Author/s:
Wallace, MW;Hood, AVS;Woon, EMS;Hoffmann, KH;Reed, CP

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Corresponding Author: Dr. Malcolm Wallace,

Corresponding Author's Institution: School of Earth Sciences

First Author: Malcolm W Wallace, PhD

Order of Authors: Malcolm W Wallace, PhD; Malcolm Wallace; Ashleigh V Hood, BSc Hon; Estee M Woon, PhD; Karl-Heinz Hoffmann, PhD; Christopher P Reed, PhD

Abstract: Previously undescribed chambered structures are common and widespread in the Cryogenian (post-Sturtian glacial) carbonates of the Oodnaminta Reef Complex (Adelaide Geosyncline, South Australia), the Rasthof-Berg Aukas Formation (Namibia) and the Gauss Formation (Namibia). These carbonate structures have millimeter to centimeter-scale chambers separated by well-defined and generally thin micritic walls. Chamber walls now consist of dolomite, but were probably originally aragonitic. The chambers may have a lobate, polygonal or dendritic morphology and are often further subdivided into smaller chambers. Chambered structures occur as reefal growth frameworks; as cavity-fillings in neptunean dykes and growth cavities; and as intercolumnar material within stromatolite frameworks. In the Oodnaminta Reef Complex, these structures are only present in the sub-photic deep water framework.

These structures probably represent the calcified remains of an organism or community of organisms that was globally distributed and widespread for a significant time period following the Sturtian glaciation. No precisely analogous structures have apparently been previously described from modern or ancient settings, but the complexity and degree of organization suggests a significant evolutionary advance over older Proterozoic fossils. The closest morphological analogues for the structures are: a) some types of reef-dwelling sponges; and b) some complex microbialites from Archean and Paleoproterozoic carbonates. The structures lack spicules and ostia found in sponges, ruling out a true Poriferan origin. However, it is plausible that they are proto-sponges, or a complex microbial precursor to sponge-grade organisms.

Highlights

- Previously undescribed chambered structures are widespread and common in post-Sturtian-glacial Cryogenian carbonates from Namibia and Australia
- The structures probably represent the remains of an organism or community of organisms that was globally distributed
- The most morphologically similar structures previously described are some complex microbialites and some chambered reef-dwelling sponges.
- It is plausible that the structures represent proto-sponges, or a complex microbial precursor to sponge-grade organisms

Enigmatic chambered structures in Cryogenian reefs: animal, vegetable or mineral?

Malcolm W. Wallace[a]*, Ashleigh vS Hood[a], Estee M. S. Woon[a,d], Karl-Heinz Hoffmann[b] and Christopher P. Reed[c]

[a]*School of Earth Science, University of Melbourne, Parkville, Victoria 3010, Australia*
[b]*Namibian Geological Survey, Ministry of Mines and Energy, Windhoek, Namibia*
[c]*Teck Namibia Ltd., Windhoek, Namibia*
[d]*Present address: Shell Development (Australia) Pty Ltd, 2 Victoria Avenue, Perth WA 6000, Australia*

*Corresponding Author, Email: mww@unimelb.edu.au, Postal address: School of Earth Science, University of Melbourne, Parkville, Victoria 3010, Australia, Phone: 61-3-8344-6526, Fax: 61-3-8344-7761

Abstract

Previously undescribed chambered structures are common and widespread in the Cryogenian (post-Sturtian glacial) carbonates of the Oodnaminta Reef Complex (Adelaide Geosyncline, South Australia), the Rasthof-Berg Aukas Formation (Namibia) and the Gauss Formation (Namibia). These carbonate structures have millimeter to centimeter-scale chambers separated by well-defined and generally thin micritic walls. Chamber walls now consist of dolomite, but were probably originally aragonitic. The chambers may have a lobate, polygonal or dendritic morphology and are often further subdivided into smaller chambers. Chambered structures occur as reefal growth frameworks; as cavity-fillings in neptunean dykes and growth cavities; and as intercolumnar material within stromatolite frameworks. In the Oodnaminta Reef Complex, these structures are only present in the sub-photic deep water framework.

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Key Words

Cryogenian carbonates, reefs, chambered structures, ancestral sponges

1. Introduction

The sudden and widespread appearance of soft-bodied metazoan organisms during the Ediacaran and the later development of organisms with hard mineralised skeletons at the beginning of the Cambrian are events which challenge our understanding of early life (Conway-Morris, 1993). The relatively sudden appearance of these advanced organisms in the geological record and the lack of ancestral precursors has focussed attention on the preceeding early Ediacaran and Cryogenian periods. The discovery of biomarkers and spicules derived from demosponges from this time (Du and Wang, 2012; Love et al., 2009) and possible sponge-grade calcified fossils from the latest Cryogenian (Maloof et al., 2010) suggests that the Cryogenian is highly prospective for the discovery of complex fossils.

However, there has been considerable debate about the origin of many Precambrian structures that are purported to be fossils and the literature abounds with such controversies (e.g. Neuweiler et al., 2009; Planavsky, 2009; Brain et al., 2012). Even if a biological origin is confirmed, the affinity of many fossils from the Precambrian has also proven to be problematic, this being the case even with the well documented Ediacaran fossils themselves (e.g. Seilacher et al., 2003, Narbonne 2005).

Here, we describe chambered structures consisting of carbonate from Cryogenian interglacial successions in Australia and Namibia. The structures are widely distributed and common, but have not previously been described. We can find no precisely analogous structures documented from any time period and we compare the structures with a variety of inorganic and organic structures in order to deduce their possible affinity.

2. Geological Setting

The chambered structures described here occur within Cryogenian interglacial successions of South Australia (Northern Adelaide Geosyncline) and Northern Namibia (Otavi Mountainland and the Kaokoveld (Figs.1 and 2). Cryogenian sediments from the Adelaide Geosyncline (Australia) and Northern Namibia are closely comparable, with the Sturtian and Marinoan glacials being recognized in both successions (Fig. 3). The main difference between the two successions is the greater abundance of carbonates in the Namibian succession.

