Fossil hypercalcified sponges; types, relationships and geological history

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Abstract

Hypercalcified sponges are poriferans with a calcareous skeleton secreted on and in the soft tissue. Living examples and fossils of some such sponges in Mesozoic and Cenozoic strata contain sponge spicules and can be classified within modern poriferan groups of the Classes Demospongiae and Calcarea, which are otherwise almost entirely soft-bodied. However, other fossil forms, largely Palaeozoic archaeocyaths, stromatoporoids and chaetetids, lack spicules, so their classification relies on the calcareous skeleton alone. Because of these discrepancies, although the hypercalcified skeleton is useful for low-level taxonomy in fossils, it has no proven phyletic value, so the systematic position of non-spiculate forms is problematic. Thus the hypercalcified skeleton has for many years been considered a grade of organisation of the skeleton, and the terms archaeocyath-grade, stromatoporoid-grade, chaetetid-grade, sphinctozoan-grade and inozoan-grade are applicable. Nevertheless, archaeocyaths have been separated as a class, by sponge researchers. Two older classification terms are redundant: sclerosponges (for hypercalcified sponges in general) and pharetronids (for a subgroup divided into sphinctozoans and inozoans). Pharetronids are polyphyletic within the Demospongiae and Calcarea.

Hypercalcified sponges history began with archaeocyaths (Early Cambrian). Prominence of stromatoporoid-grade in the mid-Palaeozoic, and chaetetid-grade in the Carboniferous, was followed by a sparse record in both groups for much of the Permian while sphinctozoan- and inozoan-grades expanded. The Mesozoic has a good record of sphinctozoans, inozoans, stromatoporoids and chaetetids up to the end-Cretaceous. Cenozoic forms are uncommon but 19 genera of modern-day demosponges and calcarean sponges encompass all five grades, versus the total modern sponge diversity of 680 genera. Hypercalcification is diverse in modern sponges, involving aragonite, high-Mg & low-Mg calcite; ancient groups reflect this range in their variation of preservation (including widespread diagenetic alteration) that makes understanding of hypercalcification mechanisms problematic.

Presence of hypercalcified sponges from Early Cambrian to modern times, with short breaks associated with extinction events, demonstrate hypercalcification was an iterative evolutionary feature. This means that, for example, the stromatoporoid-grade, which appeared in the Early to Mid-Ordovician, continued through history to the modern representatives, albeit with taxa turnover through time. Stromatoporoids are traditionally viewed as becoming extinct at the end-Devonian Hangenberg event, but because this is a grade, rather than a proven phyletic group, discussion of the extinction of stromatoporoids as a group has little meaning; it is more appropriate to consider that certain sponge taxa, possessing stromatoporoid-grade skeletons, became extinct. Rare stromatoporoid-grade taxa in the Lower Carboniferous support such a view. Although their polyphyletic nature was recognized for Mesozoic and Cenozoic forms, the 2015 Treatise on hypercalcified sponges treats stromatoporoids and archaeocyaths as distinct groups. However, hypercalcified sponges are a complex of sponge taxa that just happened to hypercalcify, occurring across the classes of Demosponge and Calcarea. Thus fossil hypercalcified sponges may be considered as being an integrated system of hypercalcification, alongside the evolutionary history of the phylum Porifera, to aid understanding of their changes in time.

Keywords: Hypercalcified sponges, archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, inozoans, *Calathium*, pulchrilaminids

1. Introduction and aims

Of the 680 recognised genera of living sponges (van Soest et al., 2012), a small number (only 19 genera) have an additional component of large-scale mineralisation of calcium carbonate, that overprints the soft skeleton and spicules (Fig. 1). The result is fully lithified sponge skeletons previously called coralline sponges because of their superficial similarity to the calcification of modern corals (Hartman, 1969; Hartman & Goreau, 1970). This pervasive mineralization led to these sponges to be called hypercalcified sponges, rather than calcified sponges, by Termier & Termier (1973), to discriminate them from sponges of the Calcarea class (that have calcite spicules). Hypercalcified sponges occur in the Demospongiae and Calcarea Classes of sponges. Hypercalcification comprises aragonite and hi-magnesium calcite (HMC), and is secreted by the soft tissue, to form a calcified hard skeleton.

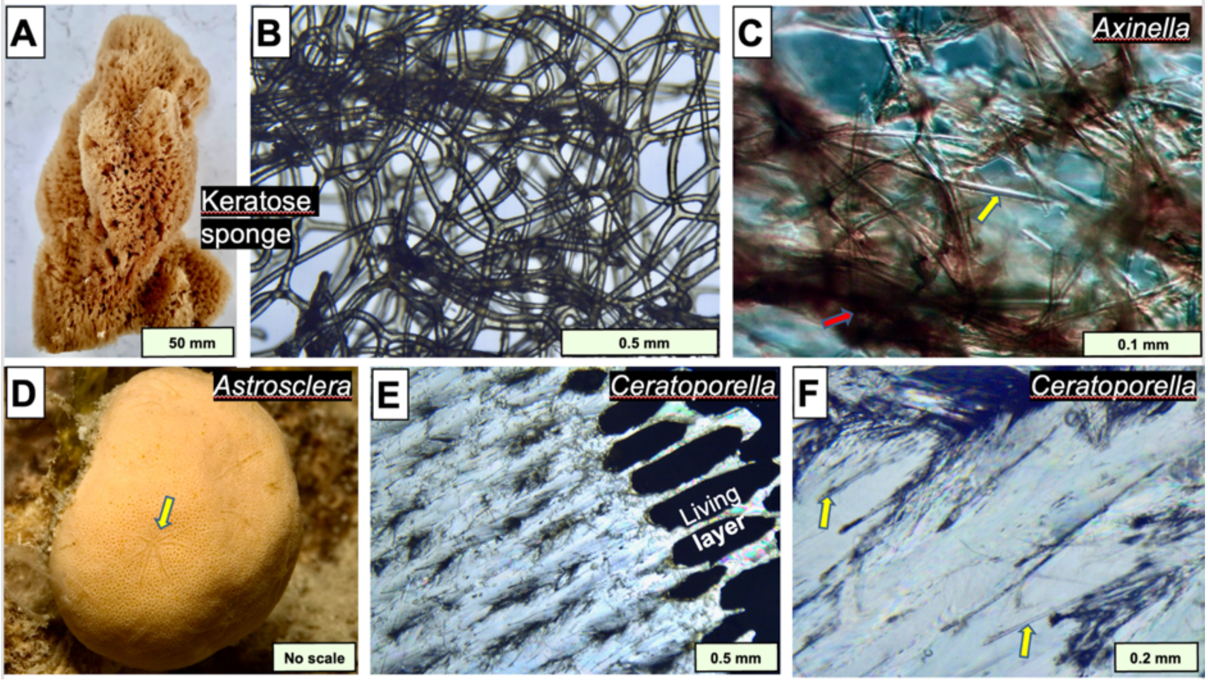


Fig. 1 Features of hypercalcified and non-calcified sponges. **A) detail in B)** Non-calcified bath sponge composed of a keratose framework. **C)** Non-calcified sponge with keratose framework and spicules (arrowed). **D)** Top view of living hypercalcified sponge *Astrosclera willeyana*, showing astrorhizae on surface (arrowed); reproduced under CC-BY-4.0 licence from Global Biodiversity Information Facility. **E) detail in F)** Vertical thin section in cross-polarised light of *Ceratoporella*, showing spicules (arrowed in F) embedded in hypercalcified skeleton; no keratose framework preserved. A & C are reproduced from Neuweiler et al. (2022) under CC-BY-4.0 licence.

Despite their rarity in modern assemblages, hypercalcified sponges are abundant and diverse in the rock record, from early Cambrian times onwards (Fig. 2). They occur as five principal groups (archaeocyaths, stromatoporoids, chaetetids, sphinctozoans and inozoans) that were originally considered to be phyletically separate. Apart from archaeocyaths, the other 4 types occur as living taxa, although archaeocyaths are considered to be similar to one living genus (*Vaceletia*) (see Debrenne & Vacelet, 1984). In addition are some other calcified fossils considered to be sponges that do not fit into those five groups (Fig. 2). The 19 living hypercalcified sponge genera were placed in a separate class (Sclerospongiae) by Hartman & Goreau (1970) but the approach to classification changed in the 1980s when sponge biologists realized that modern hypercalcified sponges may be grouped on the basis of their spicules into different orders of the Demospongiae and Calcarea (e.g. Vacelet, 1985). Thus the hypercalcified skeleton was recognized as polyphyletic in the modern forms (see also Chombard et al 1997). Later research culminated in a revised Treatise on fossil hypercalcified sponges, wherein those containing spicules were placed in the appropriate sponge classes and orders based on the taxonomy of modern sponges (West et al., 2015). However, Palaeozoic hypercalcified sponges are almost totally devoid of spicules, so classification relies on the different forms of hypercalcified skeletons. Therefore there is a significant problem regarding their phyletic relationships because it is not possible to prove whether or not they formed phyletically distinct groups. Nevertheless, the view of most sponge workers is that they are polyphyletic because polyphyly is present in their modern counterparts. However, archaeocyaths are considered to be a separate class of the Porifera (Debrenne et al., 2002), which is addressed later.

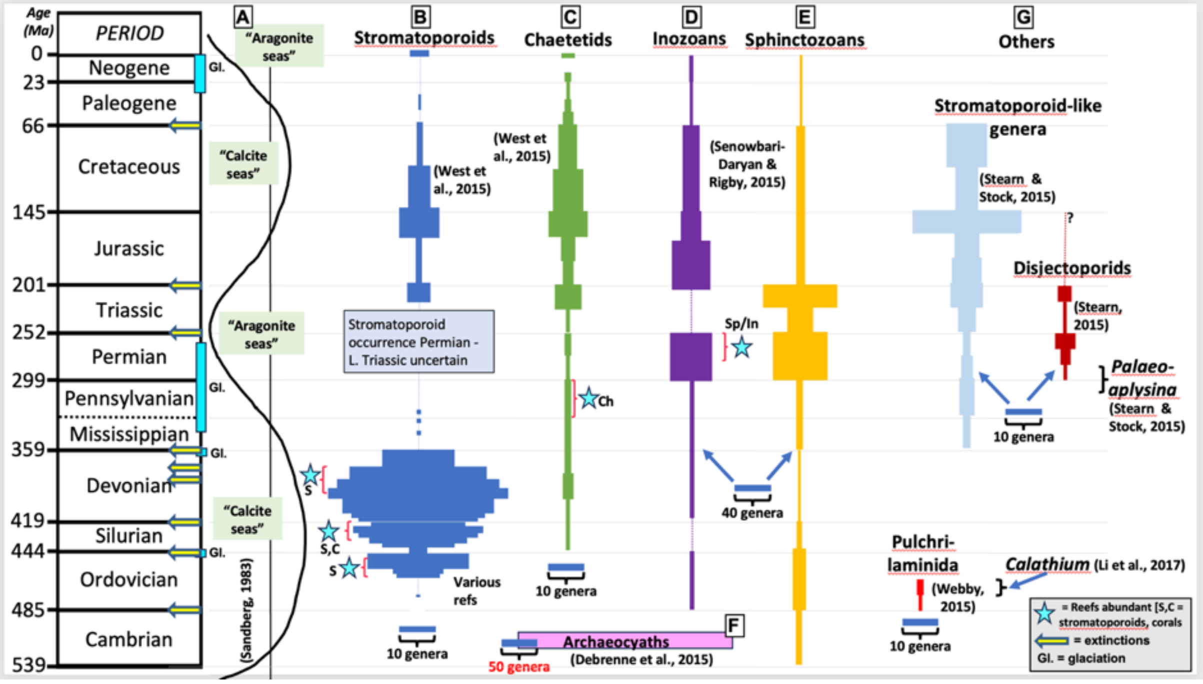


Fig. 2 Stratigraphy of hypercalcified sponges, including some global palaeoenvironmental parameters. **A)** Geological changes in aragonite-calcite deposition according to the Sandberg (1983) curve; episodes of glaciations (blue boxes); occurrence of extinction events (yellow arrows). **B)** Stratigraphy of stromatoporoid-grade sponges, Mesozoic forms compiled from West *et al.* (2015); Palaeozoic forms compiled from sources cited in Kershaw & Jeon (2024). **C)** Stratigraphy of chaetetid-grade sponges (Ch = chaetetid-dominated reefs. **D), E)** Stratigraphy of sphinctozoans and inozoan-grade sponges (Sp/In = reefs dominated by sphinctozoans and inozoans. **F)** Stratigraphy of archaeocyath-grade sponges, limited to the Cambrian Series (see also Fig. 3); note the number of genera is significantly larger than the other sponge grades. **G)** Other hypercalcified sponge grades.

