Stromatoporoids and extinctions

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Abstract

Stromatoporoids are common shallow marine hypercalcified sponges in two major episodes with distinctive skeletal architectures: 1) Palaeozoic: Early to Middle Ordovician, to Late Devonian; and 2) Mesozoic: Late Triassic to Cretaceous and rare Cenozoic, but not confirmed in Permian and earlier Triassic strata. Stromatoporoids appeared in Early to Middle Ordovician strata, important in buildups from late Middle Ordovician metazoan expansions (Great Ordovician Biodiversification Event). Throughout the Palaeozoic, some stromatoporoid taxa occur across several palaeocontinents, and, if they are the same *biological* taxa, presumably migrated as larvae across oceans, implying biotic resilience. Palaeozoic stromatoporoids suffered 5 events of decline; Event 1): end-Ordovician Mass Extinction; surviving forms are more typical of the Silurian, marking change of abundance from labechiid to clathrodictyid forms. Event 2): late Silurian to Early Devonian contraction: stromatoporoids became scarce with low generic diversity, presumably related to global sea-level fall. Intra-Silurian extinction events principally affecting conodonts and graptolites, associated with positive carbon isotope excursions, seem not to have affected stromatoporoids, likely because of their shallow marine benthic habit, contrasting pelagic oceanic planktonic and nektonic fauna influenced by oceanographic changes. Expansion to their late Early to Middle Devonian (Eifelian and Givetian) acme, as one of the Phanerozoic's major global reef systems, was likely linked to global sea-level rise, when epeiric seas expanded, but followed by Event 3): end-Givetian extinction, likely related to sea-level fall; Event 4): Frasnian-Famennian (F-F) extinction; and Event 5): end-Devonian (Hangenberg Event) extinction; 4 and 5 may be related to cooling, anoxia and potentially, magmatism. The apparent stratigraphic gap between end-Devonian and Triassic occurrence is normally interpreted as extinction of Palaeozoic stromatoporoids, but rare Carboniferous examples in England, Russia, USA and Japan prove survival in shallow marine environments. An interpretation that stromatoporoid-grade sponges lost ability to calcify is unlikely, because chaetetid hypercalcified sponges expanded and built reefs in the Carboniferous. Important is those skeletal architectures of hypercalcified sponges, such as stromatoporoids and chaetetids, are regarded as 'grades of organisation' of the skeleton, lacking phyletic value; living stromatoporoid- and chaetetid-grade sponges occur in the Demosponge and Calcarea sponge classes based on spicules. This implies that extinction of sponge taxa that just happened to have been stromatoporoid-grade hypercalcifiers may explain stromatoporoid loss in the end-Devonian, and may point to an unpreserved crisis in non-calcifying Porifera, noting a poor sponge record in end-Devonian strata. Having also survived the end-Permian and end-Triassic extinctions, sponges with ability to produce stromatoporoid-grade skeletons expanded again in the Jurassic, together with sphinctozoan and inozoan grades, then survived the K-Pg extinction although are rare after the Cretaceous. Stromatoporoids seem to be more abundant during calcite seas times, so there may be both an oceanographic chemical control on their development and bias in preservation towards calcite rather than aragonite mineralogy. Overall, the hypercalcifying ability of sponges was not lost throughout their Phanerozoic history; thus, stromatoporoids and other hypercalcified sponges are preserved evidence of resilience of sponges in Earth history, contrasting other celebrated reef-building forms, such as tabulate and rugose corals, and rudist bivalves, that died out.

Keywords: end-Ordovician Mass Extinction; Frasnian-Famennian extinction; Hangenberg extinction; end-Cretaceous extinction; hypercalcified sponges; stromatoporoids; chaetetids

1. Introduction and aims

Stromatoporoids are hypercalcified sponges (Fig. 1), that is they have a calcareous skeleton secreted by soft tissue, overprinting the original organic framework, so the remaining structure found as a fossil is the calcareous skeleton.

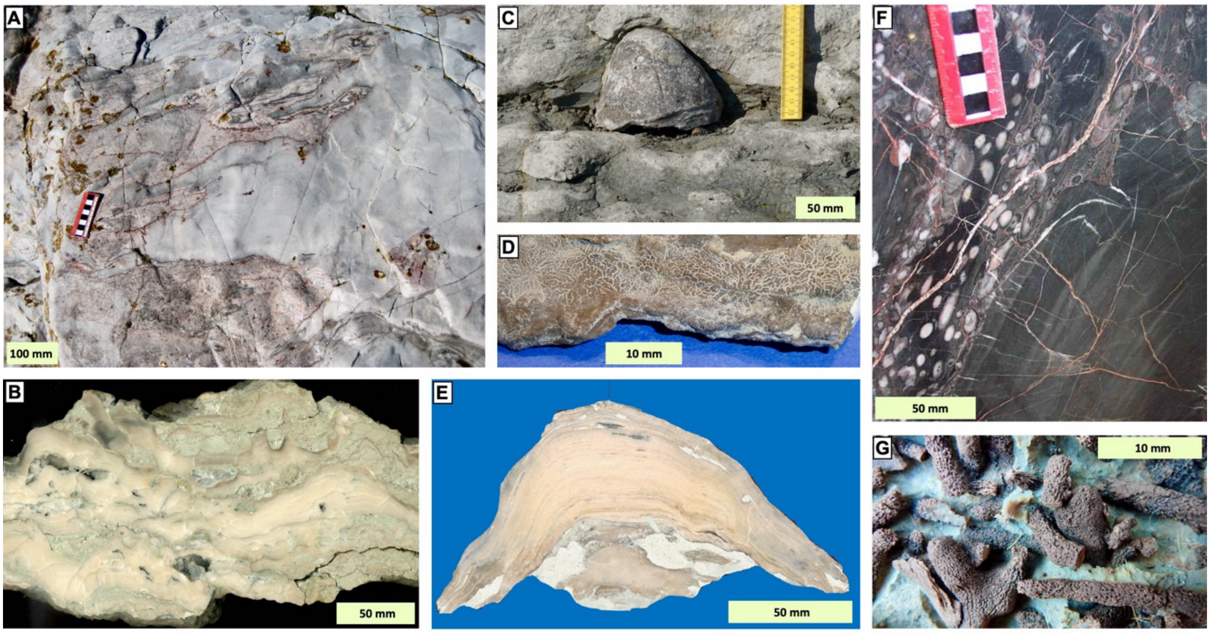


Fig. 1. Examples of fossil stromatoporoids from a range of facies to illustrate their variation. **A.** Vertical section of part of Middle Devonian reef with large laminar to domical stromatoporoids in crinoidal grainstone. Givetian, Long Quarry Point, Torquay, England. **B.** Stromatoporoid framestone of laminar stromatoporoids in Högklint Fm reef, Wenlock, Gotland. Sample donated by Nigel Watts. **C.** Domical stromatoporoid in limestone-marl alternations of open shelf facies. **D**. Detail of encrusting stromatoporoid with astrorhizae on the base of a prior stromatoporoid. **E.** Vertical section through low profile stromatoporoid encrusting a lithoclast comprising

wackestone and a tabulate coral. **C–E** from upper Visby Fm, Wenlock, Gotland. **F.** Back-reef facies wackestones with large bulbous stromatoporoid and branching stromatoporoids and corals, Devonian, southwest England, from a decorative facing stone (Ashburton limestone) in London. **G**. Fragments of branching stromatoporoids: *Amphipora* (thin sticks) and *Stachyodes* (thick pieces); fore-reef facies, Devonian, Canning Basin, Australia.

Stromatoporoids are found in two major episodes of Phanerozoic history (Fig. 2) (Kazmierczak et al., 1985; Wendt, 1980): a) Palaeozoic strata from the Middle Ordovician to the end-Devonian time as major components of carbonate reef systems, having developed during the Great Ordovician Biodiversification Event (GOBE), recognised as a process of change rather than a single event (Servais et al., 2021); b) the Late Triassic to modern times (West et al., 2015), but are scarcely known in the post-Cretaceous record: in the Eocene, and a small number of living sponges with stromatoporoid-grade architectures (Hartman & Goreau, 1970; West et al., 2015). However, although stromatoporoids are indicated in literature in the Permian and the Lower to the Middle Triassic rocks (Kazmierczak, 1985; Wendt, 1980) the compilation by West et al. (2015) did not confirm these.

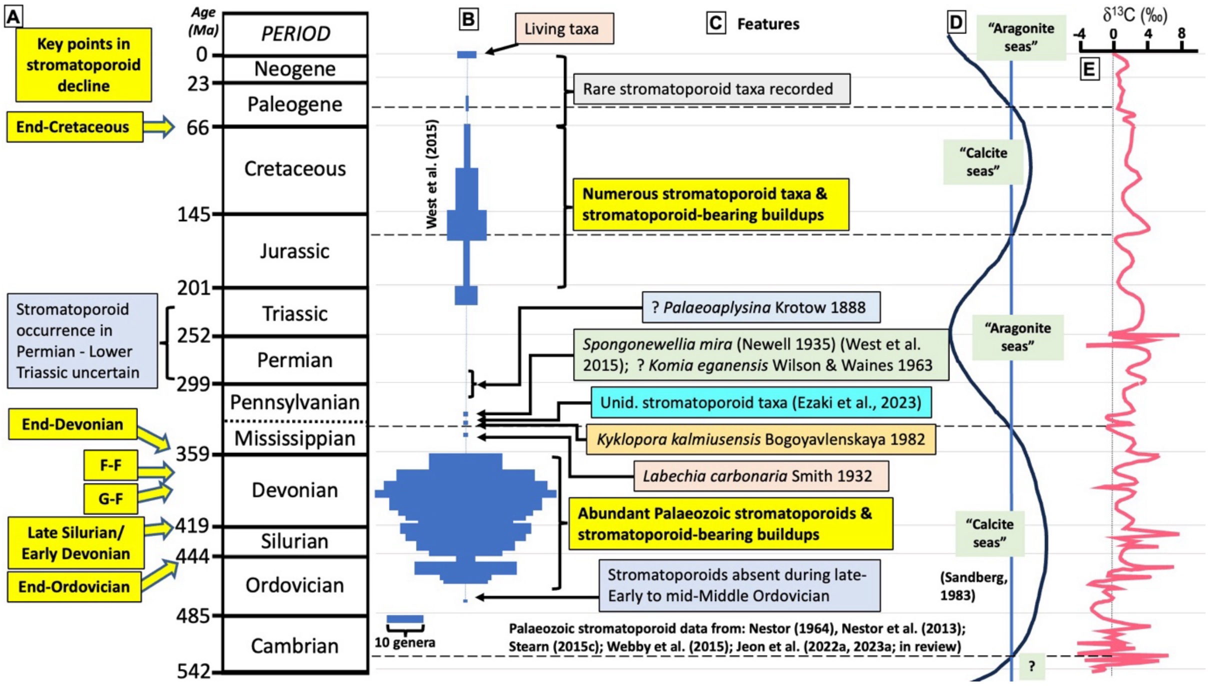


Fig. 2. Summary history of stromatoporoids from Early Ordovician to modern times, discussed in the text. **A.** Key points in stromatoporoid decline against the Phanerozoic time scale; **B.** blue-coloured spindles demonstrate there were two major periods of expansion, in middle Palaeozoic and Mesozoic; **C.** brief statements of abundance, including rare occurrence of stromatoporoids in the Carboniferous, demonstrating that stromatoporoids did not become extinct. *Palaeoaplysina* and *Komia* are included because they are abundant calcified taxa with controversial affinity, but are interpreted as sponges in the Carboniferous by Stock & Stearn

(2015), although are not stromatoporoids; **D.** summary drawing of the Sandberg (1993) curve with crossover points between aragonite and calcite seas; **E.** carbon isotope curve for Phanerozoic.

Stromatoporoids have been widely researched since their first recognition in the Devonian by Goldfuss (1826), with most work focussed on their Palaeozoic forms. Chapters of the Treatise on Paleontology (Nestor, 2015; Stearn, 2015b; Stock, 2015; Webby, 2015b; West et al., 2015) updated their taxonomy and addressed aspects of their palaeobiology and historical development, including extinction. However, in the intervening years several studies warrant an updated synthesis of stromatoporoid changes in time, with a particular need to link their geological history to extinction processes in the light of modern environmental change in the oceans. Literature records that stromatoporoids were affected by extinction events in the latest Ordovician Hirnantian, the Middle to Upper Devonian Givetian-Frasnian transition, the Upper Devonian Frasnian-Fammenian boundary, the end-Devonian Hangenberg event and the end-Cretaceous (Copper, 2002a, b; Stearn, 2015a; Webb, 2002), the causes of which continue to be debated.

Therefore, this study addresses the relationship between stromatoporoids and extinction events, that also requires examination of their historical development. The aims are: 1) to bring stromatoporoids, as hypercalcified sponges, into focus as survivors of extinction and explore the reasons for their survival, all the way through to the present day; and 2) to identify gaps in knowledge to point the way forward for future work. Comment is also made on the history of the other hypercalcified sponges (chaetetids, inozoans and sphinctozoans; see Figs. 3, 4) especially the chaetetids, which have a history partly in parallel with stromatoporoids. In this paper we do not explore details of causes of mass extinctions, a topic for which there is a copious literature; here we focus on how stromatoporoid faunas reacted to extinction and offer interpretations on the controls on the stromatoporoids.

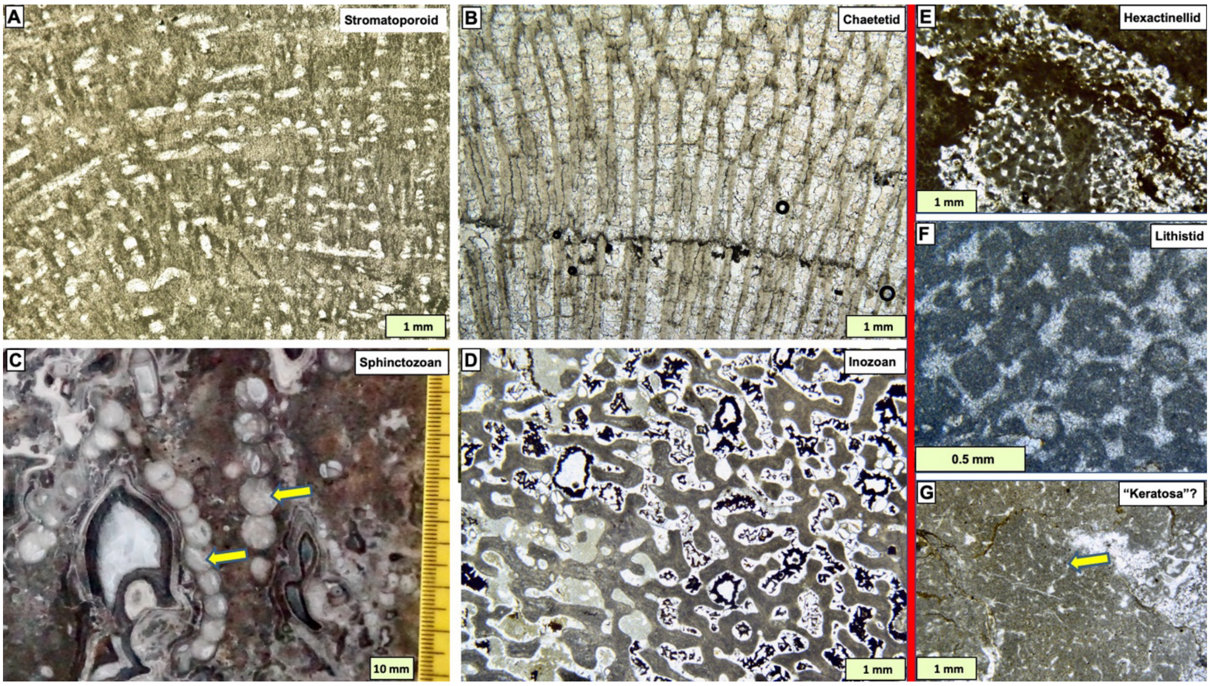


Fig. 3. A-D. Examples of hypercalcified sponge skeletons of sponges, all vertical sections. **A.** Stromatoporoid grade, Wenlock, Shropshire, England; **B.** Chaetetid grade, Mississippian, north Wales, UK; **C.** Sphinctozoan grade, Upper Permian, China; **D.** Inozoan grade, Cretaceous, central England; **E.** Calcified skeleton of hexactinellid sponge, Cretaceous, southern England; **F.** Calcified skeleton of lithistid sponge, Ordovician, Utah, USA. **G.** Post-extinction microbialite with matrix of mottled micrite, interpreted by some authors as a keratose sponge, requiring verification, Permian-Triassic boundary, Sichuan, China.