Chambered structures from Australia occur within Cryogenian reef complexes of the Umberatana Group in the northern Adelaide Geosyncline of South Australia (Giddings et al., 2009c) (Fig. 4). These reefs are of late Cryogenian age, overlying Sturtian diamictites and underlying Marinoan glacigenic sediments (Giddings et al., 2009c). The reef-rimmed platforms consist of dolomite of the Balcanoona Formation that is laterally equivalent to the basinal Tapley Hill Formation calcareous and dolomitic shales (and also laterally equivalent to the peritidal Angepena Formation, Fromhold and Wallace, 2011). Fanning and Link (2008) reported a U-Pb zircon age of 659 ± 6 My BP from a tuffaceous horizon within the uppermost Sturtian diamictites of the Northern Adelaide Geosyncline. This would suggest that the overlying Balcanoona Formation is approximately 650 My BP. The recently discovered possible sponge-grade fossils from the central Adelaide Geosyncline (Maloof et al., 2010) were found in the Trezona Formation, which is significantly younger than the Balcanoona Reef complex (probably around 10-15 million years younger).

The reefs of the Balcanoona Formation consist of a high-energy platform facies, underlain by a massive reef margin facies. The uppermost portion of reef margin facies consists of stromatolitic frameworks, while the lower, deeper water portion of the reef margin consists of a non-stromatolitic organic framework (Fig. 5). Underlying this non-stromatolitic framework facies are allochthonous breccias of the lower slope. The breccia facies directly overlies and interdigitates with the basinal calcareous shales of the Tapley Hill Formation (and the basal Yankaninna Formation). Basinal shales contain large allochthonous blocks and megabreccias shed from the reef margin. The regional and internal geometry of the platform indicates a strongly progradational reef history, with the platform margin having advanced at least 12 km as exposed in continuous outcrop in the Oodnaminta platform. The shallow water portion of the reef framework consists almost exclusively of stromatolites. The deep-water framework ranges from 0 to ~400 m in stratigraphic thickness and largely consists of chambered calcified structures.

Paleo-water depths for the reef facies can be estimated using the base of the platform facies as a proxy for sea level. This assumes that the outer edge of the platform facies was approximately at sea level and would result in minimum depth estimates. Using measured stratigraphic thicknesses from the base of the platform facies indicates that the stromatolitic reef margin facies grew in water depths ranging from 0 to 500 m. The microbial reef margin facies grew in depths from 180 to 1000 m. These depth estimates indicate that all of the microbial framework facies (and some of the stromatolitic facies) grew in sub-photic zone depths, indicating a non-photosynthetic origin for the microbial framework builders.

In Namibia, the chambered structures similarly occur in late Cryogenian sediments of the Rasthof-Berg Aukas formations (lateral equivalents in the Kaokoveld and Otavi Mountainland respectively) and the Gauss Formation (Otavi Mountainland and Fransfontein Ridge regions).

The Rasthof and Berg Aukas formations directly overlie Sturtian glacials of the Chuos Formation in the Kaokoveld and Otavi Mountainland districts respectively (Fig. 3). The Rasthof Formation (Hedberg, 1979; Hoffmann and Prave, 1996) has been divided into three informal units (from base to top, "abiotic", "microbial" and "epiclastic" units) that attain a total thickness of 200-400 m (Hoffman and Halverson, 2008) (e.g. Fig. 6). Le Ber et al. (2013) also use this three-fold subdivision of the Rasthof Formation, with a slightly modified nomenclature (basal cap dolostone; microbial member and epiclastic member). Importantly, Le Ber et al. (2013) only consider the lower unit which has a laminated texture as the cap dolostone. This lower unit is generally quite thin at most localities (~10m at Rasthof Farm, Le Ber et al. 2013) and this is consistent with Sturtian cap dolomites from elsewhere (e.g. Giddings and Wallace, 2009a). Chambered structures are abundant within the microbial unit of the Rasthof Formation, at many localities in the Kaokoveld (e.g. Ongongo Gorge, Okaaru Syncline). They occur in stromatolitic framestones that are widespread in the microbial member. At Ombepera, chambered structures also occur within the non-stromatolitic upper unit (epiclastic member) of the Rasthof Formation.

At most localities in the Kaokoveld, the upper two members of the Rasthof Formation constitute by far the greatest thickness (several hundred meters) of the Rasthof Formation as defined by Hoffman and Halverson (2008). In the Otavi Mountainland district, the equivalent unit is the Berg Aukas Formation, which also directly overlies the Chuos glacials and contains abundant microbial fabrics. This dark grey stromatolitic dolomite is overlain by light grey dolomites of the Gauss Formation. Locally, a thin shale unit separates the Gauss Formation dolomites from the underlying Berg Aukas Formation. Chambered structures are present in both the Berg Aukas and Gauss formations. Chambered structures are particularly common in the lowermost Gauss Formation and upper Berg Aukas Formation.

Comparing the Kaokoveld and Otavi Mountainland successions, the uppermost unit of the Rasthof Formation (epiclastic unit of Hoffman and Halverson, 2008) in the Kaokoveld are probably the lateral equivalent of the Gauss Formation in the Otavi Mountainland (Fig. 6).

At Fransfontein (Fig. 2), south of the Kamanjab Inlier, distinctive partially dolomitized carbonate clasts within the upper Ghaub Formation glacials also contain well-developed chambered structures. The Ghaub Formation here has been described in detail by Hoffman and Halverson (2008) and consists largely of carbonate-dominated diamictite. The source of the clasts is difficult to determine, but Hoffman and Halverson (2008) suggest most of the clasts are derived from the underlying Ombaatjie Formation. The clasts containing chambered structures also have abundant cavities and marine cements, perhaps indicating derivation from a reefal facies.

3. Morphology of Chambered Fabrics

The chambered structures from Namibia and Australia consist of multiple macroscopic and microscopic cavities (ranging from 1 to 30 mm diam.) with walls consisting of micritic carbonate (almost invariably now dolomite). The chamber walls are commonly thin (20- 100 microns) but may be up to 1 mm thick (Fig. 7). Where the walls are thin, they are generally homogeneous. When the walls are thicker, they often display a laminated microstructure (Fig. 7B). The chambers are filled by a variety of carbonate cement types, ranging from fibrous marine dolomites (Hood et al., 2011; Hood and Wallace, 2012) through to late stage coarsely crystalline dolomite or calcite. Areas of recrystallization are sometimes evident in the walls (e.g. Fig. 7B).

Chambered structures are associated and intergrown with clotted or indistinctly dendritic micrite masses (Fig. 7C) that resemble the previously described "carbonate shrubs" or "pendent clot microstructure" from the Neoproterozoic Noonday Dolomite and Little Dal reef respectively (Fraiser and Corsetti, 2003; Turner et al., 1993). We therefore interpret these masses as possible calcified microbial material.