The literature on hypercalcified sponges and their history is widespread and complex. It would benefit from a simple overview to show relationships between the various forms and their history. Therefore the ***aim of this study*** is to draw together the suite of hypercalcified sponges, and provide an integrated account of Phanerozoic hypercalcified sponges, with implications for their palaeogeographic distribution.

2. Brief perspective of hypercalcified sponge study

Sponges (Phylum Porifera) are metazoans that lack discrete organs, most of them being composed of a soft skeleton framework of the collagen protein spongin producing a simple structure (Fig. 1), yet they have a lifestyle variability and adaptability that points to them having more complexity (Wulff, 2016). The majority of sponge soft skeleton frameworks contain embedded mineralised skeletal elements called spicules, that strengthen the framework. Most sponges have spicules made of silica, and form the Class Demospongiae, representing 81-85% of living sponges (Hooper and Van Soest, 2002; Morrow & Cardeas, 2015) (Greek *demos* = '*the common people'*, origin of the concept of democracy, so the name demosponges is partly metaphorical). Spicules of calcite define the Class Calcarea and a third class, Hexactinellida, informally called glass sponges, comprise a network of silica spicules, but lack a spongin soft skeleton. A fourth group, the Homoscleromorpha, is recognized as a Class (Gazave et al., 2012), but has a very poor fossil record (Botting and Muir, 2018). Furthermore, although these classes are traditionally recognised as the major divisions of sponges, molecular work in recent years has raised questions as to the validity of the classification and work continues to develop these ideas (Botting and Muir, 2018).

Hypercalcified sponges (abbreviated to HSs in appropriate places through this text) were recognised as sponges in a landmark study by Hartman and Goreau (1970), but as mentioned above, the name ‘hypercalcified sponges’ was coined by Termier and Termier (1973) to distinguish them from the Class Calcarea. Of considerable interest is that HSs live in deeper water than the dominant corals in reefs, down to a few hundred metres (Vacelet et al., 2015, p11), contrasting soft sponges in reefs that live from near-surface waters down through mesophotic depths to 150 m (Lesser & Slattery, 2018), although some non-hypercalcified sponges can live in depths greater than 1000 m (Downey et al., 2018).

Vacelet et al. (2015, p. 5) noted that in nearly all cases, the hypercalcified skeleton does not develop on the spicules. In many hypercalcified sponges, the hypercalcified skeleton is formed largely below the soft tissue that forms a layer on the skeleton and is hence termed ‘basal skeleton’ (Vacelet et al., 2015). However, in at least one case (*Astrosclera willeyana*) the mineralisation is intracellular (Wood, 1991). Stearn (2015a, p561) summarized hypercalcification to occur in three places: basal pinacoderm (forming the basal skeleton), intracellular and within collagenous soft tissues, so although the term basal skeleton is commonly used, it is not applicable to all these sponges.

The calcareous skeleton of HSs is preserved, in contrast to the soft skeleton (found largely in lagerstätten, e.g. the Chengjiang biota, Luo et al., 2019) and spicules may or may not be present, so that the fossil record of sponge bodies overall is taphonomically biased in favour of hypercalcified sponge skeletons. Thus although hypercalcified sponges dominated shallow-marine reef systems in, for example the middle Palaeozoic, the importance of non-calcifying sponges as contributors to fossil reefs and communities is poorly known. Nevertheless, the abundance and diversity of fossil HSs underlines the ecological difference between many ancient sponge-dominated reefs and modern coral-dominated reefs; the latter are typified by the photoresponsive character of modern coral ecology, in contrast to the unknown photoresponse in ancient reef HSs.

Because hypercalcified sponges became viewed as polyphyletic, and the names of the various groups were no longer of phyletic value, the term ‘grades’ was applied to the different forms. For example, modern stromatoporoid-grade genus *Astrosclera* and chaetetid-grade genus *Acanthochaetetes* are both members of the Class Demospongiae (Vacelet, 1985). Fossil HSs are abundant in shallow marine carbonate systems, with different grades being prominent at different times during the Phanerozoic Eon (Fig. 2); at present HSs have a minor position in modern seas.

3. Hypercalcified sponge form-groups and their history.

3.1. Archaeocyath grade

Archaeocyaths are cup-shaped sponges with a form reminiscent of solitary corals, and occur in the early Cambrian (Greek *Arkhaios* = to begin [= ancient]; *kyathos* = tall, round, tapering vase; *kyatheion* = little cup). Debrenne and Vacelet (1984) provided a key study supporting inclusion of archaeocyaths as sponges, and

Debrenne et al. (2002) formally placed archaeocyaths as a class of sponges, Class Archaeocyatha. Similarity between archaeocyath structure and the modern sphinctozoan hypercalcified sponge *Vaceletia* provides a link between archaeocyaths and modern hypercalcified sponges (Debrenne and Vacelet, 1984; see also overview by Webby, 2015a, p. xix).

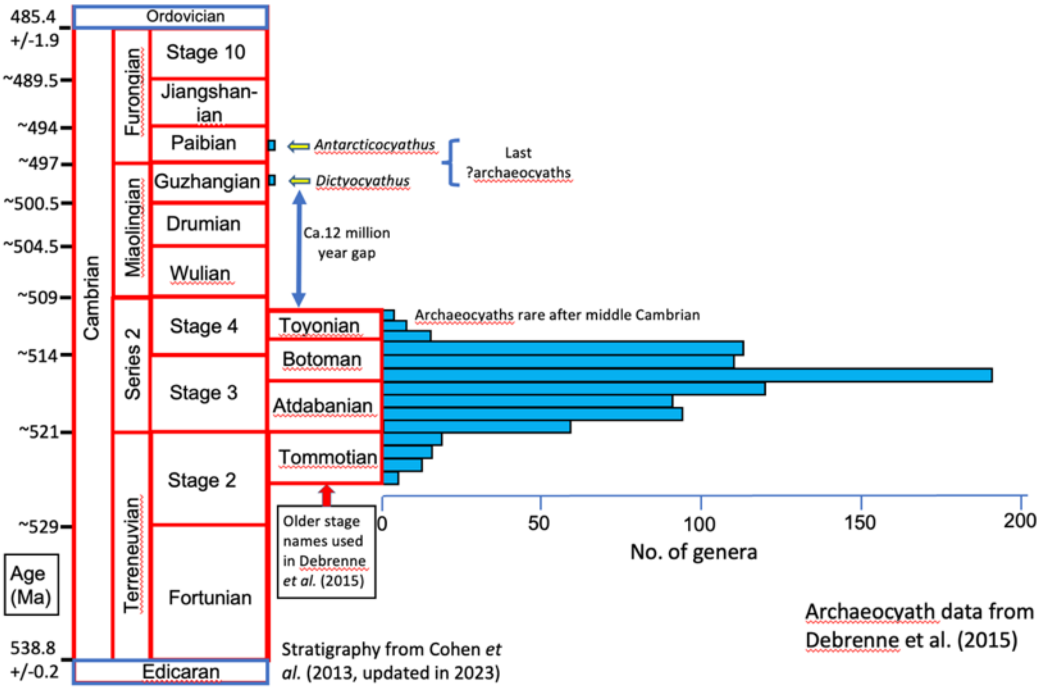


Fig. 3 Details of stratigraphy of archaeocyath-grade sponges, indicating they are almost completely restricted to lower-middle Cambrian strata.

Figures 2 and 3 show the narrow stratigraphic range of archaeocyaths but also emphase their extraordinary diversity of 305 genera (Debrenne et al., 2015), contrasting the next most-abundant group, the stromatoproids, which have 127 formalised genera in the Middle Ordovician to Lower Carboniferous. Thus archaeocyaths are highly diverse in structure (Fig. 4). Archaeocyaths have wide distribution in low-latitude reefs (Pruss et al., 2024).

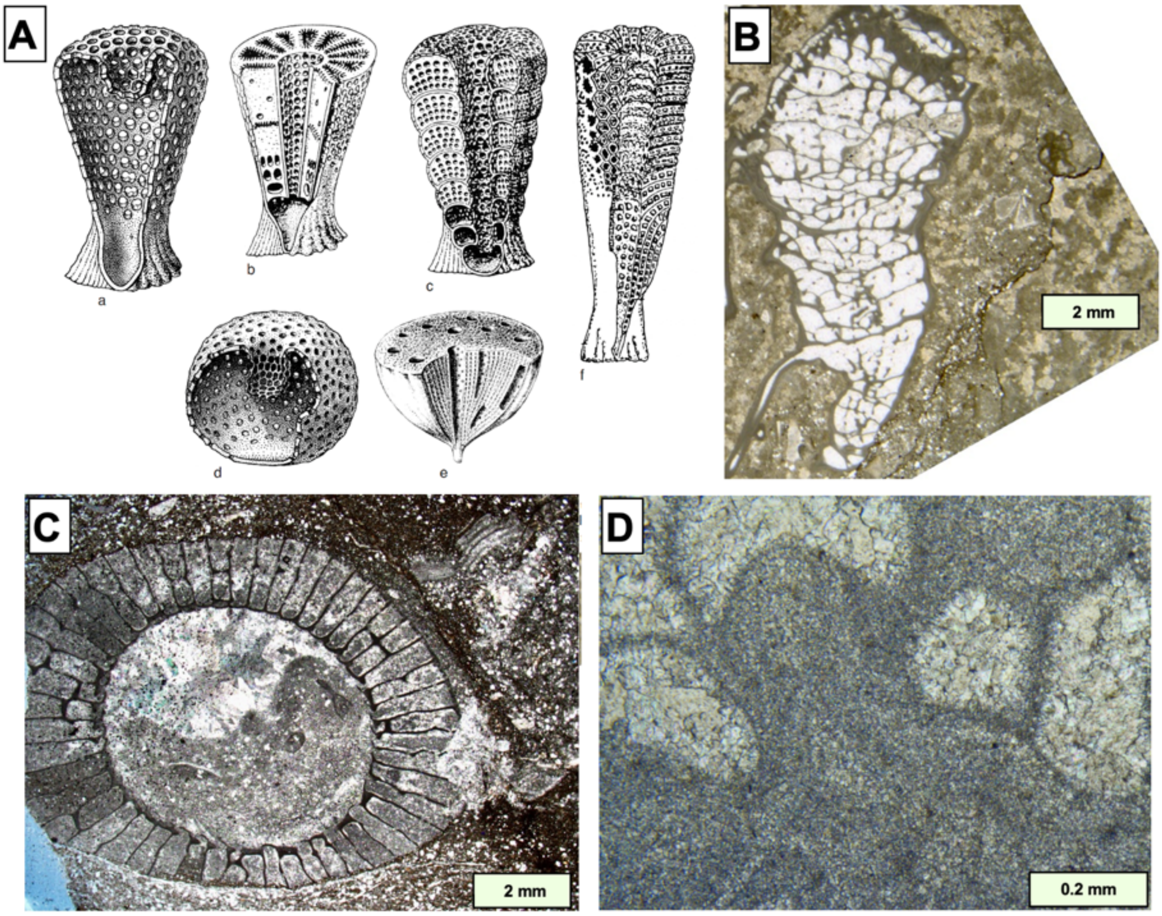


Fig. 4 Features of archaeocyath-grade sponges. **A)** diagrams of range of archaeocyath structure, reproduced from Debrenne *et al.* (2015, Fig. 491) under CC-BY-4.0 licence; the meaning of archaeocyath as “ancient cup” is apparent (“ancient cups”; cyathe is French, derived from Greek kyatheion = little cup). **B)** Vertical section of archaeocyath *Metacyathellus Lepidus*, reproduced from Tang et al. (2019, Fig. 6g, under CC-BY-4.0 licence), Xiannüdong Fm, Cambrian Series 2, Sichuan, China. **C)** Transverse section of unidentified archaeocyath. Sample from Jindingshan Fm, Cambrian Series 2, Guizhou, China. **D**) Transverse thin section of unidentified archaeocyath, showing micritic granular structure typical of archaeocyaths. Xiannüdong Fm, Cambrian Series 2, Sichuan, China. Sample provided by Hao Tang (Chengdu).

