin, dark, or light compact layer (0.01–0.03 mm thick) and upper and lower flocculent layers that are variable in thickness. However, diagenetic alteration of the skeletal structure in the current samples from Britain means that the tripartite structure is mostly lost, but is preserved in some cyst plates (Text-fig. 48). Nevertheless, British material is consistent with Mori's (1970, p. 79) description that there are 2–6 cyst plates in 1 mm measured vertically (3 or 4 on average). The growth lines in the pillars are easily discernible both in vertical and tangential sections. Mori (1970, p. 79) recorded that some pillars have light, circular centres which are 0.04–0.13 mm in diameter, which are also considered to be growth lines, but these features are not present in the British specimens because of recrystallization. Astrorhizae are absent and the microstructure is compact.

*Remarks.* The type species is a neotype, *Labechia conferta* (Lonsdale), designated by Smith (1932). Further description of *Labechia conferta* and its history of study is provided by Webby (2015a, pp. 720–722).

*Range.* Webby (2015a, p. 720) recorded for *L. conferta* a range of Middle Ordovician to Upper Devonian (Famennian), and noted geographical variations. Mori (1970, p. 81) recorded for *L. conferta* on Gotland a Wenlock age (middle Silurian), matching its occurrence in the British Silurian. It is very curious why *L. conferta* is missing from the Ludlow on Gotland. As an addendum to this range information, Smith's (1932) work also described a new taxon, *Labechia carbonaria* Smith 1932, from Lower Carboniferous limestones in Britain (see Kershaw & Sendino 2020), not included in the present study that focuses on Silurian rocks.

### **Lophiostroma schmidti** (Nicholson, 1886) Pl. 2; Text-figs 15, 40

1886 *Labechia ?schmidti* Nicholson; p. 16, pl. 2, figs 6–8.
1908 *Chalzodes granulatum* Parks; p. 36.

*Material.* NMW 99-35G-2582 (Pl. 2) [thin section] and NMW R48326 [acetate peel].

*Locality and horizon.* NMW R48326 locality and horizon unknown; NMW 99-35G-2582 Haugh Wood, Woolhope Inlier; plus one other sample from Lea South Quarry, not figured. All samples from Much Wenlock Limestone Formation, Wenlock Series, Silurian. Total 2 specimens.

*Diagnosis of* Lophiostroma *(Nicholson).* From Webby (2015a, pp. 749–752):

> Encrusting laminar, latilaminate, composed of much thickened, tangential skeletal layers almost completely filling interskeletal space, sharply undulated skeletal layers forming pillarlike upgrowths appearing as papillae on the upper surface; discrete longitudinal and tangential elements rare. […] Skeleton commonly latilaminate and laminar, consists of, dominantly, much thickened, superposed, sheet-like layers, sharply and regularly undulating into columnar, pillar-like upgrowths, giving a kind of cone-in-cone structure; these upgrowths expressed as papillae on upper surfaces; sheetlike layers almost entirely occupy interiors and do not represent true laminae, only rarely discernible cysts preserved; compact microstructure has a transverse fibrosity within sheetlike layers.

*Description of* Lophiostroma schmidti *(Nicholson).* Dominantly a laminar growth form in the Ludlow of Gotland (SK observations) very distinctive in the field because of its prominent papillate surface, due to protrusion of its large pillars on the upper surface. Only two samples were available for measurements, small samples up to 60 mm in basal diameter and maximum 10 mm high. This taxon lacks galleries and vertical pillars, the skeleton being composed of solid skeletal structure. Dark growth lines are frequently observed in VS that are easily recognized as growth interruption surfaces obvious in Text-fig. 15 where very thin layers of sediment lie in the growth lines (see Kershaw *et al.* 2018 for discussion), that appear in some specimens (including that shown in Text-fig. 15) as regular. Astrorhizae are absent and the microstructure is multi-layered. The skeleton is composed of very thin densely spaced, thin horizontal elements, recorded by Mori (1970, p. 141) as numbering 10–16 in 0.1 mm. However, we have not been able to verify Mori's metric; Pl. 7, figs 5–8 from Gotland material show the structure is composed of horizontal elements, but the structure is altered and the clarity of measurement is degraded. Nevertheless, the delicate elements are bent upwards into vertical columns recorded by Mori (1970, 141) as 4–6 per mm, although Pl. 7, fig. 3 shows only 3 per mm; in TS in Pl. 7, fig. 4, the columns are not very clear. The comparative specimen from the Ludlow of Gotland (Pl. 7, figs 5–8) has a larger scale structure of only 2 columns per mm, contrasting Mori's (1970, p.141) measurements of similar specimens from Gotland.

*Remarks.* The taxon is composed of solid crystalline structure composed of laterally amalgamated crystalline vertical structures resembling the pillars in *Labechia*, but lacks any internal spaces, in particular it lacks cyst plates. Furthermore, classification of *L. schmidti* as a type of stromatoporoid is questionable because it lacks the vertical and horizontal features that define stromatoporoids. The term 'stromatoporoid' is a combination of Greek-derived words; 'stroma' is a mattress in Greek, and '-poroid' refers to the empty spaces within the structure. *Lophiostroma schmidti* has a layered structure but is a solid skeleton and it lacks astrorhizae. Not all stromatoporoids have astrorhizae, but their layered porous architecture and features such as astrorhizae allow them to be identified as sponges; but *Lophiostroma* stands apart from the other taxa in lacking characters that link it unequivocally to phylum Porifera and to the other stromatoporoids. Nevertheless, it also lacks any features that could link it to the tabulates; it lacks any corallites. There are no other fossil groups in the Silurian rocks into which *Lophiostroma* can be placed, so phylum Porifera is a reasonable place, and the hypercalcified sponges is an obvious choice; nevertheless, this choice is a default option, in the absence of verification.

Webby's (2015a, p. 749) description quoted above refers to the traditional family Lophiostromatidae as being encrusting. This is presumed to mean that these stromatoporoids encrusted a substrate; however, it is clear from *Lophiostroma schmidti* in the Ludlow of Gotland observed by SK to be repeatedly not encrusting a solid surface such as represented by another stromatoporoid or tabulate, but instead to have grown on the sediment surface, perhaps forming primary cavities. Growth rings on the base of most samples of *L. schmidti* are considered evidence that they formed primary cavities, so the base was not in contact with the sediment. In some cases, *L. schmidti* encrusted its substrate but more commonly it was other stromatoporoids, corals and tabulates that used the presumed dead surfaces of *L. schmidti* as a substrate, although because there are only two samples in the British suite, this palaeobiological aspect of this taxon is not observed. Sample NMW R48326 (acetate peel) is from the collections of John Powell deposited in the National Museum of Wales.

*Range.* Webby (2015a, pp. 749–751) recorded for *Lophiostroma* a range of Darriwilian (Middle Ordovician) to Frasnian (Upper Devonian). Mori (1970, p. 143) recorded *L. schmidti* as being Wenlock and Ludlow ages (Silurian).

### **Lophiostroma ?schmidti** (Nicholson, 1891) Pls 3–7

1891 *Labechia scabiosa* Nicholson; p. 160, 161, pl. 20, figs 4–6.
1915 *Labechia rotunda* Johnston; pl. XV.

*Material.* NHMUK PI H969 (Pls 3–5), *Labechia rotunda,* holotype, VS and TS thin sections of holotype, described by Johnston (1915) as a new species of stromatoporoid, as several specimens of which the holotype is one; NHMUK PI P6145 (Pls 6–7), *Labechia scabiosa,* holotype, VS and TS thin sections of holotype, described by Nicholson (1891, pp. 160, 161) as a new species. Total 2 specimens.

*Locality and horizon.* NHMUK PI H969 was collected from Shadwell Rock Quarry on Wenlock Edge; NHMUK PI P6145 was collected from Dudley (presumably Wren's Nest).

*Diagnosis of* Lophiostroma *(Nicholson).* See *Lophiostroma schmidti* above.

*Description of* Lophiostroma ?schmidti *(Nicholson).* Laminar growth form. The structure of *L. rotunda* has characters of *Lophiostroma schmidti*; see Pl. 2, figs 3–6 for comparison with *Lophiostroma schmidti* from Gotland. In the two holotypes of *Labechia rotunda* and *L. scabiosa*, the structure is poorly preserved, but its structure is sufficiently visible to validate its lack of pillars and cyst plates required to be diagnostic of *Labechia*.

*Remarks.* Discussion by Mori (1970, pp. 142, 143) drew attention to the similarity between *Lophiostroma schmidti* and both *Labechia rotunda* and *Labechia scabiosa* (Nicholson) and he regarded both as being synonyms of *Lophiostroma schmidti*. We understand that it was Kei Mori who arranged making of thin sections of *L. rotunda* and *L. scabiosa* of the NHMUK collections studied here. The description above of *L. schmidti* matches the structure of both NHMUK PI P6145 (*Labechia scabiosa*) and NHMUK PI H969 (*Labechia rotunda*), making them junior synonyms of *L. schmidti*, but they are listed here as *L. ?schmidti* rather than *L. schmidti* because of poor structure preservation.

*Range.* Webby (2015a, pp. 749–751) recorded for *Lophiostroma* a range of Darriwilian (Middle Ordovician) to Frasnian (Upper Devonian). The only samples of the taxa described by Nicholson (1891) and Johnston (1915) were collected from the MWLF at Wenlock Edge. The range of *L. ?schmidti* is presumed the same as *L. schmidti*.

**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.

*Material.* CAMSM X.50347.99 (Pl. 8); CAMSM X.50347.225 (Text-fig. 16); also thin sections in NHMUK, NMW, and CAMSM. Total 26 specimens.

*Locality and horizon.* CAMSM X.50347.99, Lea South Quarry, Wenlock Edge; CAMSM X.50347.225, Wren's Nest, Dudley, West Midlands. Much Wenlock Limestone Formation, Wenlock Series, Silurian.

*Diagnosis of* Ecclimadictyon *Nestor, 1964.* From Nestor (2015, p. 758):

> 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. [...] Growth form laminar to domical; laminae crumpled, forming cassiculate network; pillars oblique or indistinct; galleries labyrinthine, subangular in longitudinal section; astrorhizae fasciculate, irregular.

*Description of* Ecclimadictyon macrotuberculatum *(Riabinin).* This taxon forms low domical to high domical growth forms, with a range of sizes up to 380 mm basal diameter and 350 mm high (see reconstruction diagram in Text-fig. 14), therefore the largest stromatoporoid in the MWLF suite. Samples from Britain are identical to those on Gotland, recorded by Mori (1970, p. 97) as having strongly crumpled and zigzag shaped laminae, 0.05–0.09 mm thick, with 5–7 (6 on average) in 1 mm of vertical section. Galleries are small and generally isometric. Well-developed astrorhizae are 4–5 mm in diameter and have 5 or 6 main canals in each astrorhiza in TS, with canals being 0.09 mm wide. Microstructure is compact.

*Remarks.* The difference between *E. macrotuberculatum* and *E. astrolaxum* (described below) is that *E. astrolaxum* has a consistently finer-scale structure than *E. macrotuberculatum* (compare Pl. 8, fig. 3 with Pl. 9, fig. 1, and Pl. 8, fig. 4 with Pl. 9, fig. 3). Both taxa differ from that figured in the *Treatise on Invertebrate Paleontology* volume, named as *E. fastigiatum* (Nestor 2015, fig. 418, 2a, b), which has a more prominent zigzag appearance of the laminae in vertical section. *Ecclimadictyon macrotuberculatum* is typical of many stromatoporoids that show evidence of ability to grow on soft substrates (Text-fig. 16) and was affected by frequent growth interruption and recovery. This taxon is Nicholson's *Clathrodictyon vesiculosum* reported in Nicholson (1889, pp. 147–150); NHMUK sample P5498-226 and 226A are identified in this study as *E. macrotuberculatum*. Nicholson (1889, p. 149) noted it was found in the Woodland Beds of Woodland Point in Girvan, SW Scotland, which places it in the Llandovery Series of the UK; and at May Hill, Gloucestershire, England, which is in the MWLF (although the sample is not recorded in the NHMUK).

*Range.* Nestor (2015, p. 758) recorded *Ecclimadictyon* as ranging from Katian (Upper Ordovician) to Silurian. Mori (1970, p. 98) and Nicholson (1889 p. 149) recorded Llandovery and Wenlock ages for *E. macrotuberculatum*, placing it in the lower to middle Silurian.

**Ecclimadictyon astrolaxum** (Nestor, 1966) Pl. 9; Text-fig. 40

1966 *Ecclimadictyon astrolaxum* sp. nov. Nestor; p.18, pl. 5, figs 5, 6, pl. 6, figs 1, 2.

*Material.* CAMSM X.50347.95 (Pl. 9). Also thin sections in NHMUK and CAMSM. Total 21 specimens.

*Locality and horizon.* Lea South Quarry, Wenlock Edge, Shropshire. Much Wenlock Limestone Formation, Wenlock Series, Silurian.

*Diagnosis of* Ecclimadictyon *Nestor, 1964.* See under *Ecclimadictyon macrotuberculatum* above.

*Description of* Ecclimadictyon astrolaxum *(Nestor).* Has a laminar to domical growth form and only one sample was complete enough to be plotted on Text-fig. 40, and is only 60 mm in basal diameter and 5 mm in height. Mori (1969a, p 61) recorded laminar, conical, and irregularly massive forms on Gotland, 330 mm in basal diameter and 120 mm high. The small size of samples of this taxon in Britain is a reflection of the general pattern that stromatoporoids are much smaller in the British Silurian than on the stable intracontinental platform of Gotland. Mori (1969a, p. 61) reported the skeleton is composed of irregularly crumpled laminae, 4–6 in 1 mm and 0.05–0.08 mm thick, consistent with the British material. Mori (1969a, p. 61) also noted that there are no definite vertical pillars. The galleries vary in size and shape but generally the galleries are more equidimensional than in *E. macrotuberculatum.* Mori (1969a, p. 61) notes presence of discontinuous horizontal dissepiments but neither his illustrations nor the samples in the British material contain dissepiments, the skeleton is composed of only crumpled-form laminae. Mori (1969a, p. 61) also recorded well-developed astrorhizae, consistent with the British material, in which the maximum diameter of astrorhizal canals is 0.30 mm in tangential section. The microstructure is compact.

*Remarks.* Differences between *E. astrolaxum*, *E. macrotuberculatum*, and *E. fastigiatum* are noted under *E. macrotuberculatum* above.

*Range.* Nestor (2015, p. 758) recorded *Ecclimadictyon* as ranging from Katian (Upper Ordovician) to Silurian. Mori (1970, p. 98) and Nicholson (1889 p. 149) recorded Llandovery and Wenlock ages for *E. macrotuberculatum*, placing it in the lower to middle Silurian.

**Petridiostroma simplex** (Nestor, 1966) Pl. 10; Pl. 12, figs 1, 2; Text-figs 17–21, 31B, 32, 33, 34C, 40

1887 *Clathrodictyon regulare* Rosen; Nicholson, p. 10, pl. 11, figs 5, 6.
1966 *Simplexodictyon simplex* Nestor; p. 25, pl. 8, figs 1–6.
1991 *Faciledictyon* Lessovaya; p. 28.

*Material.* CAMSM X.50347.47 (Pl. 10). Also samples and thin sections in NMW, and thin sections in NHMUK and CAMSM. Total 32 specimens.

*Locality and horizon.* CAMSM X.50347.47 from Lea South Quarry, Wenlock Edge Shropshire; other material in museums from Wenlock Edge and Wren's Nest.

*Diagnosis of* Petridiostroma *Stearn, 1992.* From Nestor (2015, pp. 761, 763):

> Skeletal elements very well differentiated; laminae continuous, planar (straight); pillars simple, rodlike, short or long (superposed); galleries open, subrectangular in longitudinal section; astrorhizae rare. Irregular. […] Growth form laminar to domical; laminae planar, continuous; pillars short, rodlike to spool shaped; galleries open, rectangular, oval to arch-shaped in longitudinal section; astrorhizae rare, inconspicuous.

*Description of* Petridiostroma simplex *(Nestor).* An abundant Wenlock-age stromatoporoid, occurring as small specimens commonly encrusting other fossils (see Kershaw 1984), forming laminar to domical forms; maximum recorded basal diameter in British material is 80 mm, and height of 70 mm (Text-fig. 40). Mori (1969a, p. 58, where it is named *Clathrodictyon simplex*) noted that the surface shows edges of what he referred to as exfoliated laminae in several specimens; in fact, they are not exfoliated, laminae simply terminate on the surface, resulting in contour-line effect (Text-fig. 17B, C). In vertical section, laminae also terminate at the lateral margins of the skeleton (Text-figs 17A, D, 18), and are encased in micritic sediment, which also invades the upper and outer laminae of the skeleton, presumably after death. Mori (1969a, p. 58) recorded that laminae are slightly crumpled, matching the character of *Petridiostroma* (see Nestor 2015, fig. 420, 3a, b), are generally 0.04–0.08 mm thick and 5–7 in 1 mm, consistent with the British material. Interlaminar spaces are usually wider than the thickness of the laminae.

The pillars are short, 0.05–0.1 mm thick. The number of pillars is 4–6 in 1 mm. In tangential sections, the pillars are small and circular, 0.05–0.1 mm in diameter. Mori (1969a, p. 58) noted that pillars may be connected by thin curved dissepiments, although these are not observed in British material. Mori (1969a, p. 58) also recorded in thin sections short vertical wall-less tubes up to 0.30 mm in diameter, which he considered may be astrorhizae; again, such structures are not observed in the British samples, noting that tubes may be intergrown organisms. In this study analysis of intergrown organisms (Text-fig. 46) records only one of the total 32 samples of *P. simplex* contains intergrown tubes; such tubes are uncommon in British stromatoporoids in contrast to such occurrences in stable intracontinental platforms such as the current location of Gotland. The microstructure is compact of transversely fibrous.

*Remarks*. Nestor (1998) recorded four stromatoporoids in the Telychian (uppermost lower Silurian) of Ireland, two of which (*Petridiostroma* cf. *simplex*, and *Eostromatopora ringerikensis*) closely resemble taxa in the Wenlock of the MWLF. Nestor regarded the late Llandovery to Wenlock period as a time of major change in stromatoporoids.

*Range*. Nestor (2015, p. 763) recorded *Petridiostroma* as ranging from Telychian (uppermost Llandovery, lower Silurian) to Middle Devonian.

**Petridiostroma linnarssoni** (Nicholson, 1887) Pl. 11; Pl. 12, fig. 3

1887 *Clathrodictyon linnarssoni* Nicholson; p. 5, pl. 1, figs 7, 8.
1991 *Faciledictyon* Lessovaya; p. 28.

*Material*. CAMSM X.50347.37, one specimen, partly altered, a vertical thin section only. It is compared here with a well-preserved specimen from Gotland: CAMSM X.50347.37.1.

*Locality and horizon*. CAMSM X.50347.37, Wenlock Edge Shropshire; Much Wenlock Limestone Formation, Wenlock Series, Silurian. CAMSM X.50347.37.1, Upper Visby Formation, lower Wenlock, Kneippbyn, Gotland, Sweden.

*Diagnosis of* Petridiostroma *Stearn, 1992*. From Nestor (2015, pp. 761, 763):

> Skeletal elements very well differentiated; laminae continuous, planar (straight); pillars simple, rodlike, short or long (superposed); galleries open, subrectangular in longitudinal section; astrorhizae rare. Irregular. […] Growth form laminar to domical; laminae planar, continuous; pillars short, rodlike to spool shaped; galleries open, rectangular, oval to arch-shaped in longitudinal section; astrorhizae rare, inconspicuous.

*Description of* Petridiostroma linnarssoni *(Nicholson)*. There is only one incomplete specimen in a single vertical thin section, but its structure is unmistakably consistent with *P. linnarssoni*. Mori (1969a, p. 56) described samples from Gotland where it is more common and named *Clathrodictyon linnarssoni* in Mori's previous taxonomy. In Gotland material, this taxon forms a range of growth forms from laminar to domical, 39–1000 mm in basal diameter and 18–600 mm high. Mori (1969a, p. 56) recorded:

> The skeleton is composed of thin laminae and short pillars. The laminae are rather even, but in part slightly crumpled. Their thickness is 0.03–0.08 mm, rarely less than 0.03 mm. The number of the laminae is 5–8, rarely 9 in 1 mm. The interlaminar spaces are usually wider than the thickness of the laminae. The pillars are short and straight. They are oval or circular, 0.04–0.14 mm in diameter in tangential sections. The number of the pillars is 4 or 5 in 1 mm. Astrorhizae are developed. They are composed of vertical canal systems which are frequently cut by the laminae. The microstructure is compact.

*Remarks*. Text descriptions of *Petridiostroma simplex* and *P. linnarssoni* by Mori (1969a, pp. 56, 58) record the number of laminae per mm in each taxon and they are very similar. Photographs of the two taxa in Mori (1969a, pl. IV, fig. 5 for *P. simplex*, and pl. V, fig. 3 for *P. linnarssoni*) show the latter is finer structured with a few more laminae per mm but there is little difference in laminae spacing between the two taxa, consistent with the comparison between *P. linnarssoni* and *P. simplex* of this study. However, as with Gotland material, there is much more variability of skeletal structure in *P. simplex* between and within samples, and Text-fig. 14E–G shows that the structure of *P. simplex* can be much coarser than *P. linnarssoni*. Specimens with larger spacing were referred to by Mori (1970, pl. III, figs 1–4) as *Clathrodictyon* [= *Petridiostroma*] *striatellum*, but Mori (1969a) himself illustrated samples of *Clathrodictyon* [= *Petridiostroma*] *simplex* in his 1969a, pl. III, fig. 1 and pl. IV, fig. 5 with laminae spacing no different from the illustration of *P. striatellum* in his 1970 pl. III, figs 1–4. Therefore, we feel justified in our view that *P. simplex* and *P. striatellum* are synonyms. *Petridiostroma linnarssoni* is not common on Gotland (Mori 1969a, p. 55 recorded six specimens) and there is only one specimen in the British Silurian suite studied here.

*Range.* Nestor (2015, p. 763) recorded *Petridiostroma* as ranging from Telychian (uppermost Llandovery, lower Silurian) to Middle Devonian.

**Actinostromella vaiverensis** Nestor, 1966 Pl. 13; Text-figs 8C, 22, 23, 40, 43, 44

1966 *Actinostromella vaiverensis* Nestor; p. 52, pl. 13, fig. 7, pl 15, figs 5, 6.

*Material.* CAMSM X.50347.64, CAMSM X.50347.165. Total 32 specimens.

*Locality and horizon.* CAMSM X.50347.64, Lea South Quarry, Wenlock Edge, Shropshire; CAMSM X.50347.165, Major's Leap, Wenlock Edge, Shropshire.

*Diagnosis of* Actinostromella *Boehnke, 1915.* From Stock (2015, pp. 775, 776):

> Skeleton a microreticulate mass pierced by elongate, vertical spaces. [...] Micropillars long, connected by microcolliculi that may or may not align horizontally; longitudinal spaces autotubes.

*Description of* Actinostromella vaiverensis *Nestor, 1966.* Low to high domical form, up to 300 mm in basal diameter and height. Astrorhizae not visible on surface but occur in thin section, 20 mm diameter, with canals 0.1 mm diameter. *Actinostromella vaiverensis* is distinguished from another Silurian taxon, *A. slitensis* by diameter of vertical spaces; in *A. vaiverensis* they are 0.07–0.15 mm in diameter, in *A. slitensis* they are 0.04–0.05 mm (Mori 1970, p. 116); the latter does not occur in the British Isles.

*Remarks. Actinostromella* was named by Boehnke (1915), but the illustrations are poor and also all the type material was lost in the Second World War, so *A. vaiverensis* became the reference taxon illustrated by Stock (2015, pp. 775, 776). As described in the text, we consider *A. vaiverensis* to be a synonym of *Stromatopora antiqua* illustrated by Mori (1970), and we abandon *S. antiqua*, because the taxon does not have the structure of *Stromatopora* defined by Stearn (2015a).

*Range.* Reported by Mori (1970, pp. 117) as Wenlock and Ludlow Series.

**Araneosustroma fistulosum** Lessovaya, 1970 Pls 14, 15; Text-figs 24, 27, 40, 49, 50

1970 *Araneosustroma fistulosum* Lessovaya; p. 81.
1983 *Petschorostroma* Bogoyavlenskaya; p. 84.

*Material.* CAMSM X.50347.258. Total 15 specimens.

*Locality and horizon.* CAMSM X.50347.258 is from Crew's Hill Quarry, Abberley Hills, Worcestershire. All from new material from Wenlock Edge, Shropshire; Wren's Nest, Dudley, West Midlands; and Malverns-Abberley Hills area, Worcestershire.

*Diagnosis of* Araneosustroma *Lessovaya, 1970.* From Stock (2015, pp. 778, 779):

> Skeleton microreticulate, uninterrupted by accessory spaces. [...] Microreticulate structure orthoreticular to acosmoreticular, in some species combined with microlaminae; microcolliculi horizontally aligned at some levels, not aligned at other levels; in some species, micropillars clustered into indistinct, narrow subcolumns, giving impression of closely packed microreticulate pillars.

*Description of* Araneosustroma fistulosum *Lessovaya, 1970.* This is the holotype figured by Stock (2015, p. 778, fig. 433, 3a, b) and the information given in the diagnosis above is sufficient to describe this taxon.

*Remarks.* The comparison between *Densastroma* and *Araneosustroma* is considered here to create problems of identification below traditional genus level. The relatively poor state of preservation of the samples used for this study makes the notion of recognizing subdivisions as traditional species in these two taxa difficult if not impossible. It is unfortunate that the photographs in Stock (2015, p. 778) of both *Densastroma* and *Araneosustroma* are poor quality due to restrictions in the *Treatise on Invertebrate Paleontology* to use photographs of holotypes. Therefore, although we have assigned a traditional species-level name to each taxon (*Densastroma pexisum* and *Araneosustroma fistulosum*) we would not be confident to recognize other taxa within the traditional genera of *Densastroma* and *Araneosustroma*.