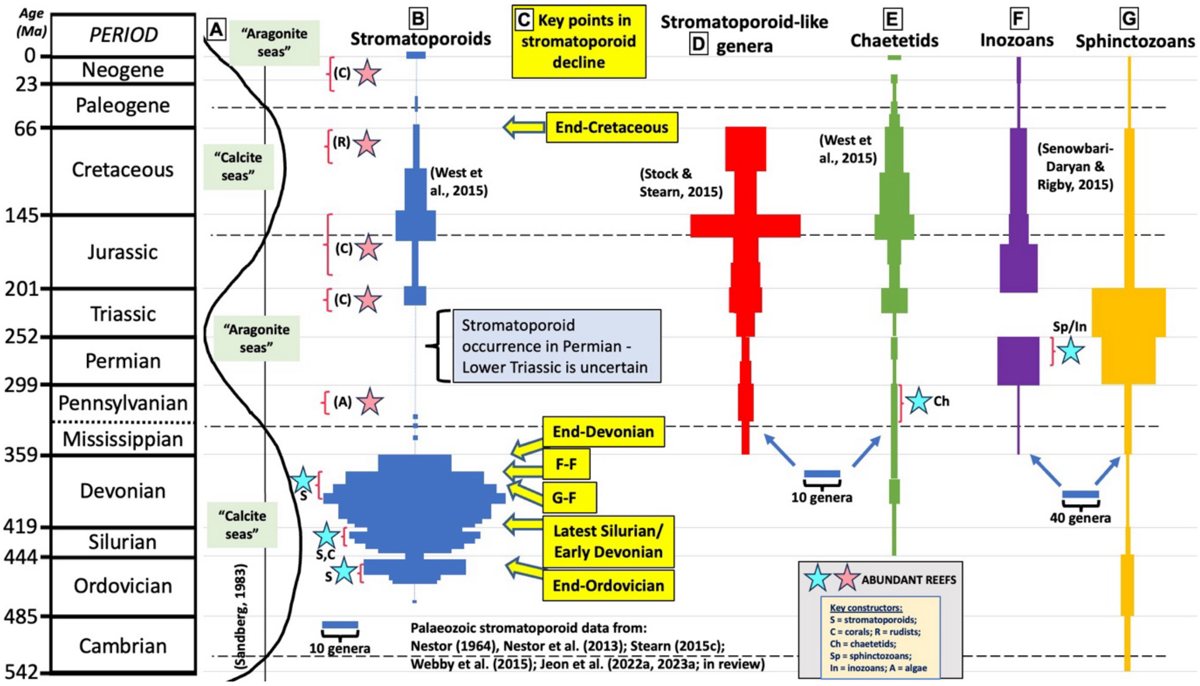


Fig. 4. Summary geological history of hypercalcified sponges, **A–C** are repeated from Fig. 2, for clarity of comparison of hypercalcified sponges. **A.** Phanerozoic timescale and summary of Sandberg (1993) curve aragonite-calcite seas; **B**. Summary history of stromatoporoids, highlighting times of growth of stromatoporoid-rich reefs. Blue stars indicate episodes where reefs contained abundant hypercalcified sponges; pink stars indicate reefs built by organisms other than sponges, included for reference; **C.** Key points of stromatoporoid decline discussed in the text (see also Figs 6, 7); **D**. Stromatoporoid-like genera distribution, from Stock & Stearn (2015), a list of poorly-researched fossils that resemble stromatoporoids; **E-G.** Summary histories of genera diversity of the other three hypercalcified groups, to compare with stromatoporoids, discussed in the text.

2. Stromatoporoid history and phylogeny: impact on understanding their extinctions

2.1. A brief history of stromatoporoids

Search for stromatoporoids earlier than the Middle Ordovician by Webby (2015a) did not confirm their presence, but there is more recent evidence that stromatoporoids are present in strata before the Middle Ordovician (*Cystostroma* and other early stromatoporoids in the Early Ordovician, see Jeon et al., 2023a), so stromatoporoid-grade architectures have a record from the Early Ordovician to modern times. Traditional stromatoporoid studies sought to develop evolutionary trends in stromatoporoid history using stratigraphic changes in the calcareous skeleton (see example compiled by Webby, 2015a, fig. 359), wherein authors interpreted changes of the skeletal structure through time as evidence of stromatoporoid evolution. Furthermore, there are some very large differences of the calcareous skeleton amongst co-eval Palaeozoic stromatoporoids, with some groups having significantly different skeletal architectures from others; such differences may be found in stromatoporoids of different taxa side-by-side in outcrops. Probably the best example is the labechiids, traditionally classed as an order within the class Stromatoporoidea (Webby, 2015b). Labechiid-form stromatoporoids (Fig. 5A, B) are composed of mainly cyst plates with or without vertical elements (e.g., denticles, pillars), sharply contrasting taxa with the more familiar laminae-pillar structure, a good example of which is the clathrodictyid-form (Fig. 5C, D). Labechiid-forms were most abundant during the Ordovician, where they occur along with taxa with clathrodictyid forms, but their diversity declined sharply in the latest Ordovician (Fig. 6) in the first of five events of reduction in stromatoporoid diversity. In most continents, labechiids could not recover their diversity from the Hirnantian losses; only South China shows relatively diverse labechiid taxa compared to their counterparts of Baltica, Siberia and Laurentia (Nestor & Webby, 2013; Stock et al., 2015). However, recent re-confirmation of those early Silurian stromatoporoid specimens from South China by the authors of this paper drew attention to the issue of taxonomic over-splitting. Labechiid-forms became subordinate during most of middle Palaeozoic time, but rebounded after the F/F extinction (Stearn, 2015a). As in Ordovician time, labechiids became dominant after the F/F event, and were primary reef components as in the earlier Ordovician (Stearn et al., 1987; Stearn, 1988; Webby, 2002; Copper, 2002a, b). Labechiids interestingly survived through the end-Devonian Hangenberg event, and occur in the Early Carboniferous (Fig. 5E, F) (Kershaw & Sendino, 2020).

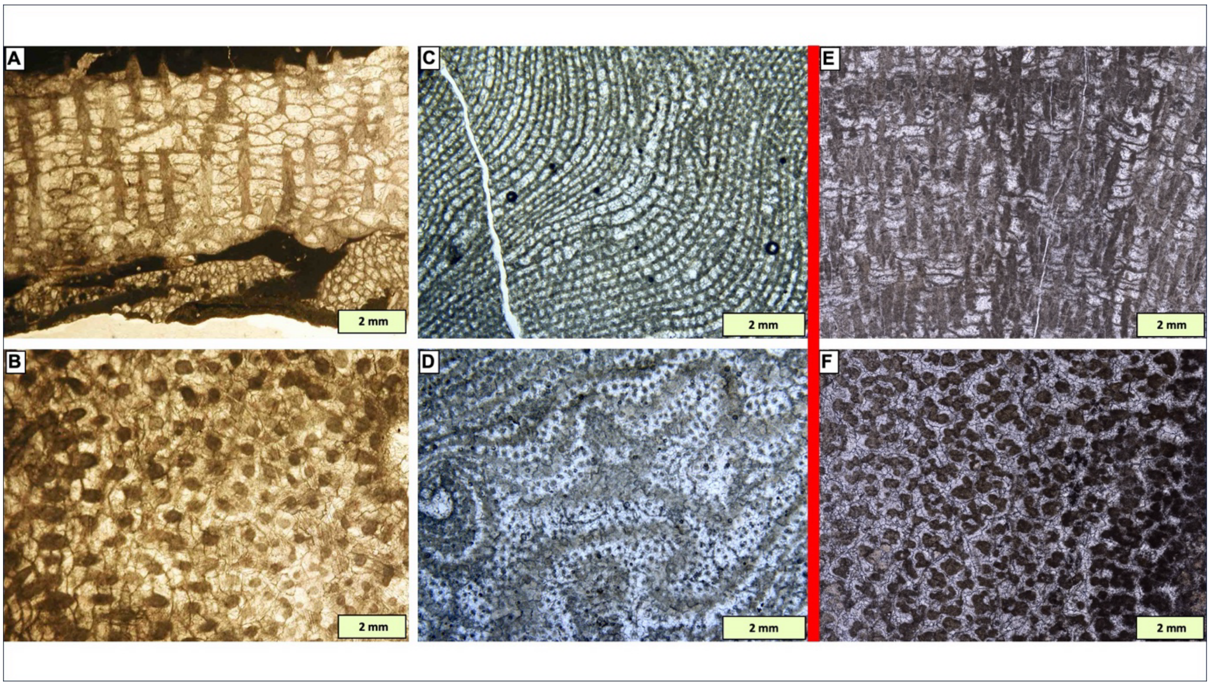
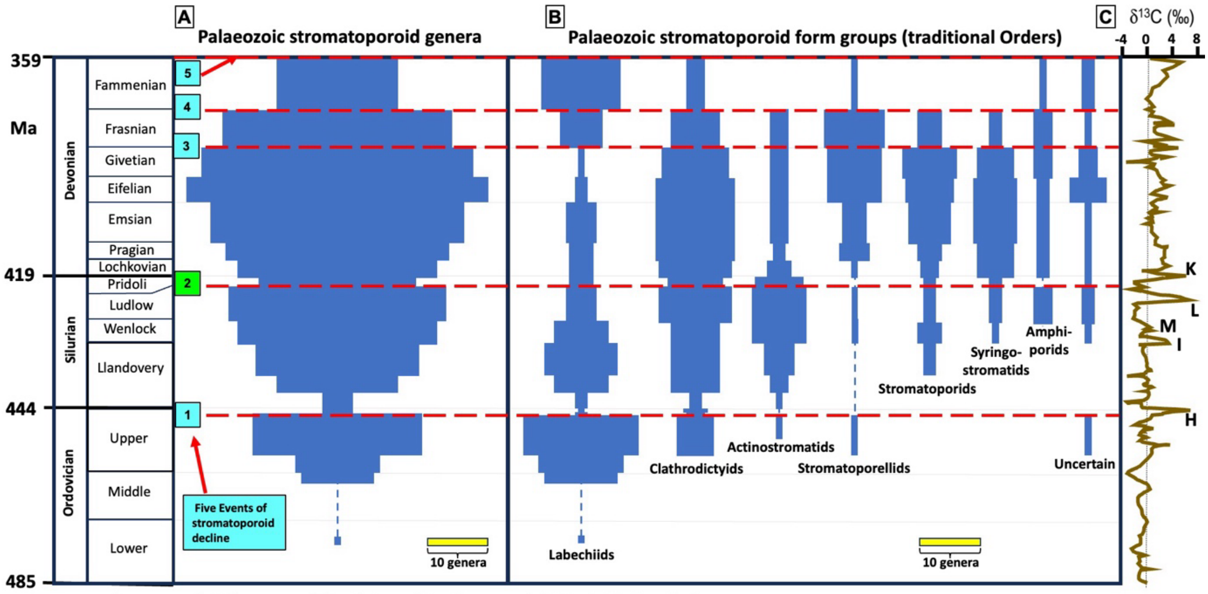


Fig. 5. Contrasts in stromatoporoid architecture, discussed in the text. **A, B.** Vertical and transverse thin sections respectively of *Labechia conferta*, a key labechiid-form stromatoporoid typified by curved cyst plates, and in the case of *Labechia* there are thick pillars. Wenlock, England; **C, D.** Vertical and transverse thin sections respectively of *Petridiostroma simplex*, typified by well-developed laminae and pillars. Wenlock, Gotland, Sweden. **E, F.** Vertical and transverse thin sections respectively of *Labechia carbonaria*, demonstrating a rare stromatoporoid that survived the end-Devonian extinction event, to compare with **A, B**. Mississippian, northern England (after Kershaw & Sendino, 2020).

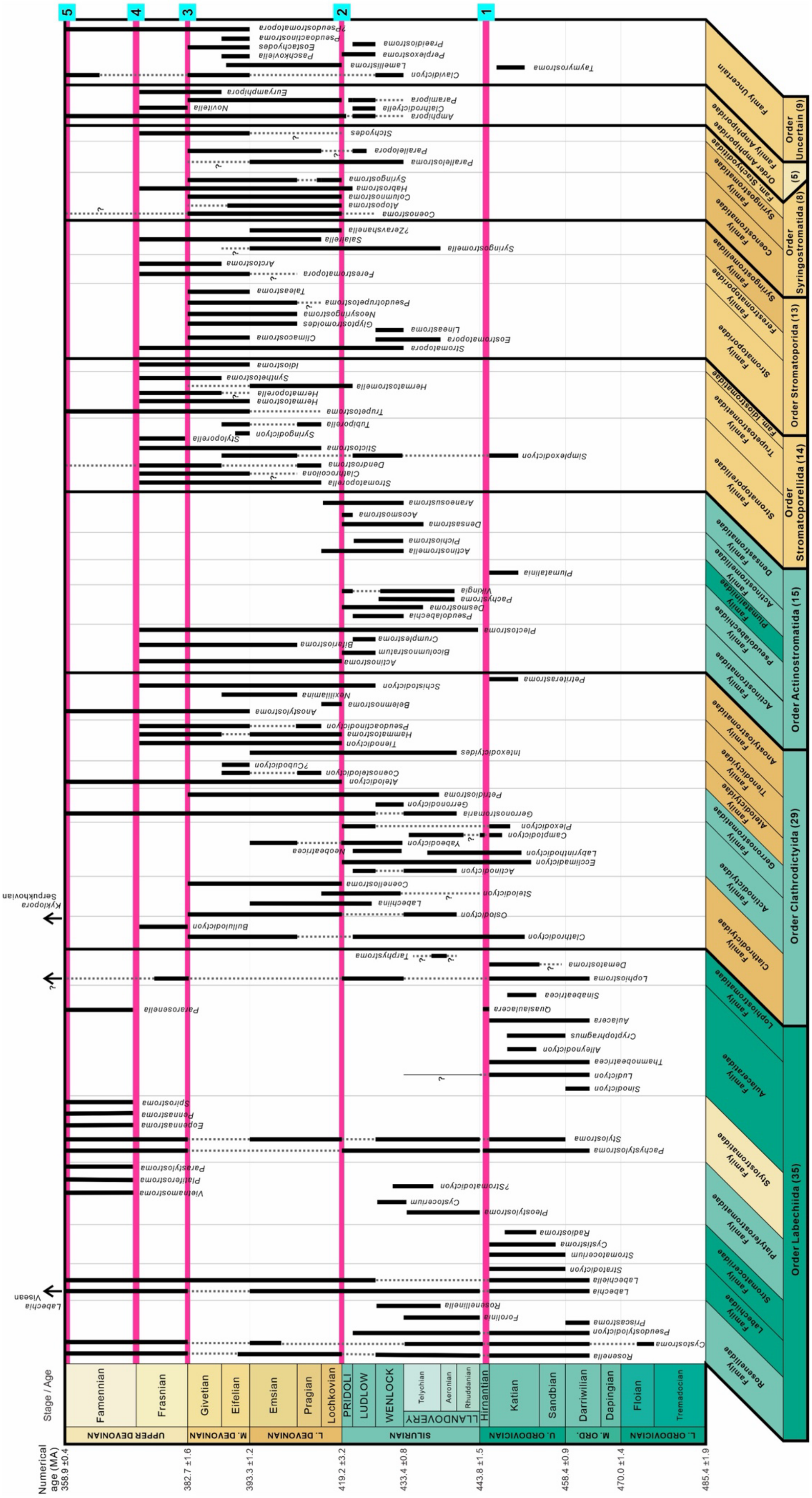


Data from: Nestor (1964), Nestor et al. (2013); Stearn (2015c); Jeon et al. (2022a, 2023a; in review)

Fig. 6. Palaeozoic stromatoporoid generic diversity, based on Stearn (2015c, figs. 360, 361 with updates from the cited references below the figure). **A.** All Palaeozoic stromatoporoid genera, showing expansion in upper Silurian and Middle Devonian times, when the major stromatoporoid-dominated reefs developed. Decline of numbers of genera are linked to five events 1–5, discussed in the text; Events 1, 3, 4 & 5 are classed as extinctions in the literature; Event 2 (distinguished in green colour) is not considered as an extinction, yet shows significant contraction of generic diversity. **B.** Generic diversity within the traditional stromatoporoid Orders, expressed here as form groups, to emphasise the uncertainty of biological relationships within and between the groups, discussed in the text. The diagram emphasises that form groups expand and contract their generic diversity without any specific interrelationship, evidence that they were under different controls in the Palaeozoic history. **C.** The carbon isotope curve for the Palaeozoic, redrawn from Saltzmann & Thomas (2012) and discussed in the text. H = HICE [Hirnantian Isotope of Carbon Excursion]; I = Ireviken CIE; M = Mulde CIE; L = Lau CIE; K = Klonk CIE.

Several stromatoporoid genera continued to occur throughout the Ordovician-Silurian interval, indicating survival of stromatoporoids from the end-Ordovician Mass Extinction events. Faunal turnover during this time shows reduction in a large number of labechiid genera, so that reef construction was principally by non-labechiid stromatoporoids. In particular, major taxa of typical Silurian stromatoporoids, including *Clathrodictyon* and *Ecclimadictyon* forms, first appeared globally and built reefs, at least in the peri-Gondwanan regions, in the Late Ordovician (Webby, 2002, 2015a; Jeon et al., 2022a). Among the peri-Gondwanan regions, North China is characterized by distinctive stromatoporoid assemblage in the Katian Stage of the Late Ordovician, represented by the occurrence of *Plexodictyon*, *Petriterastroma* and *Simplexodictyon* (Jeon et al., 2023b). These genera are rather commonly found in Siluro-Devonian rocks and similar to those typical Middle Palaeozoic stromatoporoids, which are characterised by laminated architectures (Nestor & Stock, 2001; Nestor, 2015; Jeon et al., 2023b).

Throughout the Silurian, groups with prominent laminated architectures, particularly clathrodictyid and actinostromatid forms, were abundant (Fig. 7). There is a significant contraction of stromatoporoid taxa and abundance in the late Silurian to the Early Devonian time, Event 2 of their decline (Fig. 6) that is most likely related to global sea-level fall at that time (Boucot, 1985). However, this episode of decline is not considered as an extinction event for stromatoporoids, largely because many taxa survive into the Devonian (Fig. 7), but clearly stromatoporoids were adversely affected at this time. Thus, stromatoporoids are uncommon from the late Silurian to the first part of the Early Devonian time, but they expanded again in the Eifelian (Fig. 6), when stromatoporoids have their taxonomic acme with a range of skeletal architectures divided into the most diverse of the traditional stromatoporoid orders and families (Nestor, 2015; Stearn, 2015b; Stock, 2015; Webby, 2015b). Devonian stromatoporoids have somewhat different details of architecture from Silurian forms, and thus different taxa but with some overlap between the two periods. Stromatoporoids became globally-distributed reef-builders in low to mid-latitudes of the Givetian (Middle Devonian) (Copper, 2002a, b), with significant development in biostromal settings (e.g. Tian et al., 2024). Stromatoporoids suffered some loss of taxa in the late Givetian, regarded here as Event 3 of their decline (Fig. 7).