Textural preservation of the chambered structures is quite variable, ranging from complete recrystallization, through to near-perfect preservation. In the Oodnaminta Reef Complex, samples with the best preservation of texture generally come from partially dolomitized (mimetic) allochthonous blocks encased in shale from the slope facies (Fig. 5). In the best-preserved samples, only the chamber walls of the fossils have been mimetically replaced by dolomite, the remainder of the sample being calcite. In allochthonous blocks that are completely undolomitized, textural preservation is very poor, with the fossils being either preserved as sparry-calcite-filled moulds (with no internal structure visible) or as poorly preserved "ghosts" in sparry calcite. This style of preservation and the evidence of partial recrystallization suggests an original aragonitic mineralogy, in common with other depositional constituents in the carbonates (e.g. ooids, Hood et al., 2011; Hood and Wallace 2012).

The chambered structures can be divided into at least three morphological variants: lobate, dendritic, and polygonal types (Fig. 8).

3.1 Lobate Structures

In the lobate form, the bulbous chambers grow on one another to produce encrusting or short branched structures (Figs. 7 and 8). These short-branched structures typically consist of a central ellipsoidal or near-circular chamber with a series of bulbous or hemispherical chambers encrusting around the central chamber (Fig. 7A). The large central chamber commonly has cusps projecting into the chamber. Chambers may be further subdivided into secondary chambers with a more polygonal shape. The secondary chamber walls commonly have a meandering shape and again consist of micrite (Fig. 7B). Lobate structures make up the youngest frameworks within the Oodnaminta Reef. The lobate form is also common in allochthonous blocks within the most basal Yankaninna Formation in the Adelaide Geosyncline. Clasts within the Marinoan glacials of the Ghaub Formation, at Fransfontein, Namibia also contain well developed lobate chambered structures. Lobate structures are also present in the upper Rasthof Formation (epiclastic member) at Ombepera, Kaokoveld, Namibia.

3.2 Dendritic Structures

Dendritic chambered structures consist of elongate chambers that branch in the direction of growth. In cross section, the branching chambers have a tendency towards a close-packed polygonal morphology (Fig. 9). The dendritic chambered masses are usually encircled by peloidal and/or micritic carbonate (Fig. 9A). The dendritic chambers sporadically have thin convex walls that subdivide the branches (Fig. 9B). Dendritic chambered structure is an important component of the deep-water framework in the Oodnaminta Reef Complex of the Balcanoona Formation, Adelaide Geosyncline. This dendritic form is also found as massive frameworks in the Gauss Formation of Namibia (e.g. at Farm Matunda, near Outjo).

3.3 Polygonal Structures

Polygonal chambered structures have equidimensional polygonal chambers that are generally larger (up to 50 mm diam.) than the lobate or dendritic forms (Fig. 10).

Polygonal structures are common in the lower Gauss, Berg Aukas and Rasthof formations of Namibia. Particularly well developed polygonal chambered structures occur within the lower Gauss/upper Berg Aukas at Farm Hurisib, Otavi Mountainland. Polygonal structures have not yet been found within the Adelaide Geosyncline.

4. Macroscopic Occurrence of Chambered Structures

The chambered structures described here from both Australia and Namibia have a variety of stratigraphic associations, although virtually all occurrences of the structures are in some way associated with reefal frameworks (Figure 11). Chambered structures occur as:

1. Reefal growth frameworks
2. Intercolumnar material within stromatolitic frameworks
3. Within cavity systems in neptunean dykes and breccias

Chambered structures of various types are also reworked as allochthonous blocks in reefal debris and sometimes as clasts within glacials (e.g. Ghaub Formation, Namibia).

4.1 Growth Frameworks

Within the Oodnaminta Reef, the dominant deepwater framework consists of a mass of intergrown chambered structures. Much of the Oodnaminta deepwater framework consists of dendritic chambered structures. These frameworks commonly have well-defined growth surfaces. The branches of the dendritic structures are generally oriented roughly perpendicular to these growth surfaces. The youngest frameworks within the Oodnaminta Reef consist of lobate chambered structures. In both lobate and dendritic frameworks, carbonate shrubs-clotted micrite makes up a subordinate proportion of the framework. No polygonal chambered structures have yet been found that form a dominant framework constituent. A reconstruction of the lobate and dendritic chambered structures as a framework is shown in Figure 12.

4.2 Stromatolite-Associated Chambered Structures

Polygonal and lobate chambered structures commonly occur as inter-columnar material within stromatolite frameworks (e.g. Fig 10B). The associated stromatolites can have a wide variety of morphologies, varying from vertical upright columns (with resultant, vertically-oriented masses of chambers) through to more meandering Tungussia-like columns (with more irregularly spaced chambered masses). In many cases, the stromatolites appear to have been growing on steep slopes, with adjacent stromatolite laminae stepping down across each column. The morphology of the stromatolites is commonly reminiscent of the deep-water "scalloped" stromatolites described by Playford et al. (1976).

This is the dominant mode of occurrence for chambered structures within the microbial member of the Rasthof Formation, Namibia. Inter-columnar chambered structures are also common within allochthonous blocks in the forereef facies of the Oodnaminta Reef. Well- developed intercolumnar chambered structures are also present within the lower Gauss Formation in the Otavi Mountainland district.

4.3 Cavity-filling Chambered Structures

Polygonal chambered structures occur in both synsedimentary fractures (neptunean dykes) and in intergranular space within breccias. Chambered structures in neptunean dykes are particularly common within the Berg Aukas Formation of the Otavi Mountainland. Here, the chambered structures can both line large neptunean dykes, and completely fill smaller fractures. Small neptunean sills filled by chambered material have been found within the Rasthof Formation from the Kaokoveld (Fig. 10D). Intergranular breccia porosity may be completely filled by polygonal chambered structures within the lower Gauss Formation/Berg Aukas Formation on Farm Hurisib, Otavi Mountainland.

5. Possible Affinities for Chambered Structures

The structures described here have a relatively complex arrangement? consisting of multiple chambers with well-defined walls. The chamber size is relatively large, with a maximum size of up to several centimetres in diameter. The three major morphological variants (lobate, dendritic and polygonal) all have similar chamber walls that consist of micritic carbonate. No precisely analogous structures have apparently been previously described, producing obvious problems in the interpretation of the origin and affinity of these chambered structures. We therefore compare these chambered structures with similar previously described void structures from the geological record.