*Range.* Stock (2015, p. 779) recorded a range of middle Silurian (Wenlock) to Lower Devonian (Lochkovian).

**Densastroma pexisum** (Yavorsky, 1929) Pl. 16; Text-figs 25, 26, 28, 29, 34D, 40

1867 *Stromatopora astroites* Rosen; p. 62.
1929 *Actinostroma pexisum* sp. nov. Yavorsky; p. 82, pl. 6, figs 1, 2.
1966 *Densastroma pexisum* (Yavorsky) Nestor; p. 37, pl. 13, fig 1, pl. 14, figs 1, 2.
1970 *Pycnodictyon densum* Mori; pp. 104–107, pl. 7, figs 1–6, pl. 8, figs 1, 2, pl. 30, fig. 4.

*Material.* CAMSM X.50347.257. Total 51 specimens.

*Locality and horizon.* Crew's Hill Quarry, Abberley Hills, Malverns area, Worcestershire. Other samples from Wenlock Edge, Shropshire; Wren's Nest, Dudley. Much Wenlock Limestone Formation, Wenlock Series, Silurian.

*Diagnosis of* Densastroma *Flügel, 1959.* From Stock (2015, pp. 777, 778):

> Skeleton microreticulate, uninterrupted by accessory spaces. […] Microcolliculi horizontally aligned, giving impression of microlaminae; micropillars short; forming orthoreticular pattern.

*Description of* Densastroma pexisum *(Yavorsky).* This is the second-most abundant taxon in the British Silurian stromatoporoid suite. Growth form varies from low to high domical, up to 250 mm basal diameter and 150 mm high, and therefore *D. pexisum* is also one of the largest stromatoporoids in the British suite. Its size characteristics parallel its occurrence and large size in the Silurian of Gotland (Mori 1969a, p. 73). Specimen surfaces are generally smooth and lack astrorhizae.

*Remarks.* See captions for Pls 14 and 15 for comparison with *Araneosustroma*, noting the more uniform structure of *Densastroma*. Mori (1969a, pp. 75, 76) described *Densastroma podolicum* as a separate taxon from *D. pexisum*. Comparisons of Mori's (1969a) illustrations and descriptions with those provided by Stock (2015, pp. 777–779) leads to uncertainty of the status of *D. podolicum*. We query that, given the very fine skeletal structure of *Densastroma* and *Araneosustroma*, whether it is really feasible to distinguish lower-level taxa within those traditional genera. CAMSM X.50347.257 thin sections illustrated in Pl. 16 are from a sample donated by Margaret Rodway of Malvern.

*Range.* Stock (2015, p. 777) recorded a range of lower Silurian (Llandovery) to upper Silurian (Pridoli).

**Plectostroma intertextum** (Nicholson, 1886) Pl. 17; Text-figs 7D, 8A, 40

1886 *Actinostroma intertextum* Nicholson; p. 233.

*Material.* CAMSM X.50347.163.

*Locality and horizon.* CAMSM X.50347.163 from Coates Quarry, Wenlock Edge, Shropshire; other material from Lea Quarry, Wenlock Edge; Ironbridge (the northernmost outcrop of Wenlock Edge in Shropshire); Wren's Nest, Dudley; Malverns area. Nine samples from Ludlow-age strata. Total 48 specimens.

*Diagnosis of* Plectostroma *Nestor, 1964.* From Stock (2015, pp. 769, 771):

> Skeleton consists of well developed, parallel pillars, usually more prominent than colliculi; microstructure compact. […] Pillars long, continuous; colliculi not horizontally

aligned, in many cases not perfectly horizontal.

*Description of* Plectostroma intertextum *(Nicholson).* This is one of the most abundant stromatoporoids in the British suite. Its growth form is low to high domical, with maximum basal diameter of 220 mm and maximum height of 180 mm. Nicholson (1889, pp. 138, 139): described its surface as smooth or gently undulated, lacking mamelons. In fact, mamelons occur sporadically in stromatoporoids for reasons that are currently undetermined and are unrelated to taxonomy. Nicholson further noted presence of astrorhizae (see Pl. 17, figs 5, 6 of this study). Nicholson recorded astrorhizae are not arranged in vertical groups, and the skeleton is, therefore, not traversed by vertical astrorhizal canals. Nicholson (1889, pp. 138, 139) observed that the surface of specimens "is covered with exceedingly minute, close-set tubercles, representing the upper ends of the radial pillars" that penetrate much of the skeleton, although because pillars are never entirely coincident with the plane of section their lengths are not determined. There are approximately five pillars in 1 mm when viewed in vertical section. Although not composed of laminae, the skeleton has a laminated appearance (Pl. 17, fig 1) shown in Pl. 17, figs 2, 3 as caused by variations in density of skeletal elements which are presumed due to growth rate variations.

*Remarks.* Nicholson (1889, pp. 138, 139) noted that *Plectostroma intertextum* (which he called *Actinostroma intertextum*), is distinguished from most of the species of *Actinostroma* (which thus now includes other traditional genera, including *Plectostroma*) by general characters of its delicate radial pillars, the loosely reticulate structure of the growth layers. *Plectostroma intertextum* is the only taxon under the traditional genus *Plectostroma* in the British suite, but it has not been described from Gotland, which in the Wenlock Series has *P. guticum* (Mori 1969a) and in the Ludlow Series has the common taxa *Plectostroma scaniense*, *P. intermedium* (Kershaw 1990), and *P. atterdagi* (Mori, 1970). All these taxa on Gotland differ from *P. intertextum* in Britain in the arrangement and characters of skeletal elements.

*Range.* Stock (2015) recorded this taxon as in the Wenlock Series, Silurian.

**'Stromatopora' venukovi** Yavorsky, 1929 Pl. 18

1929 *Stromatopora venukovi* Yavorsky; p. 99, pl. 11, figs 8, 9.

*Material.* CAMSM X.50347.283, one specimen.

*Locality and horizon.* Pebble of Wenlock-age limestone in Devonian-age Peel Sandstone, Isle of Man (Crowley *et al.* 2009).

*Diagnosis*. The reason this traditional genus taxon is called '*Stromatopora*' is because it has no likeness to *Stromatopora* as described by Stearn (2015c).

*Description of* 'Stromatopora' venukovi *Yavorsky*. Mori (1970, p. 127) described this taxon as being domical to irregularly massive in form; samples from the Ludlow of Gotland collected previously by SK are up to 500 mm in basal diameter and 200 mm high. Plate 18 shows the skeleton is composed of an amalgamated network, in some parts laminae and pillars are continuous in vertical sections. In transverse sections pillars merge into a skeletal mass (Pl. 18, figs 5–7). The British sample matches Mori's (1970, p. 127) description that:

> galleries are circular to irregularly elongate vertically and horizontally, but in tangential specimens they are mostly circular, 0.07–0.13 mm in diameter. Very thin dissepiments may occur (0.01 mm or less in thickness). The astrorhizae are abundant and easily recognizable in tangential sections. They are 5–9 mm in diameter and composed of 6 or 7 main canals. The maximum diameter near the centre of the astrorhizal canals is 0.17 mm. The microstructure is cellular.

Mori (1970, p. 127) also stated that 13 out of his total of 22 samples from Gotland are associated with intergrown tubes of *Syringopora* sp. (tabulate) and solitary rugose corals. Mori also noted that the holotype described by Yavorsky is associated with *Syringopora*. The British sample described here (Pl. 18) contains intergrown syringoporid tabulate tubes. Unpublished material from Gotland collected by SK includes samples that have syringoporid tabulates, branching rugose corals, and spiral (possibly worm) tubes together in one specimen and grew to a large size (500 mm diameter), and it is clear that this stromatoporoid taxon was able to thrive as a host to up to three intergrown organisms.

*Remarks.* *'Stromatopora' venukovi* has some similarity to *Eostromatopora* but is not sufficiently similar to accept it is the same taxon. Thus, it continues to be classed as a separate low-level taxon.

*Range.* Mori (1970, p. 126) recorded its occurrence in the Klinteberg, Hemse and Eke strata on Gotland, thus upper Wenlock to middle Ludlow. The British samples were assigned to Wenlock strata by (Crowley *et al.* 2009).

### **Simplexodictyon yavorskyi** (Nestor, 1966) Pl. 19

1929 *Clathrodictyon regulare* var. nov. Yavorsky; p. 83.
1966 *Diplostroma yavorskyi* sp. nov. Nestor; p. 29, pl. 9, fig. 4, pl. 10, figs 4, 5.
1972 *Nuratadictyon* Lessovaya; p. 48.

*Material.* NMW 99.35G.853.

*Locality and horizon.* NMW 99.35G.853, Farley Dingle, Wenlock Edge, Shropshire. Another sample, also from Farley Dingle, was reported by Powell (1991). Much Wenlock Limestone Formation, Wenlock Series, Silurian. Total 2 specimens.

*Diagnosis of* Simplexodictyon *Bogoyavlenskaya, 1965.* From Stearn (2015c, p. 785):

> Laminae extensive, composed of two compact layers separated (in the same skeleton) by either or all of spar cement, sediment, epibionts, a line of cellules; or fused into a single layer. Pillars compact, simple, post-like, commonly incomplete or oblique.

*Description of* Simplexodictyon yavorskyi *Nestor.* Mori (1970, p. 101), who used the prior name of *Diplostroma yavorskyi,* noted that specimens are columnar or massive, up to 500 mm in basal diameter and up to 220 mm high. All samples observed by SK on Gotland were domical. In Britain, the one sample available was a broken piece; *Simplexodictyon yavorskyi* is not common in Gotland either. Mori (1970, p. 101) reported that the specimen surfaces may show what he termed exfoliated laminae, but as in *Petridiostroma simplex* described above, such a feature is due to laminae terminating at the stromatoporoid margins, without exfoliation or erosion, it is simply a characteristic of the growth of this taxon. Mori (1970, p. 101) also reported commensal corals at the surface but it is not clear if that means the corals were intergrown with the stromatoporoid; such has not been observed by SK in Gotland material. Mori noted the lack of astrorhizae in this taxon. Mori (1970, p. 101) recorded laminae to be "straight and persistent, rarely crumpled, numbering 14–24 in 5 mm" and are 0.06–0.21 mm thick; however the current material, and samples studied from Gotland by SK show that the skeleton is composed of units made of pairs of laminae, separated by pillars; these units are *c.* 0.4 mm thick, so laminae are much less densely spaced than Mori (1970, p. 101) indicated, although the laminae thickness range reported by Mori (1970, p. 101) is consistent with the specimen studied here. Pillars are generally simple and post-like, counted by Mori (1970, p. 101) as numbering 8–17 in 5 mm; in tangential section the pillars are circular or oval, 0.06–0.19 mm in diameter. These measurements are consistent with the British specimen. Mori also recognized dissepiments in some specimens, but these are not present in the British specimen and his photographs seem to show that these dissepiments may instead be crystal boundaries of the diagenetic sparite that pervades the structure.

*Tripartite laminae.* Laminae in *S. yavorskyi* are unusual because they have been described as tripartite, with a central layer between two other layers. Within the same thin section, adjacent laminae may have a light central layer and two dark layers, or *vice versa*. Pairs of adjacent laminae are so closely spaced that they look like single laminae. Mori (1970, p. 101) contended that "there is a difference in microstructures between each member of the pair: the microstructure of the lower lamina in each pair is more compact and the specks are more densely spaced than in the upper one. The microstructure is vacuolate in the upper lamina". It is unfortunate that the skeletal structure of the British specimen is at least partly recrystallized and that the features of microstructure outlined by Mori are not confirmed. Stearn (2015g, pp. 494, 495, 563–567) discussed the implications of such pairs of laminae in some stromatoporoids, proposing that they constitute growth modules for the growth of stromatoporoids, because laminae pairs with their intervening pillars may form discrete layers projecting from the margins of the stromatoporoid (Stearn 2015g, figs 353, 354). Mori (1970, p. 101) expressed the view that "pairs of adjacent laminae are so closely spaced that that they look like a single lamina". Powell (1991) illustrated examples from his material from Wenlock Edge that showed encrusting microbia between laminae. Stearn (2015g, fig. 438) shows examples with a similar appearance, but in that case, peloidal material lies between laminae. It appears that tripartite laminae are simply an artefact of adjacent laminae lying close to one another. If so, then the reason why the NMW 99.35G.853 sample illustrated in Pl. 20 shows dark and light layers in the tripartite structure may be that the dark central layers are simply micrite sediment and the light central layers are simply sparite filling tiny voids (the structure is obfuscated by alteration). If this interpretation is correct, then tripartite laminae do not exist.

*Remarks.* Powell (1991) described an association between this taxon and calcareous algae in Wenlock Edge, but the samples are not present in the NMW collections where Powell's material was deposited. John Powell (personal communication to SK in 2018) confirmed all his material was passed to the NMW, so those samples from his 1991 paper are presumed missing.

*Range.* Mori (1970, p.103) recorded Wenlock and Ludlow ages for *S. yavorskyi* on Gotland, consistent with the British samples.

**Eostromatopora impexa** (Nestor, 1966) Pl. 20; Text-figs 30, 40

1966 *Stromatopora impexa* Nestor; p. 44, pl. 16, figs 1–4.

*Material.* CAMSM X.50347.57.

*Locality and horizon.* CAMSM X.50347.57, Lea South Quarry, Wenlock Edge, Shropshire; other material from Woolhope Inlier, Malverns area, other sites on Wenlock Edge, Wren's Nest, all in the Much Wenlock Limestone Formation, Wenlock Series, Silurian, 29 samples. It is also recorded in the Ludlow, one sample. Total 30 samples.

*Diagnosis of* Eostromatopora *Nestor, 1999.* From Stearn (2015a, pp. 797, 802, 803): *Eostromatopora* is one of the taxa in the traditional Order Stromatoporida "with cellular or obscurely cellular microstructure and structure dominated by pachysteles and pachystromes forming amalgamate networks". The traditional family Stromatoporidae are "dominated by pachystromes, laminae, and/or cassiculate structure". *Eostromatopora* has "structure amalgamate, structural elements occupying most of skeleton, pierced by thin, tangential, vermiform canals and short, curved autotubes and allotubes with tabulae. Tangential canals in irregular layers simulating galleries and vaguely defining thick, irregular pachystromes. Microstructure compact or obscurely cellular. [This earliest representative of the (traditional) order Stromatoporida appears to be the only genus without clear cellular microstructure.]".

*Description of* Eostromatopora impexa *Nestor.* It has a range of growth forms beginning as laminar and progressing through low to high domical and seems to have been capable of growing directly on soft sediment (Kershaw *et al.* 2018). It ranges from a few millimetres to 100 mm in basal diameter and up to 70 mm high. It is characterized by well-developed distinct astrorhizae on the surface and throughout its structure in transverse sections. As described by Mori (1969a, p. 83) the skeleton comprises amalgamated transverse and vertical components, lacking recognizable pillars and laminae. Galleries are more or less regularly distributed; some are equidimensional, but most occur either as horizontally or vertically elongated (Pl. 20, fig 3); vertically elongated galleries usually have thin horizontal dissepiments. Mori (1969a, p. 83) also noted that astrorhizae are well developed, 8–12 mm diameter, comprising more than four main canals which bifurcate into smaller canals. Astrorhizae occur throughout the stromatoporoid and in transverse section their centres are generally 6 or 7 mm apart, rarely up to 12 mm and the diameter of the main canals is 0.15–0.25 mm. Mori (1969a, p. 83) also noted the microstructure as being "obscurely cellular", but in the current samples microstructure is poorly preserved, and cannot be recognized as described by Mori.

*Remarks.* In vertical section *Eostromatopora impexa* can resemble *Syringostromella borealis* in some specimens, but the transverse section shows the structure to be very different; *S. borealis* being readily recognizable from its vermiform pachysteles in transverse section.

*Range.* Stearn (2015a, p. 802) recorded upper Llandovery to Wenlock series for *Eostromatopora*; *E. impexa* certainly occurs in the Wenlock on Gotland and in Britain.

**Syringostromella borealis** (Nicholson, 1891) Pl. 21; Text-figs 31–33, 34C–F, 40

| | |
|---|---|
| 1891 | *Stromatopora borealis* Nicholson; p. 319, pl. 9, figs 7, 8. |
| 1951 | *Stromatopora paadla* Riabinin; p. 41, pl. 34, figs. 7, 8. |
| 1966 | *Syringostromella borealis* (Nicholson); Nestor, p. 48, pl. 17, figs 3, 4, pl. 18, figs 1–5. |
| 1968 | *Yavorskiina* Khalfina; p. 148. |

*Material.* CAMSM X.50347.91 (Pl. 21).

*Locality and horizon.* CAMSM X.50347.91, Lea South Quarry, Wenlock Edge, Shropshire. Other material from Usk Inlier, Woolhope Inlier, Malverns area, Wenlock Edge, Shropshire; Wren's Nest, Dudley. Much Wenlock Limestone Formation. One specimen from Ludlow-age rocks. Total 56 specimens.

*Diagnosis of* Syringostromella *Nestor.* From Stearn (2015a, pp. 810, 811):

> Stromatoporida with structure dominated by pachysteles and dissepiments. […] Pachysteles long, continuous, joining and dividing in longitudinal section; pachystromes rudimentary or absent, dissepiments common. In tangential section, pachysteles vermiform or loose labyrinthine network. Microstructure cellular, some species may appear microreticulate.

*Description of* Syringostromella borealis *(Nicholson).* External shape varies from low to high domical, maximum basal diameter of 200 mm and maximum height of 80 mm. For Gotland, Mori (1970, pp. 128, 129) recorded this taxon as being mostly laminar growth form, with maximum basal diameter of 3 m, and also notes that it has distinct astrorhizae without mamelons visible on the surface. The skeleton is composed of prominent pachysteles and dissepiments. Mori's (1970, pp. 128, 129) description, paraphrased here, is consistent with the British specimens. Dissepiments are straight or slightly arched and very thin (0.01 mm or less thick). Several dissepiments are continuous, intersecting the pachysteles and there is no regularity in the dissepiment distribution. The pillars are vermiculate in tangential section, forming sinuous networks (Pl. 21, figs 4, 5). The number of pachysteles is 3 or 4 in 1 mm measured in vertical section and their diameter ranges from 0.09–0.20 mm. The galleries are thus tubes are circular or vermiculate in tangential sections. Astrorhizae are 8–11 mm in diameter, with centre-centre distances of 8–12 mm. Each astrorhiza is composed of 8 or 9 main canals and numerous smaller canals bifurcate from the main ones. The maximum diameter of the main canals is 0.21 mm in tangential section. The microstructure is coarsely cellular.

*Remarks.* Nicholson (1891, pp. 174, 175) provided a description of *Stromatopora borealis*. On page 175, paragraph 3, lines 8–10, Nicholson noted the similarity between *Stromatopora carteri* and *Stromatopora borealis*, then goes onto describe the differences between them. Clearly Nicholson considered they are different, but such similarity and overlap of structure creates difficulty in separating them. Therefore, *Syringostromella borealis* is considered a synonym of *Stromatopora carteri* in Mori (1970), discussed in the text.

In vertical section *S. borealis* can resemble *Eostromatopora impexa*, but the transverse section shows the structure to be very different, *S. borealis* being readily recognizable from its vermiform pachysteles in transverse section.

*Range.* Mori (1970, p. 129), recorded a Ludlow age for *S. borealis*, but Stearn (2015a, p. 811) notes the range for the traditional genus *Syringostromella* is Llandovery (lower Silurian) to Lower Devonian.

**Parallelostroma typicum** (Rosen, 1867) Pl. 22; Text-figs 40–42, 47

| | |
|---|---|
| 1867 | *Stromatopora typica* Rosen; p.258, pl. 1, figs 1–3, pl. 2, fig. 1. |

*Material.* CAMSM X.50347.77

*Locality and horizon.* CAMSM X.50347.77, Lea South Quarry, Wenlock Edge, Shropshire.

Much Wenlock Limestone Formation, Wenlock Series, Silurian. Other material from Woolhope Inlier, Herefordshire; other sites on Wenlock Edge, Shropshire; Wren's Nest, Dudley, West Midlands. All from Much Wenlock Limestone Formation, Wenlock Series, Silurian. Total 13 specimens.

*Diagnosis of* Parallelostroma *Nestor, 1966.* From Stearn (2015c, p. 819):

> Syringostromatida of laminar, bulbous, and domical growth forms with structure dominated by pachystromes and microlaminae; microstructure largely orthoreticular. […] Pachystromes thick, composed of orthoreticular skeletal material enclosing multiple microlaminae and micropillars; short autotubes separate pachysteles at their base. Pachysteles of orthoreticular microstructure, largely confined to space between pachystromes, some superposed; in tangential section forming closed network penetrated by autotubes.

*Description of* Parallelostroma typicum *(Rosen).* Growth form is domical, and only two of the 13 specimens could be measured, but include a relatively large sample 200 mm in basal diameter and 200 mm high. Mori (1970, pp. 137, 138) noted from Gotland material that many specimens have repeated growth interruptions, so that sections of skeleton 5–10 mm are separated by thin layers of sediment. In addition to the description above of *Parallelostroma*, thickness of pachystromes is greatly variable even within a single specimen, ranging from *c.* 0.1–1.0 mm. Pachysteles are very short and are part of the microreticulate structure of pachystromes. Persistent microlaminae are developed in some specimens at the top of some laminae (Text-figs 41B, 47); they are very thin, 0.01–0.02 mm thick. Dissepiments may occur. Mori (1970, pp. 137, 138) recorded distinct astrorhizae on the surface and in thin sections, and are 4–8 mm in diameter, consistent with the British material. The distances between their centres are generally 4–6 mm. The central astrorhizal canals are vertical elongate tubes, 0.15 mm in diameter on average. Astrorhizal canals are slightly larger than the galleries. Mori (1970, pp. 137, 138) reported the microstructure as microreticulate.

*Remarks.* The preservation of detailed structure in the British samples is not as good as some other deposits, such as Gotland (Mori 1970) and New York State (Stock 1979), and a particular issue is recognition of microreticulate microstructure; in the British material this occurs in only small portions of skeletons, but the material also contains both the clinoreticulate and acosmoreticulate structure described by Stock (1989). Although lack of clearly recognizable microreticulate structure creates a problem of firm identification, we draw attention to two points: (1) the gross structure of the skeleton is more like *Parallelostroma typicum* than other taxa, and (2) alteration of the skeleton that degrades the microstructure underlines the problem of relying on microstructure for identification. Thus, the identification remains as *P. typicum* for the present study and may revised in future if appropriate.

*Range.* Mori (1970) recorded an upper Wenlock to upper Ludlow (thus middle to upper Silurian) age for this taxon on Gotland; Stock (1979) extended this into the Pridoli (top Silurian); Stearn (2015a, p. 819) indicated it may range to the middle Devonian.

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## INDEX

Numbers in bold type indicate a page on which a description or diagnosis is given or commences; numbers in italics indicate pages where a text-figure occurs. Plate numbers are included.