5
4
3
2
1
?Pseudostromatopora
Pseudoactinostroma
Eostachyodes
Paschkoviella
Praeidiostroma
Perplexostroma
Lamellistroma
Clavidictyon
Taymyrostroma
Euryamphipora
Paramipora
Clathrodictyella
Novitella
Amphipora
Stachyodes
Parallelopora
Parallelostroma
Syringostroma
Habrostroma
Columnostroma
Atopostroma
Coenostroma
?Zeravshanella
Salairella
Syringostromella
Arctostroma
Ferestromatopora
Taleastroma
Pseudotrupetostroma
Neosyringostroma
Glyptostromoides
Lineastroma
Climacostroma
Eostromatopora
Stromatopora
Idiostroma
Synthetostroma
Hermatostromella
Hermatoporella
Hermatostroma
Trupetostroma
Tubuliporella
Syringodictyon
Styloporella
Stictostroma
Simplexodictyon
Dendrostroma
Clathrocoilona
Stromatoporella
Araneosustroma
Acosmostroma
Densastroma
Pichiostroma
Actinostromella
Plumatalinia
Vikingia
Pachystroma
Desmostroma
Pseudolabechia
Plectostroma
Crumplestroma
Bifariostroma
Bicolumnostratum
Actinostroma
Petterastroma
Schistodictyon
Nexililamina
Belemnostroma
Anostylostroma
Pseudoactinodictyon
Hammatostroma
Tienodictyon
Intexodictyides
?Cubodictyon
Coenostelodictyon
Atelodictyon
Petridiostroma
Gerronodictyon
Gerronostromaria
Plexodictyon
Camptodictyon
Yabeodictyon
Neobeatricea
Labyrinthodictyon
Ecclimadictyon
Actinodictyon
Coenellostroma
Stelodictyon
Labechina
Oslodictyon
Bullulodictyon
Clathrodictyon
Tarphystroma
Dermatostroma
Lophiostroma
Sinabeatricea
Quasiaulacera
Pararosenella
Aulacera
Cryptophragmus
Alleynodictyon
Thamnobeatricea
Ludictyon
Sinodictyon
Spiostroma
Pennastroma
Eopennastroma
Stylostroma
Pachystylostroma
Parastylostroma
Platiferostroma
Vietnamostroma
?Stromatodictyon
Cystocerium
Pleostylostroma
Radiostroma
Cystistroma
Stromatocerium
Stratodictyon
Labechiella
Labechia
Rosenellinella
Forolinia
Priscastroma
Pseudostylodictyon
Cystostroma
Rosenella
Kyklopora Serpukhovian
Labechia Viséan
Family Uncertain
Family Amphiporidae
Order Amphiporida
Fam. Stachyoididae
Family Syringostromatidae
Family Coenostromatidae
Family Syringostromellidae
Family Ferestromatoporidae
Family Stromatoporidae
Fam. Idiostromatidae
Family Trupetostromatidae
Family Stromatoporellidae
Family Densastromatidae
Family Actinostromellidae
Family Plumatalinidae
Family Pseudolabechiidae
Family Actinostromatidae
Family Anostylostromatidae
Family Tienodictyidae
Family Atelodictyidae
Family Gerronostromatidae
Family Actinodictyidae
Family Clathrodictyidae
Family Lophiostromatidae
Family Aulaceratidae
Family Stylostromatidae
Family Platyferostromatidae
Family Stromatoceriidae
Family Labechiidae
Family Rosenellidae
Order Uncertain (9)
(5)
Order Syringostromatida (8)
Order Stromatoporida (13)
Order Stromatoporellida (14)
Order Actinostromatida (15)
Order Clathrodictyida (29)
Order Labechiida (35)
Stage / Age
Famennian
Frasnian
Givetian
Eifelian
Emsian
Pragian
Lochkovian
PRIDOLI
LUDLOW
WENLOCK
Telychian
Aeronian
Rhuddanian
LLANDOVERY
Hirnantian
Katian
Sandbian
Darriwilian
Dapingian
Floian
Tremadocian
UPPER DEVONIAN
M. DEVONIAN
L. DEVONIAN
SILURIAN
U. ORDOVICIAN
M. ORD.
L. ORDOVICIAN
Numerical age (MA)
358.9 ±0.4
382.7 ±1.6
393.3 ±1.2
419.2 ±3.2
433.4 ±0.8
443.8 ±1.5
458.4 ±0.9
470.0 ±1.4
485.4 ±1.9

Fig. 7. Stratigraphic ranges of each stromatoporoid genus within the traditional stromatoporoid orders and families, together with timelines of the five events of stromatoporoid decline during Palaeozoic history; dashed lines indicate stratigraphic gaps in each stromatoporoid genus; the fine line of Silurian *Ludictyon* with a question mark indicates uncertainty of its occurrences, it is reported in only South China by Dong & Yang (1978); question marks indicate uncertain occurrences which require further confirmation. The numbers in brackets in the lowermost box are the estimated numbers of genera for each order. The colours of traditional orders and families in the bottom of the chart indicate when those higher-taxonomic groups of stromatoporoids show high diversity among the Ordovician, Silurian and Devonian. Pink horizontal lines indicate the five events of stromatoporoid decline; Event 1): end-Ordovician Mass Extinction, Event 2): late Silurian to Early Devonian, Event 3): end-Givetian extinction, Event 4): Frasnian-Famennian extinction, and Event 5): end-Devonian (Hangenberg Event) extinction from the bottom to top of the chart. Data are mainly based on Webby et al. (2015), but also included new taxa in Jeon et al., (2022b, 2023b), and the extended range of *Labechia* into the Early Carboniferous, which was confirmed by Kershaw & Sendino (2020).

Stromatoporoid extinction is best known for the Frasnian-Famennian (F/F) boundary (Event 4) and the end-Devonian Hangenberg (Event 5) (Stearn, 2015a). After the collapse of stromatoporoid-dominated communities at the end of the Devonian Period, stromatoporoids have a poor fossil record in the Carboniferous, Permian and Triassic (Wendt, 1980). However, verification of their presence in Carboniferous rocks (Kershaw & Sendino, 2020; Ezaki et al., 2023; Nestor, 2015; Newell, 1935; Wood et al., 1989) is a clear demonstration that stromatoporoids did not become entirely extinct at the end of the Devonian, but locally survived, represented by a few relicts. Subsequently, there are no recorded Permian and Early to Middle Triassic stromatoporoids in the most up-to-date compilation of the 2015 Treatise (see West et al., 2015). Thus, in their confirmed Mesozoic return (Late Triassic to Cretaceous) stromatoporoids display very different details of skeletal architecture from the Palaeozoic, and of great importance is the abundance of spicules in Mesozoic stromatoporoids; spicules are absent from all except one specimen of Palaeozoic stromatoporoids (Da Silva et al., 2014). Spicules are critical because modern sponge taxonomy relies upon them, and therefore it was possible to relate Mesozoic stromatoporoids to modern sponges (Cuif & Gautret, 1991a; Vacelet, 1981, Wood, 1987), in contrast to Palaeozoic stromatoporoids. Cuif & Gautret (1991b) applied study of microstructures in an attempt to link ancient and modern hypercalcified sponges, but this approach does not work for Palaeozoic stromatoporoids because they are extensively recrystallised so that microstructures are not reliable (Kershaw et al., 2021a). Fig. 8 shows a detailed comparison between stromatoporoid and chaetetid grades, whereby microstructure of a Carboniferous chaetetid calicle walls is well-preserved in contrast to stromatoporoids (Fig. 8D,E); however, a Jurassic chaetetid in Fig. 8F-I shows partial recrystallisation, with fabric-retentive diagenetic overprinting, as in stromatoporoids; Fig. 8C also contrasts the well-preserved character of rugose corals and the partly recrystallised syringoporid tabulates, these are both taxa that form intergrowths with stromatoporoids so that all three organisms were alive together. In addition to their survival of Ordovician, Devonian and Cretaceous extinctions (three of the traditionally-recognised “Big Five” mass extinction events of the Phanerozoic [not to be confused with the five events shown in Figs 6, 7], the occurrence of Mesozoic stromatoporoids demonstrates that the hypercalcifying ability of sponges clearly also survived the other two extinctions (end-Permian and end-Triassic), contrasting groups such as tabulate and rugose corals (extinct at end-Permian), and even rudist bivalves (extinct at end-Cretaceous).

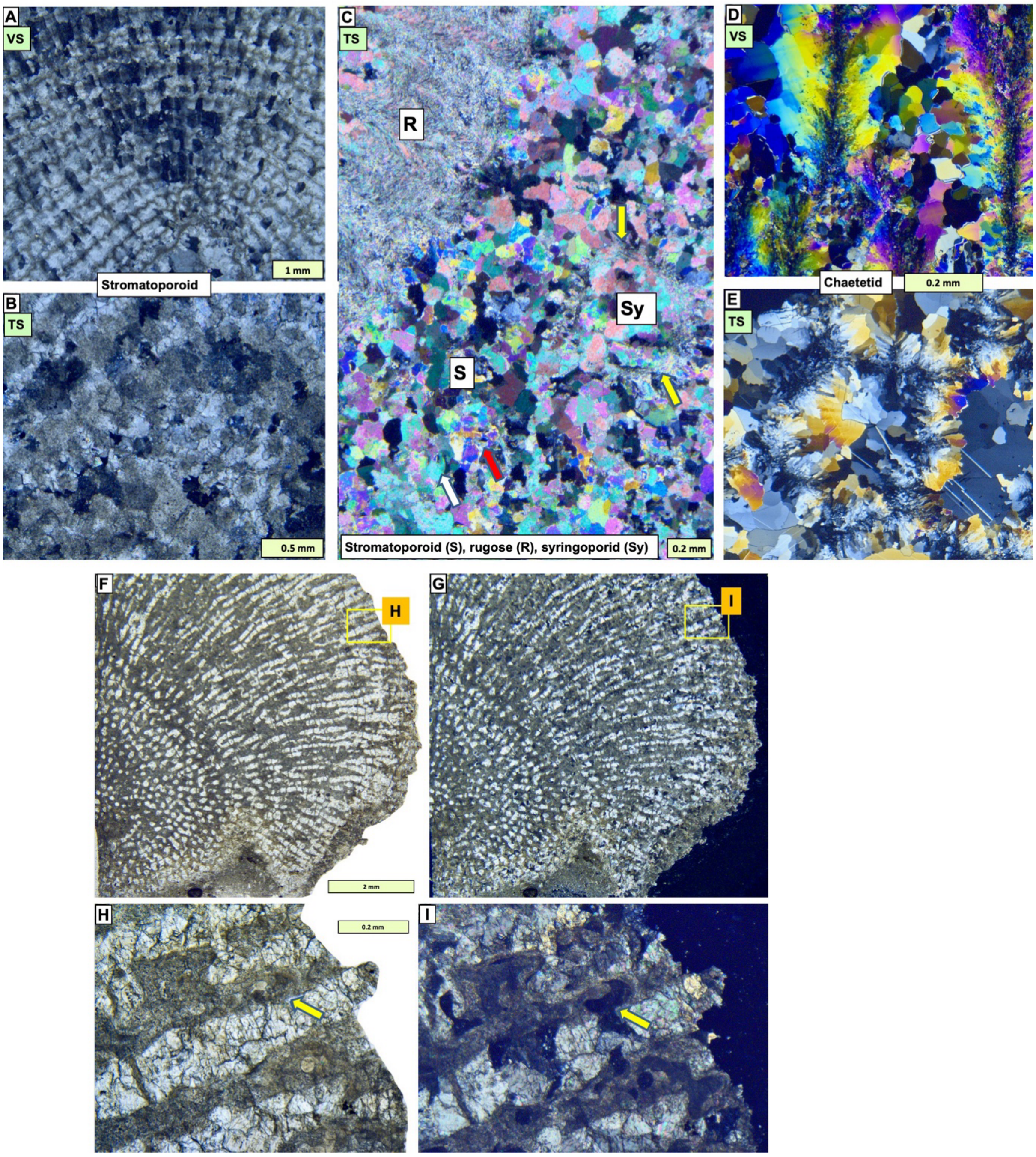


Fig. 8. Details of characteristics of hypercalcified skeletons of stromatoporoid-grade and chaetetid-grade sponges, demonstrating variation in preservation, together with intergrown corals. **A–E** in cross-polarised light. **A, B.** Vertical and transverse sections respectively of *Petridiostroma simplex* from Wenlock of Gotland. The

skeleton is indurated with fabric-retentive irregular calcite (FRIC) crystals (Kershaw et al. 2021a) that overprint the skeleton and demonstrate it is partially recrystallised. This raises a key problem of the original skeletal composition of stromatoporoids, in relation to the aragonite-calcite seas debate, see text for discussion. **C.** Thinner than normal transverse thin section of *Petridiostroma convictum*, Ludlow of Gotland, showing the skeleton, **C** (red arrow), is difficult to see within the irregular FRIC crystals, but can be distinguished from the gallery cement (white arrow) in the skeleton. The stromatoporoid contrasts the well-preserved rugose coral wall, upper left (R) and the partially altered transverse section through a symbiotic syringoporid tube, that has a laminated wall that is partly recrystallised, the yellow arrows show location of opposite outer margins of the tube wall. **D, E.** Vertical and transverse sections of very thin thin sections of chaetetid, Pennsylvanian, Kansas, showing the wall fibres are very well-preserved, in contrast to the altered stromatoporoid. **F-I.** PPL (**F, H**) and XPL thin section views of a Jurassic chaetetid showing fabric-retentive recrystallisation where diagenetic overprinting crosses the calicle walls and calicle cavity cements (compare yellow arrow location in **H, I**). Basal Cabaços Formation, middle Oxfordian, at Cabo Mondego, Lusitanian Basin, central Portugal (Azaredo et al, 2002); sample provided by Simon Schneider.

2.2. Stromatoporoid classification issues

Stromatoporoids had been considered as possible sponges in earlier literature of late 19th and early 20th Centuries, from the work of Kirkpatrick, Twitchell, von Rosen and others (see Wood 1990 for a review), but confirmation came from 1960s onwards. Hartman (1969) reported calcified sponges from Jamaica, followed by the landmark study by Hartman and Goreau (1970), confirming the poriferan affinity of stromatoporoids by comparison with modern calcified sponges, but applied the term sclerosponges to indicate the calcified sponges were a separate group within the Porifera. However, Vacelet's (1985 and references therein) synthesis from spicule studies confirmed that modern calcified sponges are representatives of different subclasses within the Demosponges and Calcarea and therefore the concept of a separate group (sclerosponges) was abandoned. Thus, it was possible to place Mesozoic stromatoporoids within the modern sponge groupings, achieved by West et al. (2015). The result of these efforts demonstrated that although the calcified skeleton of Mesozoic stromatoporoids may be used for low-level taxonomic identification (species and genera) it has no value in higher-level groupings, and led to the development of concept of grades of organisation to describe the skeletal architecture, resulting in four grades for the calcified sponges. Hence stromatoporoids form one grade, the other three are chaetetids, sphinctozoans and inozoans (Fig. 3). However, Wood (1990) pointed out that, despite the profound differences between the particular examples shown in Fig. 3, these grades do not have sharp boundaries, which implies that separation of one group (here, the stromatoporoids) as a phylogenetic system is not appropriate. A good example is the Carboniferous hypercalcifed sponge *Spongonewellia mira* (originally named *Parallelopora mira* by Newell, 1935, then named *Newellia mira* by Wood et al., 1989, but because *Newellia* is a pre-occupied genus name, Özkidmen, 2009, renamed it *Spongonewellia*). Illustrations in Newell (1935, plate 34, figs 6a, 7a) show that in vertical section this fossil may be classified as stromatoporoid grade (and was named as a stromatoporoid by Wood et al., 1989), but in transverse section the same specimen is more consistent with chaetetid grade!

The implication of the above discussion for Palaeozoic stromatoporoids leads to a significant dilemma; are the traditional orders of stromatoporoids, based on their carbonate skeletal architecture, valid phylogenetic groups or not? It may be that certain groups are phyletically distinct, in particular the labechiids, that skeletal architectures are distinctly different from other stromatoporoids (Fig. 5). Unfortunately, most stromatoporoids have sufficient similarity of construction so that discrimination into lineages has no firm basis, so that it becomes impossible to develop a reliable concept of evolution in stromatoporoids. This uncertainty led sponge workers in 1980s and 1990s cited above to disregard the traditional groupings of Palaeozoic stromatoporoids as being of no evolutionary significance.

While the consequence of the problems outlined above shows that, as an avenue of research, study of stromatoporoid evolution has no scientific basis, there is a further problem, exemplified by the report from Reitner & Engeser (1987) of three different species in specimens of the modern chaetetid-form hypercalcified sponge *Acanthochaetetes* where the calcareous skeletons are identical. However, even though *Acanthochaetetes* is not a stromatoporoid-grade taxon, within the modern stromatoporoid-like calcified sponge *Astrosclera willeyani*, Wörheide et al. (2000) found much variation in spicule morphology, and examined the sponge for variations in DNA. The result indicated there are three different species in skeletons that have the same architecture (Wörheide et al. 2000). If these revelations from modern sponges are considered for Palaeozoic stromatoporoids, they raise the possibility that more than one biological species may exist within an identical skeletal architecture. Developing this concept further, an example was found by Kershaw et al. (2021b, p. 17), working on Silurian stromatoporoids in the UK, where they noted two form-species *Ecclimadictyon macrotuberculatum* and *Ecclimadictyon astrolaxum*, that occur in the same assemblages; they are sufficiently different to warrant different names of morphological description, and they may even be different species. However, even if they are biologically different, there is no certainty that they are species in the same genus. This issue is of course applicable to most fossils of organisms generally, and is a well-known problem to palaeontologists; but the key point is that we may be lulled into a false sense of security of acceptance of these form-species as having a biological significance that has not been demonstrated.