5.1 Inorganic chambered structures

In hand specimen, the Cryogenian structures resemble some form of fenestral cavities. Shinn (1968) was the first to describe a class of fenestrae which he termed "bubblelike" or spherical fenestrae. Shinn (1968) found similar cavities forming in mine tailings around gas bubbles and suggested this as an origin for these bubblelike fenestrae. The bubblelike fenestrae described by Shinn (1968) and from elsewhere (e.g. Rainey and Jones, 2009) have similar chamber sizes (several millimetre diameter), but the general shape of the structures is dissimilar. Fenestral cavities tend to have rounded shapes, but in detail, have irregular geometries (e.g Fig. 13B). In contrast, the Cryogenian structures have very regular geometries (lobate, polygonal and dendritic, Fig. 13A). Furthermore, fenestrae do not have thin chamber walls (the margins of fenestrae usually being host sediment), whereas the Cryogenian structures have very well-defined chamber walls.

Chambered structures formed in association with gas bubbles are found in some travertines (Flugel, 2004) and in methane hydrates (e.g. globular structure of Bohrmann et al., 1998). Examples from travertines illustrated by Flugel (2004) display only small (<1 mm diam.) subspherical chambers again without well defined walls. The globular structures of Bohrmann et al. (1998) have a similar chamber size, but have thicker and more indistinct wall structures. The Cryogenian chambered carbonates also have relatively heavy carbon isotope values that are not consistent with a methane-related origin (Giddings and Wallace, 2009b).

A process that could conceivably produce a series of hemispherical chamber-like structures is marine aragonite precipitation. In some reef frameworks, hemispherical aragonite botryoids are precipitated as marine cements (James and Choquette, 1990). If individual botryoids were to be coated by thin micritic rims, and then undergo aragonite dissolution or recrystallization, the resulting structure might resemble some of the chambered structures described here. However, this hypothetical process would not explain the geometry of the other chambered forms. Neither is there evidence for aragonite botryoids ever having been present in these carbonates. No radiating aragonite pseudomorphs have yet been found within the Cryogenian chambered structures. In fact, aragonite botryoids are extremely rare in both the Australian and Namibian reefal frameworks. Marine cements in these reefs are instead dominated by isopachous fibrous dolomite cements (Hood et al., 2011, Hood and Wallace, 2012).

In summary, there is no known abiogenic structure that closely resembles these Cryogenian structures and it appears very likely that they are formed biologically.

5.2 Microbialite and calcimicrobial structures

Microbialites are defined as “organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation” (Burne and Moore, 1987). A great variety of textural morphologies can be classified under this broad definition, including stromatolites and thrombolites (Riding, 2011). The geometry of stromatolites does have some similarities with the Cryogenian structures described here. Stromatolites branch upwards, display lamination and have bulbous head, and in some instances, have rounded fenestral chambers. However, because stromatolite growth is often partly controlled by physical parameters (e.g. carbonate saturation state, light levels, and sediment input), there is a great deal of variability in their structure, rather than the very regular and repeated morphology or the Cryogenian structures. Furthermore, the fenestral chambers of fenestral stromatolites generally have an irregular wall structure.

Nevertheless, some microbialite structures like thrombolites (clotted microbialite structures, Riding, 2011) are characterized by large (cm-sized) chambers (e.g. Turner et al., 2000). Reitner et al. (2005) for example, described carbonate mounds from the Black Sea (produced in association with methane) that have large (cm size) chambered fabrics. However, as in most microbialite textures, the chambers have ill-defined and irregular chamber walls that do not at all resemble the defined Cryogenian structures.

The interaction of oxygen gas bubbles with microbial mats has been suggested as a mechanism for producing vesicular chambers in microbialites (e.g. Bosak et al., 2010). Knoll et al. (2013) described large voids in microbialites from the upper Mesoproterozoic Angmaat Formation and attributed them to oxygen bubbles forming within microbial mats. However, the voids described by Knoll et al. (2013) and Bosak et al. (2010) again have poorly defined and irregular walls, unlike the Neoproterozoic chambered structures described here.

Several authors (Sami and James, 1993; Hofmann and Mason, 1994; Sumner, 1997, 2000; Wright and Altermann, 2000; Gandin et al., 2005; Schroder et al., 2009) have described Archean and Proterozoic chambered microbialite textures (variously referred to as fenestrate microbialites, cuspate microbialites, pillared microbialites, and thesaurus stromatolites) that, in terms of size and basic structure, resemble the chambered structures described here. These chambered microbialite structures consist of large chambers with relatively thin walls. Sumner (2000) documented three major morphologies; cuspate, network and tented. The network variety has a geometry that is similar to our polygonal morphology. However, the other two morphological forms described by Sumner (2000) have no clear analogue in our chambered structures. In addition, these chambered microbialites appear to have less well defined wall structures.

Calcimicrobes (= calcified microbial microfossils, James and Gravestock, 1990) can have very regular and complex structures. Clear examples of calcimicrobes like Epiphyton are present in Early Cambrian reefs (James and Gravestock, 1990), and less well-defined calcimicrobe examples are documented from the Neoproterozoic (e.g. Little Dal reefs, Batten et al., 2004). The lobate variety of our Cryogenian structures has a morphology that is reminiscent of the Phanerozoic renalcid *Shuguria* (Fig. 13C and D). *Shuguria* has a branching morphology with the branches consisting of a series of lobate chambers. *Wetheredella* (Kazmierczak and Kempe, 1992) similarly has a lobate chambered structure. However, the size of these microbes is an order of magnitude smaller than our chambered structures (e.g. Fig. 13C). The term “calcimicrobe” as originally defined does refer to microfossils, rather than macrofossils.

In summary, cavernous microbialite structures are generally quite unlike the Cryogenian structures. Microbialite structures in general are characterized by more irregular and variable structures than those found in the Cryogenian structures. This is presumably because microbial colonies are generally not able to generate complex, well-defined and repeated structures of any form. An exception to this are the group of structures variously known as fenestrate/ cuspate microbialites or thesaurus stromatolites described by several authors from Archean and Proterozoic carbonates. These structures do appear to have several similarities with Cryogenian chambered structures.

5.3 Palaeopascichnus, Xenophyophores, and Foraminifera

Palaeopascichnus is a problematic Neoproterozoic fossil that consists of a series of lobes commonly forming a branched structure (Seilacher et al., 2003; Antcliffe et al., 2011; Lan and Chen, 2012). The lobes of the fossil have been interpreted as chambers (e.g. Antcliffe et al., 2011) and in this sense, *Palaeopascichnus* does have many similarities with the chambered structures described here. Importantly, unlike most microbial chambered fossils, *Palaeopascichnus* is a macroscopic structure (with branches several centimeters wide and chambers of similar width).