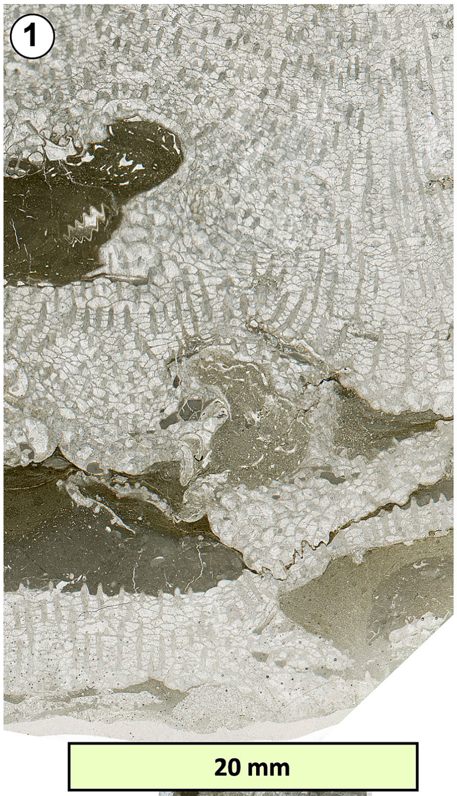
# PLATE 1

Fig. Page

*Labechia conferta* (Lonsdale, 1839) 69

Middle Silurian, Much Wenlock Limestone Formation
Wren’s Nest, Dudley, West Midlands

1–5 CAMSM X.50347.187; 1, 2, whole thin section views showing major features in vertical and transverse section respectively. 3, 4, details of vertical section (1) showing robust pillars and curved dissepiments defining the structure of this taxon. 5, detail of transverse section (2), oblique in places, showing even distribution of pillars in the sample.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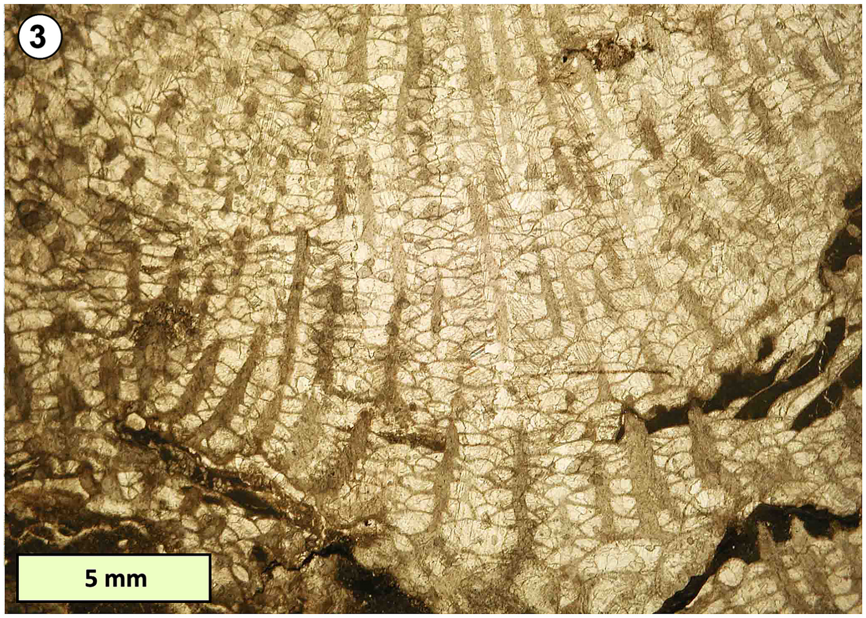
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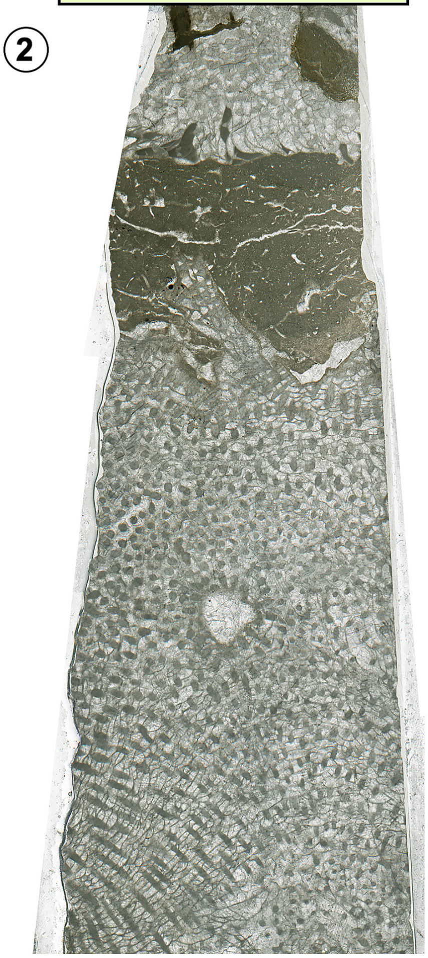
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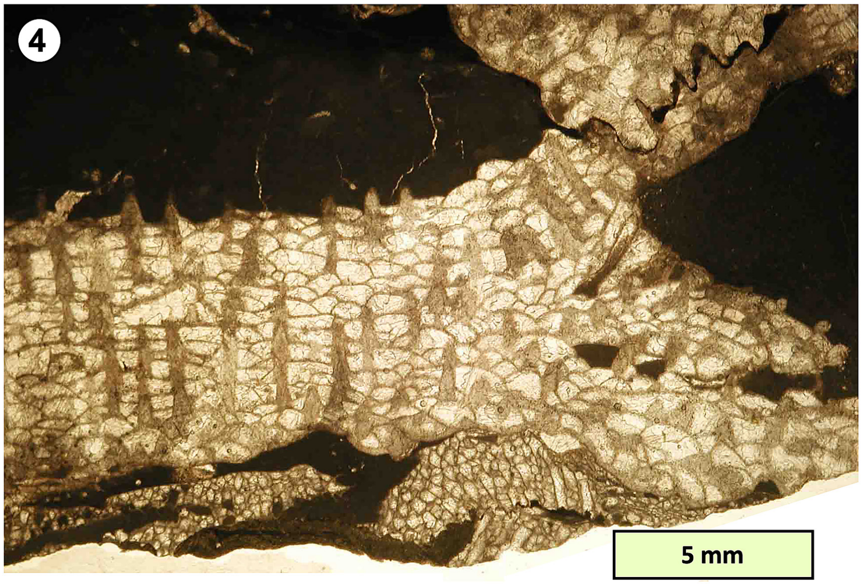
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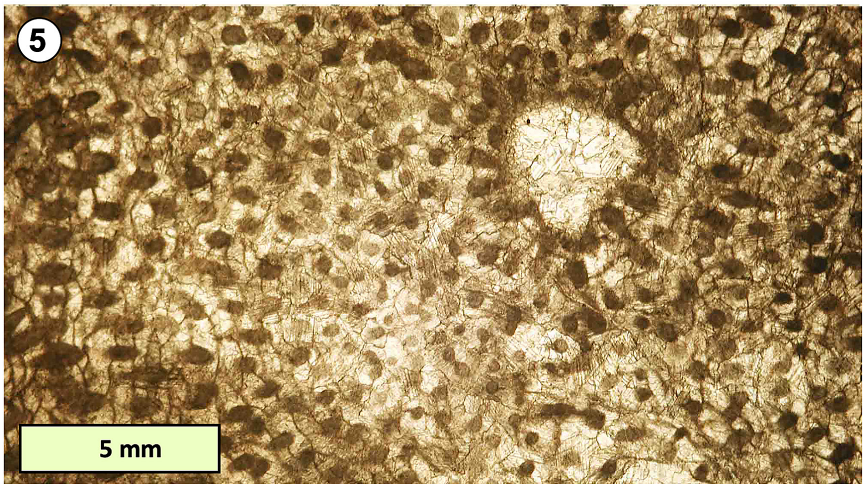

⑤
5 mm

# PLATE 2

Fig. Page

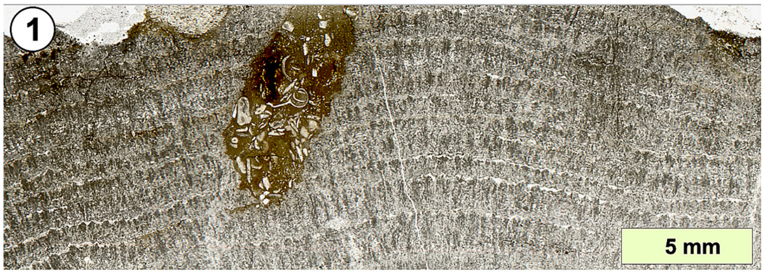
*Lophiostroma schmidti* (Nicholson, 1886) 70

Middle Silurian, Much Wenlock Limestone Formation
Haugh Wood, Woolhope, Herefordshire

1–4 NMW 99.35G.2582; vertical (1, 3) and transverse (2, 4) sections showing partly altered skeletal structure. The skeleton is penetrated by a large boring (1, 2) filled with shell debris and micritic sediment. Equally spaced growth interruptions (1) contain sparite cement (3). Shows poorly-preserved state in both transverse and vertical views.

Upper Silurian, Hemse Group
Kuppen peninsula, near Östergarn, eastern Gotland, Sweden

5–8 CAMSM X.50347.37.2; vertical plane-polarized (ppl) (5) and cross-polarized light (xpl) (6) sections; transverse ppl (7) and xpl (8) sections. This is a comparative example from the middle Ludlow Hemse Group stromatoporoid biostrome at Kuppen, Gotland, Sweden, presented as evidence that *Labechia rotunda* and *Labechia scabiosa* illustrated in Plates 3–7, are junior synonyms of *L. schmidti*.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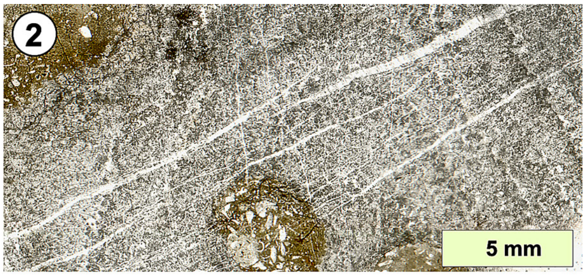
5 mm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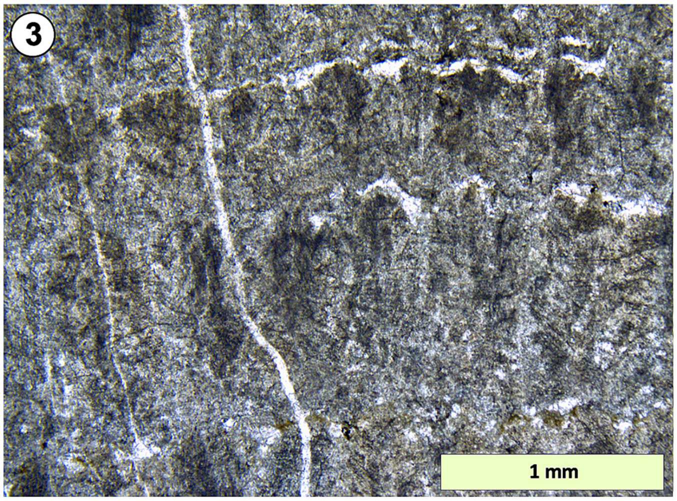
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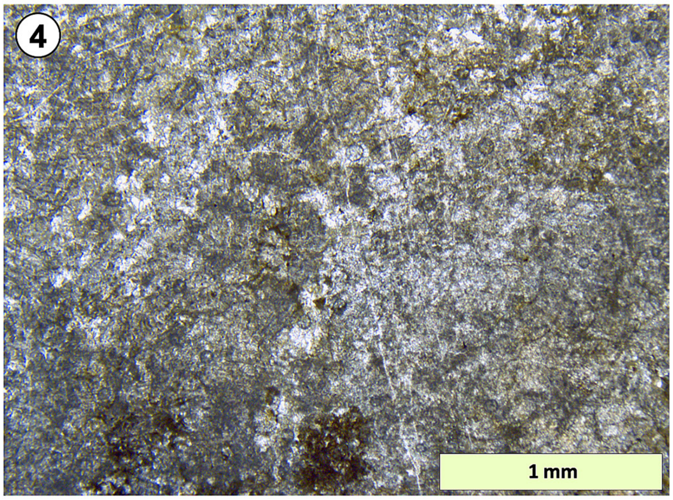
4
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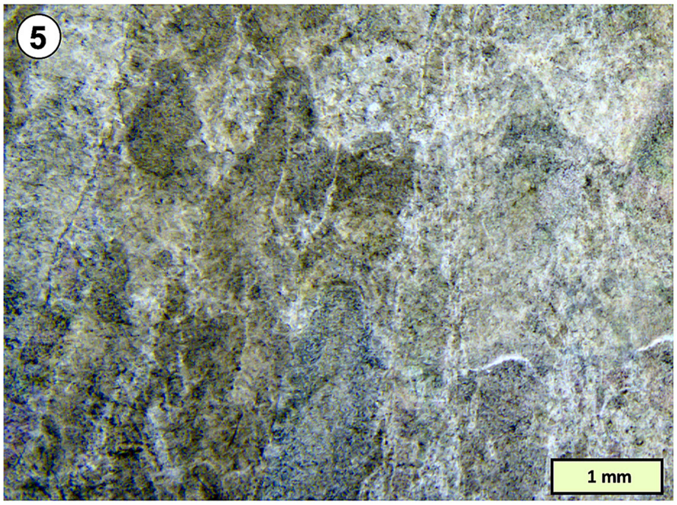
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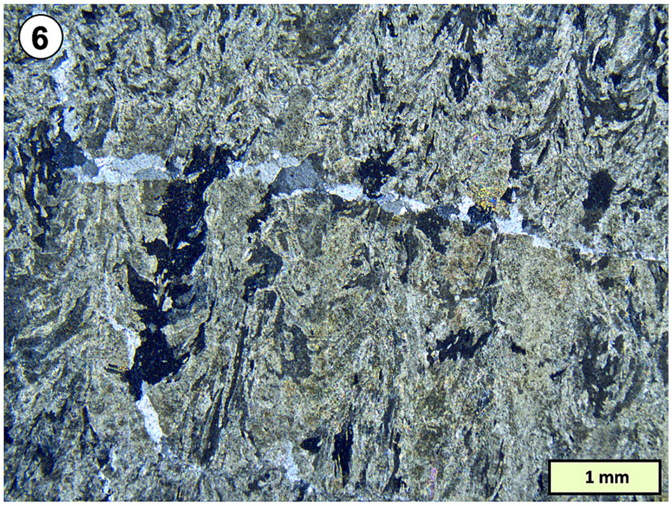
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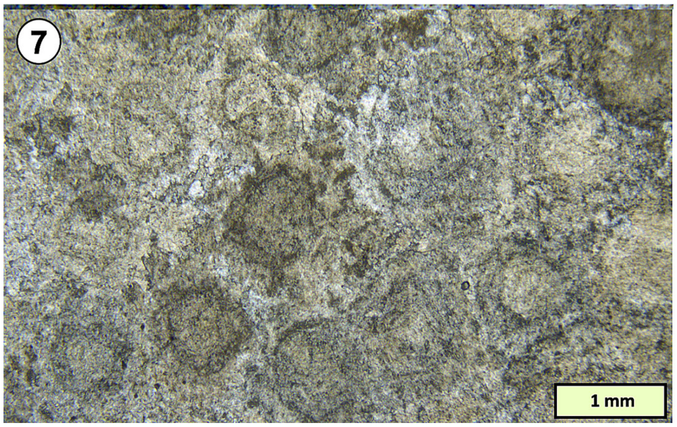
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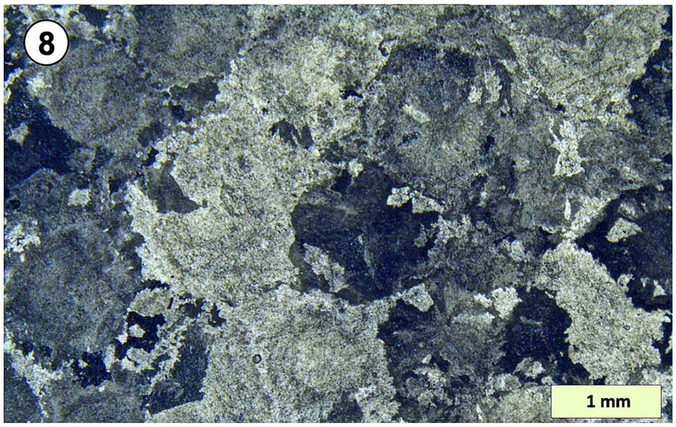

8
1 mm

## PLATE 3

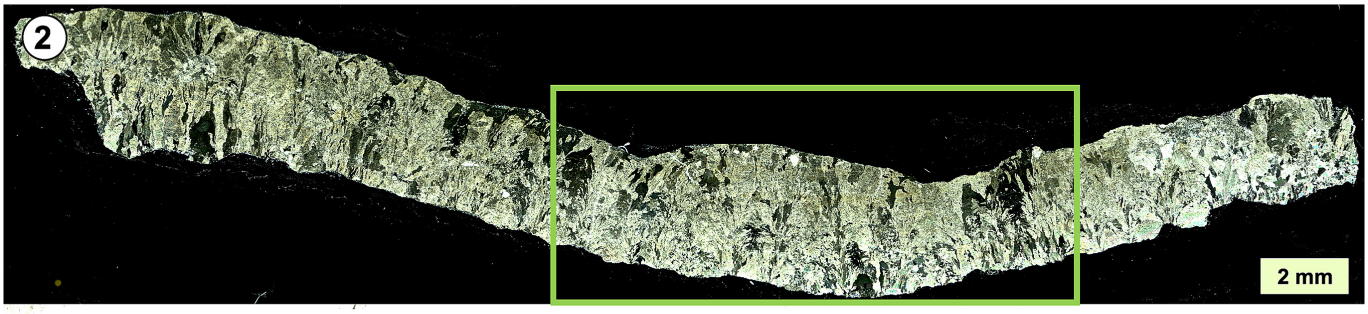
| Fig. | | Page |
|---|---|---|
| | *Lophiostroma ?schmidti* (Nicholson, 1891)<br>(*Labechia rotunda* Johnston, 1915; Holotype) | 71 |

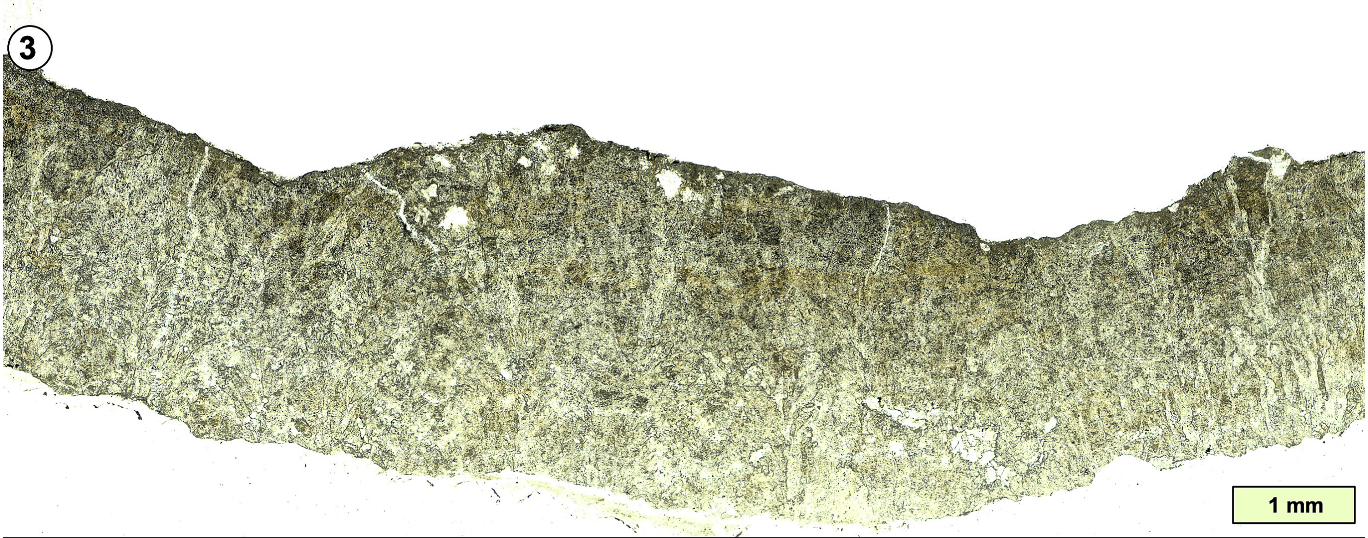
Middle Silurian, Much Wenlock Limestone Formation
Bradwell Rock Quarry, Wenlock Edge, Shropshire

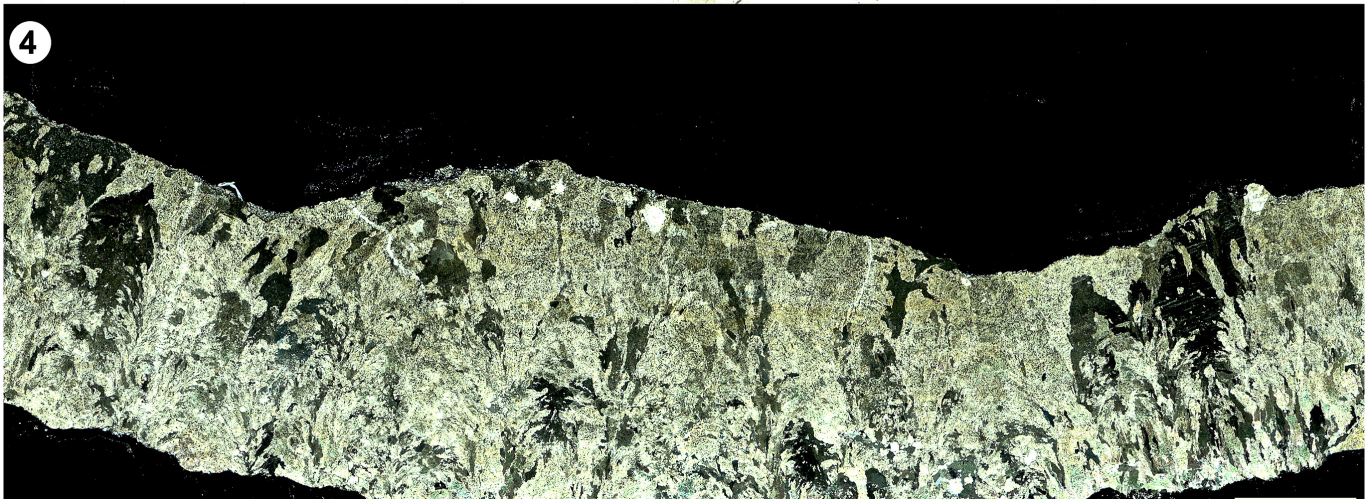
1–4 NHMUK PI H969; 1, 2, whole thin section of laminar growth form, vertical section in plane-polarized and cross-polarized light, respectively. 3, 4, enlargements of 1 and 2, of area in green box in 2, showing detail of solid columnar structure, particularly well shown in 4, where the structure is also shown as recrystallized.

Compare with enlargements in Plate 4 and transverse section in Plate 5.


1
2 mm


2
2 mm


3
1 mm


4

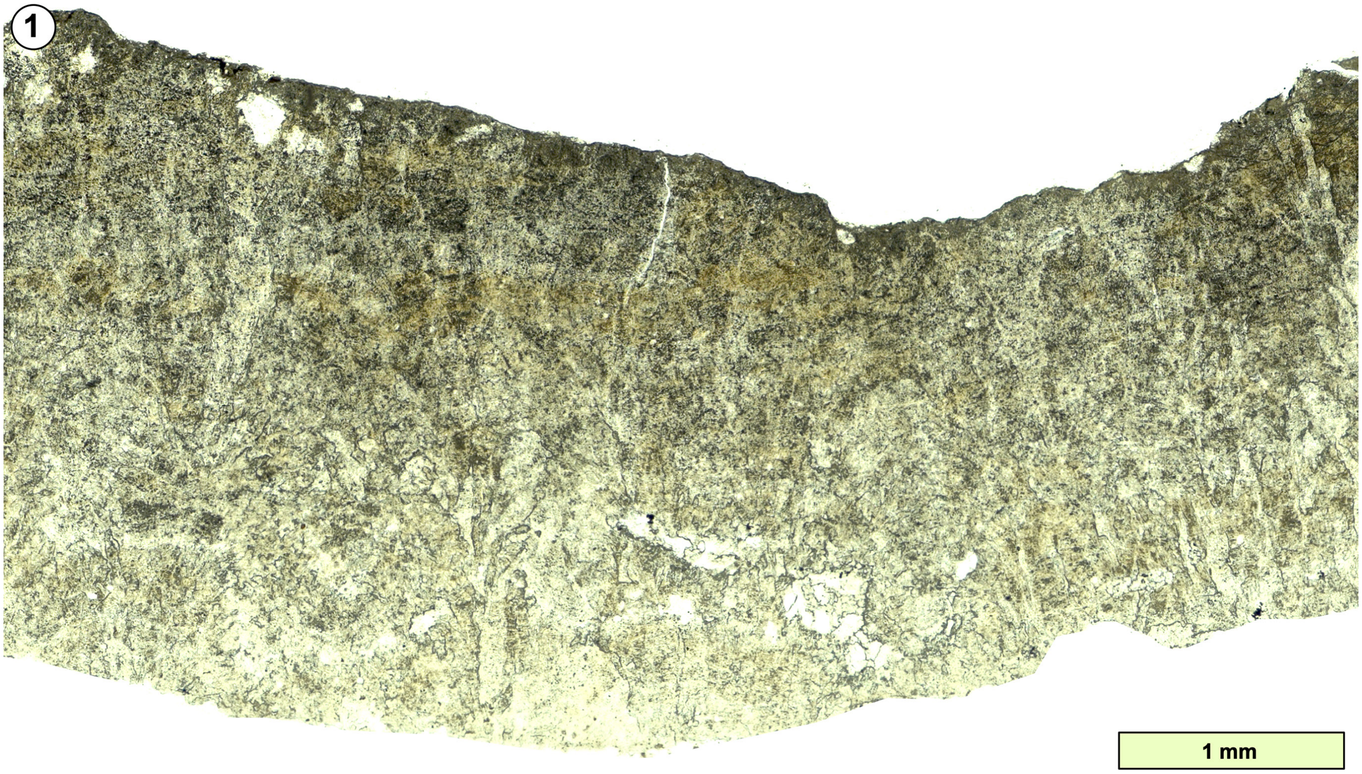
## PLATE 4

| Fig. | | Page |
|---|---|---|
| | *Lophiostroma ?schmidti* (Nicholson, 1891)<br>(*Labechia rotunda* Johnston, 1915; Holotype) | 71 |

Middle Silurian, Much Wenlock Limestone Formation
Lilleshall Quarry, Wenlock Edge, Shropshire

1, 2 NHMUK PI H969; Enlargement of central part of laminar growth form shown in Plate 2, vertical section in plane-polarized (1) and cross-polarized light (2). The base of the stromatoporoid is composed of the same recrystallized structure of the skeleton as the rest of it, and thus there is no epithecal layer at the base, consistent with all other specimens of *L. schmidti* observed by the authors.