Consequently, although there are consistent differences between traditional stromatoporoid taxa at low levels of taxonomy that would imply distinction into form-genera and form-species, it is prudent to regard them as suspect taxa groups, so that the traditional approach of describing Palaeozoic stromatoporoids using genera and species levels, may be missing potential biological variation of significance. A particular worry is that one stromatoporoid form-species in one location may look identical to a form-species in another location, yet they may be different biological entities. The same might apply for identical form-species of successive ages in a stratigraphic sequence. Such problems may have significant implications for palaeobiogeographic studies of dispersal of stromatoporoids from one palaeocontinent to another. A good example of this problem is the late Silurian of Baltica and Laurentia, that were on opposite sides of the closing Iapetus Ocean. The genus *Parallelostroma* occurs in reefs in the late Silurian of New York (Stock 1979) and the Silurian of Gotland (Mori 1970) and Estonia (Nestor, 1966) therefore may or may not indicate that the larvae of these benthic fossils could cross the ocean. *Parallelostroma* was distinguished into some different species in the New York material by Stock (1979), but there is an open question as to whether or not these are the same biological species as those found in the Baltic region. Furthermore, a co-eval taxon *Stromatopora bekkeri* originally found in Estonia by Nestor (1966), and subsequently on Gotland (Mori, 1970) and New York (Stock, 1979), has an architecture that overlaps in some specimens with that of *Parallelostroma typicum*, and also in part resembles *Coenostroma* and *Habrostroma* (see Kershaw & Motus, 2016, p. 36). Indeed, it became clear that *Stromatopora bekkeri* is not consistent with the revision of *Stromatopora* by Stearn (1993), but is a distinctive taxon, and is referred to as *"Stromatopora" bekkeri* by Kershaw & Motus (2016) pending a definitive resolution. In the cases of overlapping architecture, it seems impossible to resolve this potential problem of separating taxa, but researchers need to be aware of its possibility because of the effect it has on interpreting the palaeogeographic distribution of stromatoporoids. Nevertheless, despite overlaps of skeletal architecture in the particular stromatoporoid taxa above, most stromatoporoid taxa are distinctive enough to apply a low-level taxonomy with reasonable confidence that they are likely to be different genera and, potentially, species.

Wörheide (2008) used molecular sequencing and other analyses to show that the living sphinctozoan hypercalcified sponge *Vaceletia*, an aspiculate sponge with a hypercalcified skeleton, belongs to the keratose group of sponges. If this connection is alignment with Palaeozoic stromatoporoids, which are also hypercalcified aspiculate sponges, it raises the interesting possibility that they may have been, or included, sponges that belonged to keratose sponge. However, this remains impossible to conclusively validate and further emphasise how little we really know about the taxonomy and phylogeny of Palaeozoic hypercalcified sponges of stromatoporoid grade.

2.3. Stromatoporoid vs modern sponge diversity

Palaeozoic stromatoporoids are limited to a relatively small number of genera compared to the much larger diversity in modern Porifera. Figure 7 records 128 stromatoporoid genera grouped into 28 traditional families, and 7 traditional orders. That total of 128 genera applies through their entire Palaeozoic history, noting a maximum of 48 genera at their acme in the Givetian. Living sponges have 680 genera grouped into 128 families and 25 orders (van Soest et al., 2012), only 10 of which are hypercalcifiers, commonly viewed as being outcompeted by corals in reefs, due to their slower growth. Of course, the record of sponge genera in past history is incomplete; most sponge fossil genera are were not hypercalcifiers (Finks et al., 2004). Therefore it seems self-evident that stromatoporoid (and other hypercalcified sponge) fossils represent only a limited part of what was a much larger range of taxa and abundance of sponges in the rock record. An indication of this in modern sponges is shown from the genus *Merlia* that has four species, only two of which calcify and thus a fossil record of living *Merlia* could not represent the full range of this genus (Vacelet & Uriz, 1991; West, 2011, p 37). Furthermore, Vacelet & Uriz (1991) explored the difficulties of confirming the taxonomic stability of this sponge that has facultative calcification; they also pointed out (p. 176) that populations of *Astrosclera* in the central Pacific lack spicules. Wood (2011, p. 381) provided a poignant reminder of this issue, noting from prior studies that skeletal taxa in general (not just sponges) represent 70% of organisms on modern open-reef surfaces in Jamaica, but deeper reef facies are dominated by non-skeletal organisms, which are not always preserved in the fossil record. Studies of modern sponges note that sponges break down and disappear soon after death (Debrenne, 1999; Wulff, 2016). Nevertheless, there are no studies on the taphonomy of modern non-calcifying sponges, so details of exactly what happens to sponges after death, and the potential for their preservation, are currently unknown. This has implications for understanding the history of sponges, including non-calcified keratose sponges, for which there are controversial opinions about their existence in carbonate rocks (see Luo & Reitner 2014; Neuweiler et al. 2022); this is a field of research that needs developing.

Against the backdrop of the above discussion, it may seem that extracting useful information about extinctions of stromatoporoids is highly problematic. However, evidence is evidence, and it is an observed fact that certain form-species and form-orders underwent significant expansions and contractions, with some extinctions, at certain points in geological history, and demand explanation. We just need to be careful not to fool ourselves into believing that we are dealing with confirmed biological entities in stromatoporoid taxa, and therefore analyse the evidence with our eyes open. Thus, the approach in this paper is that each traditional stromatoporoid species is treated as the lowest-level of taxon obtainable, and each is considered of equal status to all others, with no determined relationship between them. Thus, the use of traditional orders and families is for descriptive purposes only, with no implication of biological relationship, below the level of phylum Porifera.

3. Stromatoporoids and their relationship with extinctions: key features

Stromatoporoids show decline in numbers and abundance of taxa at various times throughout their history. For their Palaeozoic record, we identified five events of decline, four are recorded in literature as extinctions, the fifth is not, and we use the term contraction to describe it. The following subsections explore these events and the response of stromatoporoids to other extinctions.

3.1. End-Ordovician Mass Extinction and stromatoporoids; Event 1

Recent literature shows that during the end-Ordovician mass extinction stromatoporoids were less severely affected than in the Devonian extinctions. It is clear that labechiid-form and clathrodicytid-form taxa continued from the Katian Stage, through the end-Ordovician mass extinctions, into the Silurian; recent focus in China revealed that both North and South China blocks were important geographic areas for development of Late Ordovician stromatoporoids, which continued to develop in Silurian and Devonian strata (Jeon et al. 2023b). Stromatoporoids common in Silurian rocks had their origins in the Late Ordovician, then became dominant and diversified through the Silurian. Consequently, the end-Ordovician mass extinction seems instead to have provided a springboard for the Silurian expansion of stromatoporoids, particularly for those with prominent laminae in their skeletal architecture (Jeon et al. work in progress). Bond & Grasby (2017, p. 6) drew attention to evidence that glaciation began before the Hirnantian and continued into the Silurian, reducing the likelihood that glaciation was the cause of the extinction, pointing instead to changes in global ocean temperature and redox conditions. Given that glaciation is itself a change in global ocean temperature, it is reasonable to interpret that stromatoporoids were affected by the cooling; overall, the effect on stromatoporoids was extreme, proven by sharp decrease of stromatoporoid diversity (Figs 6, 7).

Given that stromatoporoids are associated with warm-water environments, the occurrence of stromatoporoids in some Hirnantian rocks indicates that those environments were warm enough for stromatoporoids. Hirnantian stromatoporoids are known from only Anticosti Island in eastern Laurentia (Nestor et al., 2013), Estonia in Baltica (Nestor, 1964), and South China (Jeon et al., work in progress). Findings of Hirnantian stromatoporoids in these regions indicate that there was a favourable and hospitable environment for stromatoporoids at least along the equatorial regions, which most likely acted as refugia. It is noteworthy that the clathrodictyid-form taxon *Ecclimadictyon porkuni* occurs throughout the Hirnantian to Rhuddanian rocks of Estonia (Nestor, 1964). On Anticosti Island, *Ecclimadictyon anticostiense* and *Labyrinthodictyon angulosum* occur throughout the Hirnantian Ellis Bay Formation, and the latter taxon is most abundant in the reefal Laframboise Member (Fig. 9) of the upper formation (Nestor et al., 2013). Interestingly, a typical cold water-indicating brachiopod *Hirnantia* fauna has not been found in the Ärina Formation of Estonia and the Ellis Bay Formation of Anticosti Island, although the faunas have been reported in other Hirnantian rocks geographically close to these regions (see Rong et al. 2020; Rong Jiayu, personal communication, 2022). Hirnantian stromatoporoids in South China occur along with the warm water Edgewood-Cathay Fauna, succeeding the earlier Hirnantian cold-water *Hirnantia* Fauna (Rong et al., 2020; Jeon et al., 2022b). In particular, stromatoporoids in South China are dominated by clathrodictyid genera *Camptodictyon* and *Ecclimadictyon*, which made their appearance globally in the earlier Katian (Webby et al., 2015; Stock et al., 2015; Jeon et al., 2022a). Thus, Hirnantian stromatoporoids occur from the earlier Ordovician with the exception of *Quasiaulacera*. This genus, belonging to aulaceratid stromatoporoid, is known to occur within only the Lousy Cove Member of the Ellis Bay Formation, Anticosti Island (Copper et al., 2013). Almost all aulaceratid stromatoporoids disappeared at the end-Ordovician Mass Extinctions, one example reported in South China (Dong & Yang 1978) is unconfirmed. Nevertheless, refugia yielding stromatoporoids but lacking the *Hirnantia* Fauna may have existed beyond our current recognition. The absence of the *Hirnantia* Fauna in these aforementioned units was probably due to their warmer environments compared to locations where brachiopods belonging to the *Hirnantia* Fauna occur. Taken together, these interpreted refugia developed along the equatorial regions to provide favourable environments for stromatoporoids to continue their palaeoecological and reef-building roles through the Late Ordovician glaciation, highlighting palaeogeographic effects on stromatoporoids in extinction.

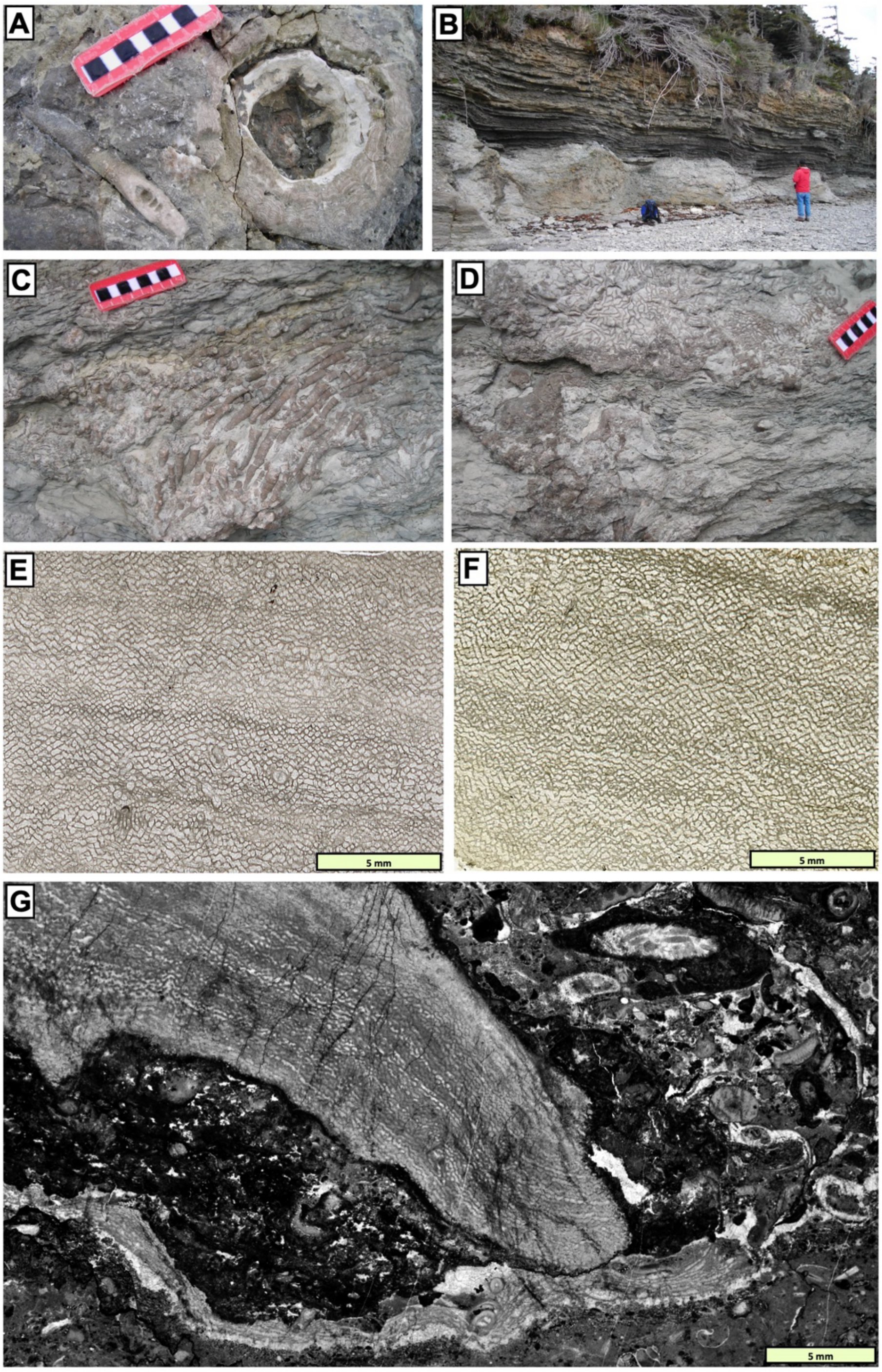

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Fig. 9. Hirnantian stromatoporoid-bearing rocks, stromatoporoids and associated biota. **A.** Field photograph of *Quasiaulacera* in the Lousy Cove Member of the Ellis Bay Formation, Anticosti Island. See Copper et al., 2013 for the detail description. **B.** general view of patch reefs in the Laframboise Member of the Ellis Bay Formation. **C, D.** Closeup view of corals in the Laframboise reefs in the Ellis Bay Formation; these reefs contain uncommon stromatoporoids (not illustrated). **E, F.** Examples of Hirnantian stromatoporoids. **E.** GIT 113-48, *Ecclimadictyon porkuni* (Riabinin, 1951) from the Porkuni Regional Stage (Hirnantian) in the Siuge quarry, Estonia. **F.** GIT 333-159, *Ecclimadictyon porkuni* (Riabinin, 1951) from the Undva 580 borehole of the Juuru Regional Stage, drilled in Tagamõisa hoiuala of Saaremaa Island, Estonia. Note that the clathrodictyid *Ecclimadictyon porkuni* occurs continuously throughout the uppermost Ordovician to the lower Silurian strata of Estonia.
G. Hirnantian stromatoporoids from the Uppermost Ordovician (Hirnantian) Shiqian Formation of South China. Note that the occurrence of the calcareous alga *Dimorphosiphon* (upper right corner) and the large clathrodictyid *Camptodictyon* enveloped by dark-coloured microbia and the labechiid *Cystostroma* (centre bottom).

3.2. Silurian extinctions, isotope excursions and stromatoporoids

Reefs took a long time to recover after the end-Ordovician extinction, with full recovery attained by the Telychian (Li & Kershaw, 2003), but throughout the Llandovery, stromatoporoids were relatively uncommon compared to their expansion in the Wenlock (Figs 6, 7). Calner et al. (2004, fig. 3) summarised the stratigraphy of the Silurian of Gotland, Sweden, that exposes strata from latest Llandovery to near the top of the Ludlow Series. The Gotland sequence is one of the best worldwide for its exposure of an almost completely continuous middle to upper Silurian record. The Gotland sequence displays abundant stromatoporoid assemblages, which were synthesised by Mori (1969, 1970), who demonstrated variations in abundance and taxonomic diversity throughout the Gotland column. In the last twenty years, research on stable isotopes revealed significant changes in carbon isotopes throughout the Gotland sequence, that have been recognised internationally (see Calner et al, 2004, and references therein). Three significant positive carbon isotope excursions (CIEs) are associated with stromatoporoid-bearing limestones on Gotland: early Wenlock Ireviken CIE, late Wenlock Mulde CIE and late Ludlow Lau CIE. These three CIEs are linked to extinction events amongst conodonts and graptolites, and three events are identified, partly overlapping the CIEs: Ireviken, Mulde and Lau Events (see Calner 2004, fig. 3 for compilation). The CIEs and events are considered to have global oceanographic significance, although verified explanations of the causes of the excursions and events are works in progress by the various authors involved. Details of these isotope excursions and events are given by Munnecke et al. (2003) and Cramer & Saltzman (2005) for the Ireviken Event; Cramer et al. (2012) for the Mulde Event (dubbed the “Big Crisis”), and Younes et al. (2017) and Bowman et al. (2021) for the Lau Event. Fig. 10 was compiled from Mori’s (1969, 1970) monographs and shows a simplified version of the stratigraphy, to show fluctuations in numbers of traditional stromatoporoid species. Nestor (1966) described the same taxa in Estonia as in Gotland, presented in broad stratigraphic divisions that likely extend into the Pridoli, noting that Pridoli-age strata do not occur on Gotland. There is no obvious correlation between stromatoporoid generic diversity and the three CIEs; instead, the stromatoporoid assemblages are much more closely related to the facies, being abundant and diverse in shallow marine carbonate-rich sediments, especially as biostromes, but with bioherms in some levels.