Using the descriptions of archaeocyath genera in Debrenne et al. (2015), Fig. 3 shows that archaeocyaths first appeared Stage 2 of the early Cambrian, indicating early development of hypercalcification in the fossil record of sponges, although reasons why some sponges became hypercalcified is not clear, see Wood (1991) for discussion. Then, archaeocyaths underwent a remarkable expansion in the lower half of Cambrian Series 2, Stage 3, culminating in a peak of 191 genera during the upper part of Stage 3, equivalent to the earlier-used Botoman Stage. However, after that they declined rapidly in the lower part of Stage 4, and by the top of Stage 4, they had almost completely disappeared from the record. Pruss et al. (2024) showed the continuation of some archaeocyaths in the later part of Stage 4, but only one genus, *Archaeocyathus*, was found. After a gap of about 12 million years, the only subsequent occurrences are in the Guzhangian and Pabian Stages of the upper Cambrian (Fig. 3). However, Lee (2022) reinterpreted the youngest occurrence, *Antarcticocyathus*, as an anathaspellid lithistid sponge, which raises the possibility that not all archaeocyaths are necessarily grouped in the Class Archaeocyatha. Nevertheless, the lower occurrence of these two latest genera, in the Guzhangian Stage continues to be considered an archaeocyath, but not present in reefs (Pruss et al. 2024), and Lee's (2022) reinterpretation as a lithistid allows for some lithistid demosponges to be included as hypercalcified forms. Thus while there is general agreement that archaeocyath-grade sponges died out in the later part of the early Cambrian, there seems to be evidence of their continuation into the late Cambrian. Pruss et al. (2024) refer to archaeocyaths as the first reef-building clade, and to *Archaeocyathus* as a "dead clade walking" (a fossil or small group of fossils, that survived an event of major decline, but never recovered and eventually died out; see Barnes et al., 2021 for discussion). However, noting that archaeocyaths are a hypercalcified sponge *grade*, then the concept of clade may or may not be appropriate, depending on whether or not archaeocyaths may be proved to be a single phyletic group.

Finally, Luo et al. (2021) offered the view that vauxiid sponges of the later Cambrian evolved from archaeocyaths, based on similarities between their architectures. Luo et al. (2021) proposed the possibility that archaeocyaths lost their ability to calcify in the late part of early Cambrian time, but survived as sponges and led to evolution of vauxiids. Their proposal is both innovative and controversial for the historical development of hypercalcification, because: a) it raises questions about how loss of hypercalcification occurs; there may alternatively have been extinction of sponge taxa that just happened to be hypercalcifiers, a suggestion raised by Kershaw and Jeon (2024); and b) it highlights the point that hypercalcified sponges are sponge genera with an ability to form easily-preservable skeletons and thus draws attention to taphonomic bias in the sponge record, potentially revealing that the preserved record of hypercalcified sponges gives us a skewed view of the overall history of Porifera in the rock record.

After the loss of archaeocyath reefs in the late middle Cambrian, reefs are populated by lithistid sponges for the rest of the Cambrian, then in early Ordovician, reefs contain lithistids, calathids and pulchriliaminids, before appearance of stromatoporoid major reef-building in the Middle Ordovician (Lee & Riding (2018).

3.2. Stromatoporoid grade

Stromatoporoid-grade hypercalcified sponges are characterised by a layered growth form with internal voids called galleries (Greek *stroma* = mattress/bed; *poros* refers to the voids), see Fig. 5. Stromatoporoid forms developed from the Early Ordovician (Jeon et al., 2019), then in Middle Ordovocian became significant reef builders. The stromatoporoid grade shows change of architecture between Ordovician, Silurian and Devonian time, leading to a progression of forms defined as genera that can be easily appreciated in a stratigraphic table of genera showing events of loss and appearance of genera (see Kershaw and Jeon, 2024, Fig. 8, not repeated here). Kershaw et al. (2021a) and Kershaw & Jeon (2024) reflected on the application of Order and Family groupings of stromatoporoids. Because of the lack of spicules, they cannot be grouped according to modern sponge taxonomic principals, so the possibility is open that the current Order groups are entirely artificial and not necessarily related to phyletic groups. Nevertheless, the lowest level of taxon available, traditionally called species in stromatoporoid literature, is a reasonable indication of taxonomic separation.

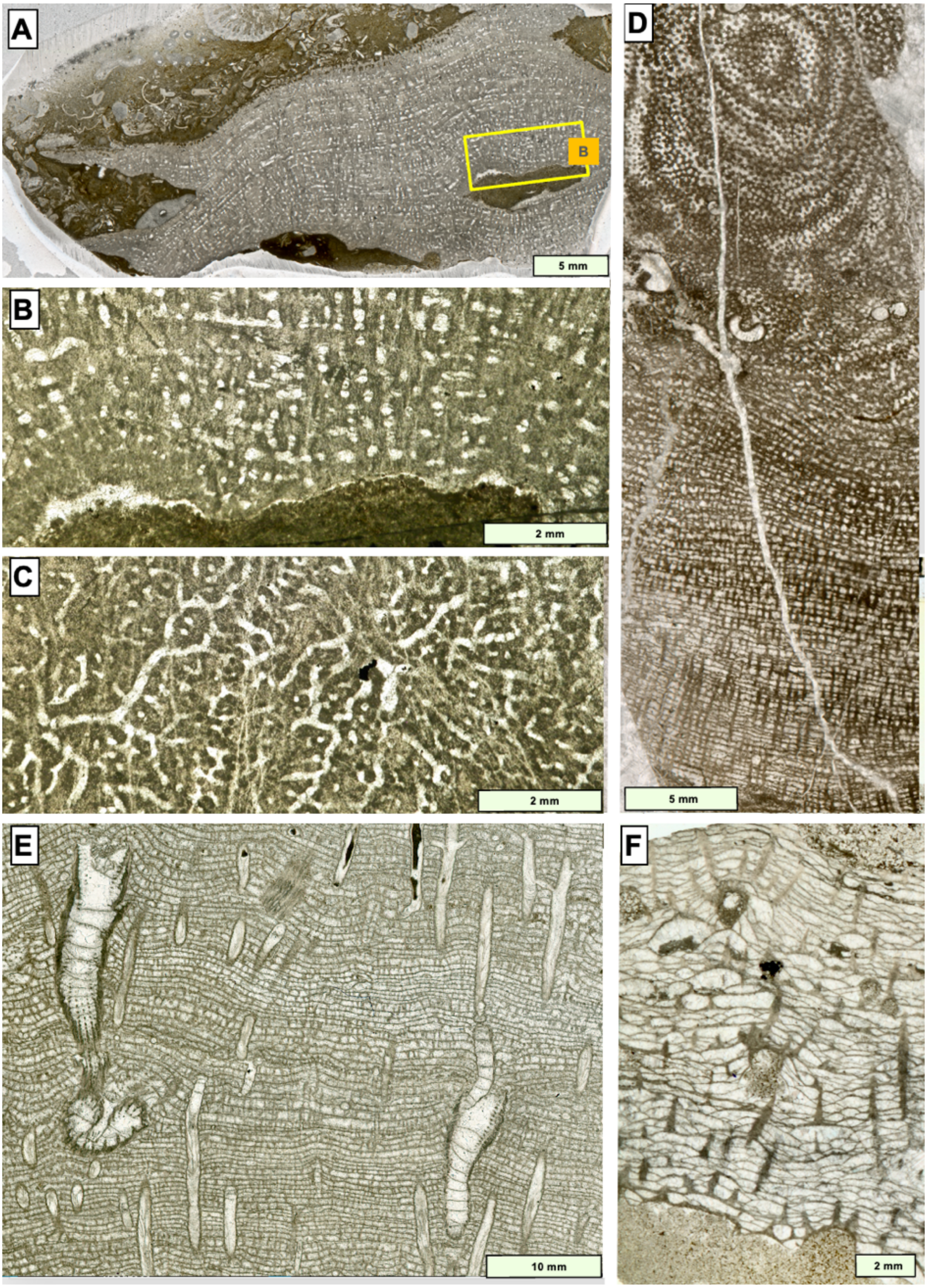


Fig. 5 Stromatoporoid-grade sponge architecture. **A)** Vertical thin section of *Eostromatopora impexa* showing layered porous structure typical of stromatoporoids. **B)** Vertical thin section view of *E.*

impexa, showing combination of vertical and transverse elements enclosing gallery space in the structure; this characteristic derives the term stromatoporoid (layers and holes). **C)** Transverse thin section view of *E. impexa*, showing prominent astrorhizal canals in this taxon, interpreted to indicate the excurrent canal system of the sponge. **D)** Thin section of *Actinostroma* showing vertical section (VS) view in the lower part and transverse section (TS) view in the upper part, caused by curvature of the specimen in relation to the thin section orientation. Prominent pillars are visible in the TS area, characteristic of this taxon. Note the tubes of a spiral intergrown organism centre and bottom. Middle Devonian, south Devon, UK. **E)** VS view of *Petridiostroma convictum* with a combination of syringoporid tabulate and branching rugose corals as intergrowths within the stromatoporoid. Upper Ludlow, Gotland, Sweden. **F)** VS of a labechiid stromatoporoid, showing prominent long pillars and curved cyst plates characteristic of this taxon. Famennian (U. Devonian), Sichuan, China; sample provided by Yue Li, Nanjing.

Stromatoporoids are typified by their layered structure, subject to common growth interruptions (Fig. 5). Many taxa show, in transverse sections, radiating canal systems, astrorhizae (Fig. 5C), interpreted as locations of exhalant water drainage from the sponge (Stearn, 1975) wherein the drainage tubes were partially embedded in the skeleton. Taxa lacking astrorhizae are presumed to have borne the exhalant drainage in tubes on the skeleton surface (Fig. 5D). Many stromatoporoids have intergrown organisms, with spiral tubes common (Fig. 5D), and some taxa contain symbiotic syringoporids and rugose corals (Fig. 5E), interpreted by Kershaw (2024) to have potential biological relationships with the host stromatoporoid. Ordovician stromatoporoid assemblages contain abundant taxa of skeletons composed primarily of horizontally-orientated cyst plates, and commonly prominent thick pillars; these are grouped as the Order Labechida. Labechiid stromatoporoids are well known to have declined in the Late Ordovician extinction, and are rare through Silurian and the Devonian strata up to the end of the Frasnian, but resurged after the Frasnian-Famennian extinction, as shown in Fig. 5F). Stromatoporoids are rarely reported from the Carboniferous (*Kyklopora,* Nestor, 2015; *Parallelopora mira,* Newell, 1935 [renamed as *Spongionewellia*, Özkidmen, 2009]). In the case of *Spongionewellia,* Newell's (1935) illustrations show that in vertical section it looks like a stromatoporoid, but in transverse section it looks like a chaetetid (Fig. 6), emphasizing the overlapping nature of hypercalcified sponge grades, discussed by Wood (1990). However, the confirmed Lower Carboniferous stromatoporoids (Kershaw and Sendino, 2021; Ezaki et al., 2024) have labechiid architecture, providing a possibility that such structures were more resilient to environmental change.