1



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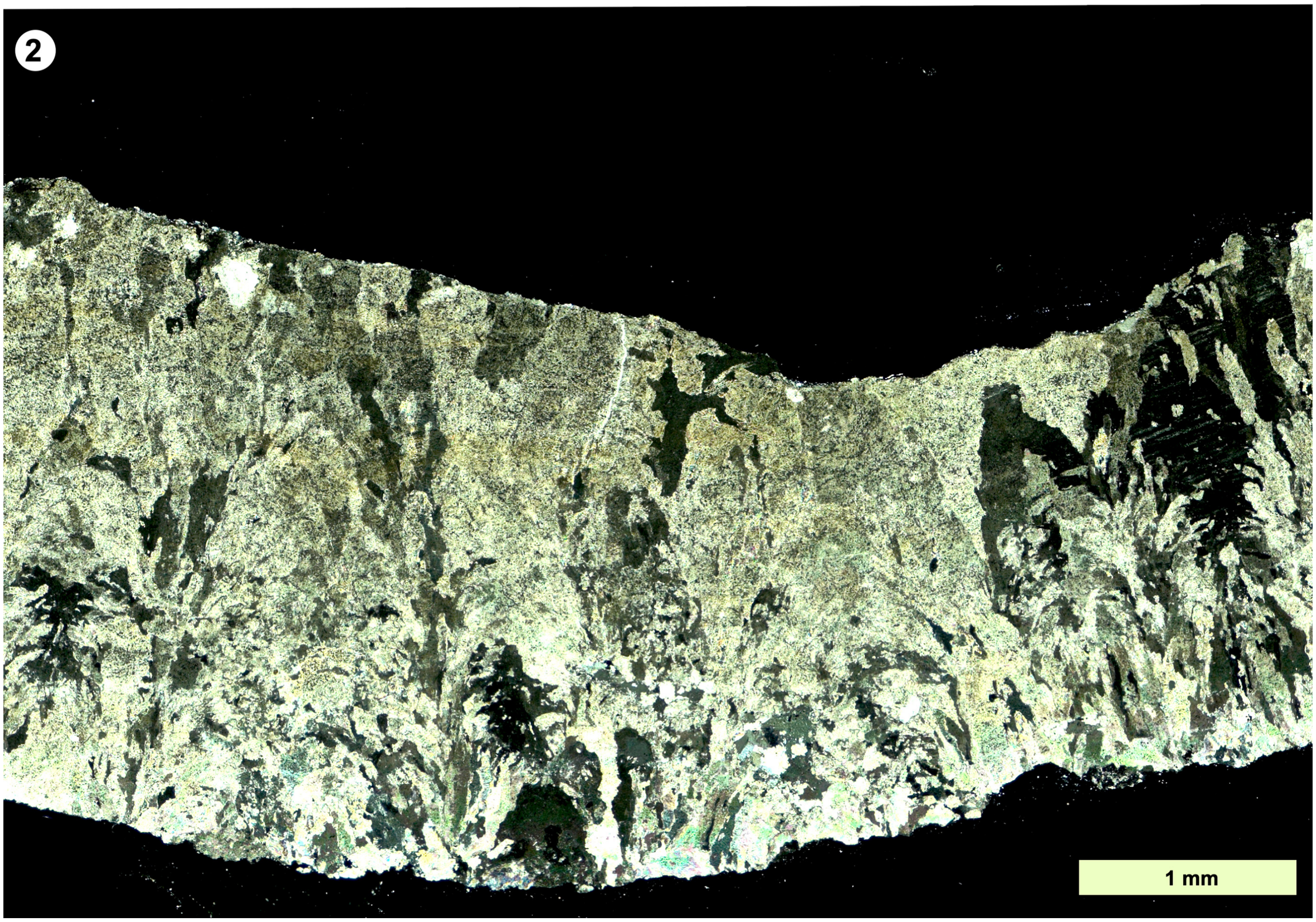
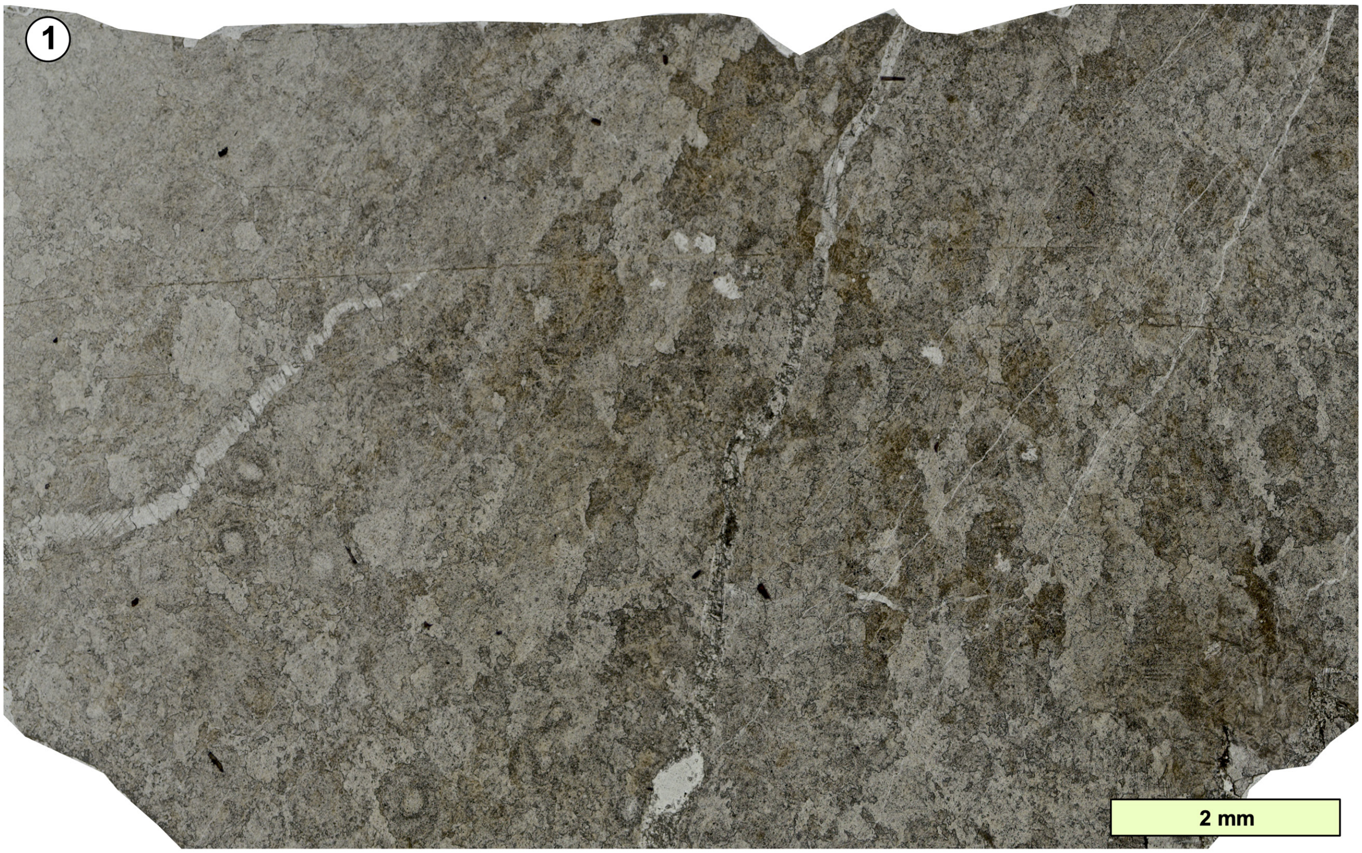


# PLATE 5

| Fig. | | Page |
|---|---|---|
| | *Lophiostroma ?schmidti* (Nicholson, 1891)<br>(*Labechia rotunda* Johnston, 1915; Holotype) | 71 |

Middle Silurian, Much Wenlock Limestone Formation
Lilleshall Quarry, Wenlock Edge, Shropshire

1, 2 NHMUK PI H969; transverse section in plane-polarized (ppl) (1) and cross-polarized light (xpl) (2). Both ppl and xpl views show approximately rounded transverse sections through the pillars. Compare with Plate 2 for comparison with *Lophiostroma schmidti* from Gotland and Plates 3 and 4 for vertical section.


1
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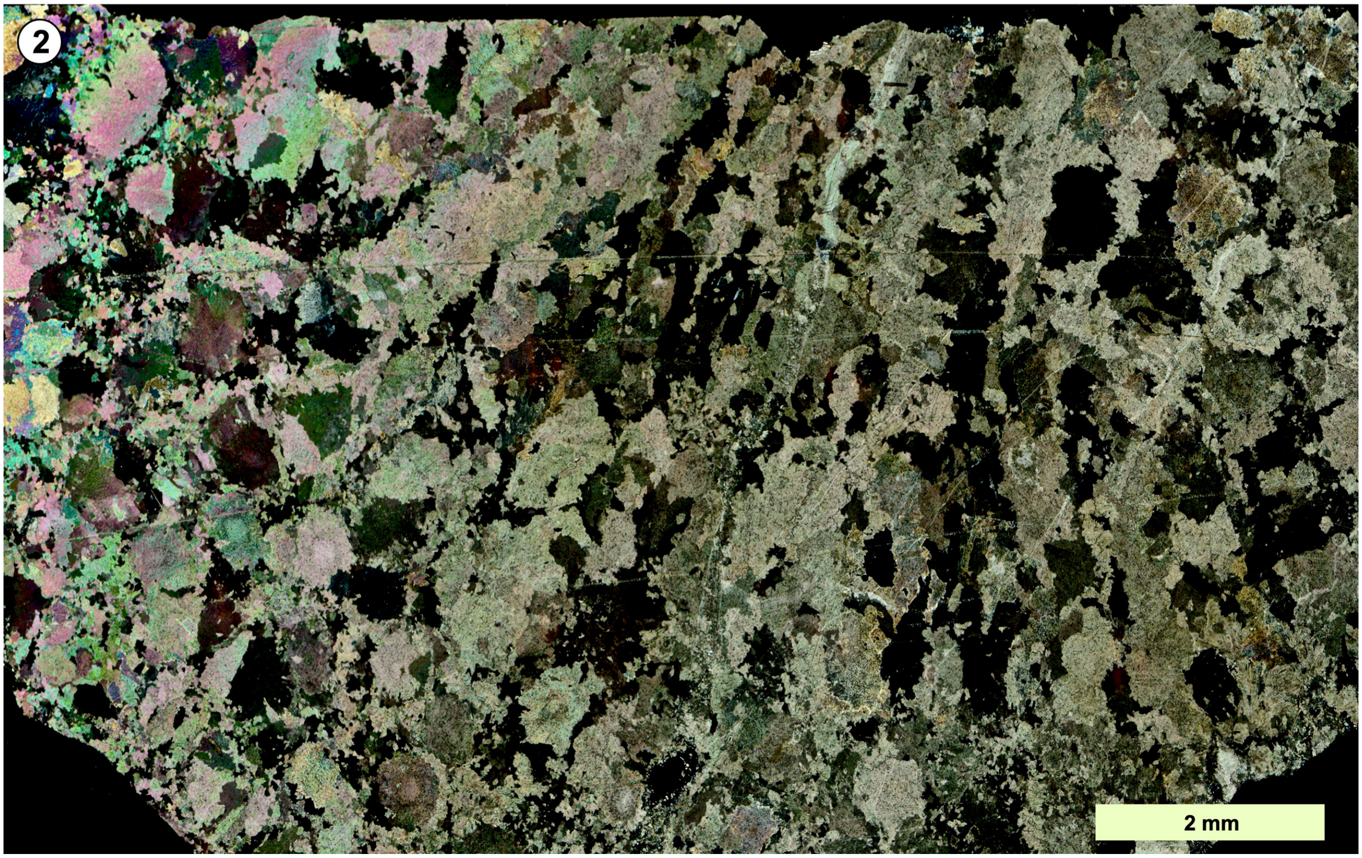

2
2 mm

## PLATE 6

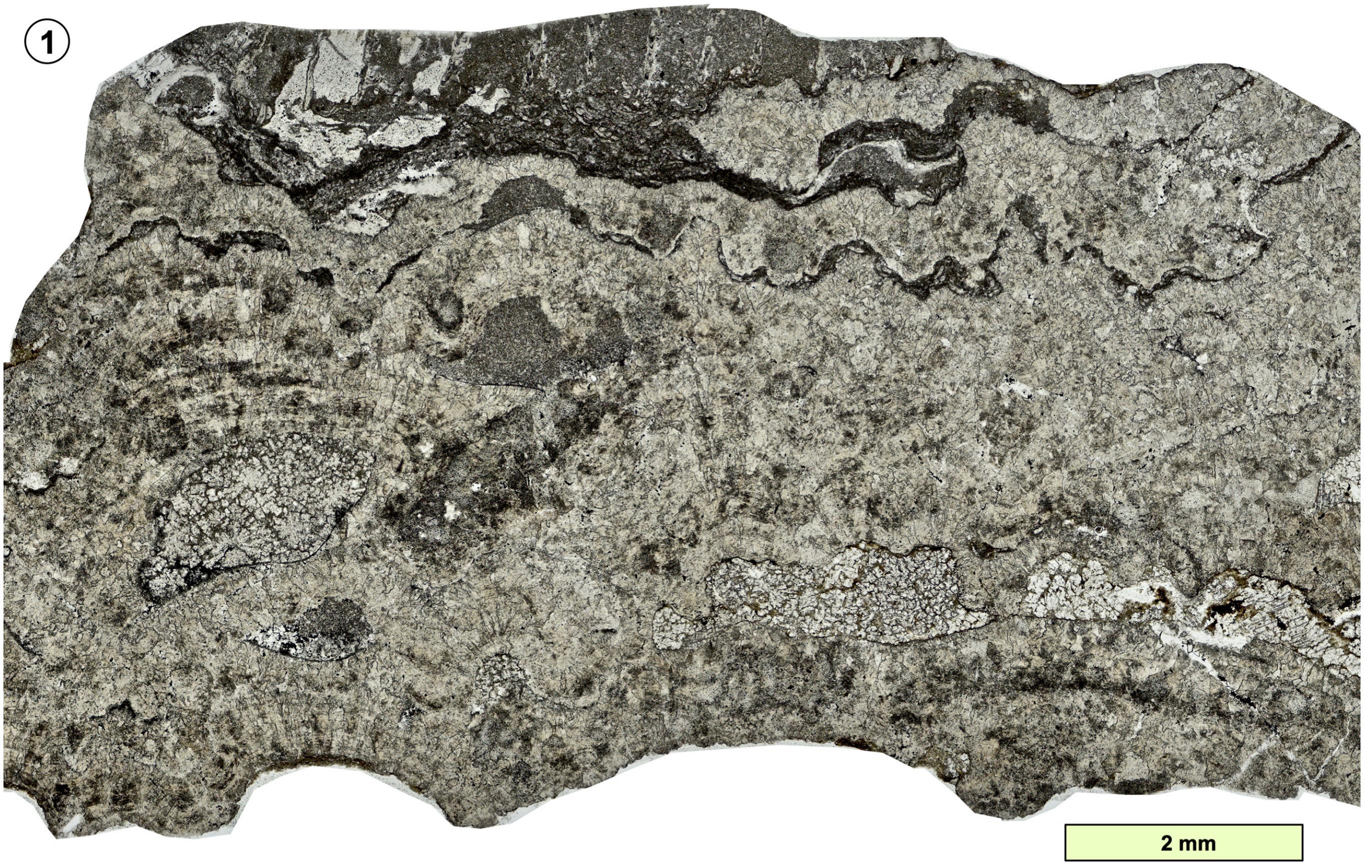
Fig. Page

*Lophiostroma ?schmidti* (Nicholson, 1891)
*(Labechia scabiosa* Nicholson, 1891; Holotype) 71

Middle Silurian, Much Wenlock Limestone Formation
Wenlock Edge, Shropshire

1, 2 NHMUK PI P6145 vertical section in plane-polarized (1) and cross-polarized light (2), showing its structure of large pillars that are recrystallized. The base of the specimen lacks an epitheca. The upper part of the specimen shows two prominent growth interruption events where sediment lies between layers of stromatoporoid skeleton. In the lower part of the thin section there are two areas of recrystallized structure, left and right, where the stromatoporoid skeleton has been replaced.

See Plate 2 for comparison with *Lophiostroma schmidti* from Gotland and Plates 3–5 for comparison with *Labechia rotunda.*


①
2 mm


②
2 mm

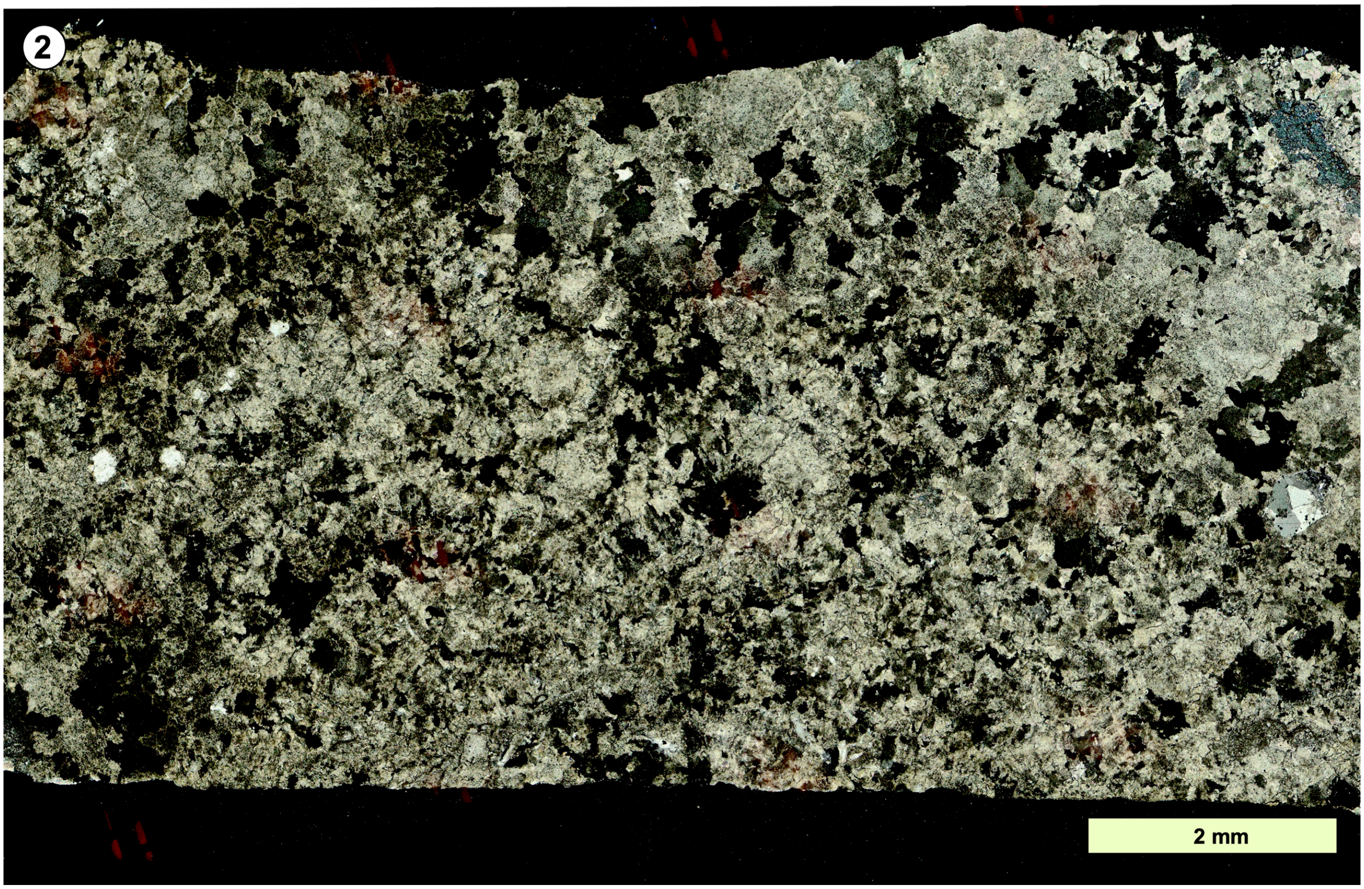
## PLATE 7

| Fig. | | Page |
|---|---|---|
| | *Lophiostroma ?schmidti* (Nicholson, 1891)<br>*Labechia scabiosa* Nicholson, 1891 | 71 |

Middle Silurian, Much Wenlock Limestone Formation
Wenlock Edge, Shropshire

1, 2 NHMUK PI P6145 (holotype of *Labechia scabiosa* Nicholson, 1891) transverse thin section views in plane-polarized (1) and cross-polarized light (2) show approximately rounded transverse sections through the pillars. See Plate 2 for comparison with *Lophiostroma schmidti* from Gotland and Plates 3–5 for comparison with *Labechia rotunda.*


1
2 mm


2
2 mm

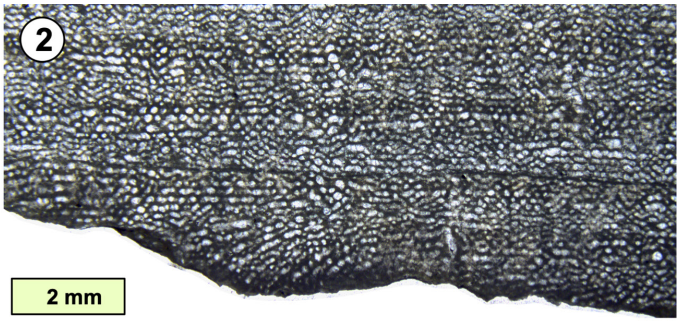
## PLATE 8

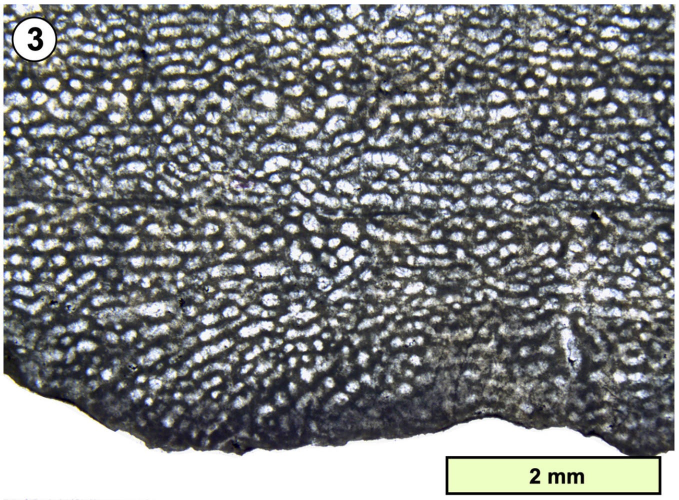
| Fig. | | Page |
|---|---|---|
| | *Ecclimadictyon macrotuberculatum* (Riabinin, 1951) | 72 |

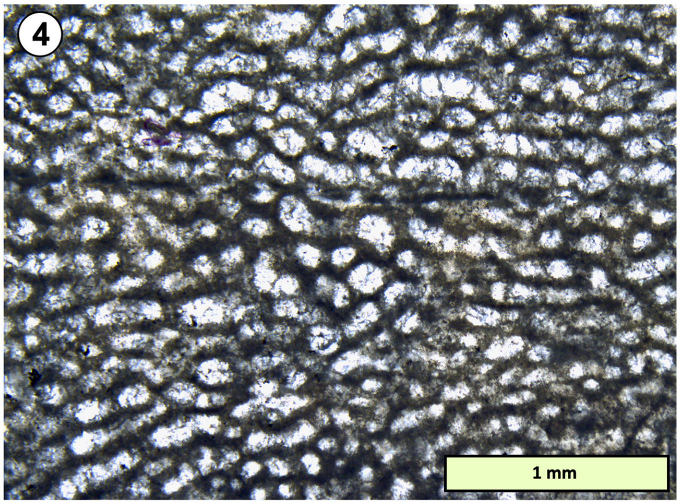
Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

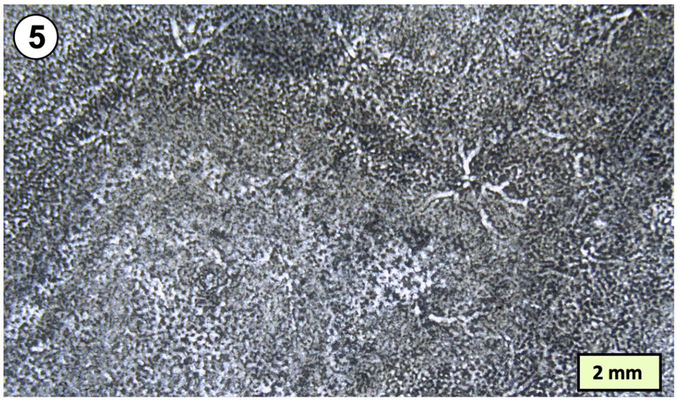
1–8 CAMSM X.50347.99; 1, vertical thin section of a large area of stromatoporoid skeleton. The base is the bottom of the stromatoporoid that grew either on sediment or as a primary cavity and shows overlapping growth of laminae, that grew upwards and laterally from right to left. 2, 3, enlargements of 1, showing details of skeletal structure and overlapping growth of laminae. The lower part shows oblique downward development of the skeleton from right to left, possible evidence that the specimen grew to form a primary cavity. Former growth surfaces are shown by the three slightly darker horizontal lines (centre and upper), evidence that growth did not progress evenly through the life of this stromatoporoid. 4, detail of 3 showing the crumpled laminae architecture with circular to elongate galleries. 5–8, transverse sections at increasing scale showing character of astrorhizae and pillars.