Palaeopascichnus has been recently found in early Ediacaran sediments from Australia (Ranford Formation of the Kimberley region, Lan and Chen, 2012) but more commonly occurs in mid and late Ediacaran sediments (e.g. Haines, 2000). The affinity of the fossil is controversial, with several authors suggesting they are related to modern xenophyophores (Seilacher et al., 2003; Lan and Chen, 2012). Modern xenophyophores are a specialized group of Foraminifera (Pawlowski et al., 2003a). Antcliffe et al. (2011) suggested that *Palaeopascichnus* was neither a xenophyophore nor a foraminiferan, but did suggest that it may have been a eukaryotic colony/organism and may have been a giant protozoan.

This raises the possibility that the Cryogenian chambered structures are foraminifera or some other related group of chambered protozoans. Pawlowski et al. (2003b) have used molecular evidence to suggest that Foraminifera may have evolved in the Neoproterozoic (see also Douzery et al., 2004). Furthermore, the presence of testate amoebae related to foraminiferans from the Chuar Group (>16 Ma ??) suggests that the group was probably present in the Cryogenian (Porter et al., 2003). The recent discovery of possible foraminiferans from the Rasthof Formation in Namibia is also consistent with this hypothesis (Bosak et al., 2012).

The large chambered morphology in our Cryogenian structures might be consistent with a foraminiferal affinity. However, McIlroy et al. (2001) suggested that the regular chambered structure of Phanerozoic foraminifera did not evolve till the Devonian. Furthermore, the absence of pores in the chamber walls (foramina) of the Cryogenian structures makes it unlikely that they are foraminifera in the strictest sense. It does however, seem possible that the chambered structures were produced by large protists that might be related to *Palaeopascichnus.*

5.4 Porifera

Some reef-dwelling sphinctozoan sponges (a polyphyletic group of Phanerozoic spicule-less chambered sponges; Finks, 1973), calcified demosponges, stromatoporoids, and some archaeocyathans have remarkably similar morphologies to the chambered structures that we describe here (Fig. 14A-F). Similarities include the presence of large (mm to cm size) bulbous to hemispherical chambers with thin micritic walls, secondary chamber subdivisions and an overall branching morphology. Moreover, many of these poriferans have similarly shaped lobate chambers. Chamber walls also tend to have non-uniform thicknesses. Significantly, all of these morphologically similar fossils are now considered to be Porifera and the majority inhabit reef frameworks as encrusters (i.e. similar environment to the Cryogenian structures).

However, in detail, many of these Poriferan fossils have a different morphology from the Cryogenian structures. Sphinctozoans, like all true sponges, have some chamber walls with regular pores (ostia). Pores are an integral part of the water circulation system employed by sponges for filter feeding (Vogel, 1974) and the lack of such pores in the Cryogenian chambered structures rules out a true Poriferan affinity. There is also a lack of spicular material associated with the Cryogenian structures (although some groups of sponges do not have spicules). The labechiid stromatoporoids are very similar morphologically to the Cryogenian structures (e.g. Fig, 14F), but have additional pillar-like skeletal elements. While the close similarity in morphology between some reef-dwelling sponges may be a result of evolutionary convergence, it may also represent a close affinity.

5.5 Bacinella and Lithocodium

Bacinella irregularis (Radoičić 1959) and *Lithocodium aggregatum* (Elliot, 1956) are problematic chambered structures that occur in Late Jurassic to Early Cretaceous reefs. They share many similarities with the Cryogenian chambered structures described here, including their enigmatic origin. *Bacinella* and *Lithocodium* have been variously described as being calcimicrobial, green algae, red algae, foraminifera, sponges, and sponge borings (Schlagintweit, 2010). These structures consist of a series of millimetre-scale chambers with thin micritic walls. The chambers can have a number of morphologies, including lobate and dendritic (Huck et al., 2012).

Bacinella and *Lithocodium* do resemble the Cryogenian chambered structures, with a similar chamber morphology, comparable micritic walls, and an analogous ecology in reefs. It is interesting to note that while these Phanerozoic structures have uncertain origins, most authors ascribe a biological affinity more complex than calcimicrobial or microbial in origin.

6. Discussion

While it is tempting to ascribe a relatively simple origin, such as bubble-calcification (e.g. Bosak et al., 2010; Knoll et al., 2013) to these Cryogenian chambered structures, the analogy breaks down on closer inspection. Spherical fenestrae produced by bubbles, and calcified bubbles in microbialites do not have the well-defined wall structure of the Cryogenian examples. Furthermore, the complexity and level of organization (dendritic morphology and secondary chambers for example) is at odds with a bubble origin. It therefore appears most likely that the structures are produced biologically, being related to microbial processes or derived from a more evolutionary advanced taxon. The latter hypothesis is only controversial because of the Cryogenian age. Morphologically similar structures found in Mesozoic reefs (*Bacinella-Lithocodium*) have generally been attributed to a non-microbial origin.

Empirically, the morphologically closest analogues to the Cryogenian chambered structures described here appear to be:

1. Fenestrate microbialites (or cuspate microbialites, thesaurus stromatolites, e.g. Hofmann and Mason, 1994; Sumner, 2000) and;
2. Chambered reef-dwelling sponges (like Sphinctozoan sponges, Finks, 1973).

Both of these comparisons have significant problems. While the large-scale morphology of fenestrate microbialites appears to match the Cryogenian structures, the chamber wall structure of the microbialites appears less well defined and the chambers less well organized than in the Cryogenian structures. Furthermore, fenestral microbialites appear to be largely restricted to older sediments (mostly Archean and Paleoprotrozoic) and ascribing this affinity would require that fenestrate microbialites reappear and become widespread over 1 billion years later in the Neoproterozoic. In addition, the origin of fenestrate microbialites themselves is debated and largely unknown (e.g. Gandin et al., 2005).