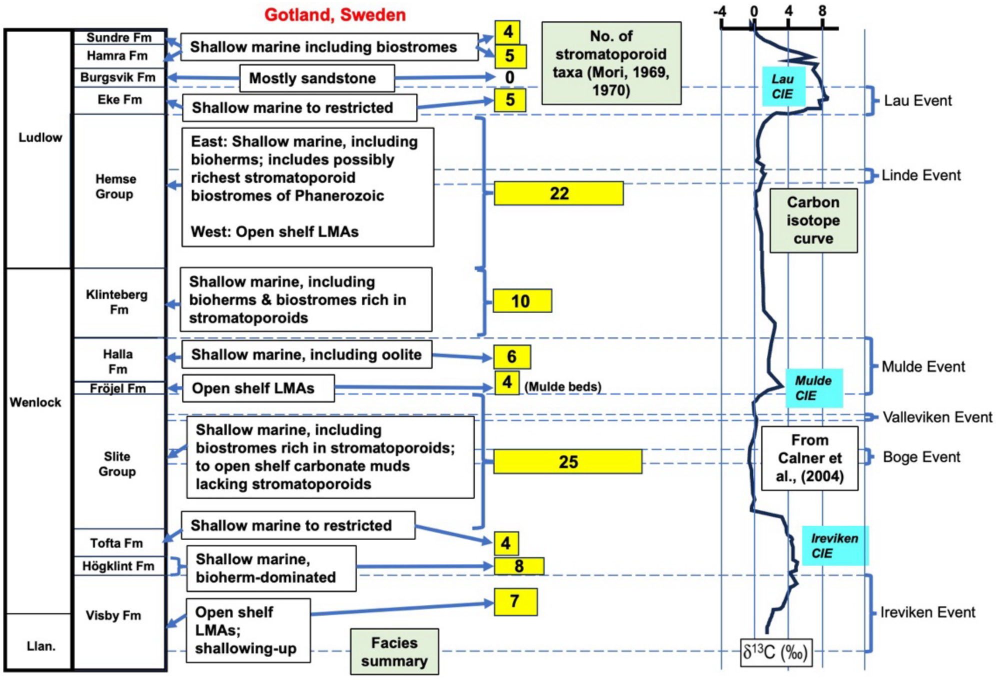


Fig. 10. Compilation of stromatoporoid taxa, based on traditional species, from Mori (1969, 1970) through the Wenlock to Ludlow stratigraphy of Gotland, Sweden. Note that the stratigraphy used by Mori was older, and in this compilation has been altered to the modern stratigraphy provided by Calner et al. (2004). Alongside the lithostratigraphic names, brief information on facies is provided, then a summary of taxa, combined from Mori (1969, Table 1) and Mori (1970, Table 1). Some revision of these taxa from prior studies has been included, and some others may require revision; nevertheless, the overall diversity variations in this diagram are an appropriate reflection of stromatoporoid occurrence in the strata. The three positive carbon isotope excursions (Ireviken, Mulde and Lau) that are associated with named extinction events are shown, right. Although the Ireviken case does not match with stromatoporoid occurrence, there seems to be some relationship with the Mulde and Lau cases, discussed in the text.

Kershaw et al. (2021b) attempted to relate stromatoporoids of the UK to Silurian extinctions. British stromatoporoids occur in the later part of the Wenlock, coinciding with the Mulde excursion. The Much Wenlock Limestone Formation of central England and parts of southeastern Wales formed in a brief episode of raised sea levels during a time when clastic supply from the adjacent Caledonian orogenic system was reduced; the stromatoporoids and corals took advantage of a time-limited window to develop the Silurian reefs found sporadically in Britain. Kershaw et al. (2021b) expressed the view that stromatoporoid and coral larvae were available plankton but were able to settle and develop only in conditions of low sedimentation rates, in carbonate-rich environments. For Gotland, Fig. 10 shows a reduction in stromatoporoids at the time of the Mulde events, but it is not clear whether the extinction affected the stromatoporoids or their reduction was simply due to shallowing, noting that oolites are abundant in the parts of the Halla Formation, conditions not suitable for stromatoporoid growth. Prior to that time, the early Wenlock Ireviken event is represented by clastics in Britain, but in Gotland the facies are largely carbonates, showing a regression from open shelf Visby Formation to shallow marine and marginal facies in the Tofta Formation (Fig. 10). Facies effects overprint any possibility of recognising extinctions on stromatoporoids.

The best possibility of recognising extinction in Silurian stromatoporoids seems to be associated with the Lau isotope excursion and Event (Fig. 10). The widespread biostromal deposits of the middle and late Ludlow on Gotland (Mori, 1970) decline in the late Ludlow. The latest Ludlow and Pridoli (displayed well in Gotland and Estonia, see Mori, 1970, Nestor, 1966), and in the Gaspé peninsula of eastern Canada (Pope, 1985; Bourque et al., 2000), preserves reduced stromatoporoid diversity. However, in the New York State area of eastern Laurentia (Figs 11, 12), Stock (1979) recorded a well-developed stromatoporoid assemblage in the Pridoli and earliest Devonian. Stock (1979) noted that stromatoporoid development was associated with shallow marine conditions in an otherwise lower sea level, when facies were marginal and affected by widespread evaporite deposition. Stock drew attention to common silicification of stromatoporoids in the New York Pridoli stromatoporoids, interpreted as related to the evaporative conditions, an example of which is given in Fig. 12. Kershaw et al. (2021a) noted silicification affected some stromatoporoids in the Ludlow biostromes on Gotland, and there are proposals (Kershaw, 2023; Samtleben et al., 2000) that those biostromes may have developed in an episode of raised salinity. Nevertheless, care needs to be applied when interpreting the reasons for stromatoporoid decline in the late Silurian: although on Gotland, the marginal marine Eke Fm has few stromatoporoids (Fig. 10), age-equivalent shallow marine facies in nearby Estonia show a diverse stromatoporoid and coral fauna (Kershaw & Motus, 2016), providing evidence that it is local facies, rather than the wider controls of extinction, that have a greater effect on the development of stromatoporoid assemblages.

A detail regarding late Silurian stromatoporoid taxa and stratigraphy demonstrates one of the problems of interpreting extinctions in relation to controls on stromatoporoid growth. Nestor (1966, Table 4) shows stromatoporoids in Wenlock and Ludlow strata in Estonia include the taxon *Clathrodictyon mohicanum* in Ludlow unit K2 (K1-K4 is the stratigraphic range given by Nestor, based on the older imprecise stratigraphy; K1 is Wenlock and lower Ludlow, K2 is the Paadla Stage for much of the Ludlow in modern terminology, K3 is uppermost Ludlow and lower Pridoli, K4 is upper Pridoli; see Ruben & Sarv, 1996). *C. mohicanum* is very abundant in the middle Ludlow Hemse Group on Gotland but does not occur in the overlying Eke Fm, and not in the remaining younger strata on Gotland (Mori, 1970). *C. mohicanum* is also missing from Eke-equivalent biostromes at Katri in Estonia (Kershaw & Motus, 2016), and likewise does not occur in younger strata in Estonia (Nestor, 1966). Thus, *C. mohicanum* has a remarkably short range, noting that it is the most abundant stromatoporoid in the Hemse Group biostromes on Gotland (Sandström & Kershaw, 2008); in one site it is 42% of the assemblage (Kershaw, 1990). In contrast to *C. mohicanum*, two other key taxa in Gotland (*Parallelostroma typicum* and *Plectostroma scaniense*) occur abundantly in the Hemse Group and become the two key taxa in the younger strata (Mori, 1970); they have the same stratigraphic range in Estonia, K2 and K3 (Nestor, 1966), noting that in Estonia Nestor (1966) used the name *P. intermedium*, although *P. intermedium* and *P. scaniense* are indistinguishable as the same taxon (Sandström & Kershaw, 2008). In these three taxa we see a small example of a single taxon (*C. mohicanum*) that is abundant in one stratigraphic unit in both Gotland and Estonia, but then disappears from the rock record shortly afterwards, regardless of facies, yet the other two taxa continue without any reduction. This example seems to emphasise the concept of background extinction, as individual taxa arise and later disappear.

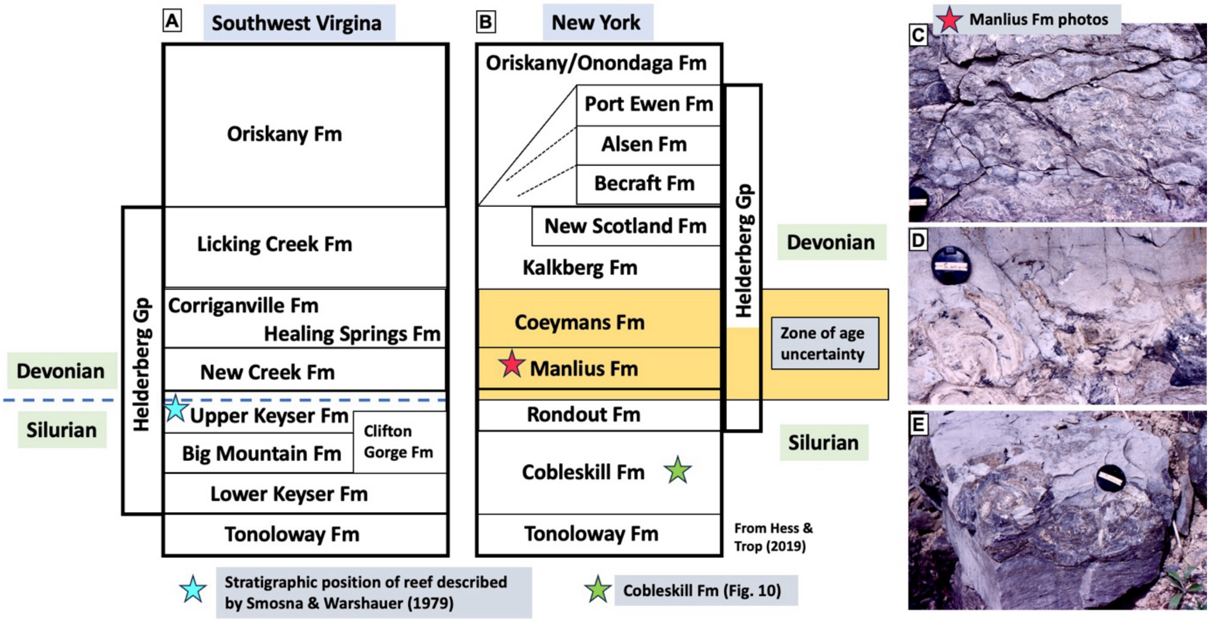


Fig. 11. A, B. Summary stratigraphy of latest Silurian to earliest Devonian stratigraphy in key parts of eastern Laurentia that have been investigated in detail, demonstrating the stratigraphic relationships between stromatoporoid-bearing units. Redrawn from Hess & Trop (2019). **C–E.** Field photos of a stromatoporoid biostrome **C** and details **D, E** from the Manlius Formation, of either late Silurian or very earliest Devonian time, New York State. These photos demonstrate a thriving stromatoporoid community during this time of contraction of stromatoporoids across the Silurian-Devonian boundary interval; see text for discussion.

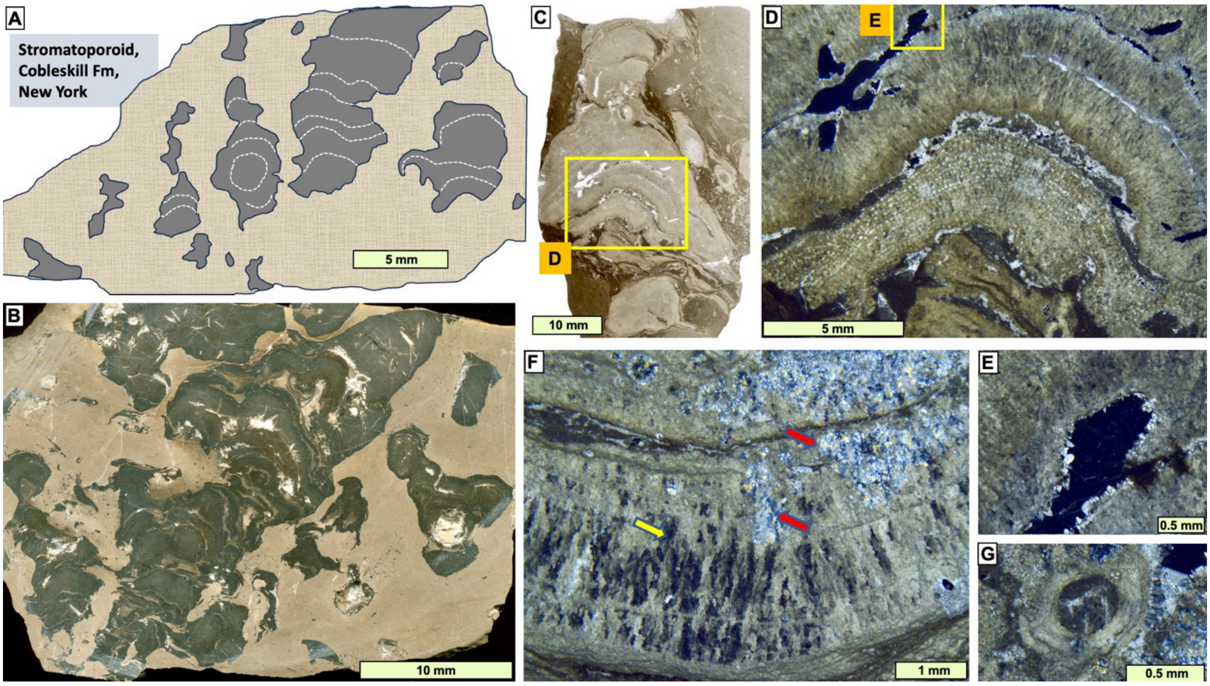


Fig. 12. Stromatoporoid growth of Pridoli age, from the Roundout Formation, Cobleskill Member, New York State, demonstrating some key features of stromatoporoids from the late Silurian to Early Devonian interval, when stromatoporoids show a diversity and abundance contraction, discussed in the text. **A.** vertical section drawing from the field, showing several vertically elongate stromatoporoids with an irregular bulbous morphology. **B.** is a vertical section polished block from A; stromatoporoid is dark brown set in a light brown matrix that is rich in microdolomite rhombs (not shown); white patches are calcite cement filling solution cavities in the stromatoporoid, probably present because of the poor preservation of stromatoporoid skeletons. **C.** Vertical thin section scan from another part of **B**, showing the vertically elongate domical growth. **D.** Enlargement of box in **C**, showing there are two taxa here, likely *Habrostroma* and *Densastroma*, that are found commonly in the Pridoli (Stock, 1979; Stock & Burry-Stock, 2020). **E.** Enlargement of box in **D**, showing dissolution cavity in the stromatoporoid, with lining of calcite crystals that grew on the cavity walls; the cavity demonstrates the relative ease with which stromatoporoids can be affected by diagenesis. **F.** Enlargement of another thin section from **B**, of *Densastroma*, showing the prominent vertically-orientated FRIC alteration that is normal to the growth layers (yellow arrow), and is universal in stromatoporoids. The photo also shows silicification overprinting the carbonate (red arrows), attributed by Stock (1979) to the shallow marine evaporative conditions of facies of this time period, and is interpreted to reflect the overall lowered sea level across the Silurian-Devonian boundary, see text for discussion. **G.** Transverse section through an encrusting auloporid tabulate tube on a partially silicified portion of *Densastroma*, demonstrating growth on an interruption surface in the stromatoporoid, a common feature in stromatoporoids.

3.3. Late Silurian to Early Devonian pinchpoint in stromatoporoid history; Event 2

Through the time period from latest Ludlow and Pridoli (Silurian) to the Lochkovian and Pragian (Early Devonian), stromatoporoids became significantly less abundant and diverse compared to the prior Silurian and later Middle Devonian widespread reef development (Figs 4, 6, 7), see also Stearn (2015c). This contraction is curious because that episode is not considered an extinction in stromatoporoids even though faunas declined. It may or may not be significant that there is a large positive CIE and an event in conodonts and graptolites (Fig. 6) (the Klonk Event; see Racki et al., 2012). Saltzman (2002) explored the impact on the global carbon cycle of this positive isotope excursion across the Silurian-Devonian boundary; shifts in nutrient delivery to the oceans from terrestrial erosion associated with sea-level fall were interpreted to have led to reduction in oxygenation in deeper waters. However, the effects on the shallow shelf, where stromatoporoids lived, are more problematic to link to oceanic changes in the carbon cycle, as is in the case of the Ireviken, Mulde and Lau excursions considered above. Haynes et al. (2018, p.11, 12) provided a succinct summary of the facies in eastern Laurentia, recounting the shallow marginal marine to evaporative nature of that region. Bełka et al. (2010) summarised Devonian facies across much of northern Europe and noted the high clastic contents of Lower Devonian sediments, followed by transgression to form carbonate platforms in the Middle Devonian. Coupled with the regressive nature of Laurentian latest Silurian facies associated with the Caledonian-Appalachian and Salinic Orogenies (e.g. Bourque et al., 2000; van Staal et al. 2009), there is an indication of widespread facies restriction reducing suitable habitat available for stromatoporoids. Stearn (2001, fig. 1) showed the range of stromatoporoids in Lower Devonian strata in Arctic and Western Canada have a low point in the Pragian. Stock (1994), considering the palaeogeography across the late Silurian to Early Devonian recognised the disappearance from North America of stromatoporoids in the Eastern Americas Realm (eastern Laurentia) during the Pragian and interpreted them to have survived in refuges in European areas, then returned to North America during the Emsian (the last stage of the Lower Devonian). However, globally the underlying Lockhovian has fewer taxa. Stock (1979), Stock & Burry-Stock (1998, 2020), Stock & Holmes (1986) detailed stromatoporoids through this interval, noting the problems of definition of the Silurian-Devonian boundary in this region (Fig. 11) (Hess & Trop, 2019, fig. 3), contrasting the definition of the golden spike in the Czech Republic (Cohen et al., 2013, updated). The papers by Stock and co-workers showed the taxa through the latest Silurian to earliest Devonian continue to reflect upper Silurian forms, but in the Emsian new taxa appear that become typical Devonian faunas (e.g. Stearn, 2001, fig. 1). Smosna & Warshauer (1979) described a small reef in the upper Keyser Limestone Fm in Virginia, presented by them as being a very early Devonian reef, although because of stratigraphic imprecision, it is more likely that this reef is latest Silurian (Fig. 11A). Fernández-Martínez et al. (2010) reported small coral-stromatoporoid reefs from earliest Pragian of northern Spain, containing 6 stromatoporoid taxa, 5 of which are rare, and include a mixture of late Silurian and Early Devonian genera. May & Rodriguez (2012) identified 10 stromatoporoid species from Pragian of Spain. More are mentioned from Spain by Copper (2002b, p. 195) as well as Lochkovian and Pragian reefs reported in the Northwest Territories of Canada (see Copper, 2002b, p. 192). The implication of these Early Devonian developments is that although there was a contraction of stromatoporoids across the Silurian-Devonian transgression, this did not disrupt the integrity of the stromatoporoid assemblages, so a loss of habitat due to sea-level fall affecting a robust sponge biota may be a reasonable explanation.