1
20 mm


2
2 mm


3
2 mm


4
1 mm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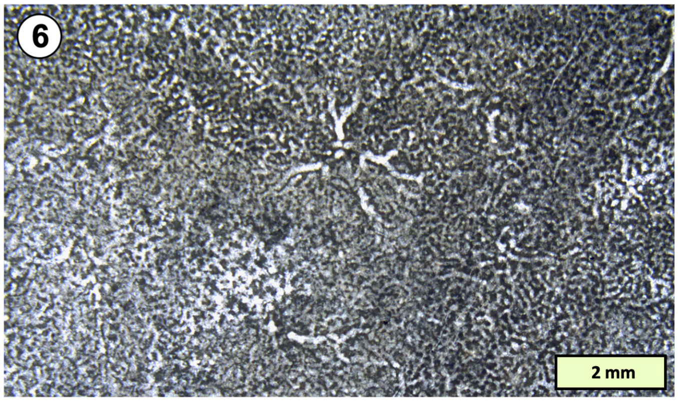
2 mm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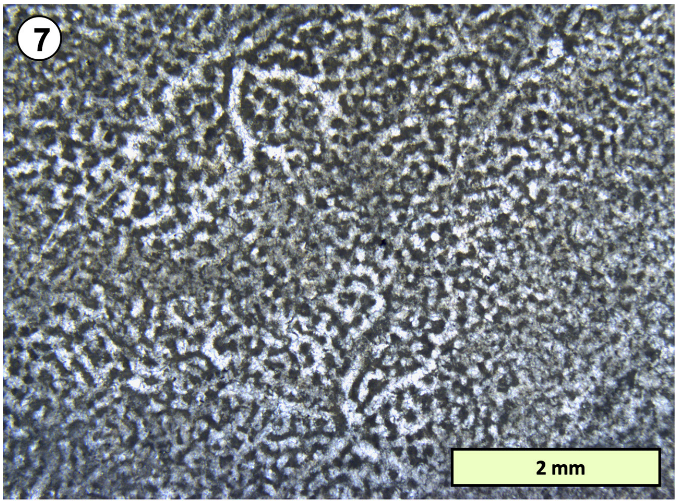
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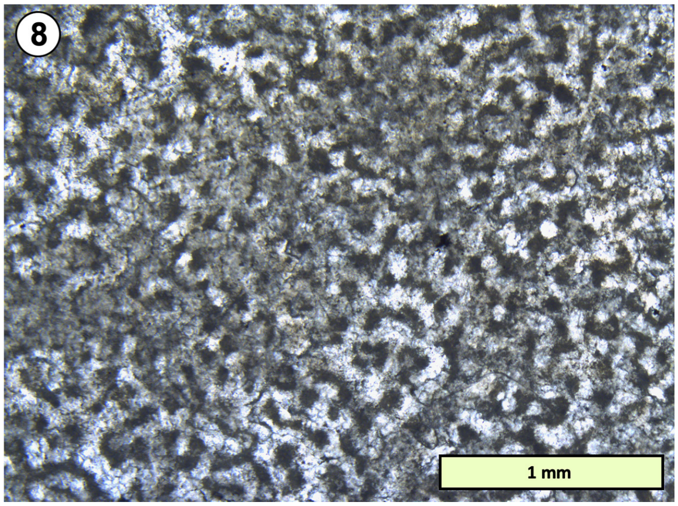

8
1 mm

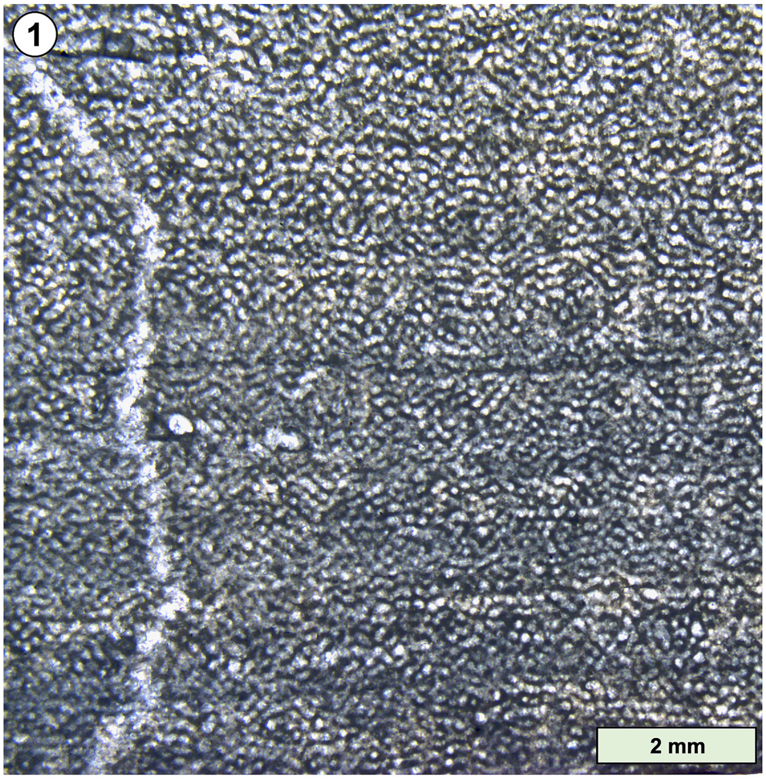
## PLATE 9

| Fig. | | Page |
|---|---|---|
| | *Ecclimadictyon astrolaxum* (Nestor, 1966) | 72 |

Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

1–6 CAMSM X.50347.95; 1–3, vertical thin sections at different scales, showing the crumpled laminae architecture characteristic of taxa classed traditionally as *Ecclimadictyon,* and the consistently finer scale of structure, indicative of *E. astrolaxum*, different from *E. macrotuberculatum* illustrated in Plate 8. 4–6, transverse thin sections at different scales. Note difference in structure from *E. macrotuberculatum* in Plate 8.

1



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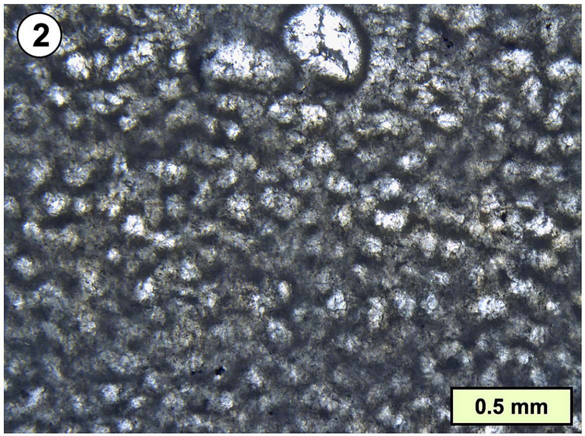

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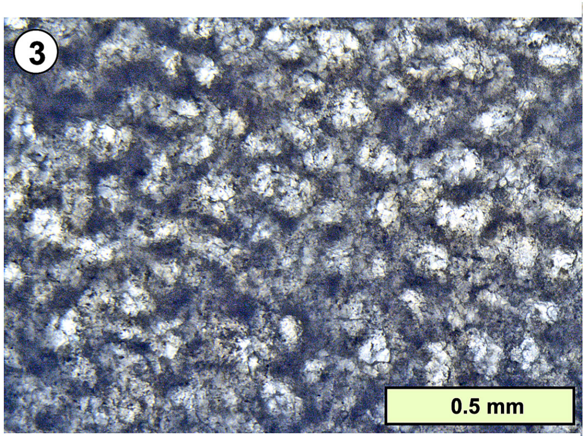

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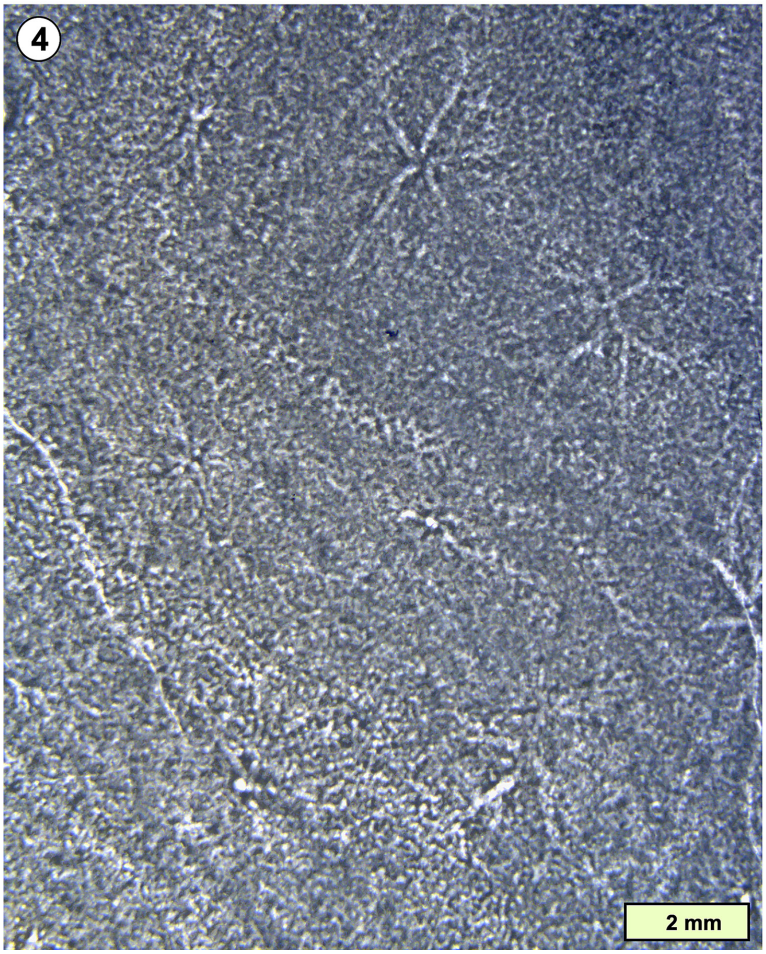

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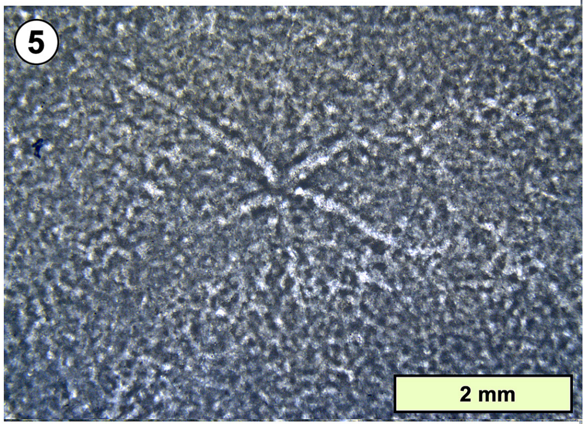

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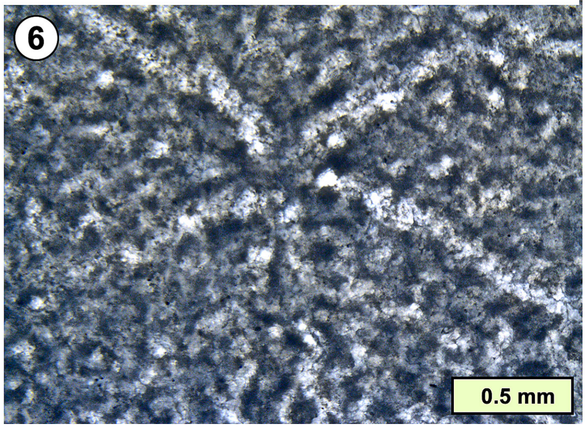


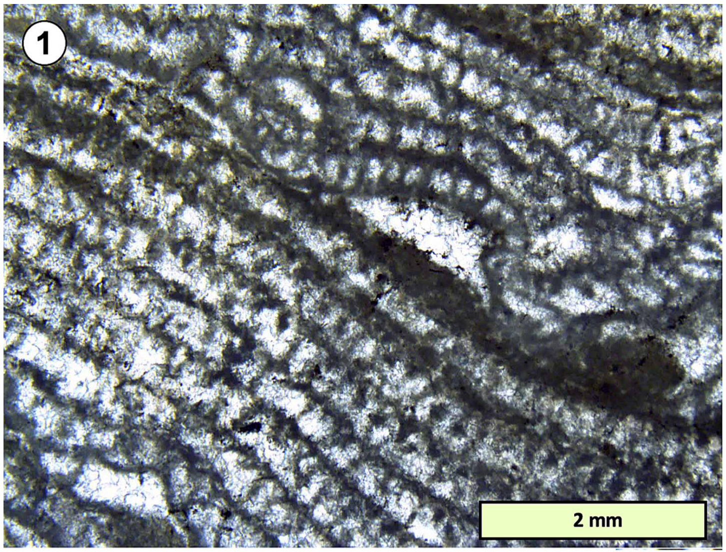
# PLATE 10

Fig. Page

*Petridiostroma simplex* (Nestor, 1966) 73

Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

1–4 CAMSM X.50347.47; 1, 2, vertical sections showing continuous laminae and the downward reflection of laminae to form pillars, characteristic of this taxon. 3, 4, transverse sections of skeletal architecture of continuous laminae and distinct rounded pillars present in this taxon.

1


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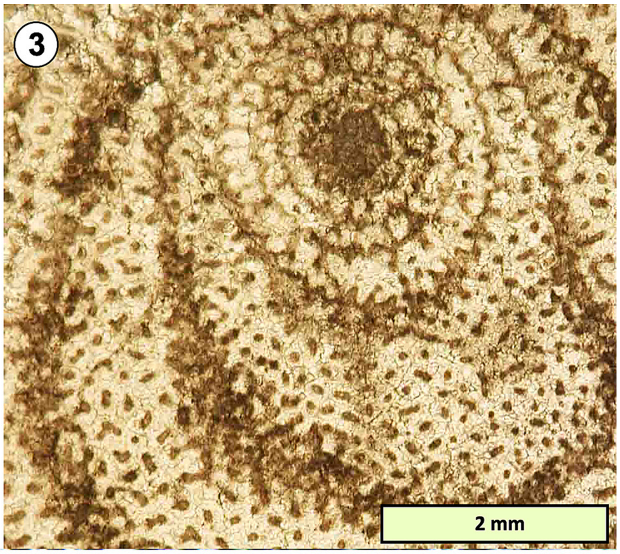

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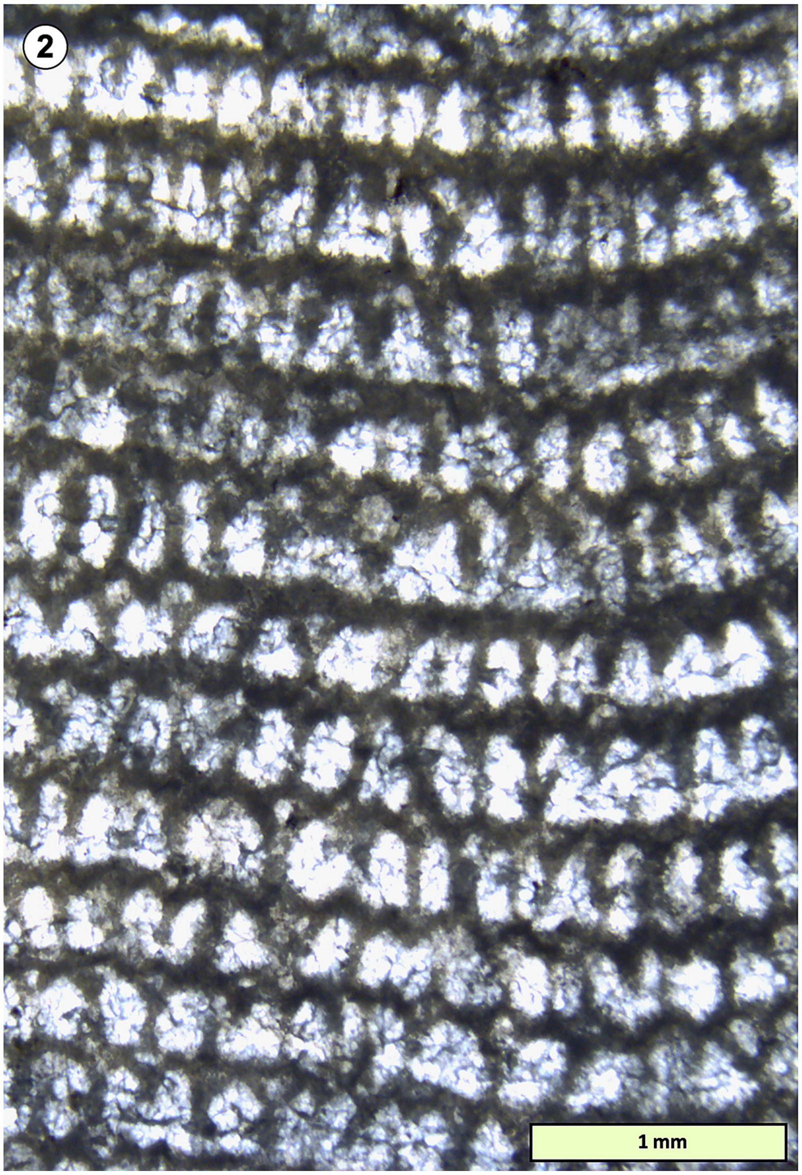

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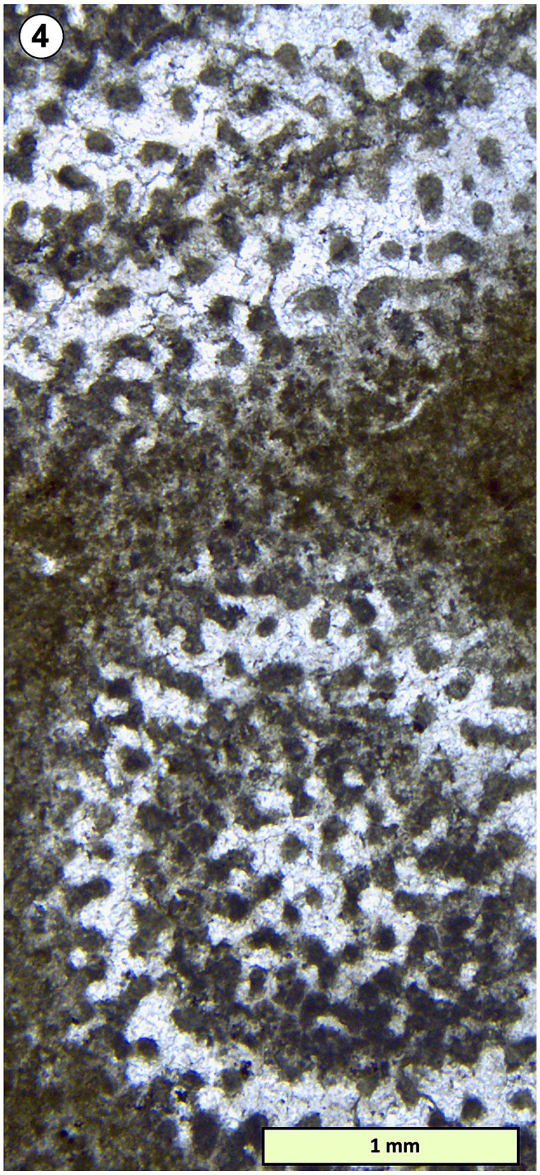


# PLATE 11

Fig. Page

*Petridiostroma linnarssoni* (Nicholson, 1887) 74

Middle Silurian, Much Wenlock Limestone Formation
Coates Quarry, Wenlock Edge, Shropshire

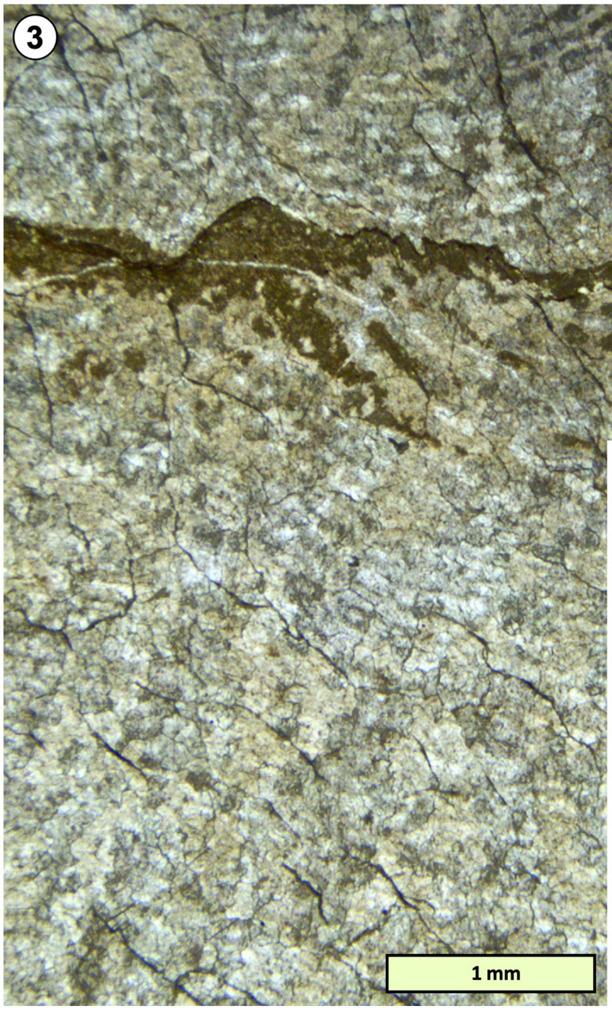
1–3 CAMSM X.50347.37; 1, vertical thin section of the only sample available; there is no transverse section of this specimen. Large area of thin section, showing the stromatoporoid in the lower one third of the photograph. 2, 3, enlargements of lower right part of 1, showing the poorly preserved structure that is somewhat recrystallized, but contains a recognizable architecture that is not consistent with any other taxon. The stromatoporoid is also affected by pressure solution between the three pieces of skeleton illustrated.

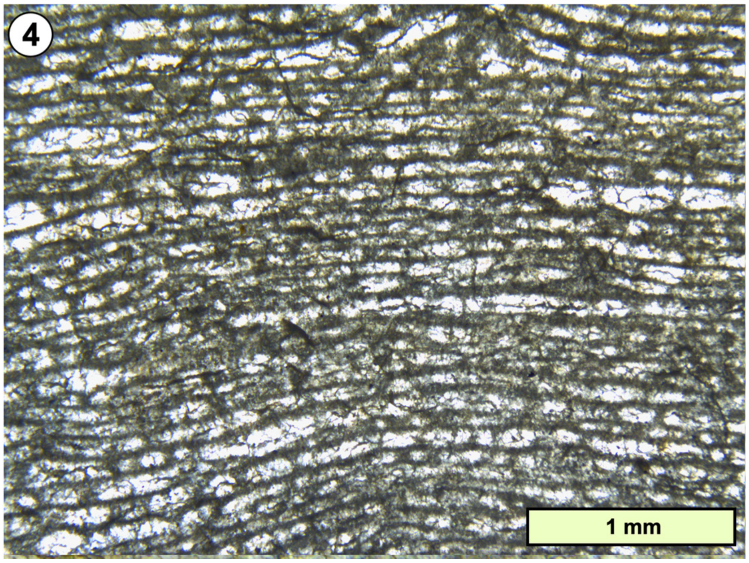
Lower Wenlock, Upper Visby Formation
Kneippbyn, Gotland, Sweden

4 CAMSM X.50347.37.1; vertical thin section view at the same scale as 3 that confirms the identification.


1
10 mm


2
2 mm


3
1 mm


4
1 mm

## PLATE 12

Fig. Page

*Petridiostroma simplex* (Nestor, 1966) 73

Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

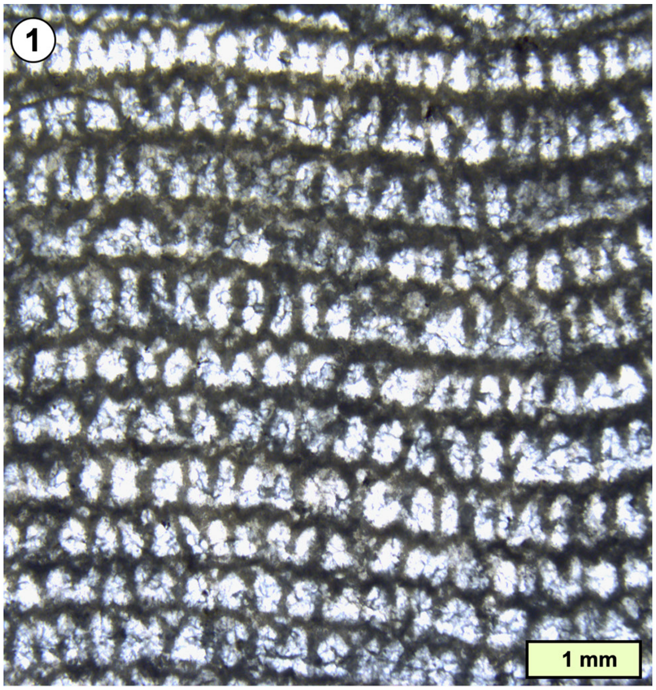
1 CAMSM X.50347.47; vertical thin section showing prominent lamina and pillar structure; compare with 2.

2 NMW 99.35G.EDG-3.23; vertical acetate peel showing an architecture the same as 1, but laminae spacing is less, reflecting the variation of the skeleton within this taxon.