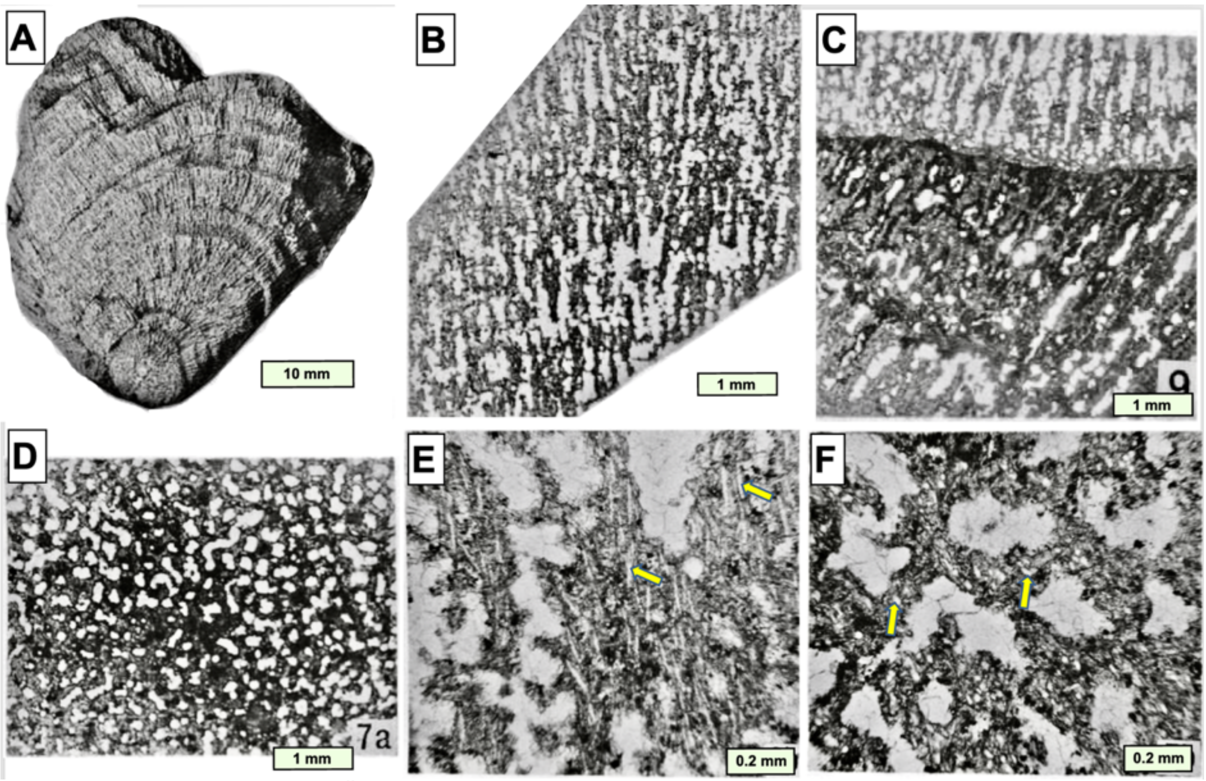


Fig. 6 *Spongonewellia mira* Özkidmen, 2009, originally identified as *Parallelopora mira* by Newell (1935). Images reproduced from Newell (1935, Plate 34) with permission from SEPM. **A)** Side view of eroded sample showing layered structure, and architecture with prominent vertical structure. **B)** Vertical thin section showing a structure comparable to stromatoporoid-grade. **C)** Vertical thin section showing variations in skeleton, with growth interruption events. **D)** Transverse thin section showing architecture comparable to chaetetid-grade. **E, F)** Enlarged vertical section (E) and transverse section (F) showing details of hypercalcified structure, plus presence of spicules as elongate clear objects (yellow arrows).

Stromatoporoids were subject to diagenetic alteration, in all cases described (Fig. 7), which creates a problem for understanding their primary mineralogy. In most cases the alteration comprises irregular calcite crystals that cut across both the skeletal carbonate and the internal voids (galleries), forming a fabric-retentive irregular calcite (FRIC) overprint (Fig. 7C-F). It is repeatedly stated in literature that stromatoporoids are better preserved than most molluscs (presumed to have original aragonite shells), but less well-preserved than brachiopods (presumed to have low magnesium calcite shells), see Kershaw et al. (2021b) for a review; the presence of microdolomite in some cases implies that stromatoporoids had a high magnesium calcite mineralogy, but the relationship is inconsistent and so currently there is no clear demonstration of their original mineralogy. In some cases cathode luminescence seems to reveal an original, or near original structure (Fig. 7G, H) but further work is needed to advance this idea.

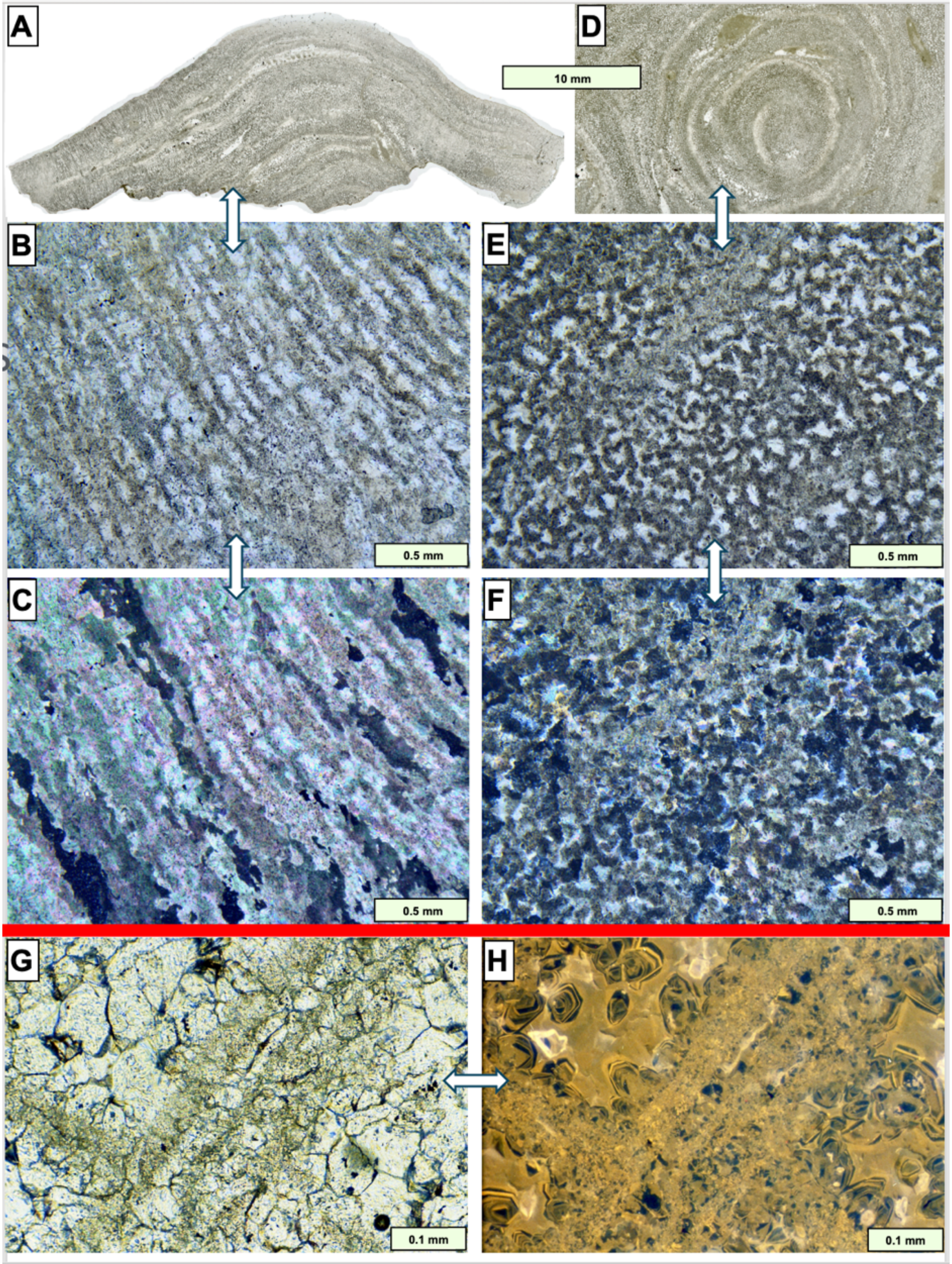


Fig. 7 Textures in stromatoporoids, showing their porous layered structure from which their name is derived. **A) – C)** Vertical section of stromatoporoid taxon *Syringostromella*, showing in A: layered nature of stromatoporoid-grade architecture; in B: plane-polarised light (PPL) view of vertical and tangential elements; in C: cross-polarised light view (same area as B) of overprinting fabric-retentive irregular calcite diagenetic alteration (C). **B) – F)** Transverse section of same sample of *Syringostromella* as in A-C, showing the same features in transverse section. A-F is from the Upper Visby Formation, lower Wenlock, Ygne site, Gotland. **G), H)** The same area of vertical section of

Simplexodictyon, showing diagenetic overprint on the skeleton in PPL (G), but H is a cathodoluminescence image that reveals cement zoning in the galleries, that grew on a structure which may be the original or near-original fabric of the stromatoporoid hypercalcified skeleton. From a biostrome in the Hemse Group, middle Ludlow, upper Silurian, Kuppen 3 site, Gotland.

Stromatoporoids commonly display vertically-orientated upward-growing columnar outgrowths whereby the skeletal structure simply grew up into columns (thus negative geotropic growth), maintaining the skeletal architecture (not illustrated here, see Kershaw et al., 2018, Fig. 12). Although most stromatoporoids grew on horizontal bed surfaces, some grew on sloping surfaces and some of those contain negative geotropic columns, which in all cases are vertically orientated, thus normal to bedding (see Kershaw, 2013, Fig. 14). Kershaw (2013) proposed such columns to be circumstantial evidence of a photoresponse in stromatoporoids. Recently Jung et al. (2024) reported nitrogen isotopes in Middle Devonian corals, evidence for photosymbiosis in Palaeozoic corals. Furthermore Jonathan Jung [pers.comm. 2nd November 2024] and colleagues in Mainz, Germany have unpublished work in progress that demonstrates nitrogen isotopes in Devonian stromatoporoids, evidence for photoresponse, consistent with circumstantial evidence found in growth forms of some stromatoporoids (Kershaw, 2013, 2022). This is an exciting development in stromatoporoid work that may significantly change our view of the biology of these fossil sponges.

3.3. Chaetetid grade

Chaetetids are known from early Silurian to modern times, with almost continuous presence in the rock record through their overall history (Fig. 2). However, the chaetetid structure is somewhat conservative, with few structures upon which to determine taxa. Chaetetid-grade derives its name from Greek *chaete* = “flowing hair” because of the structure of masses of long contiguous tubes, called calicles, that in some specimens are reminiscent of human hair (Fig. 8A, E). Palaeozoic chaetetids rarely contain spicules, but some Mesozoic taxa are spiculate (Fig. 8F, G). Some cases of Carboniferous chaetetids have astrorhizae (West & Clark, 1984), emphasizing their sponge nature. Although Fig. 2 shows that chaetetids have low diversity of skeletal structure in the Palaeozoic, Carboniferous cases developed substantial reefs. The conservative nature of the chaetetid skeleton, with few characters for taxonomic determination, may hide a problem of a more diverse biology within similar skeletons, that may not be distinguishable in fossils. This raises the possibility that Carboniferous chaetetid reefs contained more than one taxon of chaetetid-grade sponge, an issue that will be difficult to resolve.