May (2022), addressing the issue of the period of stromatoporoid contraction in the Early Devonian, proposed three possible causes: 1) raised or reduced water temperature, a suggestion that would need corroborating information; 2) Stromatoporoid taxa that built the Middle Devonian reef maximum had only just come into existence and not yet built reefs; this idea implies that the decline of stromatoporoid reefs in late Silurian to Early Devonian time was due to decline in stromatoporoids and thus has merit; 3) Stromatoporoid reefs were assisted by symbiotic organisms, such that part of the reason for their success was presence of symbiotic syringoporids. May (2022) noted there was a break in the presence of *Syringopora* commensals during the late Silurian to Early Devonian episode, and interpreted that as a cause of reef decline. Nevertheless, stromatoporoid symbionts tend to be features of the richest developed shallow marine stromatoporoid-rich reef systems (bioherms and biostromes); they are much less common in deeper water open shelf stromatoporoids, and there is evidence that such symbionts occur by chance (Kershaw, 2023). Vinn (2016) drew attention to the geological history of the organisms that formed symbionts and noted they are present in rocks before and after the mid-Palaeozoic history of stromatoporoids; thus, the symbionts may have taken opportunistic advantage of the existence of stromatoporoids through the time when they were abundant in shallow marine systems (Kershaw, 2023). Further work is required to further investigate the possible importance of symbiotic intergrowths in stromatoporoid reef development.

Malkowski & Racki (2009), and Racki et al. (2012) interpreted cooling at the Silurian-Devonian boundary, the Klonk Event, although this is right at end of Pridoli, after the major reduction in stromatoporoids in the late Ludlow. It is an open possibility that the contraction relates to loss of habitat for stromatoporoids because of sea-level fall. Also regression leads to increased clastic deposition, and we know well that stromatoporoids are found in carbonate-rich facies, they are not components of clastic facies. Capel et al. (2022), considering the "Silurian-Devonian terrestrial revolution", noted increase of plant richness in the Pragian, using material from China (Inner Mongolia, Yunnan, Zhejiang provinces), Brazil, Canada, France, Belgium. Likewise, Morris & Edwards (2014) identified increased plant complexity in Lochkovian compared to Pridoli time in the Welsh Borderland of UK. Nevertheless, if loss of habitat caused by sea-level fall is proposed as a cause for extinctions at the end of the Givetian (see below), then this contrasts the interpretation that sea-level fall caused contractions (but not extinction) of stromatoporoids across the Silurian-Devonian boundary. Perhaps the difference is the increased input of nutrients to the oceans in the Givetian case, although in modern environments sponges grow well in higher nutrient environments that cause coral decline (e.g. Bell et al., 2013).

A significant problem for knowledge of stromatoporoids in the Early Devonian is that there are no taxonomic studies in the Lower Devonian of South China, although they are recognised as one of the main reef builders along with corals (Yu et al., 2021). Previous studies simply listed stromatoporoid taxa from the Lower Devonian rocks (e.g., Hou & Wang, 1988; Dong & Wang, 1990). Low diversity of stromatoporoids has been confirmed in the Lower Devonian exposed in Guangxi and Yunnan provinces (Hou & Wang, 1988), but no taxonomic description had been made. In Sichuan Province, stromatoporoids in the Lower Devonian Ganxi and Xiejiawan formations (early to middle Emsian in age) are also characterised by relatively low diversity (listed 5 genera 7 species of traditional taxonomy from the

Ganxi Formation and one *Stromatopora* species from the Xiejiawan Formation in Dong & Wang, 1990), similar to faunal patterns from other continents (Dong & Wang, 1990). In contrast, stromatoporoids become abundant in the Ertaizi Formation (7 genera, 11 species; late Emsian in age) together with corals (Dong & Wang, 1990). Stromatoporoids become rare in the overlying Yangmaba Formation, and only one *Stromatopora* taxon has been reported (Dong & Wang, 1990). Given that Early Devonian stromatoporoids are globally rare and characterised by low diversity, South China holds great promise for expanding knowledge of the late Silurian-Early Devonian stromatoporoid transition and reef development. The low diversity of stromatoporoids reported in this time interval may or may not be due to real lower diversity, noting that less emphasis has been placed on stromatoporoids in this interval. However, many Lower Devonian outcrops in Guangxi and Yunnan provinces have not been investigated in detail, but are known to present several stromatoporoid reefs there (Yu Chang-Min, personal communication, 2023). Comprehensive study of the Early Devonian is thus required to fully explore the earlier time interval as maximum reef development was achieved in the subsequent Givetian stage (Yu Chang-Min, personal communication, 2023).

3.4. Givetian-Frasnian transition and stromatoporoid loss; Event 3

Bond & Grasby (2017) surveyed mass extinctions in geological time and noted that there were numerous events in the Devonian. The Zlichov, Daleje (Lower Devonian), Chotec and Kacak (Middle Devonian) had no recorded impacts on stromatoporoids, but the Taghanic Event in late Givetian time is recognised as having affected stromatoporoids. Ebert (1993) interpreted stepwise processes of extinction and noted regressions at that time. Copper (2002a, p. 31) viewed stromatoporoid extinctions near the end of the Givetian Stage as being more significant than those of the F-F. Stock (2005) provided a detailed discussion of stromatoporoid history throughout the Devonian, and noted that originations of stromatoporoid taxa were greater than extinctions until the end of the Givetian, after which extinctions were greater. The causes of this change for stromatoporoids are not clear because Stock (2005, fig. 3) illustrated that sea level overall rose through Givetian and Frasnian. However, neither Stock (2005) nor Stearn (2015a), in two focused treatments of the Devonian decline of stromatoporoids, mentioned the extinction of stromatoporoids at the late Givetian. Copper (2002b, p. 214) noted that this period was a time of major evaporite deposition, as was the Silurian-Devonian transition considered above. Bridge et al. (2022) summarised several studies that showed a significant temperature fall in the late Givetian, which provides an appropriate cause for increased stromatoporoid extinction at that time. Bridge et al. (2022) proposed collapse of photosymbiosis for the Late Devonian extinctions, related to the theoretical presence of photosymbionts in tabulate corals; for stromatoporoids, despite numerous attempts, there is no evidence of photosymbiosis in these sponges (Kershaw et al., 2018). Thus, there is a possibility that the reduction of the number of stromatoporoid taxa in the late Givetian to early Frasnian was related to a combination of habitat loss due to sea-level fall and lowered temperatures, potentially related to increased clastic supply as mentioned above.

3.5. Frasnian-Famennian boundary extinction effect on stromatoporoids; Event 4

Stromatoporoid reduction in the middle Palaeozoic began in the late Middle Devonian, and the Frasnian-Famennian (F-F) extinction changed the composition of stromatoporoid assemblages, because after the F-F, in the impoverished stromatoporoid fauna, labechiid-type taxa became abundant again (Figs 2, 4, 6, 7, 13) (Stearn 2015c). As in other extinctions of stromatoporoids, the F-F records regression (Copper, 2002b) and there is evidence of anoxia and cooling, as well as reduced habitat due to sea-level fall, affecting shallow marine systems (Copper, 2002a; Bond & Grasby, 2017). Bond & Grasby (2017) noted the potential for magmatism to have played a part in a large igneous province (LIP). A current perspective on this extinction comes from evidence of terrestrial development of land plants, enhancing physical and chemical weathering and thus transport of nutrients from land to the shallow seas, to promote anoxia in the environments where stromatoporoids lived. Support comes from Belka et al. (2010) who recorded clastic Famennian sediments in the southern Belgium area resulting from continental erosion. George & Chow (2002) noted that changes in the faunas of the fore-reef slope of the Canning Basin (Australia) reef system began before the F-F boundary, and the changes seem to relate to sea-level fluctuations that affected the faunas. For the F-F there is also evidence of an effect of volcanism; Liu et al. (2021) presented evidence from mercury contents of sediments across the F-F to interpret volcanism as a key component of the extinction controls. Girard & Lecuyer (2002) interpreted Ce anomalies in conodonts from the F-F facies in the Holy Cross Mountains (Poland) to indicate increased clastic input at that time.

Pujol et al (2006) noted sea-level rise occurred at the same time as hydrothermal and volcanic activity in South Laurussia and North Gondwana; they proposed that increased microbial activity after the F-F (see also Feng et al., 2010) may be related to increased nutrients. Fall in sea level relates to terrestrial ecosystem development of land plants and increased biological weathering may have played a part in stromatoporoid decline. Curiously, plants carried on growing in the millions of years after the F-F, yet reefs still thrived throughout the rest of the Phanerozoic, so the extinction at F-F can be explained only by a combination of coinciding processes. There are still therefore aspects of the F-F extinctions, and the causes of loss of the great majority of stromatoporoids, that remain unclear.

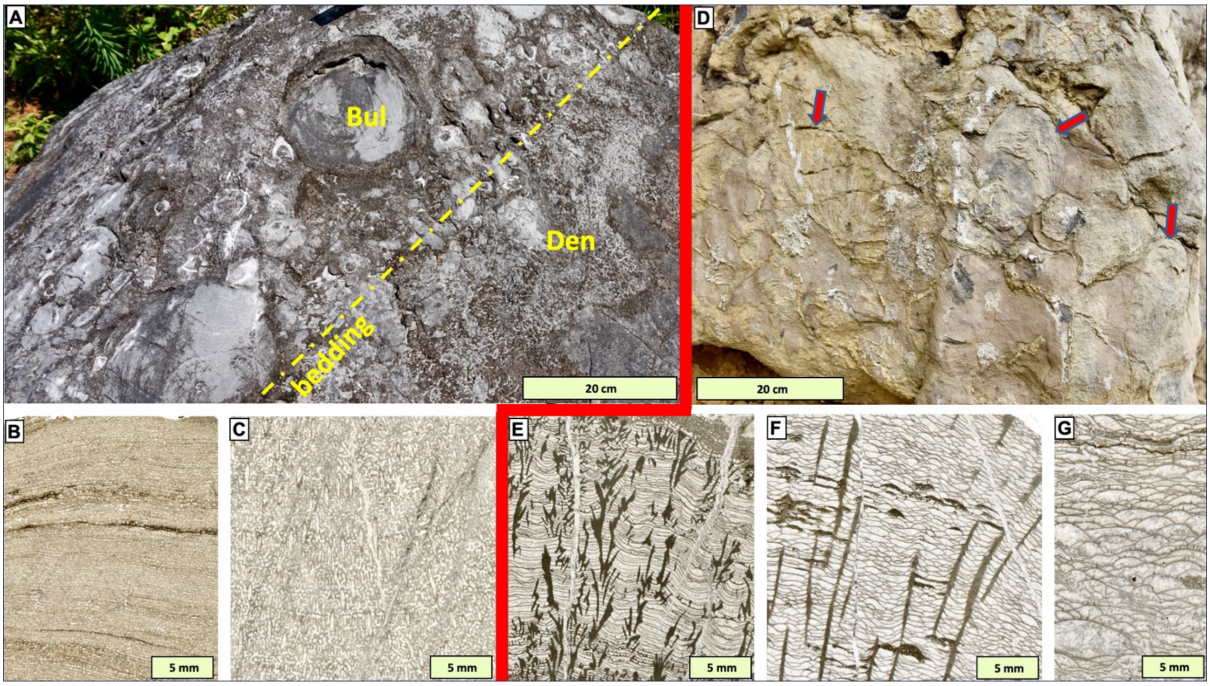


Fig. 13. Contrasts between abundant stromatoporoids of the Givetian to Frasnian stages, compared to the post F-F extinction Famennian stage. **A.** Stromatoporoid biostrome comprising a layer of fragmented dendroid (Den) skeletons of stromatoporoids and tabulates, overlain by an accumulation of bulbous (Bul) and other morphologies (light gray areas). Givetian (Middle Devonian), Tangjiawan Formation, Guangxi Province, China. **B, C.** Vertical sections of typical Givetian stromatoporoids (B) *Parallelopora* and (C) *Stromatopora* with intergrown syringoporid tabulate coral from the Jinbaoshi Formation, Pintonghe River section, Longmenshan, Sichuan. **D.** Famennian reef in Yanjiaozhai, Guizhou Province, comprising abundant labechiid-form taxa (red arrows). **E–G.** Vertical sections of three typical Famennian stromatoporoids; **E.** *Platiferastroma*, **F.** *Labechia*, **G.** *Rosenella.* Note that all taxa show the profound labechiid architecture contrasting the pre-F-F extinction stromatoporoids in B and C. All specimens were provided by Yue Li, Nanjing.

3.6. End-Devonian Hangenberg event and what happened in the Carboniferous; Event 5

The Hangenberg extinction event at the end of the Devonian is regarded as the extinction of the middle Palaeozoic stromatoporoids, attributed largely to cooling and anoxia (Copper, 2002b). Bond & Grasby (2017) drew attention to transgression at this time, which contrasts the sea-level falls in the Hirnantian, end-Silurian, late Givetian and F-F; they also note a potential impact event. However, despite the perceived end-Devonian extinction of stromatoporoids, a cluster of samples of the confirmed taxa *Labechia carbonaria* (Kershaw & Sendino, 2020) and *Kyklopora kazmiusense* (Nestor, 2015 p. 755) are known in the Early Carboniferous, indicating that stromatoporoids did not become entirely extinct at the end-Devonian. Recently, stromatoporoids have been recognised in Early Carboniferous strata of Japan, including labechiid forms (Ezaki et al., 2023), adding to the evidence that stromatoporoids did not become fully extinct after the end-Devonian. Later in the Carboniferous, *Spongonewellia mira* (Wood et al., 1989) is regarded as a stromatoporoid, noting a point made earlier that its transverse section resembles a chaetetid. Nevertheless, geographic variation of occurrence of stromatoporoids indicates that impact of the Hangenberg extinction was geographically heterogeneous, similar to the pattern in the Latest Ordovician. An interesting viewpoint is that labechiid-form hypercalcifying sponges may have been the ultimate Palaeozoic survivors, having passed through both the F-F and Hangenberg extinction events; this thus raises the question about why labechiid-form taxa do not continue through the Mesozoic and Cenozoic, yet other stromatoporoid taxa occur. Moreover, it is an open question as to why labechiid forms did not become the dominant reef stromatoporoid in the aftermath of the End-Ordovician mass extinction. These contrasts indicate complex controls on labechiid occurrence.

Chaetetids, another grade of hypercalcified sponges, present probably since the Silurian, continued in the Early Carboniferous and expanded to become significant global players in reef building of the Pennsylvanian (West, 2015). Mistiaen (1994) proposal that stromatoporoids lost their ability to calcify at the end-Devonian event is not consistent with the continued calcification of chaetetids through the same time interval, noting that both groups are simply different grade versions of hypercalcified sponges. Another aspect of changes in the Devonian to Carboniferous time is that the record of sponges in Late Devonian is quite poor (see Muir et al. 2017), which requires further studies of different sponge groups in this time interval.