*Petridiostroma linnarssoni* (Nicholson, 1887) 74

Middle Silurian, Upper Visby Formation
Kneippbyn, Gotland, Sweden

3 CAMSM X.50347.37.1; vertical thin section to emphasize the differences in physical appearance of the architecture from *P. simplex* in 1 and 2 above, but with similar laminae spacing as 2.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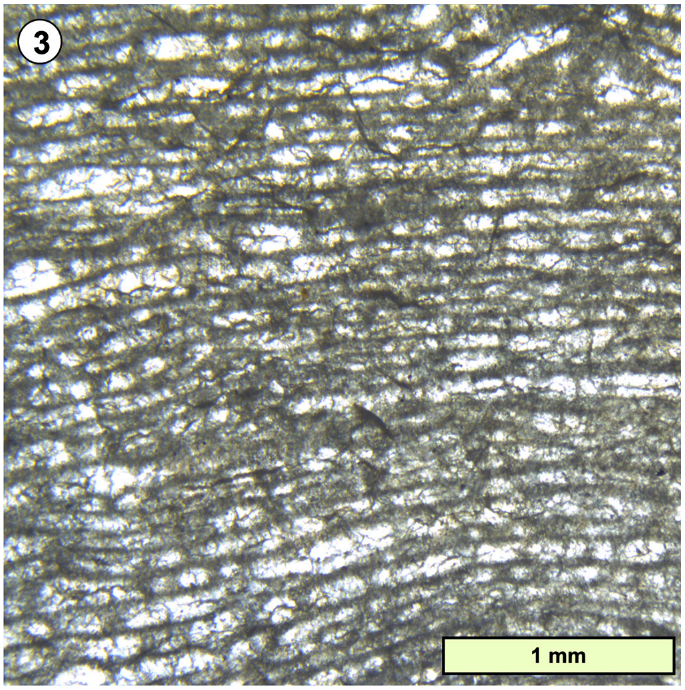
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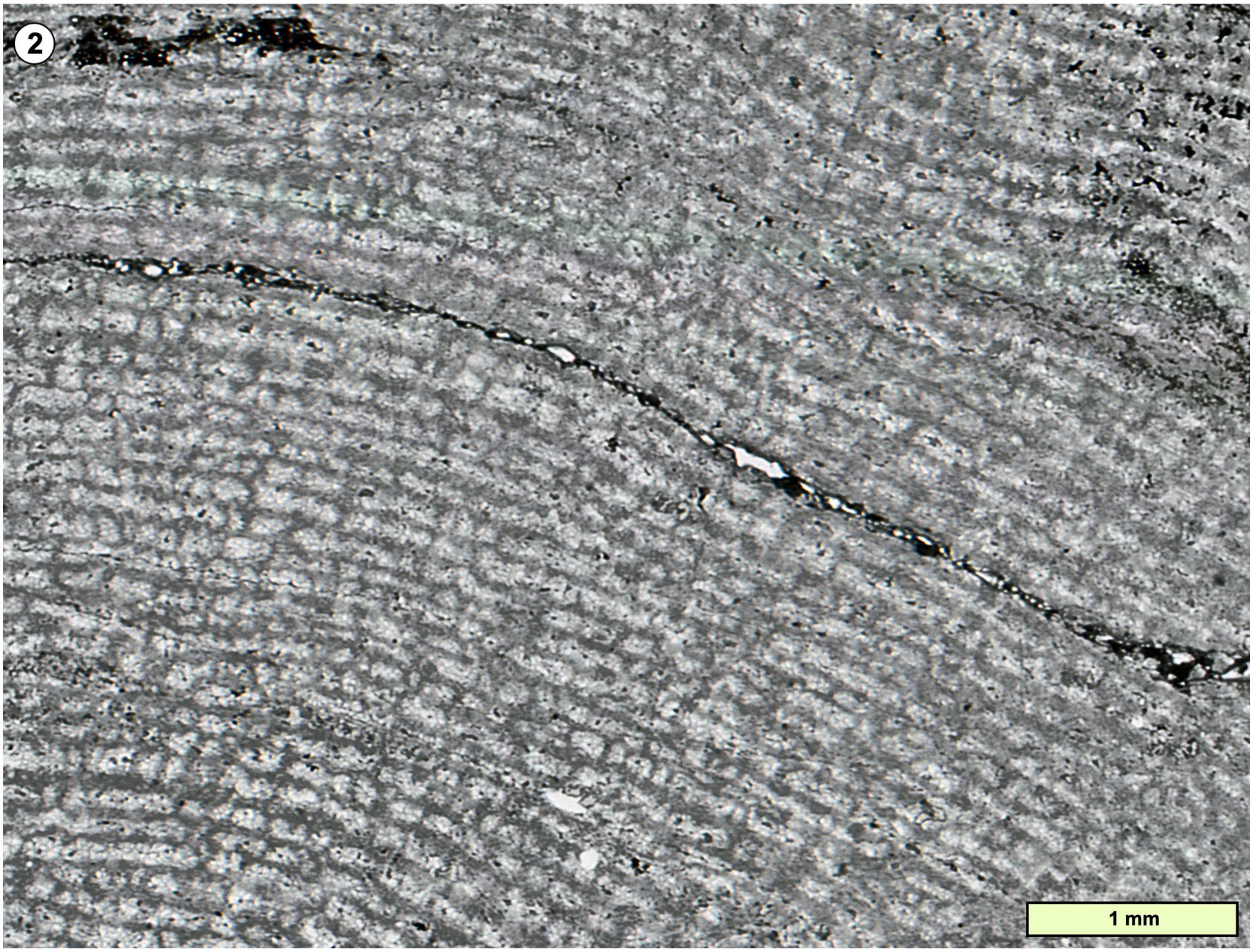

2
1 mm

# PLATE 13

| Fig. | | Page |
|---|---|---|
| | *Actinostromella vaiverensis* (Nestor, 1966) | 75 |

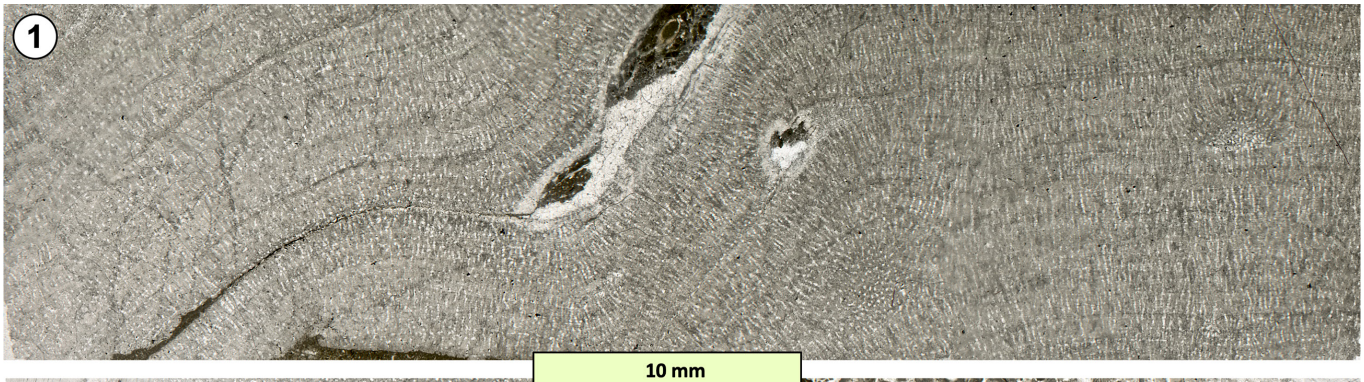
Middle Silurian, basal Elton Formation
Lea South Quarry, Wenlock Edge, Shropshire

1, 2 CAMSM X.50347.64; vertical (1) and transverse (2) views of whole thin sections. This taxon is characterized by an open network structure with narrow vertical spaces that develop as continuous vertical spaces appearing as tubes, visible as small white circles in transverse section (2, 6). Patches of sparite in the central area of 1 are interpreted as recrystallization of sediment in a sediment-interruption layer, because this photograph shows the correct way up to the top of the image.

Middle Silurian, Much Wenlock Limestone Formation
Major's Leap, Wenlock Edge, Shropshire

3–6 CAMSM X.50347.165; 3, 4, enlargements of vertical sections of the network structure. Light-coloured wavy horizontal lines in 3, enlarged in 4, show growth layers of the stromatoporoid. 5, 6, transverse sections of the network structure, showing astrorhizae. Symbiotic possible worm tubes are present as spar-filled circles; the continuous vertical spaces shown in 3 and 4 are here seen as small circles (6). Sample donated by David Walker, West Midlands, UK.

1



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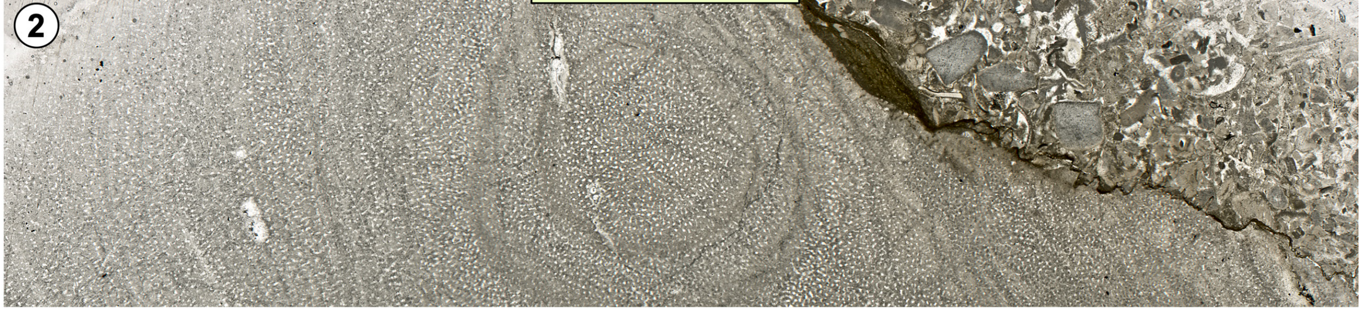

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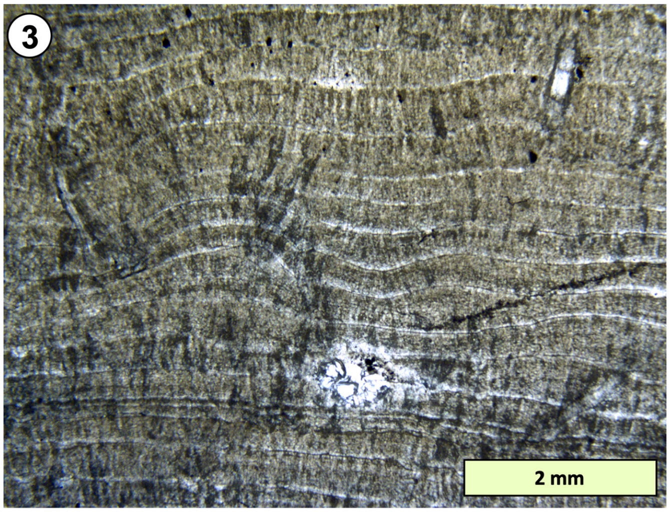

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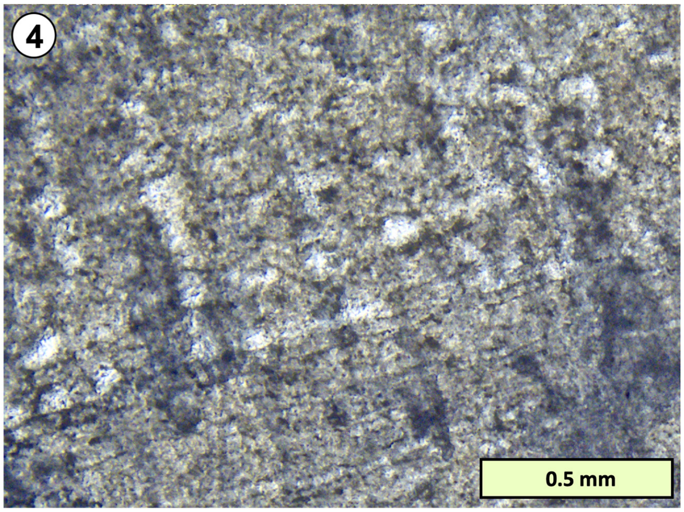

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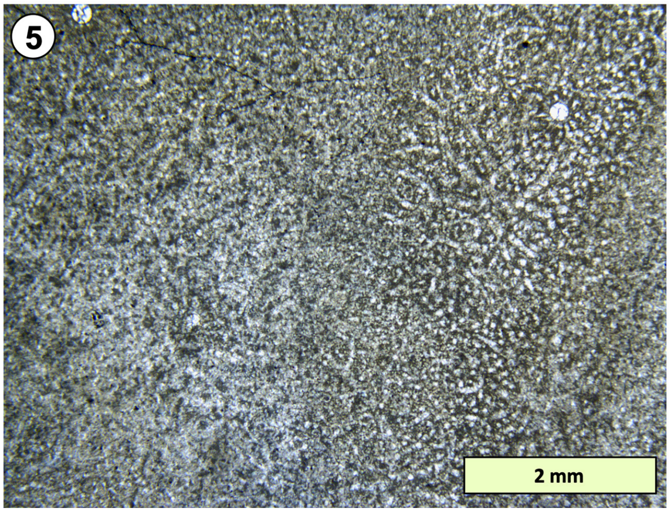

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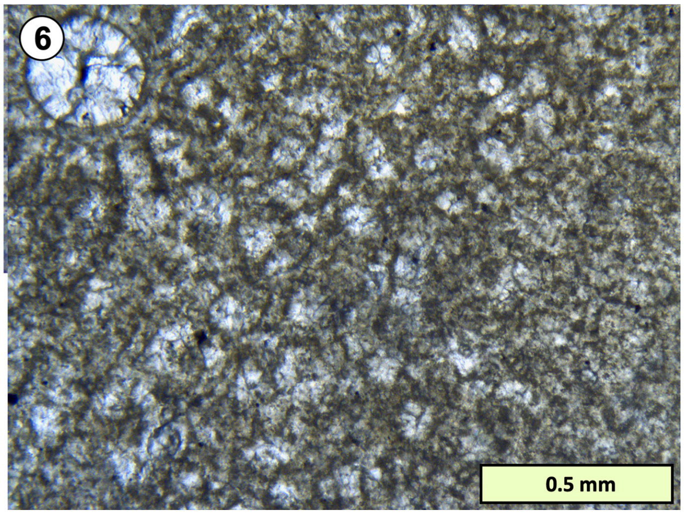


# PLATE 14

Fig. Page

*Araneosustroma fistulosum* Lessovaya, 1970 75

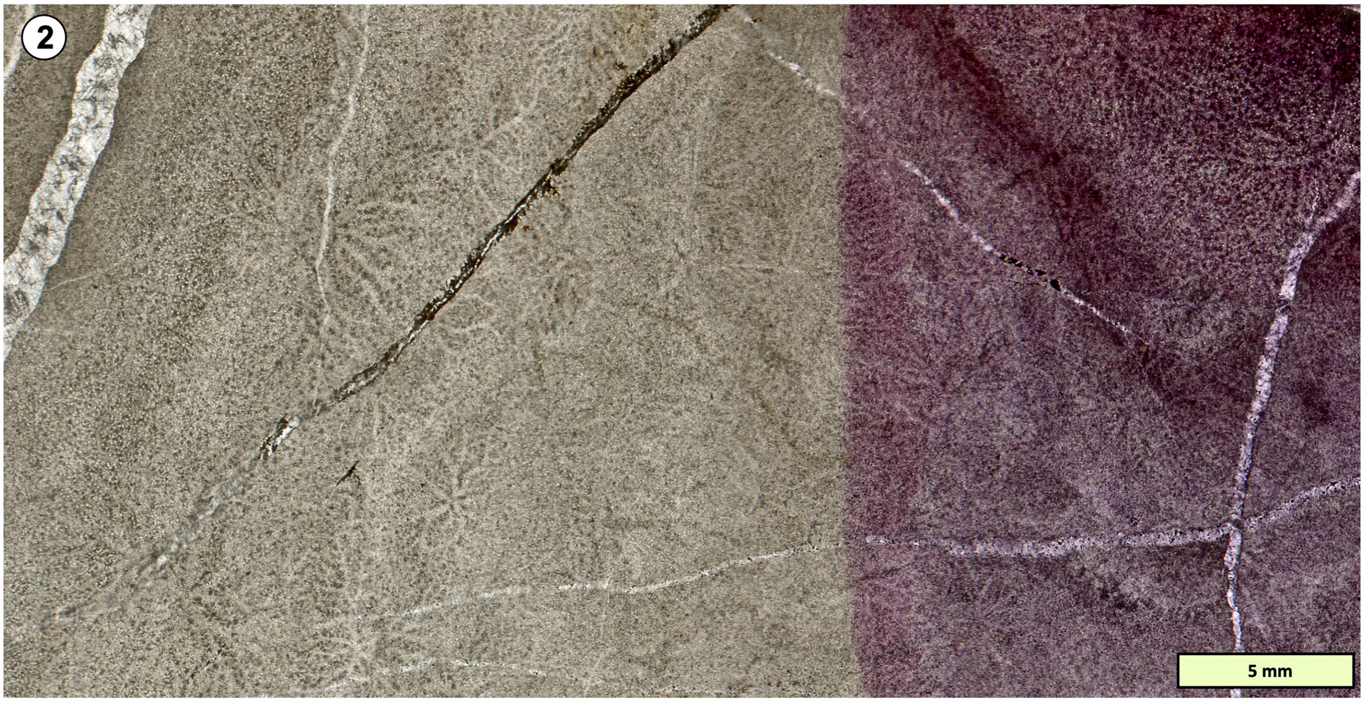
Middle Silurian, Much Wenlock Limestone Formation
Crews Hill Quarry, Abberley Hills, Worcestershire

1–4 CAMSM X.50347.258; 1, 2, vertical (1) and transverse (2) views of whole thin sections. They are partly stained with a combination of Alizarin Red S and potassium ferricyanide, producing a purple stain (darker shade in monochrome) that indicates presence of ferroan calcite, evidence of diagenesis in burial below the redox boundary. 3, 4, partial enlargement in vertical (3) and transverse (4) views. In 3 the laminate structure is more clear but even at this magnification the detail of the structure comprises narrow skeletal elements. 4 shows detail of an astrorhiza.

Compare with Plate 15. See also Text-figs. 48–51 of diagenetic change in stromatoporoids.

1

2



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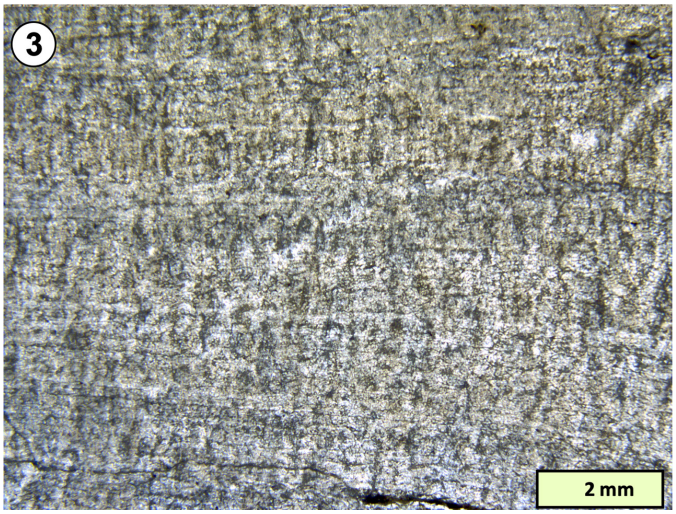

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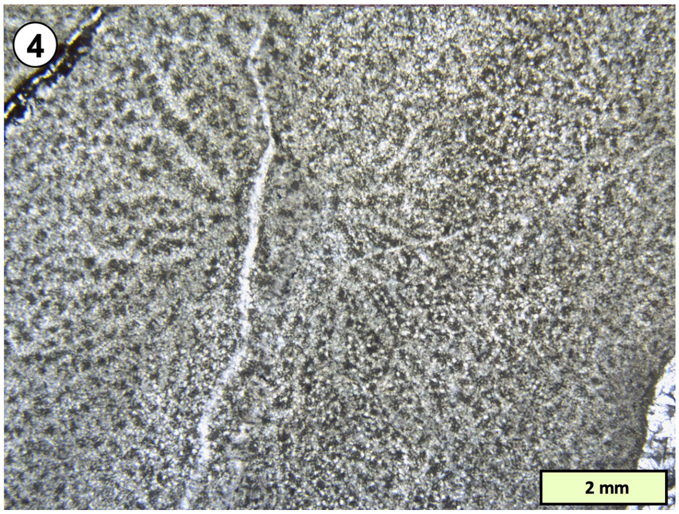


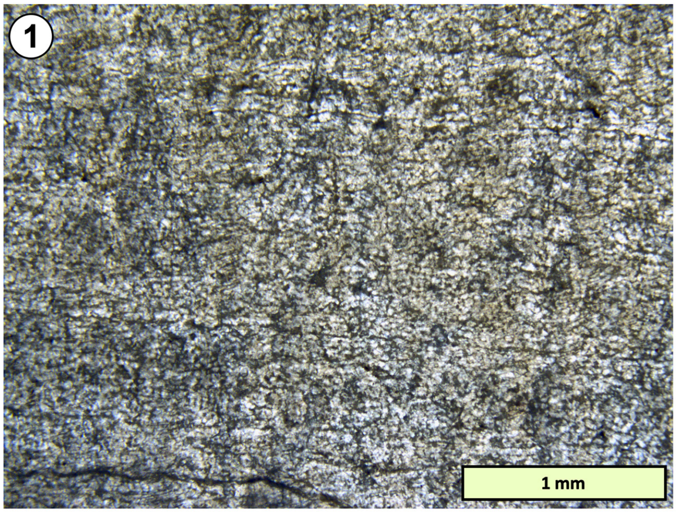
## PLATE 15

| Fig. | | Page |
|---|---|---|
| | *Araneosustroma fistulosum* Lessovaya, 1970 | 75 |

Middle Silurian, Much Wenlock Limestone Formation
Crews Hill Quarry, Abberley Hills, Worcestershire

1–6 CAMSM X.50347.258; 1–3, successive enlargements of vertical sections. In 3 the structure is revealed as an irregular network composed of non-aligned fine vertical and horizontal elements characteristic of this taxon, with scattered small spaces shown as pale areas. 4–6, successive enlargements of transverse sections showing the elements with tiny spaces represented as pale areas.

This structure contrasts with the aligned structures of *Densastroma pexisum,* that lack the small spaces, displayed in Plate 16.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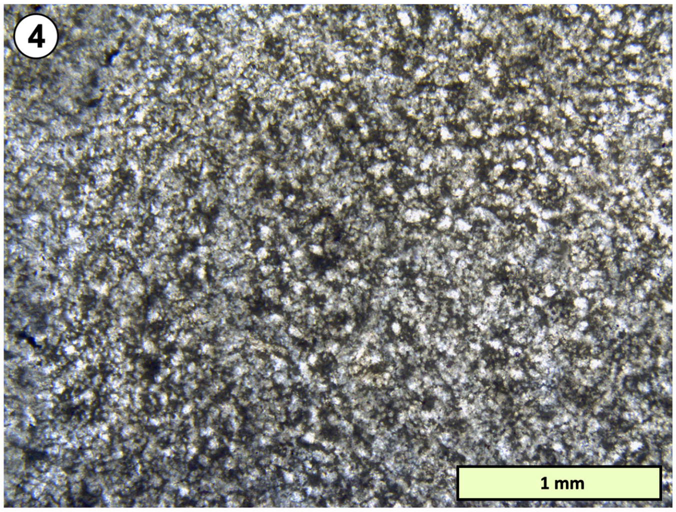
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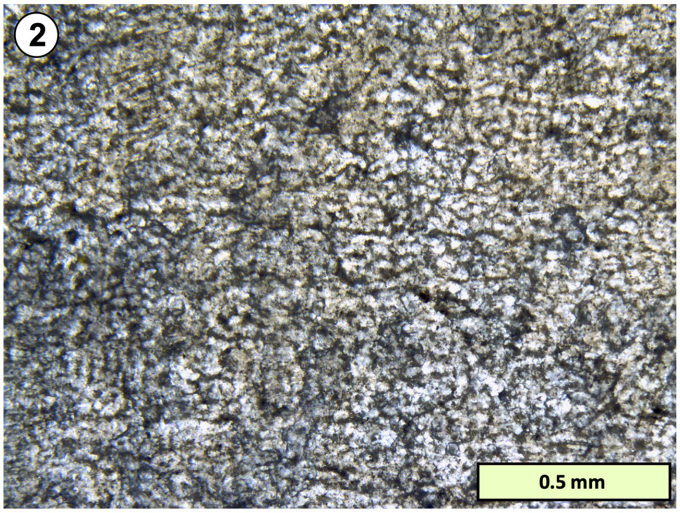
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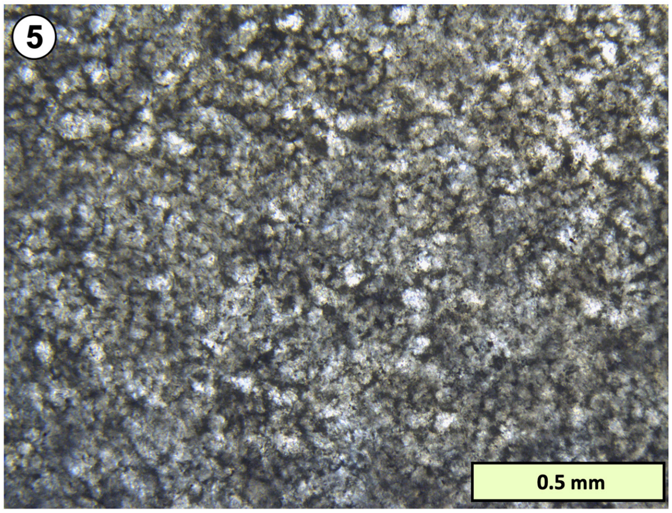
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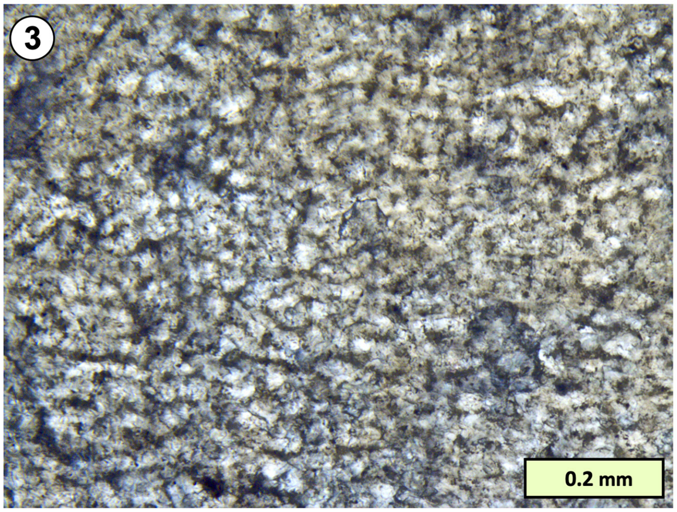
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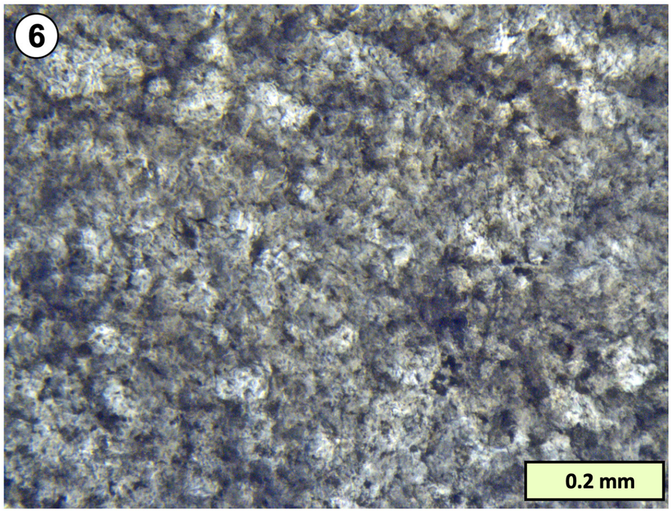
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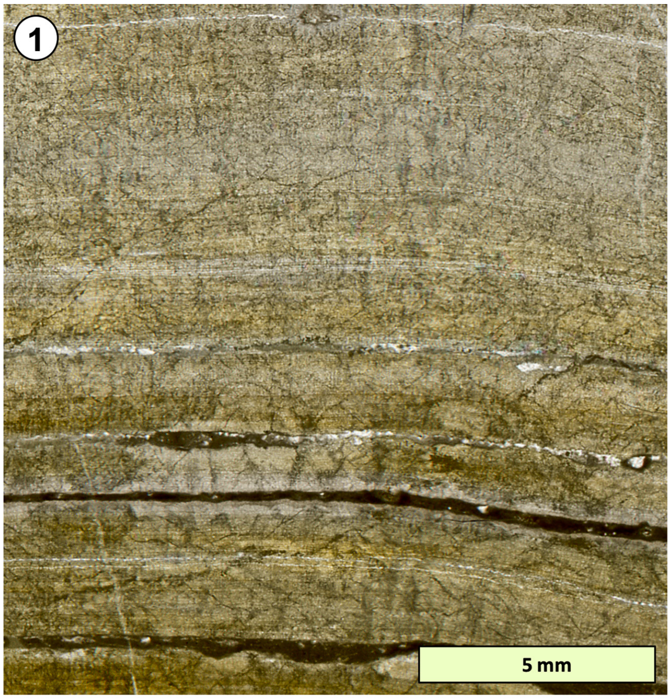
# PLATE 16

| Fig. | | Page |
|---|---|---|
| | *Densastroma pexisum* (Yavorsky, 1929) | 76 |

Middle Silurian, Much Wenlock Limestone Formation
Crews Hill Quarry, Abberley Hills, Worcestershire

1–6 CAMSM X.50347.257; 1, vertical thin section showing fine structure of this taxon, dominated by coenosteles (vertical elements), connected together by horizontal processes, so the skeleton lacks pillars and laminae. Several growth interruption events have left sediment layers in the structure, some of which pass laterally to areas lacking sediment. 2, transverse thin section showing part of a growth interruption in plan view and branched borings penetrating the sediment. 3, 5, enlargements of vertical section showing aligned horizontal processes and short vertical pillars. 4, 6, enlargements of transverse thin sections showing the uniform dense structure of the arrangement of coenosteles.