Assigning a Poriferan or proto-Poriferan affinity would obviously be evolutionarily very significant. Based on anatomical and molecular data, sponges should be amongst the earliest animals to have evolved and should be present within the Cryogenian. The existing record of Precambrian sponges is relatively consistent with this evolutionary view, since body fossil impressions and spicules have been found in late Ediacaran sediments (Brasier et al., 1997; Gehling and Rigby, 1996). Biomarker evidence suggests demosponges may have been present in the Cryogenian (Love et al., 2009) and spicules have recently been reported from early Ediacaran sediments (Du and Wang, 2012). In addition, possible sponge-grade calcified fossils have also been reported from the Latest Cryogenian Trezona Formation of the Adelaide Geosyncline (Maloof et al., 2010). However, some important anatomical attributes of Poriferans are missing in the chambered structures (like ostia and spicules) seeming to exclude the structures as being true sponges.

Nevertheless, it is still plausible that the structures could represent the calcified remains of proto-sponges. It is possible that proto-sponges had not yet evolved an active water circulation system or pore network, perhaps employing direct absorption of dissolved organic carbon (osmotrophy) as a feeding strategy (Sperling et al., 2007). Some modern sponges (particularly cavity-dwelling reef encrusters) are capable of significant dissolved organic carbon uptake (De-Goeij et al., 2008; van-Duyl et al., 2008). The morphological and ecological similarity of these chambered structures with many primitive sponges, together with molecular evidence for the early divergence of sponges (Peterson et al., 2004; Sperling et al., 2010) makes a Poriferan affinity very appealing.

An important consideration in determining the origin of these structures is the environment in which they existed. It is difficult to assess the paleo-water depth for the Rasthof and Gauss formations of Namibia, but the chambered structures from the Adelaide Geosyncline almost certainly grew in a deep subphotic environment. Given this deep-water setting, a photoautotrophic origin is highly implausible and rules out an algal affinity for the structures.

Another important environmental factor in the distribution of the chambered structures is their direct association with growth frameworks. All of the lithofacies hosting the chambered structures in Australia and Namibia (Oodnaminta Reef Complex in Australia, the Gauss and Rasthof formations of Namibia) are reefal growth frameworks. A restriction to reefal frameworks might be due to an environmental requirement such as a hard substrate, steep depositional slopes, low sediment influx, or the hypercalcifying environment of reef margins. The presently known age and geography for these chambered structures (following Sturtian glacial successions in Australia and Namibia) is suggestive of a global, but time-restricted distribution.

Anoxia may be an important environmental factor in explaining the occurrence of Cryogenian chambered structures. There is now much evidence to suggest that Cryogenian oceans were strongly anoxic and ferruginous (e.g. Canfield et al., 2008; Feng et al., 2010). Cryogenian oceans may therefore record a return to Archean-like conditions (anoxic and ferruginous). If the chambered structures are in some way related to Archean cuspate/fenestrate microbialites, then the connection might be ferruginous anoxic environments. One possible explanation might be that the Archean fenestrate microbialites were produced by an assemblage of anoxic chemotrophs that were widespread in the Archean and Paleoproterozoic. Their re-appearance in the Cryogenian, along with more complex and organized structures, in the Cryogenian may reflect a return to widespread anoxia along with evolutionary advancement over their Archean precursors. If this hypothesis is correct, then the Cryogenian chambered structures may represent the remains of evolutionary advanced anoxic chemotrophs that briefly thrived during the Cryogenian and created spectacular reef complexes. There apparent absence during much of the Proterozoic may be due to the lesser abundance of anoxic settings during this time.

Cryogenian anoxia might seem to contradict the hypothesis of an ancestral Poriferan affinity for the chambered structures, since most Metazoa require abundant dissolved oxygen. However, there is evidence to suggest that early metazoan ancestry may have occurred within anoxic settings (Mentel and Martin, 2010). Danovaro et al. (2010) for example have found modern metazoa that live permanently in anoxic environments. Low oxygen levels are a “two-edged sword” for early metazoan evolution: on the one hand, there is reduced oxygen for metabolism, but on the other, dissolved organic carbon levels are increased (Rothmann et al., 2003), allowing an osmotrophic lifestyle. It therefore appears possible that ancestral sponge-like organisms could have evolved in the anoxic and ferruginous conditions of the Cryogenian.

7. Significance

Despite their abundance in Cryogenian carbonates from Australia and Namibia, these chambered structures appear not to have been previously described. Their widespread geographic distribution as here documented (Namibia and Australia) is consistent with a global occurrence. Since no other Cryogenian or early Ediacaran reefs have yet been found, the lack of recognized similar structures elsewhere is likely due to the dearth of known reefs during this time interval. It is also probable that they have not been recognized in handspecimen due to their resemblance to large fenestrae or other cavernous sedimentary structures.

The stratigraphic occurrence of chambered structures suggests a significant time range, being recognized in Australian and Namibian sections over kilometre-scale stratigraphic thicknesses. We suggest it is highly unlikely that these structures are of inorganic origin and are probably of biological origin. The chambered structures are likely to represent the fossil remains of an organism or community of organisms that was globally distributed and existed for some significant period of time following the Sturtian glaciation.

The age distribution for these chambered structures accords well with molecular clock estimates for the divergence of Porifera within the Cryogenian (Peterson et al., 2005; Sperling et al., 2010). This timing, together with the many morphological and ecological similarities with some Phanerozoic reef-dwelling sponges makes it plausible that they could be ancestral proto-sponges. If this were the case, then these Cryogenian chambered structures would be the oldest calcified metazoan fossils ever found. This would extend the record of calcified metazoans for 100 million years earlier than previously thought (Wood et al., 2002) and would be of major significance in understanding early animal evolution.

If the chambered structures are microbially-produced (perhaps by chemotrophic anoxic microbes), then they represent a significant advance in complexity and organization over any other microbialite structures (e.g. fenestrate microbialites of Sumner, 1997). Alternatively, they may represent a “half-way house” between sponge-grade organisms and microbes. Many sponges themselves are now considered to be a microbe-sponge consortium (Webster et al., 2012). Regardless of their exact affinity, it is clear that these structures record a significant evolutionary event on the path towards organic complexity.

8. Conclusions

1. Enigmatic chambered structures consisting of carbonate are abundant in Cryogenian sediments from Namibia and Australia. The structures are hosted by the Oodnaminta Reef Complex of the Adelaide Geosyncline, Australia, the Rasthof-Berg Aukas

Formation of Namibia, and the Gauss Formation of Namibia. They are invariably associated with growth frameworks.