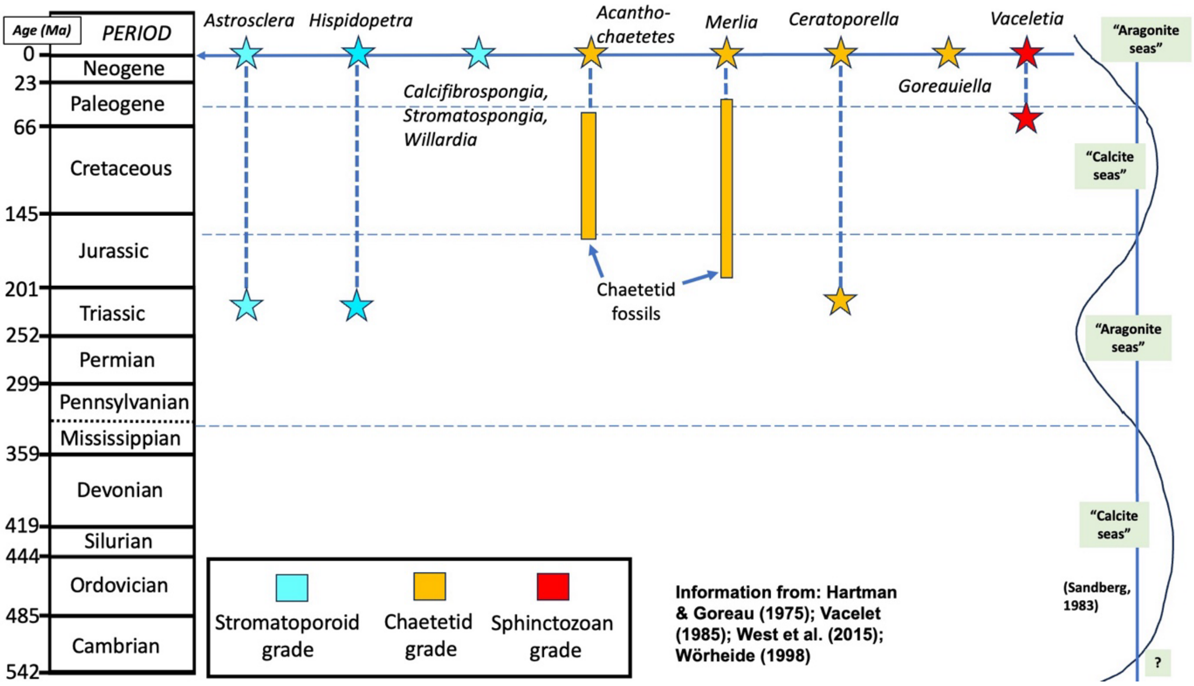
Wu et al. (2013) hypothesised that common encrustation by calcimicrobes on growth surfaces of corals and stromatoporoids caused the mass extinction of coral–stromatoporoid reef ecosystems at the end-Devonian. They interpreted the common occurrence of calcimicrobes in the outer skeletal structures of chaetetid-grade sponges (mistakenly identified as tabulate corals in their paper; see figures in Wu et al., [2013]) and stromatoporoids represents 'invasion' by bacteria and algae, and proposed that such phenomena led to the disappearance of coral–stromatoporoid reefs in the Late Devonian. However, this conclusion is controversial because although the encrustation of calcimicrobes may have resulted in growth termination of individual stromatoporoids and chaetetids, it seems an unlikely cause of extinction in the subsequent time interval. Stromatoporoids were commonly associated with microbial organisms even when stromatoporoids were highly diverse and abundant (Stearn, 2015c; Riding et al., 2019). So, collapse of the stromatoporoid-dominated reef ecosystem was most likely related to environmental changes in the Late Devonian (Stearn, 2015a), not 'invasion' of bacteria and algae.

3.7. End-Permian and end-Triassic extinctions and stromatoporoids

There is an interesting controversy regarding these two big extinction events: what happened to sponges through these events? Late Permian shallow-marine sphinctozoan sponge-hydrozoan reefs died out before the Permian-Triassic boundary because of sea-level fall, and at the boundary, facies were replaced by microbialites (Fig. 3G) in large parts of the low-mid latitudes. However, although Fig. 4F indicates a break in inozoan-grade sponges through the Permian, Fig. 4G shows that sphinctozoans expanded in the Triassic, so their hiatus at the end-Permian time and replacement by microbialites, was shortlived. Baud et al. (2021) and Ritterbush et al. (2014) proposed there were sponge takeovers of shallow marine ecosystems after the end-Permian and end-Triassic extinctions, respectively, following the notion that sponges had resilience to environmental disturbance whereas other groups did not. Fig. 4F, G, using data from Senowbari-Daryan & Rigby (2015) shows that, for sphinctozoans, there is a reasonable argument to support expansion after the end-Permian extinction, but not for inozoans; and chaetetids expanded in the last half of the Triassic (Fig. 4E, based on information in West et al., 2015). In the detail of strata after the mass extinctions there is the problem of stratigraphic scale. Certainly, for the end-Permian event, there is poor evidence for sponges in the immediate aftermath of the extinction. Sponges that are not hypercalcifiers effectively have a poor fossil record, so determining what happened to sponges in these two big extinctions remains a problem of lack of verifiable data. For the end-Triassic, Ritterbush et al.'s (2014, p. 662) discussion about sponge takeover after the end-Triassic extinction, seems to relate to siliceous sponges. Nevertheless, the increased development of stromatoporoid-grade hypercalcifiers, and chaetetids, inozoans and sphinctozoans in the overall Mesozoic and Cenozoic record, are all proof of survival from mass extinction of sponges that produced hypercalcified skeletons.

3.8. End-Cretaceous, Cenozoic, and the calcite-aragonite seas concept

Collapse of carbonate reef systems at the end of the Cretaceous is symbolised by extinction of rudist reefs that dominated Cretaceous reef (Wilson 1975), and Fig. 4 demonstrates the significant decline of all hypercalcified sponges, yet they survived to modern times (Hartman & Goreau, 1970). Although the end-Cretaceous events include substantial sea level fall that may explain loss of habitats suitable for stromatoporoids to continue developing, the thirty-five million years since the end of the Cretaceous is a long time for hypercalcified sponges to have taken a subordinate position in carbonate systems. Given the rise of scleractinian coral reefs during the Cenozoic, the maintained reduction in hypercalcified sponges may, in the broadest terms, relate to competition for space, exemplified by the modern situation in, for example, the Jamaica reefs first highlighted by Hartman & Goreau (1975). However, there is some evidence that aragonite and calcite skeletons relate to the Sandberg curve (Figs. 2, 4, 14); Cuif & Gautret (1991) proposed that sponges had poor regulation of mineralisation over their environment, so that during aragonite seas times, skeletons were preferentially aragonitic. Wörheide (1998, p.84) discussed the possibility of relationship between original aragonitic composition and geological occurrence of *Astrosclera*, proposing that the ultraconservative nature of the living *Astrosclera* was a reflection of its control on mineralisation, noting that this genus is unique in having a calcified skeleton constructed of aragonite spherules.



Information from: Hartman & Goreau (1975); Vacelet (1985); West et al. (2015); Wörheide (1998)

Fig. 14. The modern hypercalcified sponge genera and some fossil equivalents, compiled from several sources, together with the Sandberg (1993) curve. *Astrosclera, Hispidopetra* and *Ceratoporella* all have fossil counterparts, and all these three living taxa have aragonite skeletons. Fossil equivalents occur in episodes of aragonite seas. In contrast, *Vaceletia* and *Acanthochaetetes* have calcite skeletons, while *Merlia* has both calcite and aragonite; all three of these modern taxa have fossil relatives in calcite seas episodes. The information in this diagram supports the view of Cuif & Gautret (1991) that the sponges had relatively poor regulation of their mineralogy and were influenced by environmental saturation of carbonate minerals in the oceans. See text for discussion.

Investigation of modern hypercalcified sponges with a fossil record (Hartman & Goreau, 1975; West et al. 2015; Wörheide, 1998; compiled in our Fig. 14), records that the modern genera of *Hispidopetra* and *Ceratoporella* have aragonitic skeletons, as does the modern *Goreauiella* (but that has no fossil equivalent yet found). For the broad fossil record of hypercalcified sponges, Stanley & Hardie (1999, fig. 2) classed stromatoporoids as having calcite skeletons, whereas sphinctozoans and inozoans were considered to be aragonite; in their compilation, chaetetids occupied only the Pennsylvanian, and were classed as aragonite. However, chaetetids have a much longer range (Fig. 4), crossing both aragonite and calcite seas times. Furthermore, comparisons of skeletal structure in high-resolution thin sections (Fig. 8) demonstrate that mineralogy of chaetetids is best classified as calcite, whereas stromatoporoids remain enigmatic, as likely HMC mineralogy (see Kershaw et al., 2021a, for more evidence and discussion). However, chaetetids show cases of very good preservation (Fig. 8D, E), but others have fabric-retentive alteration (Fig. 8F–I) as do all stromatoporoids.

Perhaps the key point regarding mineralogy is that if the view of Cuif & Gautret (1991) is correct, that hypercalcified sponges had poor regulation of their mineral skeletons, then there is the possibility of overemphasis in the fossil record of calcite-based skeletons compared to aragonite-based skeletons. In the broadest terms, this may be the reason why Phanerozoic stromatoporoid fossils are found more commonly in calcite seas episodes (Figs. 2, 4, 14) simply because they had a greater chance of being preserved. There is no uniformity of difference in mineralogy between chaetetid-grade and stromatoporoid-grade hypercalcified sponges, so there can be no reliable argument that they had a phyletic difference. The different response of inozoan-grade and sphinctozoan-grade sponges after the end-Permian extinction (Fig. 4F, G) opens the possibility of phyletic differences, but is likely to be unresolvable.

4. Conclusions

This review of stromatoporoids and extinctions promotes the following key interpretations:

1. Overall, there are patterns of survival of stromatoporoid-grade calcified sponges through extinction events; they evidently did not die out at any of the major extinction events (Late Ordovician, F-F, End-Devonian, Permian/Triassic, end-Triassic and end-Cretaceous). They contrast other reef-building forms, notably tabulate corals that died out fully at the Permian-Triassic boundary, and rudistid bivalves at the end-Cretaceous. The rarity of post-Devonian stromatoporoids is potentially a result of extinction of calcifying taxa while non-calcifying sponges survived, and their survival was geographically heterogeneous.
2. Evidently stromatoporoids did not like clastic sediments, and although they were resilient faunas, they grew best in stabilised shallow marine carbonate systems. Therefore, sea-level fall or even deepening, plus accompanied increase in clastics might be correlated to extinction, or at least contraction of stromatoporoid diversity. Anoxia may play a part, but because stromatoporoids lived in shallow marine conditions, the impact of anoxia is less likely, given that anoxia is a feature of the deeper open ocean. Controls on stromatoporoid extinction and contraction might be quite simple: sea level fall and cooling associated with increased clastics and in some cases anoxic control and possibly toxic effects of volcanism if they

affected shallow waters. This might be a reflection of the responses of sponges to environmental conditions where they lived, so the fact that they are stromatoporoids may be less important than the fact that they are sponges.

3. Palaeozoic stromatoporoids have long been regarded to have become extinct at the end of the Devonian, but this perspective has now changed because of recognition of few relicts of Palaeozoic-type stromatoporoids in Carboniferous strata. Prior suggestions that stromatoporoids lost their ability to calcify at the end of the Devonian Period is inconsistent with the continued presence of ongoing stromatoporoid- and chaetetid-grade sponges in the Early Carboniferous; both groups are hypercalcified sponges, and so loss of ability to calcify in one grade is likely to have occurred in the other grade. A more reasonable interpretation of reason for loss of stromatoporoids is the extinction of certain stromatoporoid taxa, which just happen to have been hypercalcified. Thus, extinction is focussed on taxa loss, not loss of ability to calcify.
4. There is a broad relationship between the episodes of calcite seas (of the Sandberg curve) and occurrence of hypercalcified stromatoporoid sponges, tempting an interpretation that hypercalcification of stromatoporoids was related to ocean seawater chemistry. However, a problem with this notion is that chaetetid hypercalcified sponges occur in both calcite and aragonite seas episodes.
5. Overall, the repeated occurrence of hypercalcification in stromatoporoid grade sponges (and the other grades of hypercalcified sponges) demonstrates the resilience of sponges to environmental change in the Phanerozoic. Stromatoporoid hypercalcified sponges thus show a survival capability through geological history.
6. Because of the polyphyletic nature of hypercalcified sponges in general, and of stromatoporoid-grade sponges in particular, there is no certainty of phylogenetic relationship between Palaeozoic and Mesozoic stromatoporoids. Nevertheless, Mesozoic stromatoporoid-grade fossils are hypercalcified sponges, so the continuation of hypercalcification of sponge fossils through Phanerozoic time is unquestioned. Following from point 2, a reasonable interpretation of the expansion of Mesozoic stromatoporoids in the Jurassic and Cretaceous is due to development of sponge taxa that just happen to have been calcifiers.
7. This study helps to define the issues regarding extinction processes in stromatoporoids, with comment on other hypercalcified sponges, giving sharper focus on the problems; the “known unknowns” are now better visualised.

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Declaration of Competing Interest

S. Kershaw and J. Jeon have no conflicts of interest directly relevant to the content of this article.

References

Azeredo, A.C., Wright, V.P., Ramalho, M.M., 2002. The Middle–Late Jurassic forced regression and disconformity in central Portugal: eustatic, tectonic and climatic effects on a carbonate ramp system. Sedimentology, 49, 1339–1370.

Bełka, Z., Devleeschouwer, X., Narkiewicz, M., Piecha, M., Reijers, T.J.A., Ribbert, K.-H., Smith, N.J.P., 2010. Devonian. in: Doornenbal, J.C., Stevenson, A.G. (Eds.), Petroleum Geological Atlas of the Southern Permian Basin Area. EAGE Publications, Houten, pp. 71–79.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W., Webster, N.S., 2013. Could some coral reefs become sponge reefs as our climate changes? Global Change Biology, 19, 2613–2624.

Bond, D.P.G., Grasby, S.E., 2017. On the causes of mass extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology, 478, 3–29.

Boucot, A., 1985. Late Silurian – Early Devonian biogeography, provincialism, evolution and extinction. Philosophical Transactions of the Royal Society, London, B, 309, 323–339.

Bourque, P-A., Malo, M., Kirkwood, D., 2000. Paleogeography and tectono-sedimentary history at the margin of Laurentia during Silurian to earliest Devonian time: the Gaspé Belt, Québec. Geological Society of America, Bulletin, 112, 4–20.

Bowman, C.N., Them II, T.R., Knight, M.D., Kaljo, D., Eriksson, M.E., Hints, O., Martha, T., Owens, J.D., Young, S.A., 2021. A multi-proxy approach to constrain reducing conditions in the Baltic Basin during the late Silurian Lau carbon isotope excursion. Palaeogeography, Palaeoclimatology, Palaeoecology, 581, 110624.

Bridge, T.C.L., Baird, A.H., Pandolfi, J.M., McWilliam, M.J. & Zapalski, M.K., 2022. Functional consequences of Palaeozoic reef collapse. Scientific Reports, **12**, 1386.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013; updated. The ICS International Chronostratigraphic Chart. Episodes, 36, 199–204. URL: https://www.stratigraphy.org/ICSchart/ChronostratChart2022-02.pdf.

Copper, P., 2002a. Reef development at the Frasnian/Famennian mass extinction boundary. Palaeogeography, Palaeoclimatology, Palaeoecology, 181, 27–65.

Copper, P., 2002b. Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages, in: Kiessling, W., Flügel, E. & Golonka, J. (Eds.). Phanerozoic reef patterns. SEPM (Society for Sedimentary Geology) Special Publication 72. Tulsa Oklahoma, pp. 181–238.

Copper, P., Stock, C. W., Jin, J., 2013. *Quasiaulacera*, a new Hirnantian (Late Ordovician) aulaceratid stromatoporoid genus from Anticosti Island, Canada. Journal of Paleontology 87, 664–676.

Capel, E., Cleal, C.J., Xue, J., Monnet, C., Servais, T., Cascales-Minana, B., 2022. The Silurian-Devonian terrestrial revolution: diversity patterns and sampling bias of the vascular plant macrofossil record. Earth-Science Reviews, 231, 104085.

Cramer, B.D., Saltzman, M. R., 2005. Sequestration of ^{12}C in the deep ocean during the early Wenlock (Silurian) positive carbon isotope excursion. Palaeogeography, Palaeoclimatology, Palaeoecology, 219, 333–349.

Cramer, B.D., Condon, D.J., Söderlund, U., Marshall, C., Worton, G.J., Thomas, A.T., Calner, M., Ray, D.C., Perrier, V., Boomer, I., Patchett, P.J., Jeppsson, L., 2012. U-Pb (zircon) age constraints on the timing and duration of Wenlock (Silurian) paleocommunity collapse and recovery during the "Big Crisis". GSA Bulletin, 124, 1841–1857.

Cuif, J-P, & Gautret, P., 1991a. Étude de la 35arbonate35n des principaux types de démosponges calcifies depuis le Permien. Hypothèse d'une incidence des conditions océanologiques sur la biominéralisation carbonate des spongiaires. Bulletin de la Société Géologique de France, 162, 875–886.

Cuif, J-P, & Gautret, P., 1991b. Taxonomic value of microstructural features in calcified tissue from Recent and fossil Demospongiae and Calcarea. Pp. 159–169 In Reitner, J. & Keupp, H. (Eds.). Fossil and Recent Sponges, Springer-Verlag Berlin Heidelberg.

Debrenne, F., 1999. The past of sponges – sponges of the past. Memoirs of the Queensland Museum, 44, 9–21.

Dong, D.Y., Wang, S.-B., 1990. Stratigraphic distribution of Devonian stromatoporoids from Longmenshan of Sichuan. Journal of Stratigraphy, 14, 147–153.

Dong, D.Y., Yang, J.Z., 1978. Lower Silurian stromatoporoids from northeastern Guizhou. Acta Palaeontogica Sinica, 17, 421–436, 6 pl.

Ebert, J., 1993. Globale Events im Grenz-Bereich Mittel-/Ober-Devon (No. 59), 106 pp. Im Selbstverlag der Geologischen Institute der Georg-August-Universität Göttingen.

Ezaki, Y., Masui, M., Nagai, K., Webb, G., Shimizu, K., Sugama, S., Adachi, N., Sugiyama, T., 2023. Stromatoporoid survivors formed the Akiyoshi reefs on a Panthalassan seamount in the early late Carboniferous (Bashkirian). 2nd Asian Palaeontological Congress, 3-7 August 2023, Tokyo, Japan, Abstracts, S21-1, page 32.

Feng, Q., Gong. Y.-M. & Riding, R., 2010. Mid-Late Devonian calcified marine algae and cyanobacteria, South China. Journal of Paleontology, 84, 569–587.

Fernández-Martínez E., Fernández, L.P., Méndez-Bedia, I., Soto, F. & Mistiaen, B., 2010. Earliest Pragian (Early Devonian) corals and stromatoporoids from reefal settings in the Cantabrian Zone (N. Spain). Geologica Acta, 8, 301–323.

Finks, R.M., Reid, R.E.H., Rigby, J.K., 2004. Porifera (Demospongea, Hexactinellida, Heteractinida, Calcarea), in: Kaesler, R.L. (Ed.). Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, vol. 3. The Geological Society of America & The University of Kansas, Boulder & Lawrence, 872pp.