See Plate 15 for comparison with *Araneosustroma*, noting the more uniform structure of *Densastroma*. Thin sections from sample donated by Margaret Rodway, Malvern, Worcestershire.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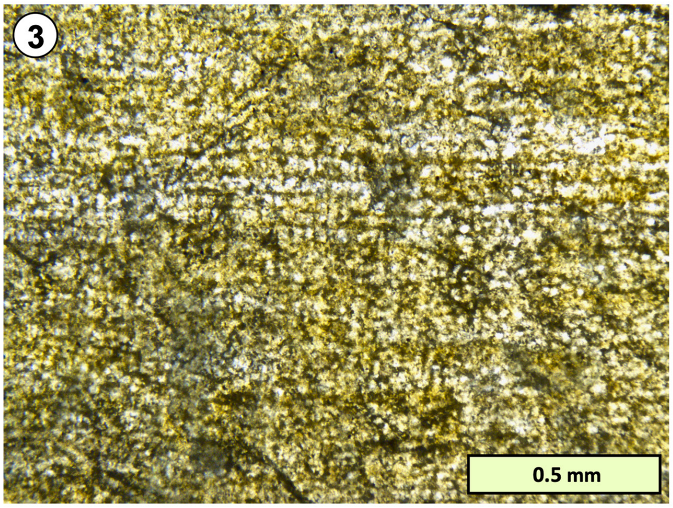
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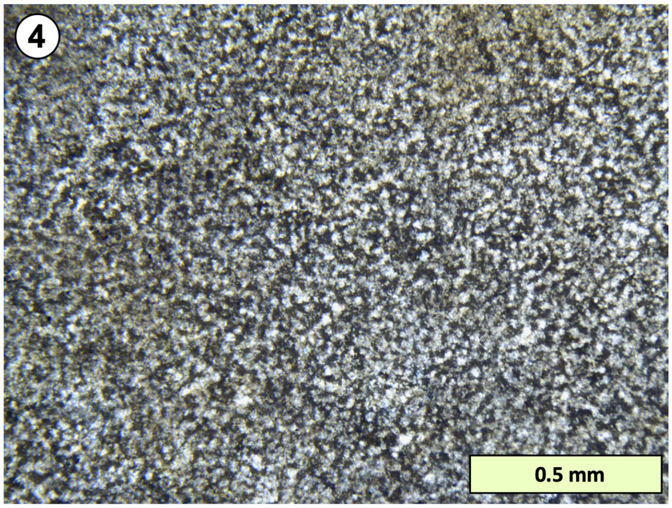
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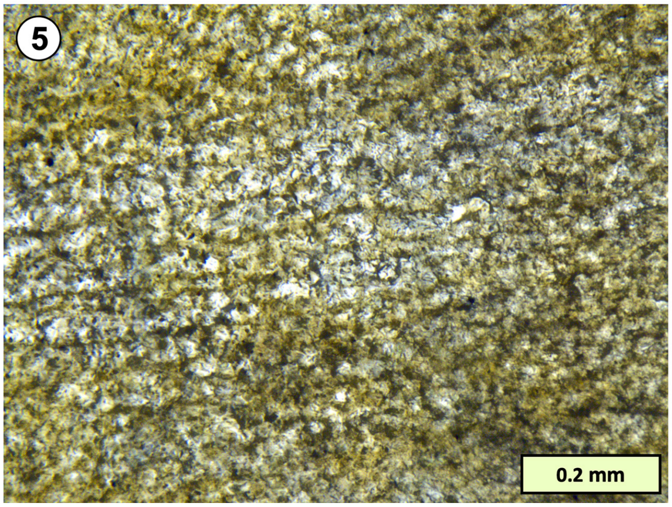
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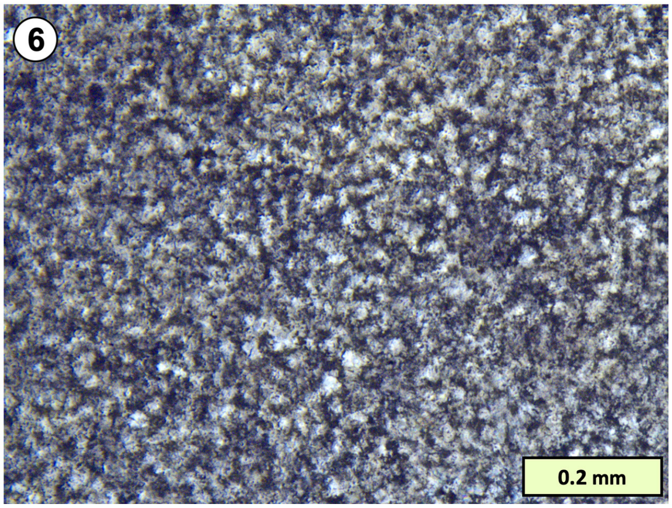
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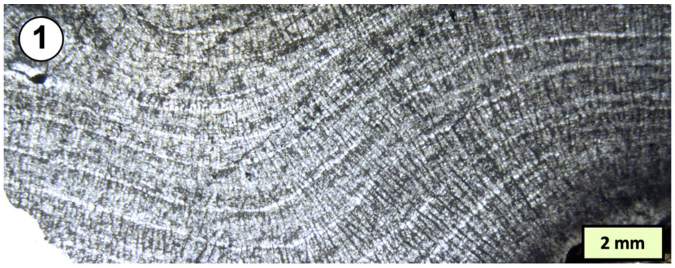
## PLATE 17

| Fig. | | Page |
|---|---|---|
| | *Plectostroma intertextum* (Nicholson,1886) | 76 |

Middle Silurian, Much Wenlock Limestone Formation
Coates Quarry, Wenlock Edge, Shropshire

1–8 CAMSM X.50347.163; 1–4, vertical thin sections with increasing magnification, to show skeletal architecture of this taxon comprising long narrow pillars and short horizontal processes. 5–8, transverse thin sections showing transverse sections through pillars; the horizontal processes are rods.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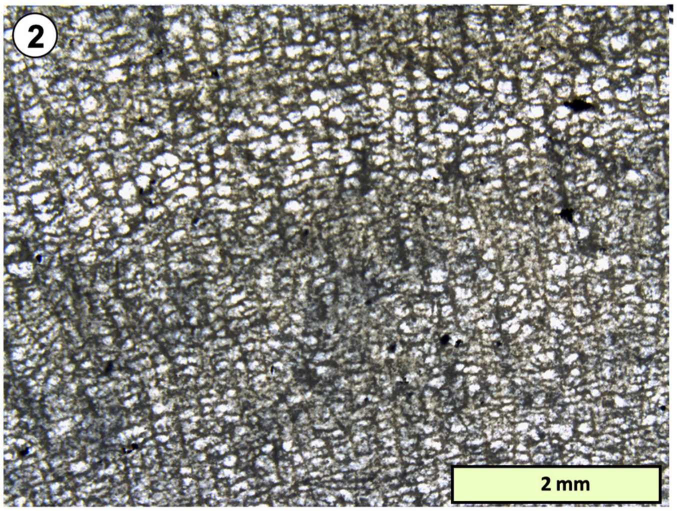
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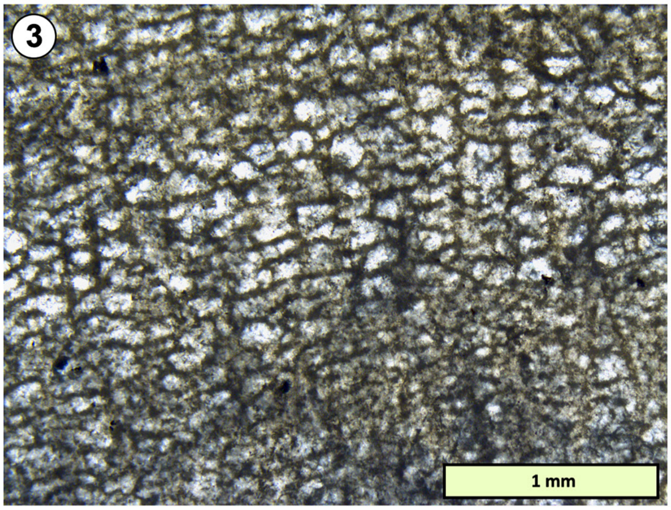
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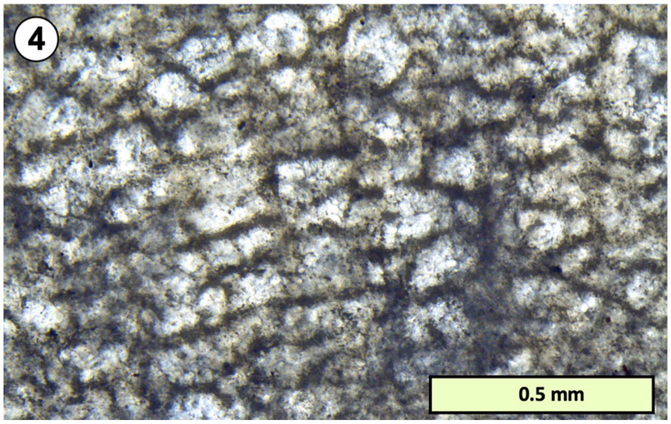
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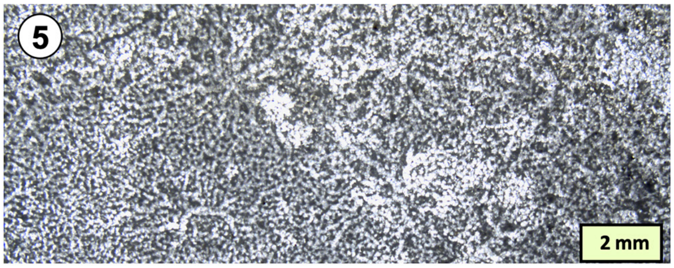
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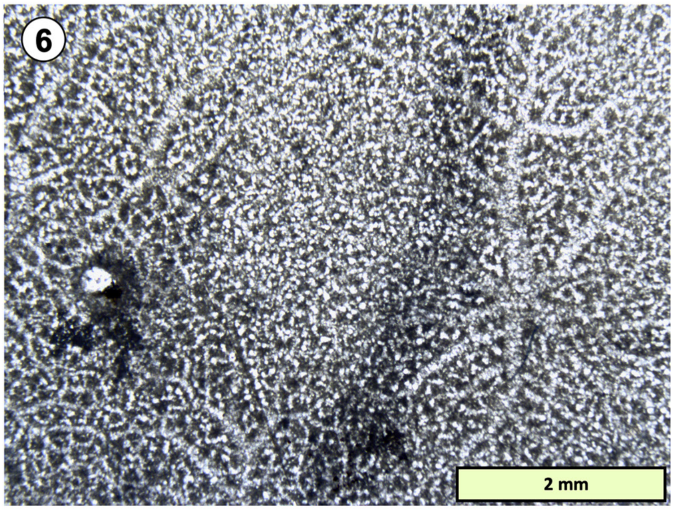
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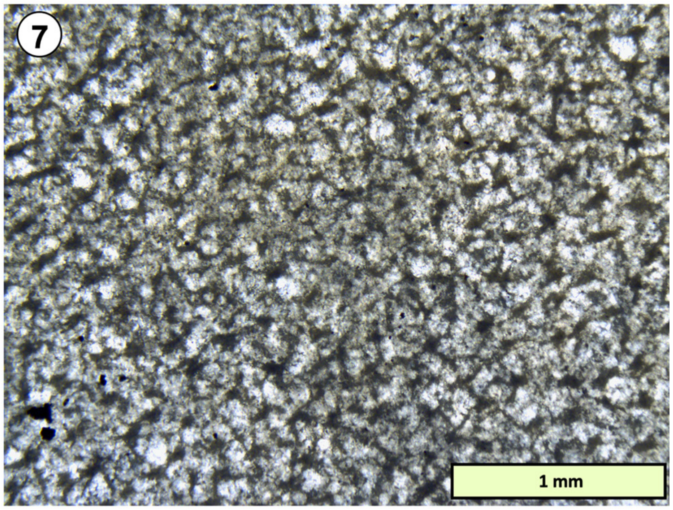
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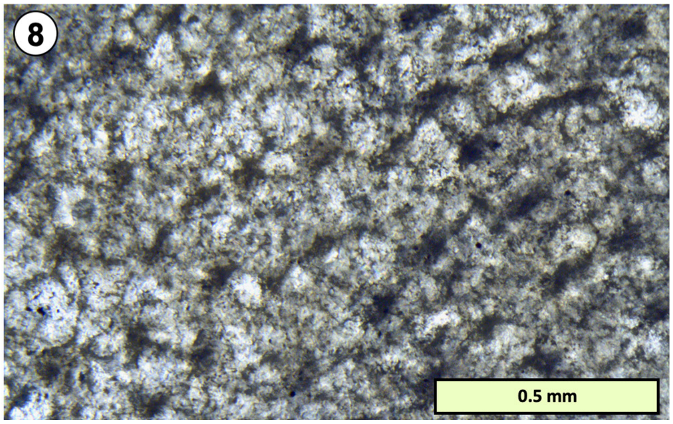
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## PLATE 18

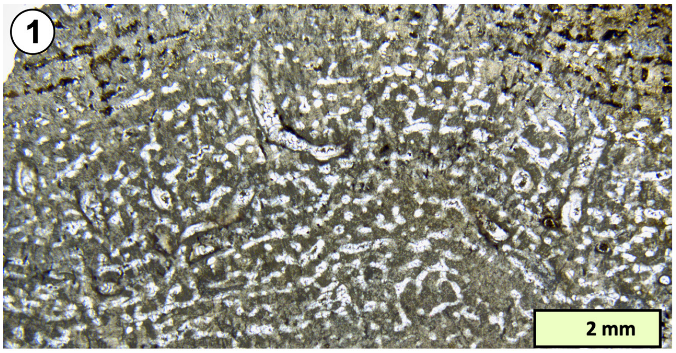
Fig. Page

*'Stromatopora' venukovi* Yavorsky 1929 77

Middle Silurian clast in Devonian Peel Sandstone
Either Whitestrand Beach or Peel Bay, north-west coast, Isle of Man

1–8 CAMSM X.50347.283; 1–4, vertical sections at increasing scale of the single available sample, showing the amalgamate skeletal architecture, with cyst plates in the galleries, consistent with this taxon described by Mori (1970) from Gotland. It is not assigned completely to a genus-level taxon, but is regarded here as a distinct low-level taxon distinct from all other taxa in this study. 5–8, transverse sections at increasing scale, of the amalgamate structure.

Numerous lined tubes in this specimen are syringoporid tabulate symbionts, common in this taxon in Upper Silurian limestones of Gotland (Mori 1970). Unlined tubes with dissepiments (3) are part of the stromatoporoid skeleton.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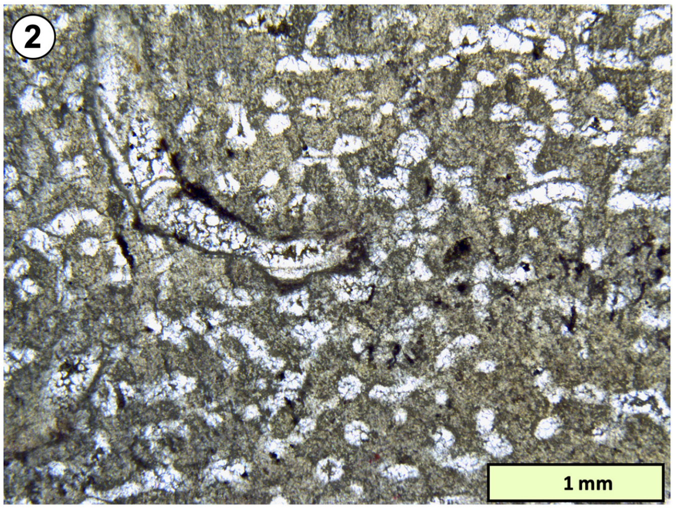
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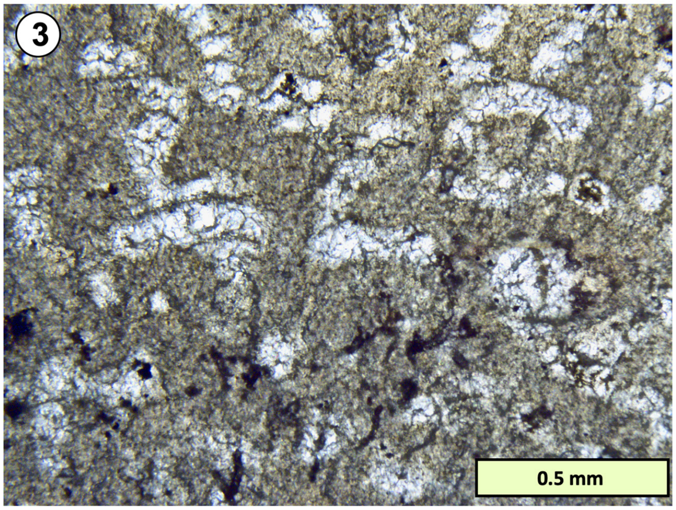
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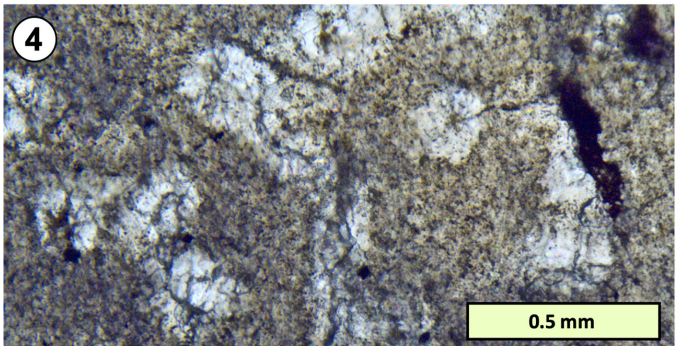
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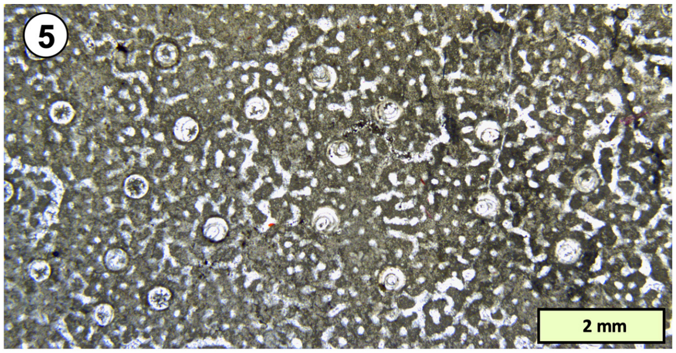
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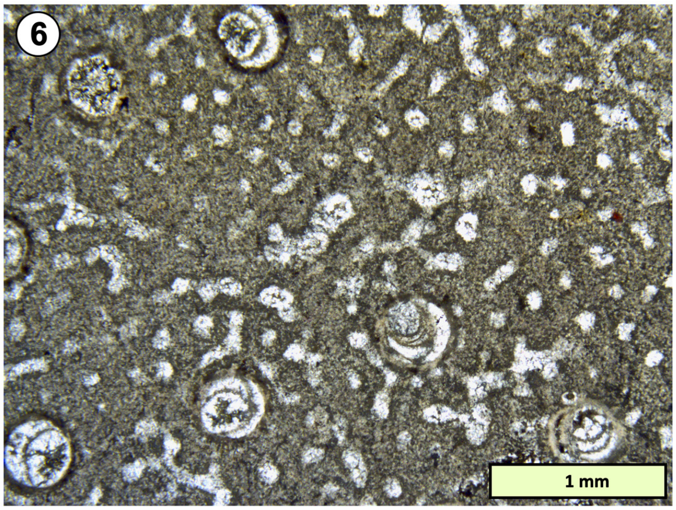
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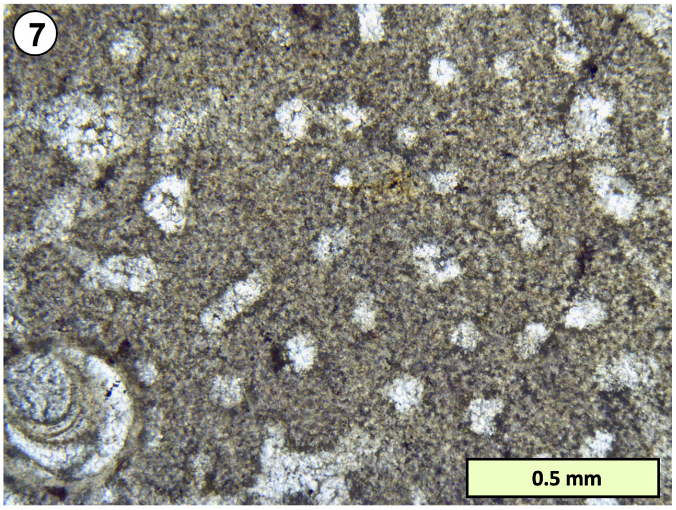
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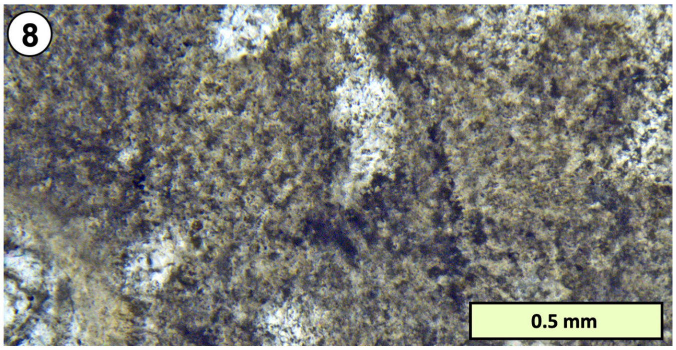
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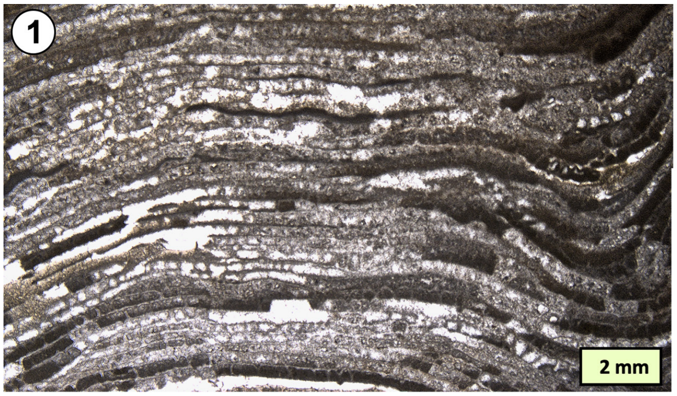
## PLATE 19

| Fig. | | Page |
|---|---|---|
| | *Simplexodictyon yavorskyi* (Nestor, 1966) | 78 |

Middle Silurian, Much Wenlock Limestone Formation
Farley Quarry, Wenlock Edge, Shropshire