2. The structures consist of lobate, dendritic or polygonal chambers (millimeter to centimeters in scale) that have thin micritic walls. Chambered structures may occur as the dominant constituent of the growth framework, as intercolumnar material between stromatolites, and as cavity filling materials in neptunean dykes and sills.
3. Precisely analogous chambered structures have not been previously described. Chambered structures probably represent the remains of an organism or community of organisms that was globally distributed and widespread for a significant period following the Sturtian glaciation.
4. Morphologically, the most similar structures previously described appear to be a) Archean-Paleoproterozoic fenestrate microbialites; and b) some chambered reef-dwelling sponges. The suggestion that they are proto-sponges or complex microbial precursor to sponge-grade organisms cannot be ruled out.

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Figure Captions

Figure 1. Adelaide Geosyncline of South Australia showing location of study area in Northern Flinders Ranges.

Figure 2. Geology of Northern Namibia with studied localities (modified from Hoffmann and Prave, 1996). G = Ghaub Farm, H = Hurisib Farm, M = Matunda

Farm, L = Luisental Farm, F = Fransfontein, O = Ongongo Gorge, Op = Ombepera, Ok = Okaaru.

Figure 3. Stratigraphic correlation between the Australian and Namibian Neoproterozoic successions with occurrence of chambered structures described here.

Figure 4. Distribution of Cryogenian reef complexes in the Northern Adelaide Geosyncline, South Australia.

Figure 5. Facies model for the Oodnaminta Reef Complex. Chambered structures occur in the deepwater non-stromatolitic framework.

Figure 6. Suggested lithostratigraphic correlation between the Otavi Mountainland and Kaokoveld in two measured sections. The upper part of the Rasthof Formation in the Kaokoveld is probably the lateral equivalent of the Gauss Formation in the Otavi Mountainland.

Figure 7. Thin section photomicrographs of lobate chambered structures from the Oodnaminta Reef Complex, Balcanoona Formation, Northern Adelaide Geosyncline, South Australia. In all samples, the micritic material is replaced by finely crystalline mimetic dolomite. (A) Typical section through a lobate form, with sub-spherical central chamber, overgrown by hemispherical chambers. Oodnaminta Reef. (B) Encrusting lobate form with a single hemispherical chamber subdivided into secondary chambers. Recrystallization of the basal chamber wall evident. White Well Reef (C) Section through a simple encrusting lobate form. The right outer side of the fossil is encrusted by clotted micrite of probably microbial origin. White Well Reef (D) Section through a complex lobate form with abundant secondary chambers. White Well Reef (E) Section through a large mass of the lobate chambered form, showing the large scale growth structure. Mt Lyndhurst Reef.

Figure 8. Major morphological types of chambered structures in Namibia and Australia.

Figure 9. Dendritic chambered structures from Namibia and Australia. (A) Outcrop of dendritic framework. Arkaroola Reef, South Australia. (B) Thinsection photomicrograph of dendritic chambered structure showing thin convex walls within dendritic chambers. Oodnaminta Reef, South Australia.

Figure 10. Polygonal chambered structures from Namibia. (A) Polished slab illustrating polygonal structures between breccia clasts. Lower Gauss Formation, Hurisib Farm, Otavi Mountainland, Namibia. (B) Polished slab illustrating polygonal chambered structures between stromatolite columns. Microbial Member, Rasthof Formation, Ongongo Gorge, Kaokoveld, Namibia. (C) Thinsection photomicrograph illustrating detail of polygonal chambered structure. Note well developed fibrous marine dolomite cements in polygonal chambers. Lower Gauss Formation, Hurisib Farm, Otavi Mountainland, Namibia. (D) Chambered structures within synsedimentary fractures, Rasthof Formation, Ombepera, Kaokoveld, Namibia.

Figure 11. Major modes of occurrence of chambered structures. Grey = pore space. Patterned = Microbial micrite. Chamber walls in black.

Figure 12. Reconstructions of the chambered structures interpreted from thin section analysis. Black indicates cut-away cross-sectional view showing internal chamber arrangement. (A) Lobate form displaying common stubby-branched habit. Internal chambers display the large central or basal chamber with hemispherical chambers encrusting it. (B) Dendritic form with more elongate and branching chambers. C. Reconstruction of lobate form growing *in situ* within the reef. D. Reconstruction dendritic form growing *in situ* within the reef.

Figure 13. Comparison of chambered structures with bubble fenestrae and calcimicrobes in thinsection. (A) Rounded bubble-like chambers in the lobate form, Mt Lyndhurst Reef, South Australia. (B) Rounded fenestrae in ooidal carbonate, Pillara Formation, Lennard Shelf, Western Australia. (C) Section through lobate form with inset of the renalcid *Shuguria* (Fig. 12D), at same scale for size comparison. (D) The calcimicrobe renalcid *Shuguria* showing chambers and dendritic growth structure. Napier Formation, Lennard Shelf, Western Australia.

Figure 14. Comparisons between Porifera and Cryogenian chambered structures. (A) Thin section photomicrograph of chambered structures, Mt Lyndhurst. (B) Sphinctozoan sponge *Aphrosalpinx textilis*, Silurian Heceta Formation, southeastern Alaska (drawn from photograph in Rigby et al., 1994). (C) Photomicrograph of chambered structure with secondary chamber walls, Oodnaminta Hut. (D) Sphinctozoan sponge *Annaecoelia maxima*, Gruber-Riff limestone, Salzburg, Austria (modified from Senowbari-Daryan, 1978). Compare chamber marked by arrow with Cryogenian structure in Fig 13C. E. Photomicrograph of chambered structures from Mt Lyndhurst. F. Devonian labechiid stromatoporoid from Poland (drawn from photograph in Flugel, 2004)

Graphical Abstract (for review)