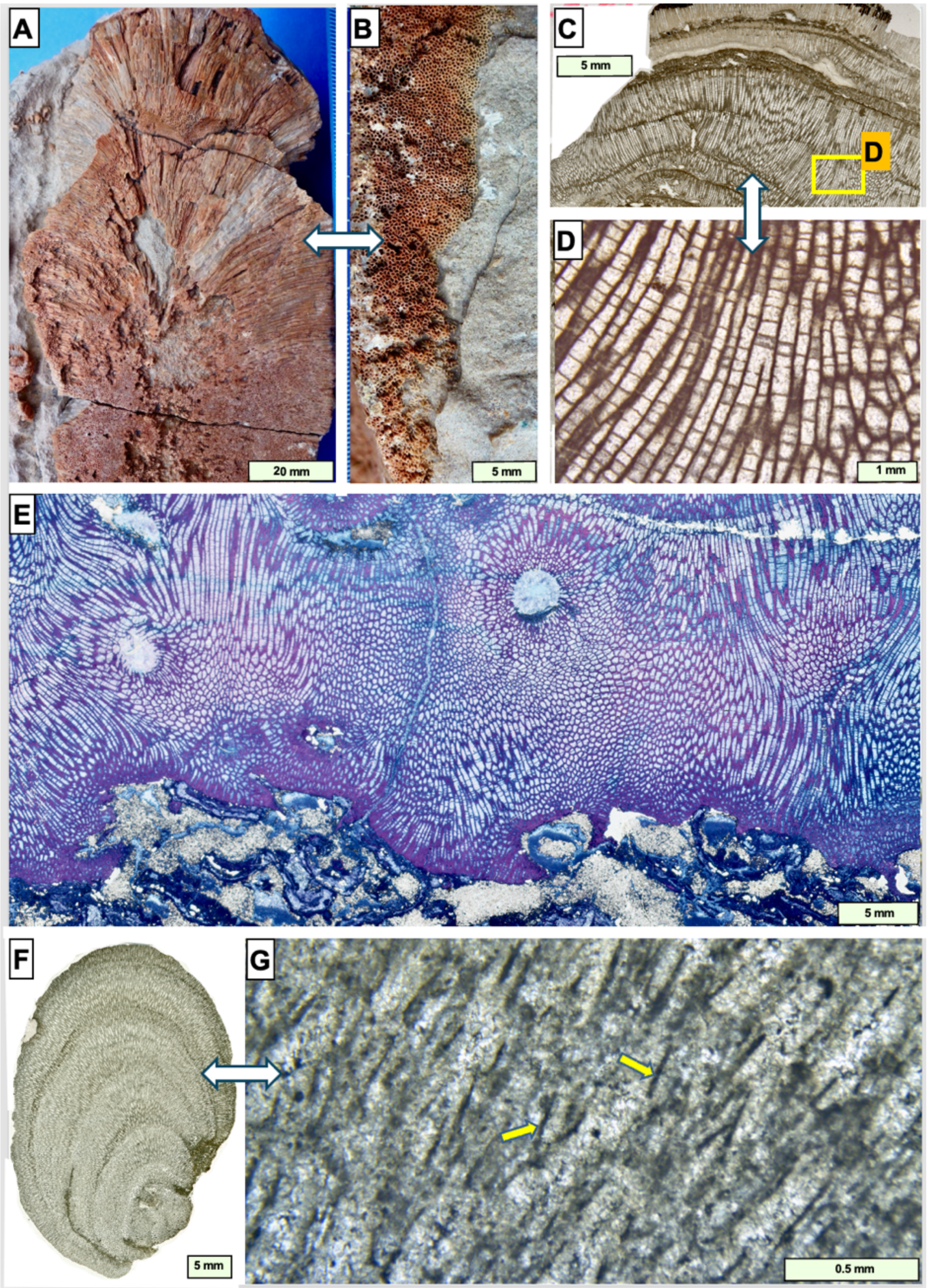


Fig. 8 Chaetetid-grade architecture, showing the calicle arrangements reminiscent of flowing hair, from which chaetetids get their name, based on Greek chaite = flowing hair. **A), B)** *Chaetetes* hand specimens showing vertical (VS, A) and transverse (TS, B) sections of calicles in a columnar form. Laberdie Limestone Member, Pawnee Formation, Pennsylvanian, Fort Scott, Bourbon County, Kansas. **C) VS** of *Chaetetes* showing repeated growth interruption events. Amoret Limestone

Member, Altamont Formation, Pennsylvanian, Labette County, Kansas. **D)** enlargement of C, showing calicles with tabulae in both VS and TS, due to curvature of the growth form. **E)** VS of acetate peel stained with Alizarin Red S and potassium ferricyanide combined stain, demonstrating the variation of preservation as both ferroan and non-ferroan calcite; Homer School Limestone Member, Holdenville Formation, Pennsylvanian, Oklahoma. **F)** VS of *Blastochaetetes*, Jurassic of Portugal. **G)** Enlargment of F showing spicules (yellow arrows) embedded in the hypercalcified skeleton. F, G: Basal Cabaços Formation, middle Oxfordian, at Cabo Mondego, Lusitanian Basin, central Portugal (Azerẽdo et al., 2002); sample provided by Simon Schneider.

Palaeozoic chaetetids have well-preserved skeletal structure, with chevron arrangements of wall elements and tabulae (Fig. 9A,B). However, poor preservation occurs in some cases, particularly seen in Mesozoic forms (Fig. 9C-F), with overprinting of the skeleton by alteration that partially retains the original structure. This arrangement is therefore a form of fabric-retentive irregular calcite (FRIC) recrystallisation reported by Kershaw et al. (2021) as being unique to stromatoporoids. Thus, the presence of a recrystallized fabric in chaetetids indicates that alteration may occur in both these hypercalcified sponge groups.

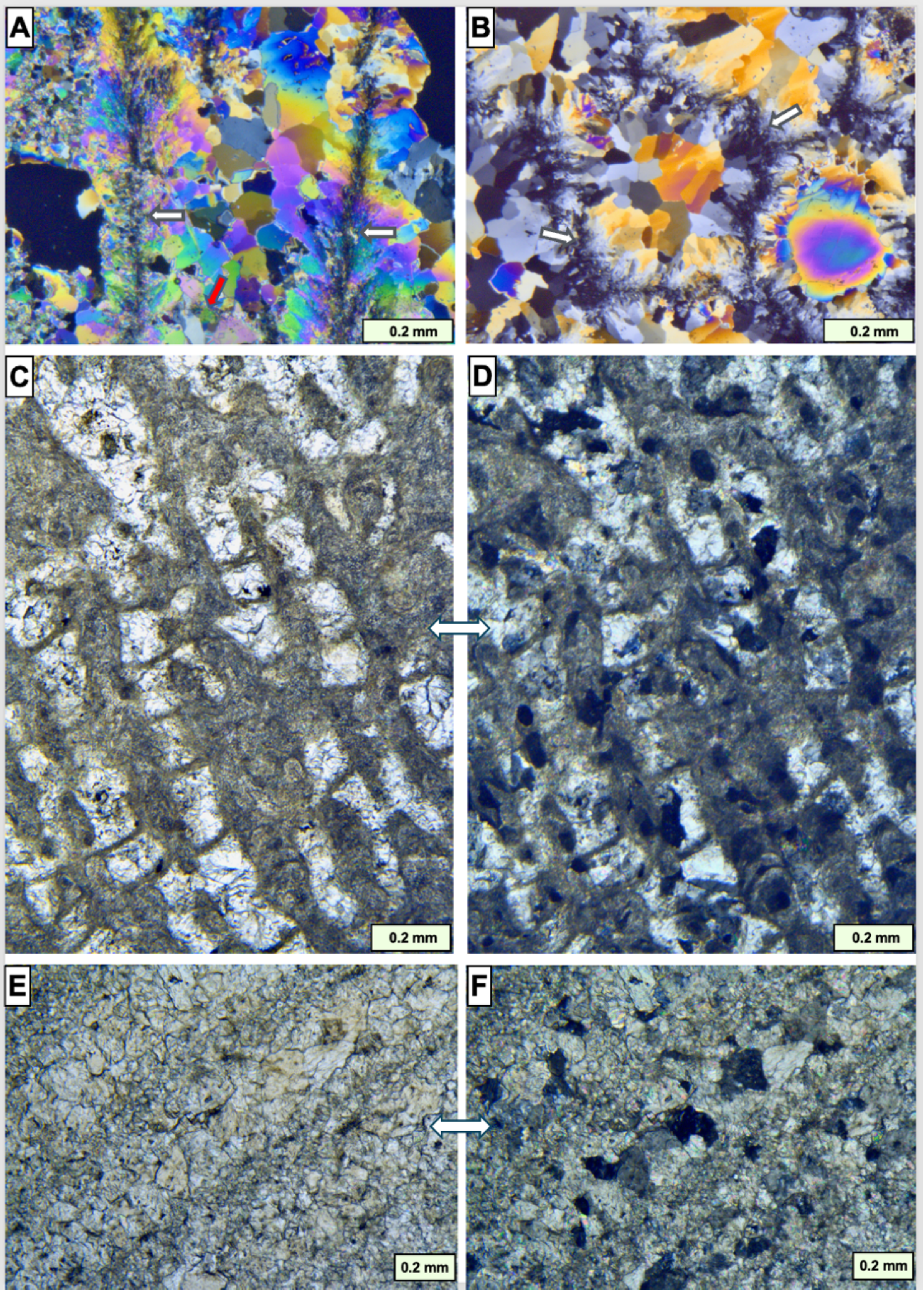


Fig. 9 Textures in chaetetids. **A), B)** Cross-polarised light views of very thin sections in VS (A) and TS (B) of Pennsylvanian *Chaetetes* from Kansas, showing well-preserved calicle walls with chevron structure (yellow arrows) typical of chaetetids, and tabula (red arrow). **C), D)** VS views of *Blastochaetetes* showing plane-polarised light (C) and corresponding cross-polarised light (D) views,

demonstrating overprinting of the hypercalcified skeleton by diagenetic calcite alteration, contrasting the well-preserved structure in A) and B). **E), F)** Enlarged view of VS of *Blastochaetetes* showing the chaetetid skeleton is substantially recrystallized; C-F from Jurassic of Portugal.

3.4. *Sphinctozoan and inozoan grades*

These are considered together here because of their common co-occurrence. Sphinctozoans may be the oldest hypercalcified sponges (Fig. 2), noting that archaeocyaths are considered to have similarity of architecture to the modern sphinctozoan genus *Vaceletia*. Sphinctozoans have a chambered structure (Fig. 10) with its hypercalcified skeleton on the outside of the chambers, so the soft tissue lies within the chambers. Sphinctozoan name derives from Greek *Sphingein* = constrict; *zoon* = animal, and sphinctozoans are one of the types of sponges previously called Pharetronids (a name derived from their commonly fibrous structure, Greek *pharetra* refers to quiver, a cylindrical container for arrows). Pharetronids are polyphyletic within the Demospongiae and Calcarea (Ilan & Vacelet, 1993). Sphinctozoans are also called thalamids (Greek *thalamus* = a chamber).

The earliest records of sphinctozoan sponges date back to the Cambrian (Senowbari-Daryan and García-Bellido, 2002). Their first major radiation occurred in the Ordovician, with 15 genera emerging (Fig. 2), marking a critical stage in the early evolution of chambered sponges (Senowbari-Daryan and Rigby, 2011). During the Late Ordovician, sphinctozoans underwent further radiation and geographic expansion, extending their ecological niche from level-bottom to reef environments (Fig. 10) (Li et al., 2015a, 2023; Carrera and Rigby, 2004). They became significant reef builders and common cryptobionts during the mid-late Permian and mid-late Triassic (Wood, 1991; Senowbari-Daryan, 2005). Sphinctozoans were strongly affected by the end-Permian and end-Triassic mass extinctions, when their key role in Late Permian reefs was terminated because of the extinction.