1–9 NMW 99.35G.853; 1–5, vertical thin sections at increasing scale, to show skeletal architecture of this taxon comprising tripartite lamina, visible particularly in 3, 4 and 5 show variations of structure in closely located portions of the skeleton in 2; such variations are common in stromatoporoids but this is clearly within one specimen that is a single taxon. 6–9, transverse sections at increasing scale, showing the prominent pillars characteristic of this taxon.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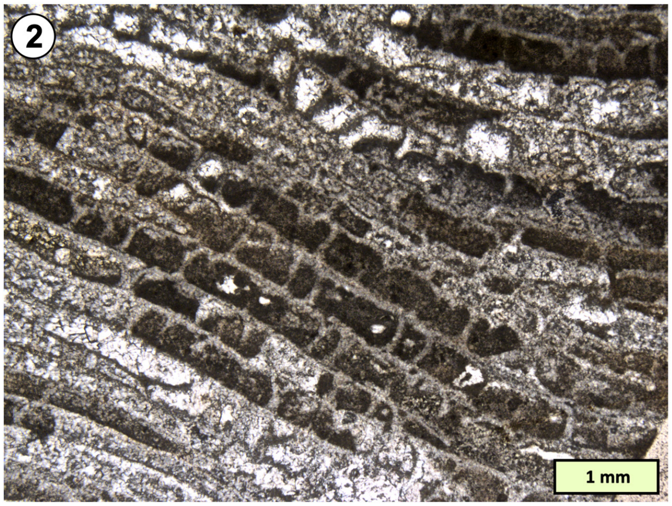
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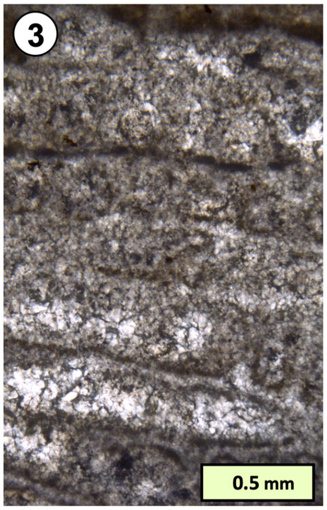
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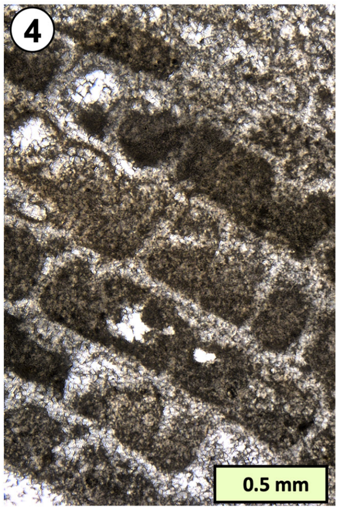
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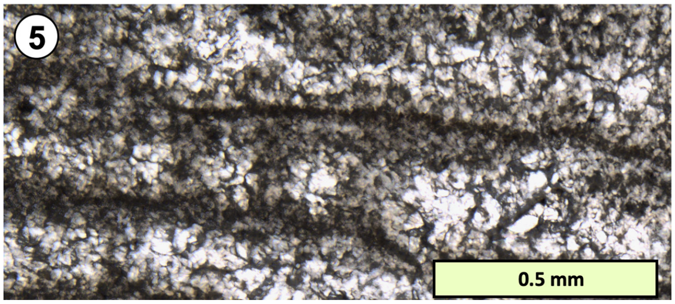
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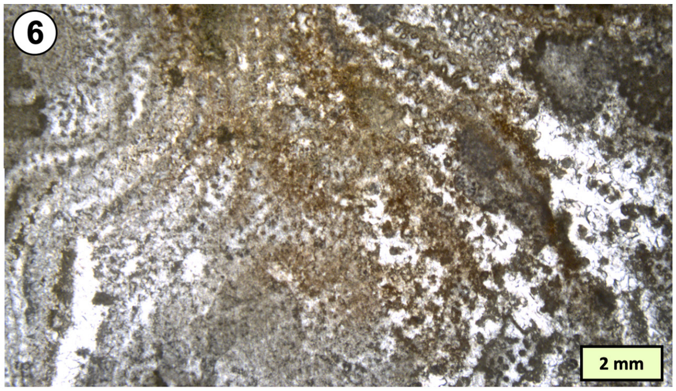
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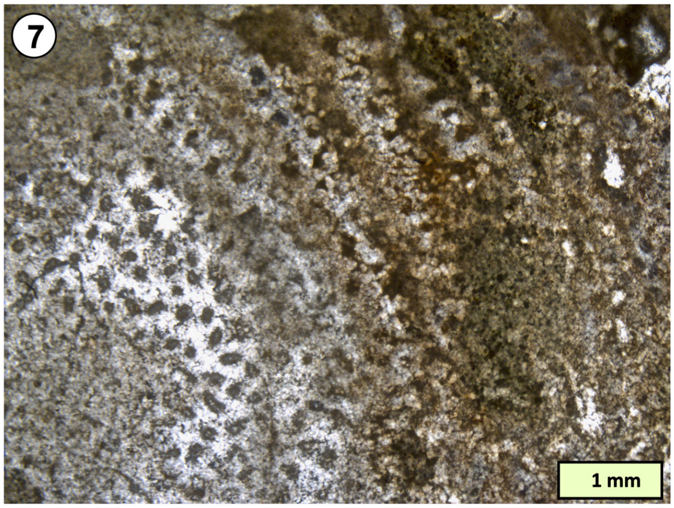
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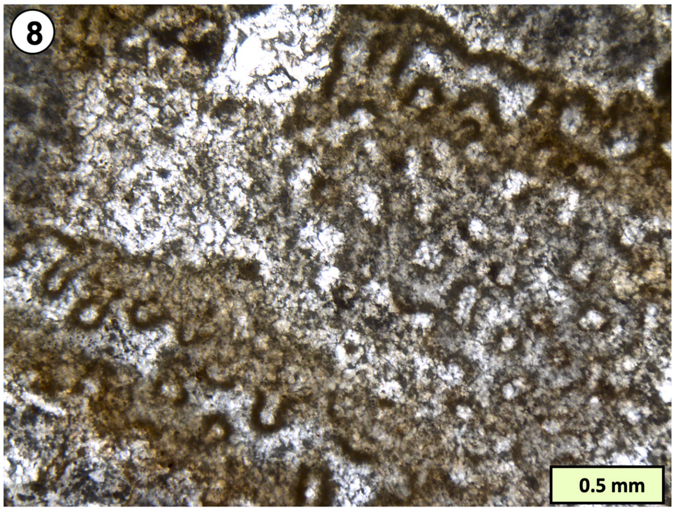
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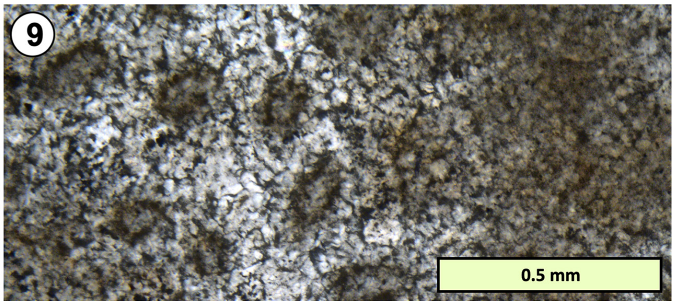
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# PLATE 20

Fig. Page

*Eostromatopora impexa* (Nestor, 1966) 79

Middle Silurian, basal Elton Formation
Lea South Quarry, Wenlock Edge, Shropshire

1–4 CAMSM X.50347.57; 1, vertical section showing typical structure of this taxon. 2, transverse section showing prominent astrorhizae in this taxon. 3, 4, vertical and transverse sections respectively, showing the dense structure dominated by vertical elements but with sufficient transverse gallery space to form a layered skeletal appearance.

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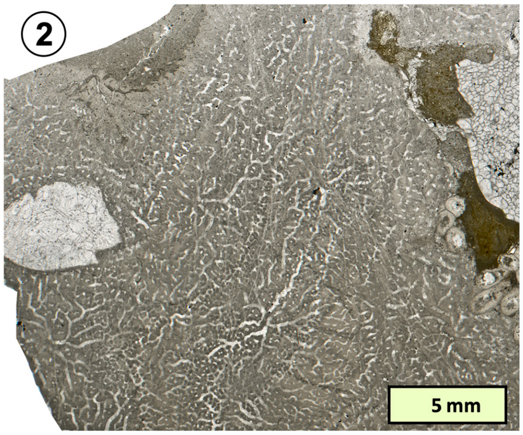

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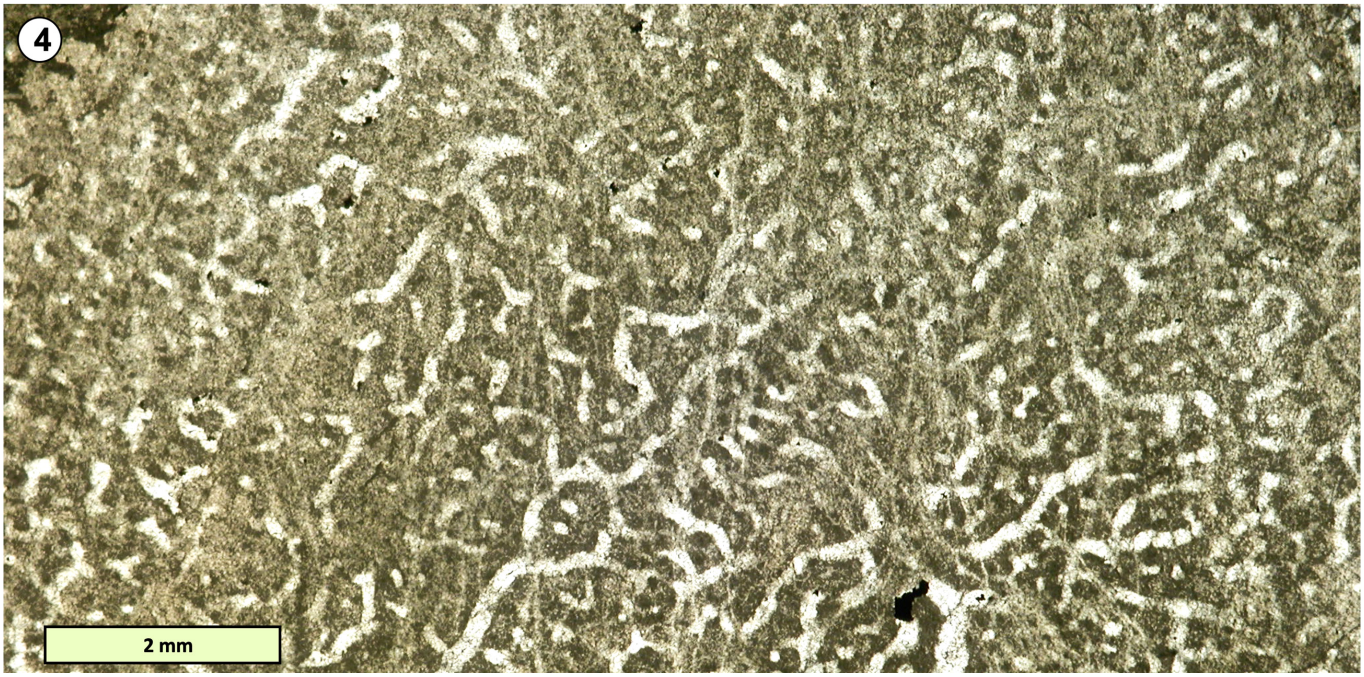


## PLATE 21

Fig. Page

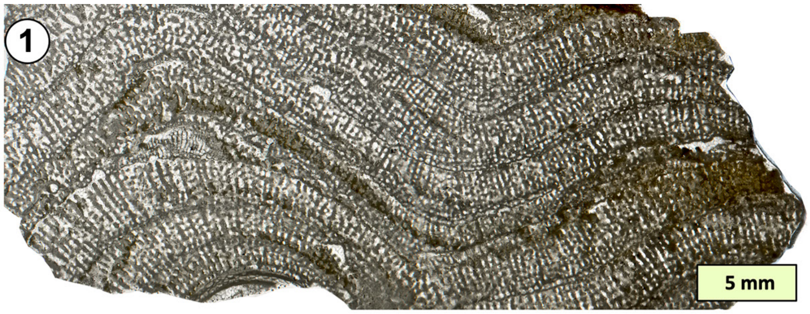
*Syringostromella borealis* (Nicholson, 1891) 80

Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

1–8 CAMSM X.50347.91. 1, 2, vertical (1) and transverse (2) views of large areas of thin sections showing the broad variation of structure across a sample. In 1 note the layering reflecting numerous growth interruptions common in stromatoporoids. 3, vertical thin section enlargement of left centre portion of 1, showing encrusting bryozoan on a growth interruption surface. 5, 7, vertical thin section enlargements, to show skeletal architecture of this taxon comprising thick verical pillars and short transverse elements. 4, 6, 8, transverse sections at increasing scales showing transverse cuts through pillars and the curved connecting elements.

In 7 and 8 the heterogenous microstructure is visible, showing what may be partial preservation of an original structure.

1



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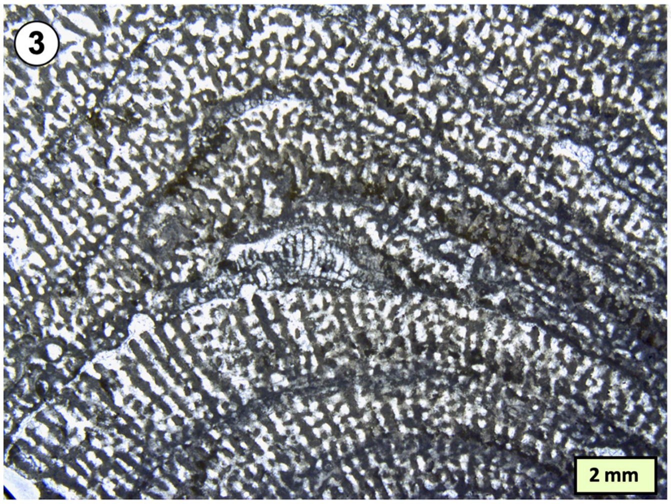

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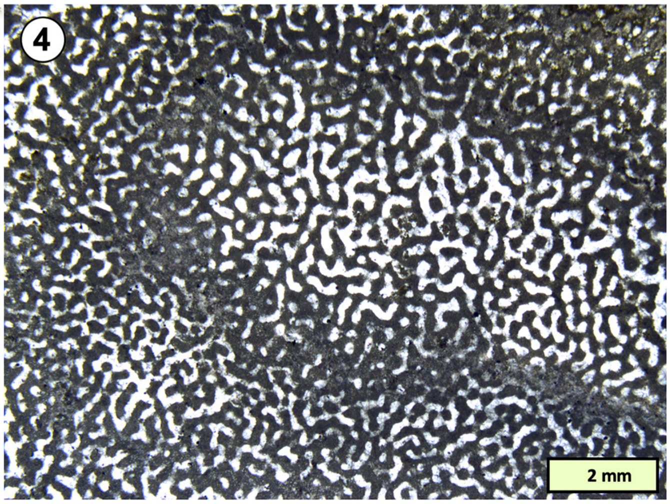

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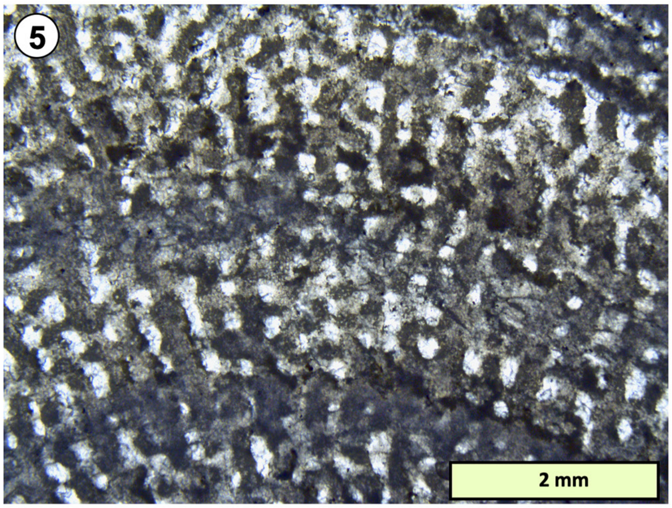

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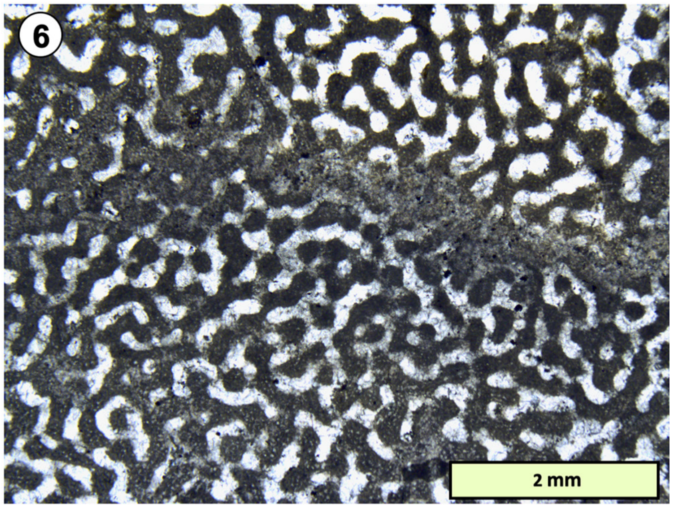

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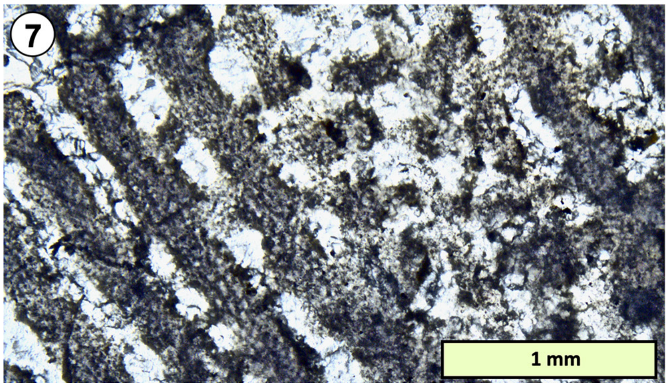

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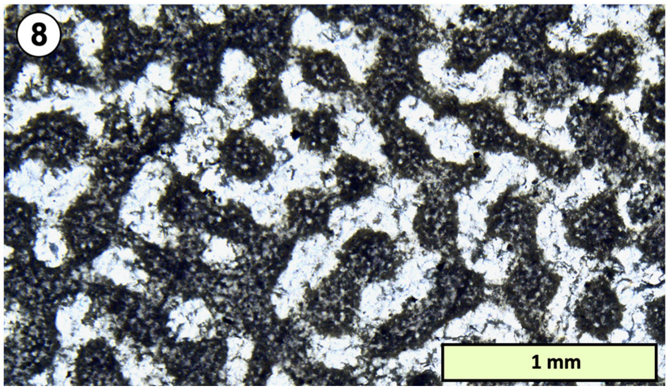


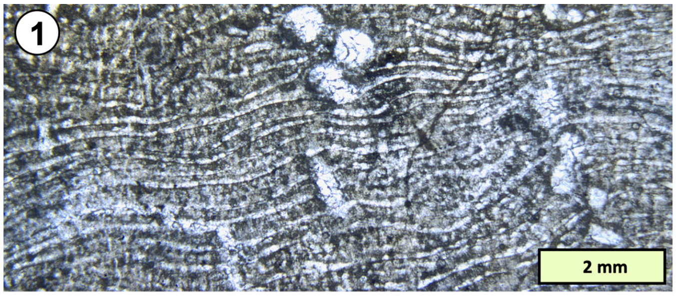
# PLATE 22

| Fig. | | Page |
|---|---|---|
| | *Parallelostroma typicum* (Rosen, 1867) | 80 |

Middle Silurian, Much Wenlock Limestone Formation
Lea South Quarry, Wenlock Edge, Shropshire

1–8 CAMSM X.50347.77; 1–4. Vertical sections at increasing scale, showing the reticulate structure with gallery spaces and some symbiotic intergrown tubes. 5–8, transverse sections at increasing scale, showing the reticulate structure with gallery spaces and some symbiotic intergrown tubes.

In samples of this taxon in the British suite, the microstructure is not well-preserved. *P. typicum* is generally characterized by orthoreticulate microstructure that is not well displayed in material from Britain.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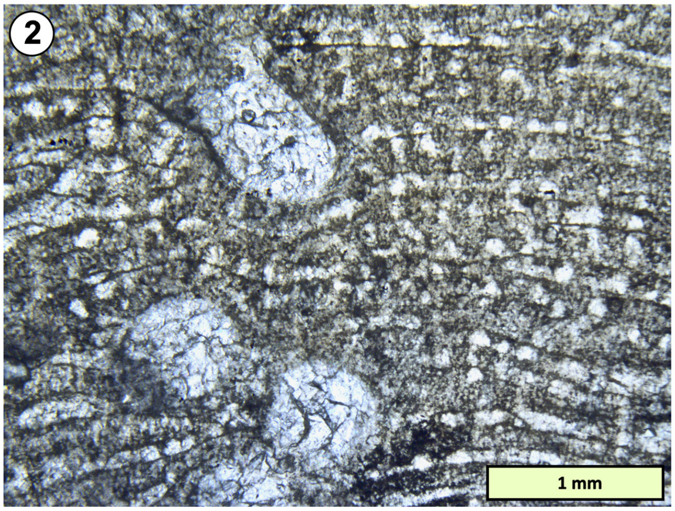
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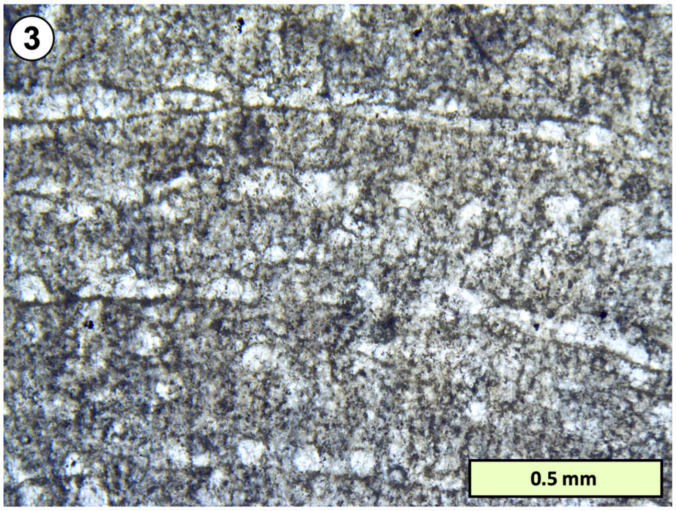
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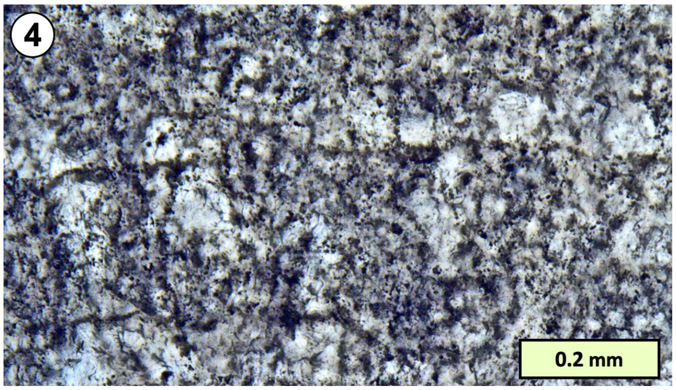
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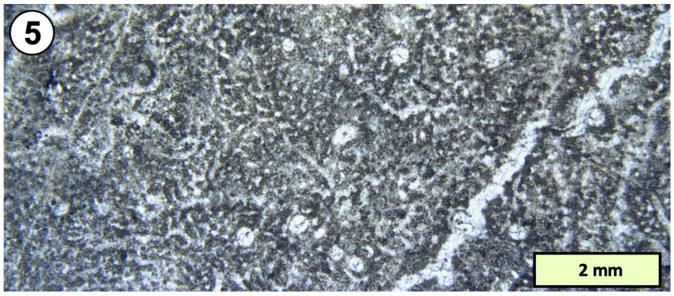
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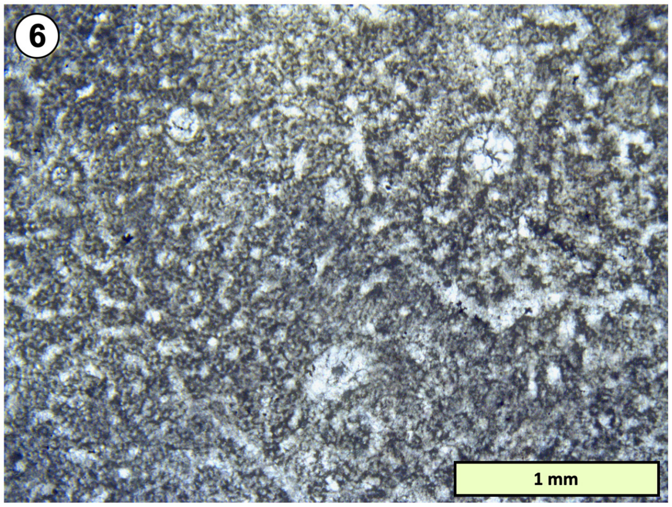
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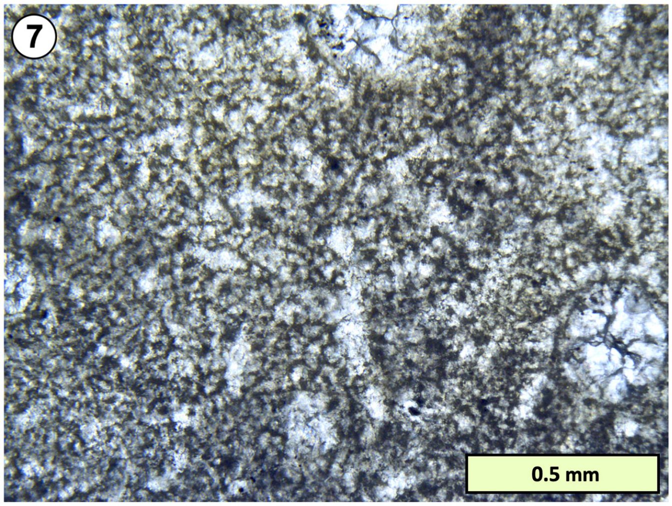
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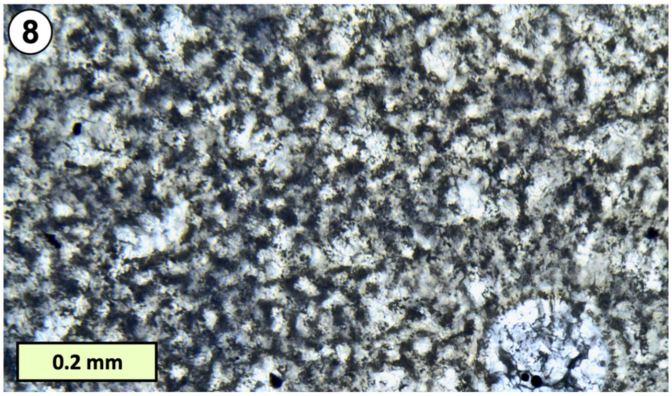
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