George, A.D., Chow, N., 2002. The depositional record of the Frasnian/Famennian boundary interval in a fore-reef succession, Canning Basin, Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, 181, 347–374.

Girard, C., Lécuyer, C., 2002. Variations in Ce anomalies of conodonts through the Frasnian/Famennian boundary of Poland (Kowala – Holy Cross Mountains): implications for the redox state of seawater and biodiversity. Palaeogeography, Palaeoclimatology, Palaeoecology, 181, 299–311.

Goldfuss, G. A., 1826. Petrefacta Germaniae, Band 1, Heft I. Arnz & Co. Düsseldorf., 1–76.

Hartman, W.D., 1969. New genera and species of coralline sponges (Porifera) from Jamaica. Postilla, 137, 1–39.

Hartman, W.D., Goreau, T.F., 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. Symposium of the Zoological Society of London, 25, 205–243.

Haynes, J.T., Pitts, A.D., Doctor, D.H., Diecchio, R.J., Blake, Jr., B.M., 2018. Appalachian Basin Stratigraphy, Tectonics, and Eustasy from the Blue Ridge to the Allegheny Front. Virginia and West Virginia: West Virginia Geological and Economic Survey, Field Trip Guide FTG-10, 86 p.

Hess, A.V., Trop, J. M., 2019. Sedimentology and carbon isotope (δ^{13}C) stratigraphy of Silurian-Devonian boundary interval strata, Appalachian Basin (Pennsylvania, USA). Palaios, 34, 405–423.

Hou, H.F., Wang, S.T., 1988. Stratigraphy of China 7. Devonian System in China [M]. Geological Publishing House, 348 pp.

Jeon, J., Liang, K., Kershaw, S., Park, J., Lee, M., Zhang, Y., 2022a. Rise of clathrodictyid stromatoporoids during the Great Ordovician Biodiversification Event: insights from the Upper Ordovician Xiazhen Formation of South China. Journal of Paleontology, 96, 1285–1317.

Jeon, J., Liang, K., Park, J., Kershaw, S., Zhang, Y., 2022b.Diverse labechiid stromatoporoids from the Upper Ordovician Xiazhen Formation of South China and their paleobiogeographic implications. Journal of Paleontology, 96, 513–538.

Jeon, J., Li, Y., Kershaw, S., Chen, Z.Y., Ma, J.Y., Lee, J.-H., Liang, K., Yu, S.Y., Huang, B., Zhang, Y., 2022c. Nearshore warm-water biota development in the aftermath of the Late Ordovician Mass Extinctions in South China. Palaeogeography, Palaeoclimatology, Palaeoecology, 603, 111182, 22 pages.

Jeon, J., Lee, J.-H., Kershaw, S., Chen, Z.-Y., Ma, J.-Y., Liang, K., Zhang, Y.-D., 2023a. The earliest known stromatoporoid and its contribution to reef construction. Estonian Journal of Earth Sciences, 72, 135.

Jeon, J., Kershaw, S., Liang, K., Zhang, Y.-D., 2023b. Stromatoporoids of the Katian (Upper Ordovician) Beiguoshan Formation, North China. Journal of Systematic Palaeontology, 21, 2234929, 42 pages.

Kazmierczak J., Ittekot, V., Degens, E.T., 1985. Biocalcification through time: environmental challenge and cellular response. Paläontologische Zeitschrift, 59, 15–33.

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

Kershaw, S., Munnecke, A., Jarochowska, E., 2018. Understanding Palaeozoic stromatoporoid growth. Earth Science Reviews, 187, 53–76.

Kershaw, S., Sendino, C., 2020. *Labechia carbonaria* Smith 1932 in the Early Carboniferous of England; affinity, palaeogeograhic position and implications for the geological history of stromatoporoid-type sponges. Journal of Palaeogeography, 9, 29, 18 pages.

Kershaw, S., Munnecke, A., Jarochowska, E., Young, G., 2021a. Palaeozoic stromatoporoid diagenesis: a synthesis. Facies, 67, 20, 43 pages and supplemental file of 18 figures.

Kershaw, S., Da Silva, A-C., Sendino, C., 2021b. British Silurian Stromatoporoids; Faunas, Palaeobiology and Palaeographical Significance. *Monographs of the Palaeontographical Society*, 175, publication 660, 1–92, Plates 1–22.

Liu, Z., Percival, L.M.E., Vandeputte, D., Selby, D., Claeys, P., Over, D.J., Gao, Y., 2021. Upper Devonian mercury record from North America and its implications for the Frasnian-Famennian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 576, 110502, 10 pages.

Malkowski, K., Racki, G., 2009, A global biogeochemical perturbation across the Silurian-Devonian boundary: ocean-continent-biosphere feedbacks. Palaeogeography, Palaeoclimatology, Palaeoecology, 276, 244–254.

May, A., Rodriguez, S., 2012. Pragian (Lower Devonian) stromatoporoids and rugose corals from Zújar (Sierra Morena, southern Spain). Geologica Belgica, 15, 226–235.

May, A., 2022. Why were reefs and stromatoporoids so rare in the Lower Devonian? Sciences of Europe: Geological and Mineralogical Sciences, 104, 24–32.

Morris, J.L., Edwards, D., 2014. An analysis of vegetational change in the Lower Devonian: new data from the Lochkovian of the Welsh Borderland, UK. Review of Palaeobotany and Palynology, 211, 28–54.

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

Nestor, H. E., 1966. Wenlockian and Ludlovian Stromatoporoidea of Estonia, ENSV TA Geoloogia Instituudi uurimused. Valgus, Tallinn. 87 pp.

Nestor, H., 2015. Clathrodictyida: systematic descriptions, in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 755–768.

Nestor, H., Webby, B.D., 2013. Biogeography of the Ordovician and Silurian Stromatoporoidea, in: Harper, D.A.T., Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography.* The Geological Society of London, Memoirs, 38, pp. 67–79.

Newell, N., 1935. Some Mid-Pennsylvanian invertebrates from Kansas and Oklahoma. II. Stromatoporoidea, Anthozoa and gastropods. Journal of Paleontology 9, 341–355.

Özkidmen, H., 2009. Substitute names for eight sponge genus group names (Porifera). Munis Entomology & Zoology, 4, 212–218.

Pujol, F., Berner, Z., Stüben, D., 2006. Palaeoenvironmental changes at the Frasnian/Famennian boundary in key European sections: chemostratigraphic constraints. Palaeogeography, Palaeoclimatology, Palaeoecology, 240, 120–145.

Racki, G., Balinski, A., Wrona, R., Malkowski, K., Drygant, D., Szaniawski, H., 2012. Faunal dynamics across the Silurian-Devonian positive isotope excursions (d13C, d18O) in Podolia, Ukraine: comparative analysis of the Ireviken and Klonk Events. Acta Palaeontologica Polonica, 57, 795–832.

Reitner, J., Engeser, T.S., 1987. Skeletal structures and habitats of Recent and fossil Acanthochaetetes (subclass Tetractinomorpha, Demospongiae, Porifera). Coral Reefs, 6, 13–18.

Riding, R., Liang, L.Y., Lee, J.H., Virgone, A., 2019. Influence of dissolved oxygen on secular patterns of marine microbial carbonate abundance during the past 490 Myr. Palaeogeography, Palaeoclimatology, Palaeoecology. 514, 135–143.

Rong, J.-Y., Harper, D.A.T., Huang, B., Li, R.-Y., Zhang, X.-L., Chen, D., 2020. The latest Ordovician Hirnantian brachiopod faunas: New global insights. Earth Sciences Review, 208, 103280.

Ruben, M., Sarv, L., 1996. Reconstruction and use of the succession of east Baltic Silurian ostracodes. Proceedings of the Estonian Academy of Sciences, Geology, 45, 177–188.

Samtleben, C., Munnecke, A., Bickert, T., 2000. Development of facies and C/O isotopes in transects through the Ludlow of Gotland: evidence for global and local influences on a shallow-marine environment. Facies, 43, 1–38.
Sandström, S., Kershaw, S., 2008. Palaeobiology, ecology, and distribution of stromatoporoid faunas in biostromes of the mid-Ludlow of Gotland, Sweden. *Acta* Palaeontological Polonica. 53, 293–302.
Saltzman, M.R., 2002. Carbon isotope ($\delta^{13}C$) stratigraphy across the Silurian-Devonian transition in North America: evidence for a perturbation of the global carbon cycle. Palaeogeography, Palaeoclimatology, Palaeoecology, 187, 83–100.
Saltzman, M.R., Thomas, E., 2012. Carbon isotope stratigraphy. in Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G.M., (Eds.) *The Geologic Timescale*. Elsevier, 207-232.
Senowbari-Daryan, B., Rigby, J.K., 2015. Sphinctozoan and inozoan hypercalcified sponges: an overview. in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 321–395.
Servais, T., Cascales-Minana, B., Harper, D.A.T., 2021. The Great Ordovician Biodiversification Event (GOBE) is not a single event. Paleontological Research, 25, 315–328.
Smosna, R.A., Warshauer, S.M., 1979, A very Early Devonian patch reef and its ecological setting. Journal of Paleontology, 53, 142–152.
Stearn, C.W., 1988. Stromatoporoids from the Famennian (Devonian) Wabamun Formation, Normandville Oilfield, North-Central Alberta, Canada. Journal of Paleontology, 62, 411–419.
Stearn, C.W., 2015a. Extinction patterns of the Paleozoic Stromatoporoidea, in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 599–612.
Stearn, C.W., 2015b. Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida, and genera with uncertain affinities; systematic descriptions, in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 781–836.
Stearn, C.W., 2015c. Diversity trends of the Paleozoic Stromatoporoidea, in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 593–597.
Stearn, C.W., Halim-Hihardja, M.K., Nishida, D.K., 1987. An oil-producing stromatoporoid patch eef in the Famennian (Devonian) Wabamun Formation, Normandville Field, Alberta. Palaios, 2, 560–570.
Stock, C. W., 1979. Upper Silurian (Pridoli) Stromatoporoidea of New York. Bulletins of American Paleontology, 76, 293–389.
Stock, C.W., 1994. Stromatoporoid paleobiogeography of the East Americas Realm during the Lochkovian Age (Early Devonian), in van Soest, R.W.M., van Kempen, T.M.G. & Braekman, J.C. (Eds.) Sponges in Time and Space. Balkema, Rotterdam, 23-28.
Stock, C.W., 2005. Devonian stromatoporoid originations, extinctions, and paleobiogeography: how they relate to the Frasnian-Famennian extinction. In Over, D.J., Morrow, J.R. & Wignall, P.B. (Eds.). Understanding Late Devonian and

Permian-Triassic biotic and climatic events: Towards an integrated approach. Developments in Palaeontology and Stratigraphy. Elsevier, 71–92.

Stock, C. W., 2015. Actinostromatida: systematic descriptions, in: Selden, P.A. (Ed.), *Treatise on Invertebrate Paleontology. Part E (Revised), Porifera*, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 769–779.

Stock, C.W., Nestor, H., Webby, B.D., 2015. Paleobiogeography of the Paleozoic Stromatoporoidea, in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 653–689.

Stock, C.W., Burry-Stock, J.A., 1998. Two new genera of upper Silurian actinostromatid stromatoporoids. Journal of Paleontology, 72, 190–201.

Stock, C.W., Burry-Stock, J.A., 2020. The stromatoporoid *Habrostroma* in the upper Silurian (uppermost Pridoli) – Lower Devonian (Lochkovian) of North America, and the paleobiogeographic significance of *H. centrotum* (Girty, 1895). Journal of Paleontology, 94, 11-27.

Stock, C.W., Holmes, A. E., 1986. Upper Silurian/Lower Devonian Stromatoporoidea from the Keyser Formation at Mustoe, Highland County, West-Central Virginia. Journal of Paleontology, 60, 555–580.

Stock, C.W., Stearn, C.W., 2015. A list of Upper Paleozoic – Mesozoic stromatoporoid-like genera; and excluded taxa, in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 307-310.

Tian, Y., Wang, L.Z., Tu, B., Xie, G.G., Huang, J.Y., Kershaw, S., Liang, K., Li, Y., Qie, W.K., 2024. Back-reef and lagoonal communities, Givetian (Middle Devonian) in Guangdong, southeast China: their role in global Devonian reef development. Palaeogeography, Palaeoclimatology, Palaeoecology, 633, 111901*.*

Vacelet, J., 1981. Éponges hypercalcifiées (Pharétronides, Sclérosponges) des cavités des récifs coralliens de Nouvelle-Calédonie. Bulletin du Museum National d'histoire, Paris, 4th Series, 3, Section A(2), 313–351.

Vacelet, J., 1985. Coralline sponges and the evolution of Porifera, in: Conway Morris, S., George, J.D., Gibson, R., Platt, H.M. (Eds.), The Origin and Relationships of the Lower Invertebrates. Clarendon Press, Oxford, pp. 1–13.

Van Staal, C.R., Whalen, J.B., Valverde-Vaquero, P., Zagorevski, A., Rogers, N., 2009. Pre-Carboniferous, episodic accretion-related, orogenesis along the Laurentian margin of the north Appalachians, in: Murphy, J.B., Keppie, J.D., Hynes, A.J. (Eds.), Ancient Orogens and Modern Analogues. Geological Society, Special Publications 327, London, pp. 271–316.

Van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., Santodomingo, N., Vanhoorne, B., Kelly, M., Hooper, J.N.A., 2012. Global diversity of sponges (Porifera). PLoS ONE 7*,* e35105, doi:10.1371/journal.pone.0035105. 23 pages.

Vinn, O., 2016. Symbiotic endobionts in Paleozoic stromatoporoids. Palaeogeography, Palaeoclimatology, Palaeoecology, 453, 146–153.

Webby, B.D., 2002. Patterns of Ordovician reef development, in: Kiessling, W., Flügel, E., Golonka, J. (Eds.), Phanerozoic reef patterns. SEPM (Society for Sedimentary Geology) Special Publication 72. Tulsa, Oklahoma, pp. 129–179.

Webby, B.D., 2015a. Early evolution of the Paleozoic Stromatoporoidea. in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 575–592.

Webby, B.D., 2015b. Labechiida: systematic descriptions, in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 709–754.

Webby, B.D., Stearn, C.W., Nestor, H., 2015. Biostratigraphy of the Paleozoic Stromatoporoidea, in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 613–630.

Wendt, J., 1980. Calcareous sponges. Development through time, in: Hartman, W.D., Wendt, J.W., Wiedenmayer, F., (Eds.), Living and fossil sponges. Notes for a short course. Comparative Sedimentology Laboratory, Division of Marine Geology and Geophysics, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami. Sedimenta, 8, pp. 169–178.

West, R.R., 2015. Paleogeography and biostratigraphy of the hypercalcified chaetetid-type Porifera (Demospongiae), in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 170-192.

West, R.R., Vacelet, J., Wood, R.A., Willenz, P., Hartman, W.D., 2015. Hypercalcified extant and fossil chaetetid-type and post-Devonian stromatoporoid-type Demospongiae: systematic descriptions, in: Selden, P.A. (Ed.), Treatise on Invertebrate Paleontology. Part E (Revised), Porifera, vol 4-5. The University of Kansas Paleontological Institute, Lawrence, Kansas, pp. 209–291.

Wilson, J.L., 1975. Carbonate Facies in Geologic History. Springer-Verlag, New York, Heidelberg, Berlin, 471pp.

Wood, R., 1987. Biology and revised systematics of some Mesozoic stromatoporoids. Special Papers in Palaeontology, 37, 1–89.

Wood, R., 1990. Reef-building sponges. American Scientist, **78**, 224–235.

Wood, R., 2011. Taphonomy of Reefs Through Time, in: Allison, P.A., Bottjer, D.J. (Eds.) Taphonomy. Aims & Scope Topics in Geobiology Book Series, vol 32. Springer, Dordrecht, pp. 375–409.

Wood, R., Reitner, J., West, R., 1989. Systematics and phylogenetic implications of the haplosclerid stromatoporoid *Newellia mira* nov. gen. Lethaia, 22, 85–93.

Wörheide, G., 1998. The reef cave dwelling ultraconservative coralline demosponge *Astrosclera willeyana* Lister 1900 from the Indo-Pacific. Facies, 38, 1–88.

Wörheide, G., 2008. A hypercalcified sponge with soft relatives: *Vaceletia* is a keratose demosponge. Molecular Phylogenetics and Evolution 47, 433-438.

Wörheide, G., Degnan, B. M., Hopper, J. P. A., Reitner, J., 2000. Phylogeography and taxonomy of the Indo-Pacific reef cave dwelling coralline demosponge *Astrosclera* '*willeyana*': new data from nuclear internal transcribed spacer sequences. in: Moosa, M.K., Soemodihardjo, A., Soegiarto, K., Romimohtarto, A., Nontji, A., Soekarno, A., Suharsonon, B. (Eds), Proceedings of the 9th International coral reef symposium. Ministry for Environment, Indonesian Institute of Sciences, International Society for Reef Studies Jakarta, pp. 339–346.

Wu, Y.B., Feng, Q., Gong, Y.M., 2013. Blooming of bacteria and algae is a biokiller for mass-extinction of Devonian coral-stromatoporoid reef ecosystems. Science China Earth Sciences, 56, 1221–1232.

Wulff, J., 2016. Sponge contributions to the geology and biology of reefs: past, present, and future, in: Hubbard, D.K., Rogers, C.S., Lipps, J.H., Stanley Jr, G.D. (Eds.), Coral Reefs at the Crossroads. Coral Reefs of the World, vol 6. Springer, Dordrecht, pp. 103–126.

Younes, H., Calner, M., Lehnert, O., 2017. The first continuous δ^{13}C record across the Late Silurian Lau Event on Gotland, Sweden. GFF, 139, 63–69.

Yu, C.-M., Li, Y., Liang, K., 2021. Devonian reef development and strata-bound ore deposits in South China. Journal of Palaeogeography, 10, 571–583.