Work by Reitner (1990) and Vacelet (1985) indicates that the sphinctozoan grade is polyphyletic, and may have evolved in both the Classes Demospongiae and Calcarea. Problematically, fossil sphinctozoans rarely contain spicules, and some spicule-bearing forms are suspected to have spicules imported into the skeleton after death (Senowbari-Daryan and Rigby, 2015, p.336), presumably by currents, so that determining the taxonomic position of the various genera cannot be reliably confirmed.

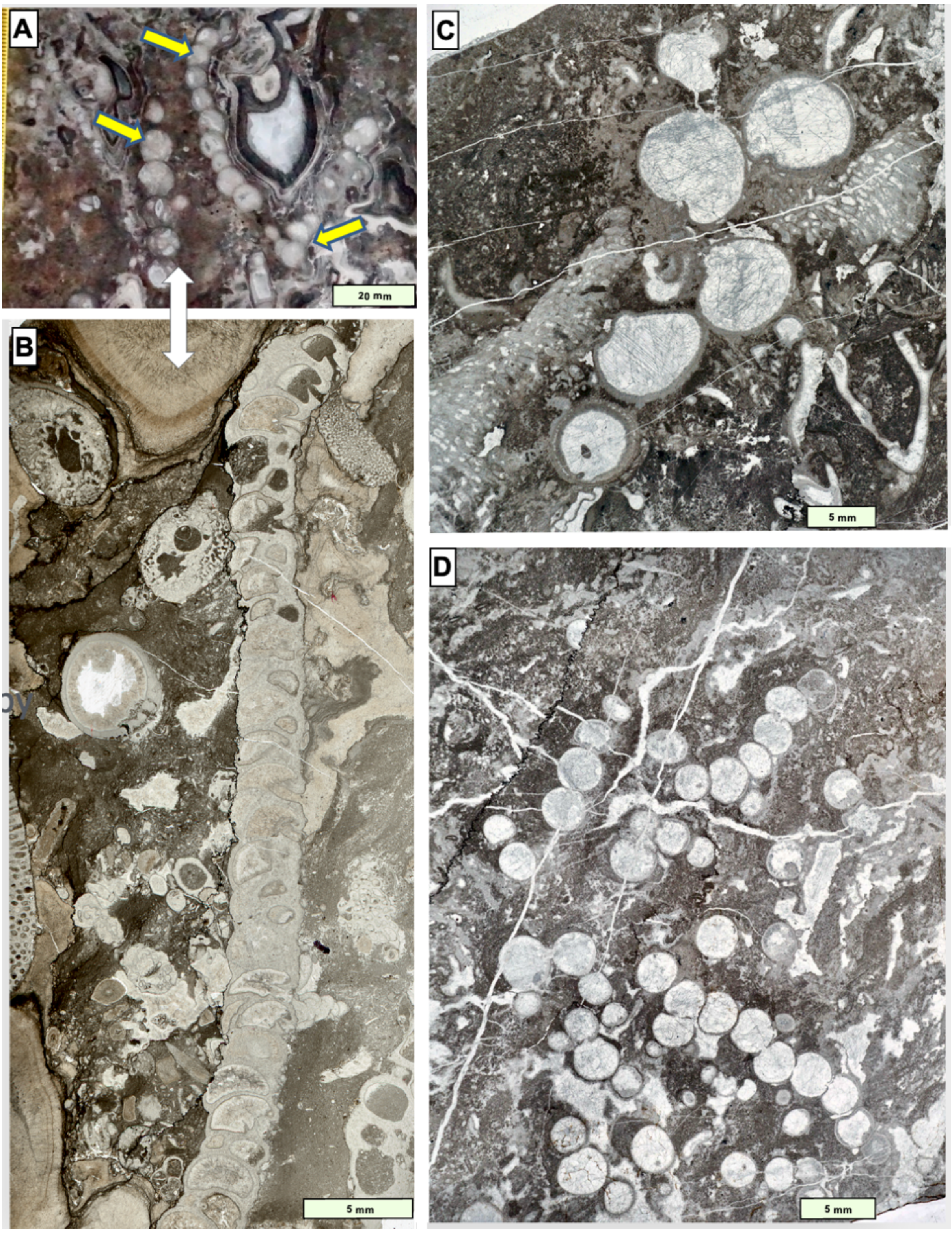


Fig. 10 Sphinctozoan-grade architecture. **A)** vertical section of polished block of reef limestone with 3 sphinctozoan individuals (arrowed), comprising chambers with walls, restricting soft tissues, giving the name (from Latin and Greek origins meaning restriction) Greek sphingein = constrict; zoion = animal. **B)** Thin section on plane parallel to the surface shown in A), illustrating an unidentified sphinctozoan (centre) and parts of others; Permian, Jiantianba, Hubei, S. China. **C), D)** Sphinctozoans in reef framework: *Corymbospongia amplia* (C); *Corymbospongia mica* (D), samples from Sanqushan Fm, Katian (Late Ordovician), Jiangxi, China.

Inozoan sponges contrast the sphinctozoans because inozoans do not have the chambered structure possessed by sphinctozoans (Senowbari-Daryan and Rigby, 2015). In particular, inozoans have a fibrous structure (Fig. 11, Greek *ina* = fibre, that accounts for the fibrous arrangement of the hypercalcified skeleton in detail). Both groups became important reef builders in the Permian (Fig. 2); although both were badly affected by the end-Permian and end-Triassic extinctions, inozoans rebounded in the Jurassic whereas sphinctozoans continued in low diversity (Fig. 2). Senowbari-Daryan and Rigby (2015, p. 371-383) surveyed distribution of sphinctozoans and inozoans, showing they both occur largely in low to mid latitudes throughout their history, and were palaeogeographically limited during most of the Palaeozoic, becoming more widespread in Permian and Triassic. However, they became more restricted in later Mesozoic time and through the Cenozoic.

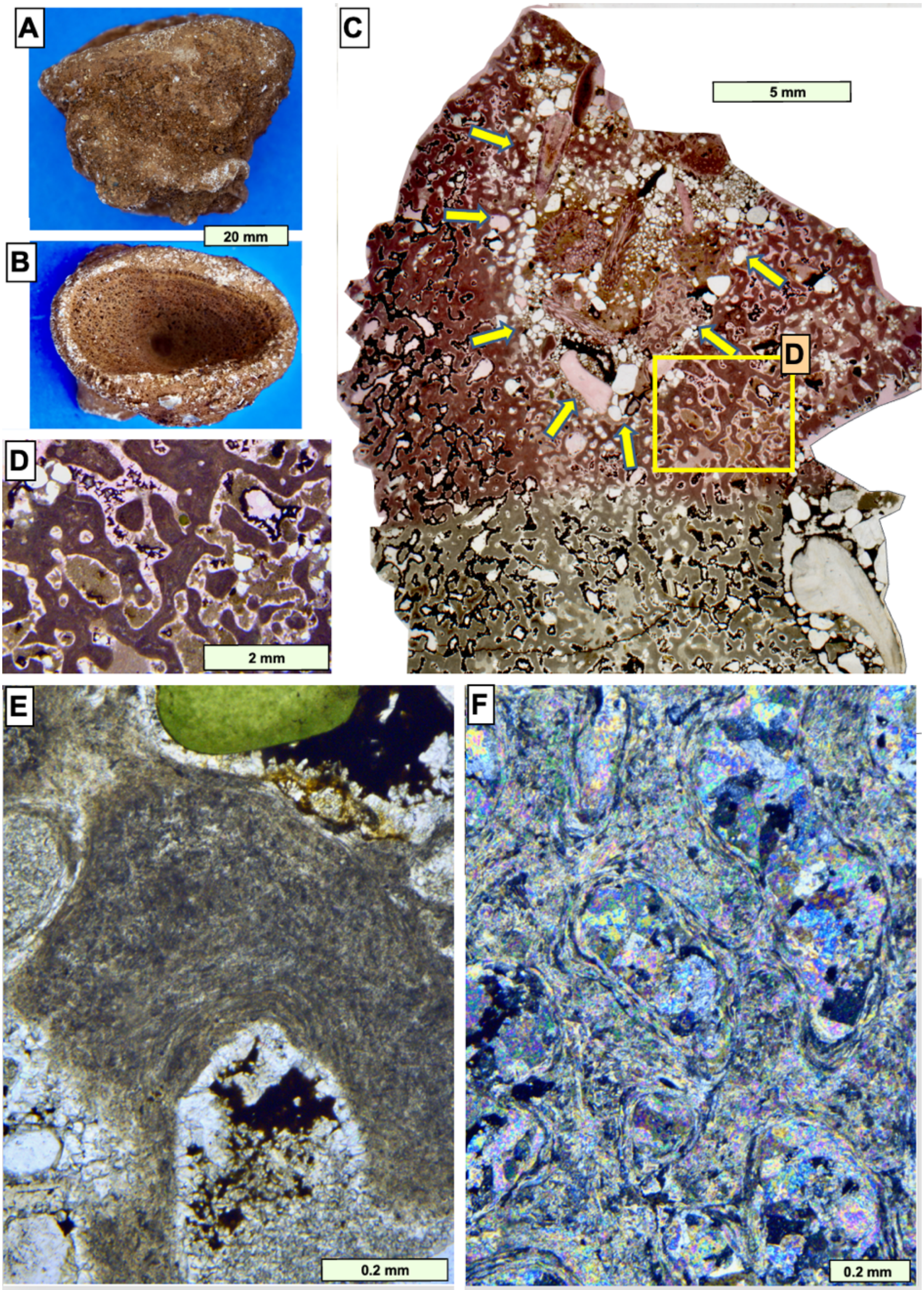


Fig. 11 Inozoan-grade architecture. **A), B)** Side (A) and top (B) views of cup-shaped inozoan sponge. **C)** Vertical section of sponge similar to A & B, showing cup-shaped form (outlined by yellow arrows); in contrast to sphinctozoans, it lacks a chamber, characteristic of inozoans. The cup is filled with clastic debris and fragments of other inozoans. **D)** Enlargement of C, showing sponge network of

hypercalcified skeleton. **E), F)** Thin section details of sample in A-D (E is PPL, F is XPL), showing fibrous structure from which the inozoan name is derived (Greek ina = fibre).

3.5. Other hypercalcified sponges and related forms

3.5.1. Calathids

As the only currently valid genus of calathids (Li et al., 2015b), *Calathium* (Fig. 12A,B) is an open, cup-shaped fossil and a common reef builder in the Early to early Middle Ordovician (Webby, 2002). It has an obconical (or cylindrical), branching body with an extensive holdfast composed of a network of calcareous structures around the base and within the cup (Guo, 1983; Li et al., 2015b; Dzik, 2024). First described by Billings (1865), *Calathium* was initially thought to belong to a unique group of sponge-like organisms. By the late 1970s and early 1980s, however, it was classified within the receptaculitids, a puzzling group of calcareous green algae in the family Soanitidae (Nitecki and Debrenne, 1979; Nitecki et al., 1981). However, *Calathium* differs from receptaculitids in terms of shape, attachment, pores, wall structure, and calcification patterns (Rowland, 2001). Its perforated inner and outer walls suggest that its assignment to algae is questionable (Church, 1991) and it likely functioned more like filter-feeding sponges (Church, 2009). Furthermore, the well-developed lateral outgrowths and budding reproduction seen in specimens indicate that *Calathium* cannot be placed within receptaculitids (Zhang, 1995; Li et al., 2015b, 2017).

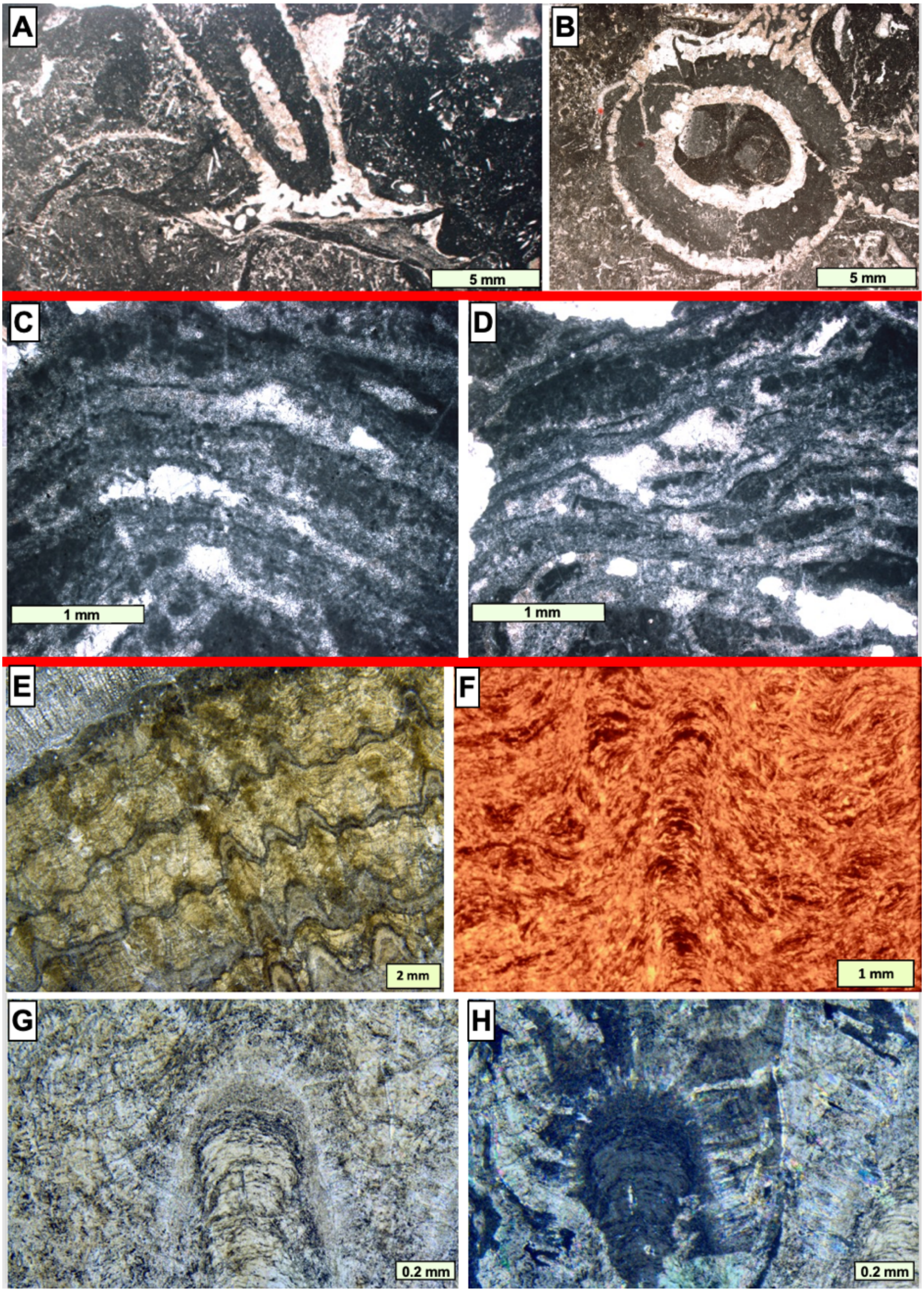


Fig. 12 *Calathium*, *Pulchrilamina* and *Lophiostroma* hypercalcified architectures. **A), B)** VS (A) and TS (B) thin section views of tapered cylindrical calcified fossil *Calathium*, regarded as a sponge. **C), D)** VS thin section views of problematic fossil *Pulchrilamina* that has similarities to stromatoporoids but sufficiently different to be considered separately (see Webby, 2015a). Samples in A-D from

Hunghuayuan Fm, Floian (Lower Ordovician), Hubei, China. **E)** VS in PPL of *Lophiostroma schmidtii*, classed as a labechiid stromatoporoid (Webby, 2015), comprising undulating small plates arranged into juxtaposed columns, revealed in **F)** under cathodoluminescence. **G), H)** Detailed matching VS views in PPL (G) and XPL (H) of *L. schmidtii*, demonstrating its unique diagenetic structure, considered in detail by Kershaw (2022). Biostrome, Hemse Group, Middle Ludlow; Kuppen site, Gotland. E-H reproduced under CC-BY-4.0 licence from Kershaw (2022).

Siberian calathids, once described as *Soanites* (Myagkova, 1965, 1984), are now considered a junior synonym of *Calathium* (Nitecki, 1986). Billings' original description did not mention outgrowths or holdfast structures, likely due to the incomplete nature of the *Calathium formosum* holotype. Rauff (1894) later introduced the name *Calathium? (Calathella) anstedi* (Billings), defining *Calathella* as a loosely defined subgenus of *Calathium*. Nitecki (1972) proposed that *Calathella* is distinguished by its prominent outgrowths, but he later revised this, suggesting that the outgrowths were due to epibionts, not part of the organism itself (Nitecki, 1986). Consequently, most authors have rejected Nitecki's definition of *Calathella*, leaving *Calathium* as the only widely accepted genus. One of the authors of this paper (QL) recently collected samples from the Fillmore Formation in Nevada, which show outgrowths in nearly all well-preserved specimens, challenging previous descriptions that calathids lack outgrowths in the Great Basin (Nitecki, 1986, p. 29). Thus, it appears that outgrowths are a characteristic feature of *Calathium*, and their absence in some specimens may be due to incomplete preservation (Guo, 1983; Zhang, 1995; Liu et al., 2005).

The main shared feature between *Calathium* and receptaculitids is their calcified elements (stellate structures with rods, also known as meroms) arranged in a similar pattern. However, this feature is not exclusive to receptaculitids and has also been noted in some cupuladriid bryozoans (Gould and Katz, 1975). Additionally, each *Calathium* rod has stellate structures at both ends, while in most receptaculitids, the rods (merom shafts) only connect at the distal ends (Rowland, 2001). Thus, these stellate structures may have evolved independently in different clades and are not diagnostic. Recent numerical simulations indicate that the radial rods in *Calathium* prolong the retention time of nutrients and gametes within the central cavity and in the surrounding water, supporting the hypothesis that calathids were filter-feeders (Feng, 2024). Updated morphological, structural, and functional analyses now suggest that calathids were hypercalcified sponges rather than receptaculitid algae, as previously believed (Li et al., 2015b, 2017).

3.5.2. *Pulchrilaminids*

Pulchrilaminids (Fig. 12C,D) are regarded as an uncertain class of hypercalcified sponges in the Lower to Middle Ordovician. Earlier work considered pulchrilaminids to be related to labechiid stromatoporoids, but this is now discounted (Webby, 2015). Webby (2015b) illustrated and described them as having laminar, domical and columnar shapes, with prominent internal lamination but dissimilar to any other hypercalcified sponge grade. Of the few taxa included within this group, the controversial genus *Zondarella* was convincingly reinterpreted as a microbialite (Cañas and Carrera, 2023). The true nature of the other few genera of pulchrilaminids is unknown, but it remains possible they are poriferans.

3.5.3. *Lophiostroma schmidtii*

Lophiostroma schmidtii (Fig. 12E-G) is included with the stromatoporoid-grades as one of the labechiids (Webby, 2015c) but we highlight it here because of its unique solid skeletal structure that does not fit well with the concept of a stromatoporoid architecture. *Lophiostroma schmidtii*, the most well-known *Lophiostroma* taxon (illustrated in detail by Kershaw, 2022) is comprised of thin plates, that may or may not be equivalent to the cyst plates found in the labechiid-type stromatoporoid. Of great interest is that the diagenetic overprinting present in all samples studied of *L. schmidtii*, differs from all other stromatoporoids; compare Figs. 6 and 12E-H, which creates uncertainty in determining the relationship between *L. schmidtii* and other stromatoporoids, such that it may or may not be appropriate to retain this taxon in the stromatoporoid grade classification. Nevertheless, its position as a member of the hypercalcified Porifera is not questioned at present.

3.5.4. Disjectoporids

Disjectoporids are poorly known hypercalcified sponges found in Permian and Triassic strata (Stearn, 2015), largely from Asia, see Fig. 13. Disjectoporids are not clearly related to any other hypercalcified sponge grade, and little work has been done on this uncommon group of fossils, a topic for future development.

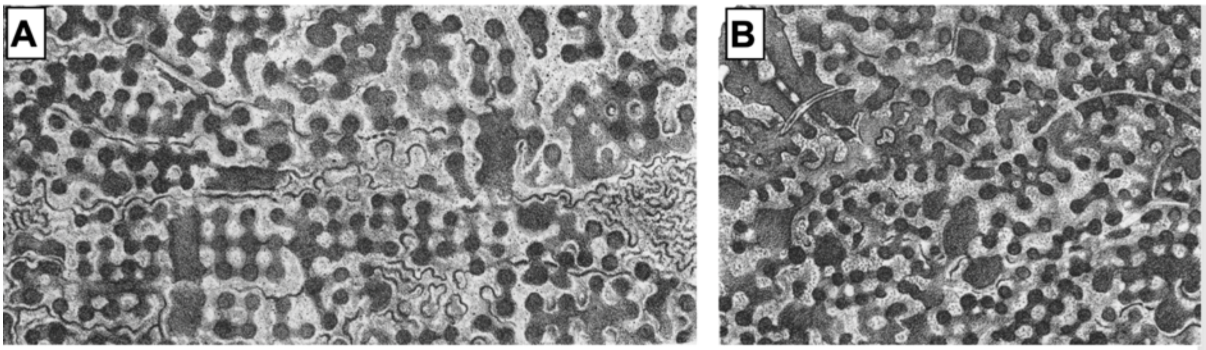


Fig. 13 Disjectoporids. **A), B)** VS (A) and TS (B) of *Disjectopora*, regarded as hypercalcified sponges of uncertain affinity (Stearn, 2015). Reproduced from Stearn (2015, Fig. 208, parts 1a, 1b) under CC-BY-4.0 licence.

3.5.5. Stromatoporoid-like forms

A list of stromatoporoid-like forms of hypercalcified fossils was compiled by Stearn & Stock (2015) as part of the 2015 Treatise, to demonstrate that there are many other fossils in the rock record that may be included within the hypercalcified sponges. Stearn and Stock's (2015) list, represented in a stratigraphic chart of hypercalcified sponges (Fig. 2G), includes taxa ranging from earliest Carboniferous to latest Cretaceous. The list includes the problematic taxon *Palaeoaplysina* (Jeon et al., 2024), that is prominent in some Carboniferous reefs. However, little work has been done on this ad-hoc grouping of fossils, lamentably related to the declining number of researchers in recent years. Thus there is much potential for development in this area.

4. Polyphyly of hypercalcified sponges

Modern hypercalcified sponges are demonstrably polyphyletic, as discussed in detail by a range of authors (e.g. Vacelet, 1985; Wood, 1990, 1991; Chombard et al., 1997; Senobari-Daryan and Rigby, 2015); thus the taxonomic determination of these fossils cross-cuts the distribution of hypercalcified skeletal forms, that shows the hypercalcified skeleton does not have phyletic value. Fig. 14 shows the four modern hypercalcified forms and their historical range, and also indicating the relationship between Cambrian archaeocyaths and the living *Vaceletia*. The overlap between hypercalcified grades and phyletic groups is notable. Nevertheless, archaeocyaths were designated as a class of sponges (Debrenne et al., 2002), and the 2015 Treatise separated the Palaeozoic stromatoporoids as Class Stromatoporoidea. The problem is that these fossils do not possess spicules, so determination of their phyletic positions must remain questionable, and thus their relationships with fossil non-hypercalcified sponges (the latter recognized largely *because* they are spicule-bearing!) continues to be problematic. This is an area of continuing debate in the research community.

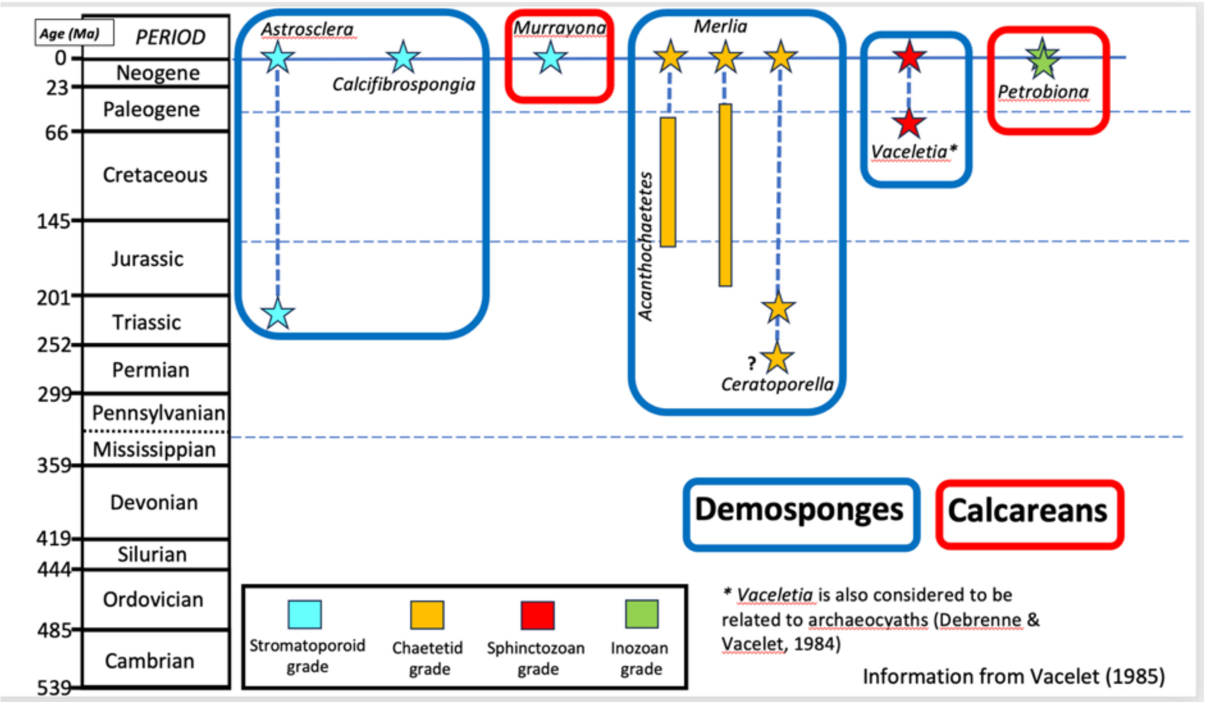
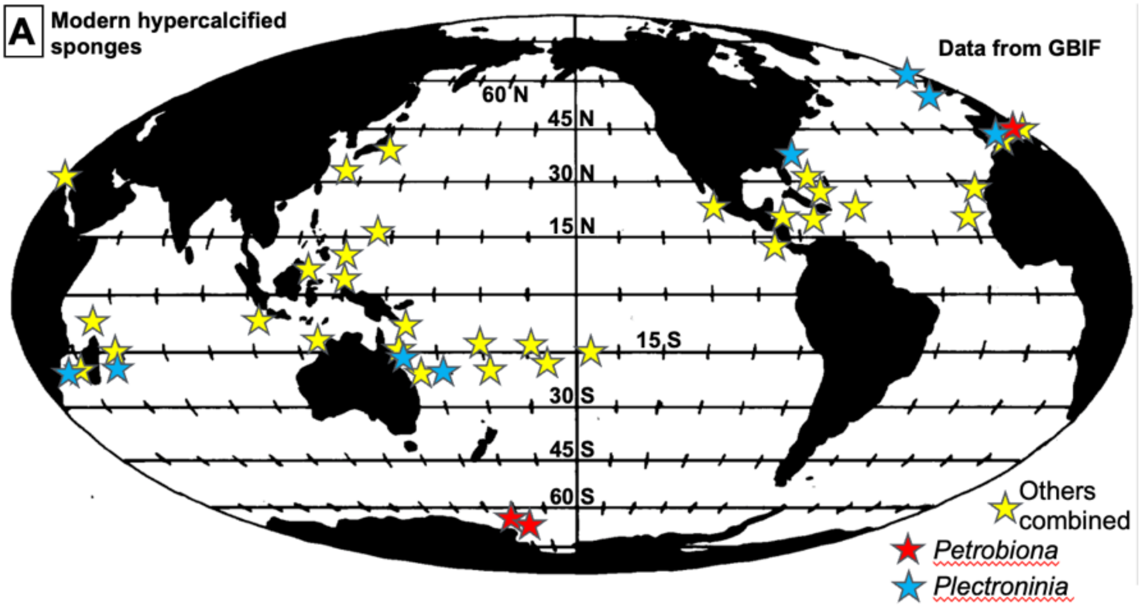


Fig. 14 Hypercalcified sponge polyphyly. Examples of modern hypercalcifed sponges in four of the grades, with coloured boxes indicating which Classes of sponges they belong to. This simple diagram illustrates the polyphyletic nature of hypercalcified sponges, and underlines the key point that the grades are not phyletic entities.

5. Palaeogeographic comparisons between fossil and modern hypercalcified sponges

Fossil hypercalcified sponges occur in low to mid-latitudes in palaeogeographic reconstructions, and for this final section of the study, we use the example of the Palaeozoic stromatoporoid-grade sponges, that were the most successful grade of the Phanerozoic Eon. Fig. 15 shows a comparison of palaeogeographic difference between the Devonian peak of stromatoporoid growth and the suite of 19 modern genera of hypercalcified sponges, collated from the Global Biodiversity Information Facility. Most of the modern genera lie in low latitudes, compatible with the distribution of reef-building Devonian stromatoporoids in warm climates of the Devonian low latitudes, which is consistent also with the other reef-building hypercalcified sponge grades (Kiessling et al., 2002). However, some modern hypercalcified sponges occur in higher latitudes, in colder waters, and may reflect a widening of their environmental tolerance compared to prior times, contrasting their loss of dominance of shallow marine assemblages.



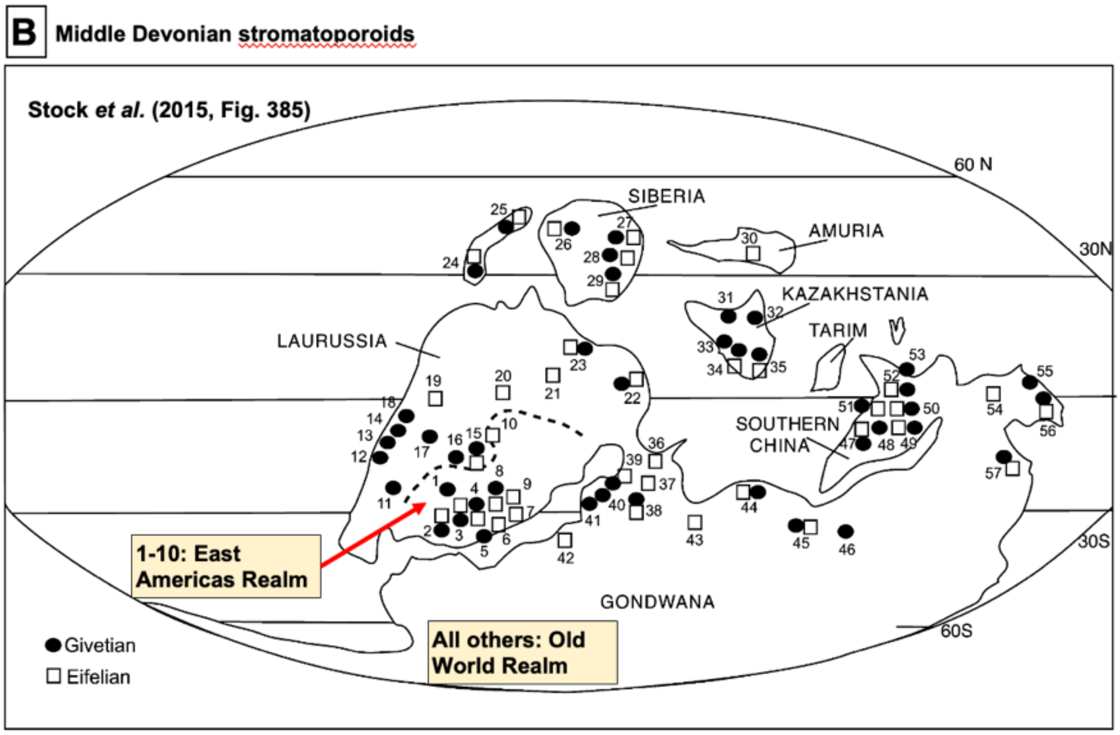


Fig. 15 Examples of hypercalcified sponge biogeography. **A)** Global distribution of all 19 genera modern hypercalcified sponges, compiled from the Global Biodiversity Information Facility (https://www.gbif.org); most taxa, including the abundant and widespread *Astrosclera* and *Acanthochaetetes* (*Spirastrella*) are grouped in yellow colour, and occur largely in tropical and subtropical areas. However, in red and blue are separated two taxa that may occur in modern high latitudes. **B)** Middle Devonian stromatoporoid distribution, reproduced from Stock (2015) under CC-BY-4.0 licence, showing the wide latitudinal occurrence and some separation into two provinces, noting that the Middle Devonian time is generally considered as a warm period allowing spread of stromatoporoid-grade sponges into higher latitudes. **C), D)** Distribution of Early and Late Carboniferous chaetetid-grade sponges, demonstrating their occurrence in low to middle latitudes. See text for discussion.

6. Conclusions

From this short survey of hypercalcifed sponges, we draw the following key points:

1. In addition to the five main form-groups (grades) of hypercalcified sponges (archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, inozoans) is a mixed bag of fossil hypercalcified taxa, not all of which have been proven as sponges. The concept of grades reflects an important point that the spectrum of hypercalcified sponges is not fixed into fully separated groups, with some merging of form-groups;

2. Sponges show ability to hypercalcify from early Cambrian, they survived all mass extinctions, continuing to present day. There is a continuous record of hypercalcification through the entire geological history of these sponges;

3. Fossil hypercalcified secondary skeletons groups cross-cut taxonomy of modern hypercalcified sponges. Fossil hypercalcified sponges bearing spicules have long been known to be polyphyletic, but a question remains as to whether archaeocyaths (Cambrian) & mid-Palaeozoic stromatoporoids were truly separate phyletic groups, noting that they lack spicules.

4. Overall maybe the best approach is to treat HSs as an integrated system of hypercalcification, with continuing major questions about phylogeny;

5. Hypercalcified sponges have a palaeogeographic context relating to continental distribution and global ocean & climate.

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Availability of data and materials

Supporting data for Fig. 2 of this study are provided in Supplemental file 1.

Authors' contributions

The authors together conceived the idea of this study and provided equal input.

Declaration of competing interest

The authors declare that they have no competing interests.

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Conflict of interests

The authors declare that they have no conflicts of interests.

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