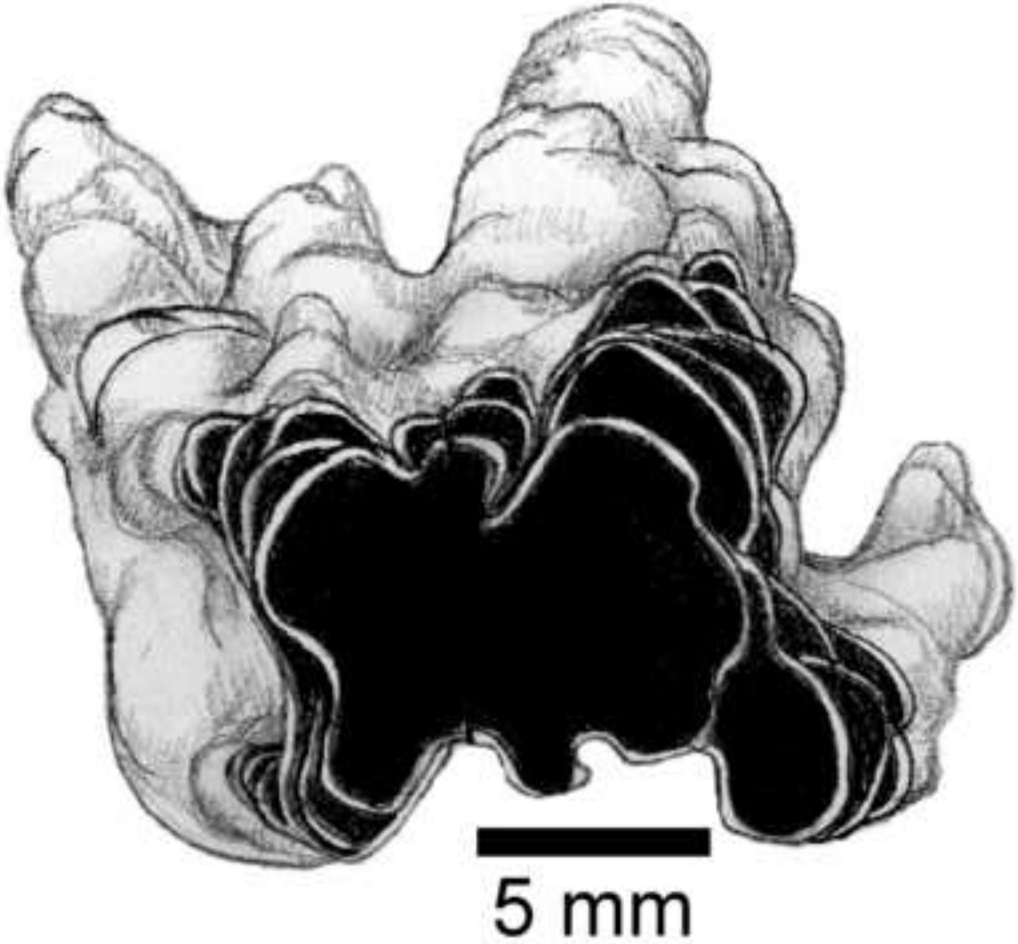


Figure 1

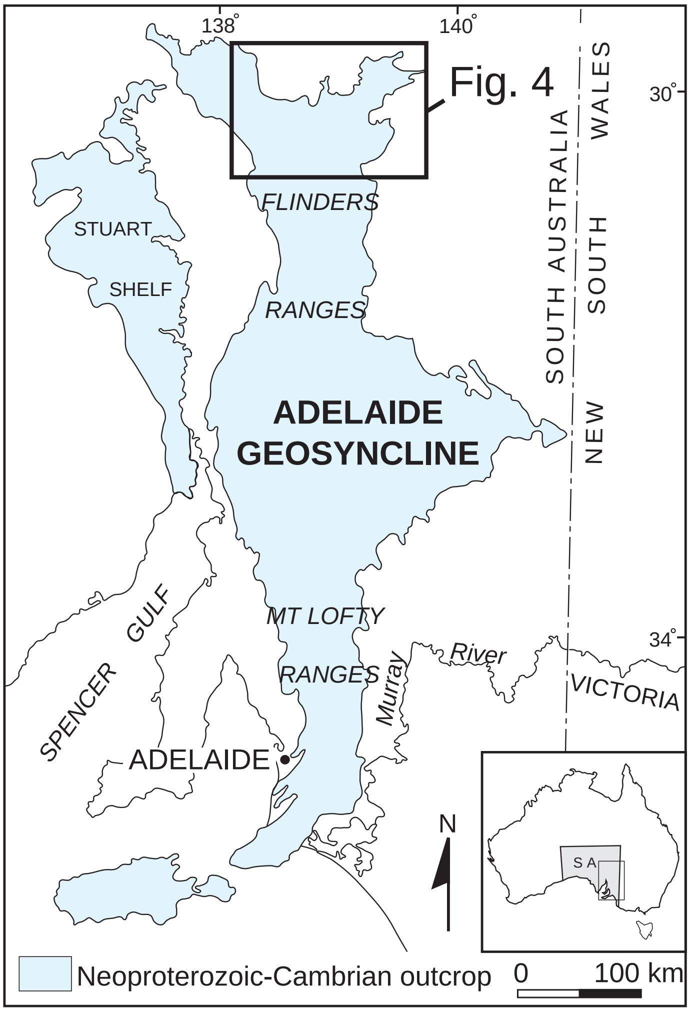


FIGURE 1

Figure 2

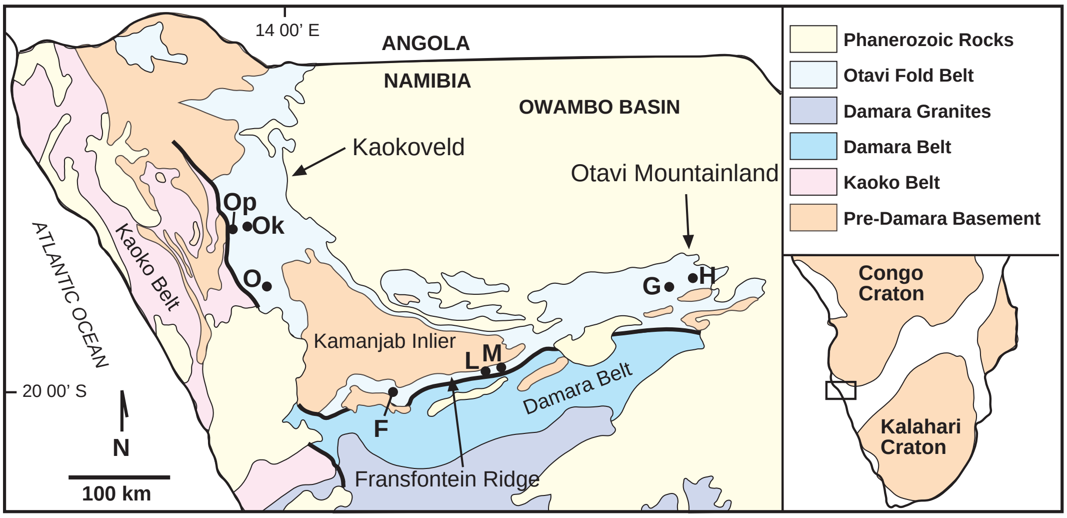


FIGURE 2

Figure 3

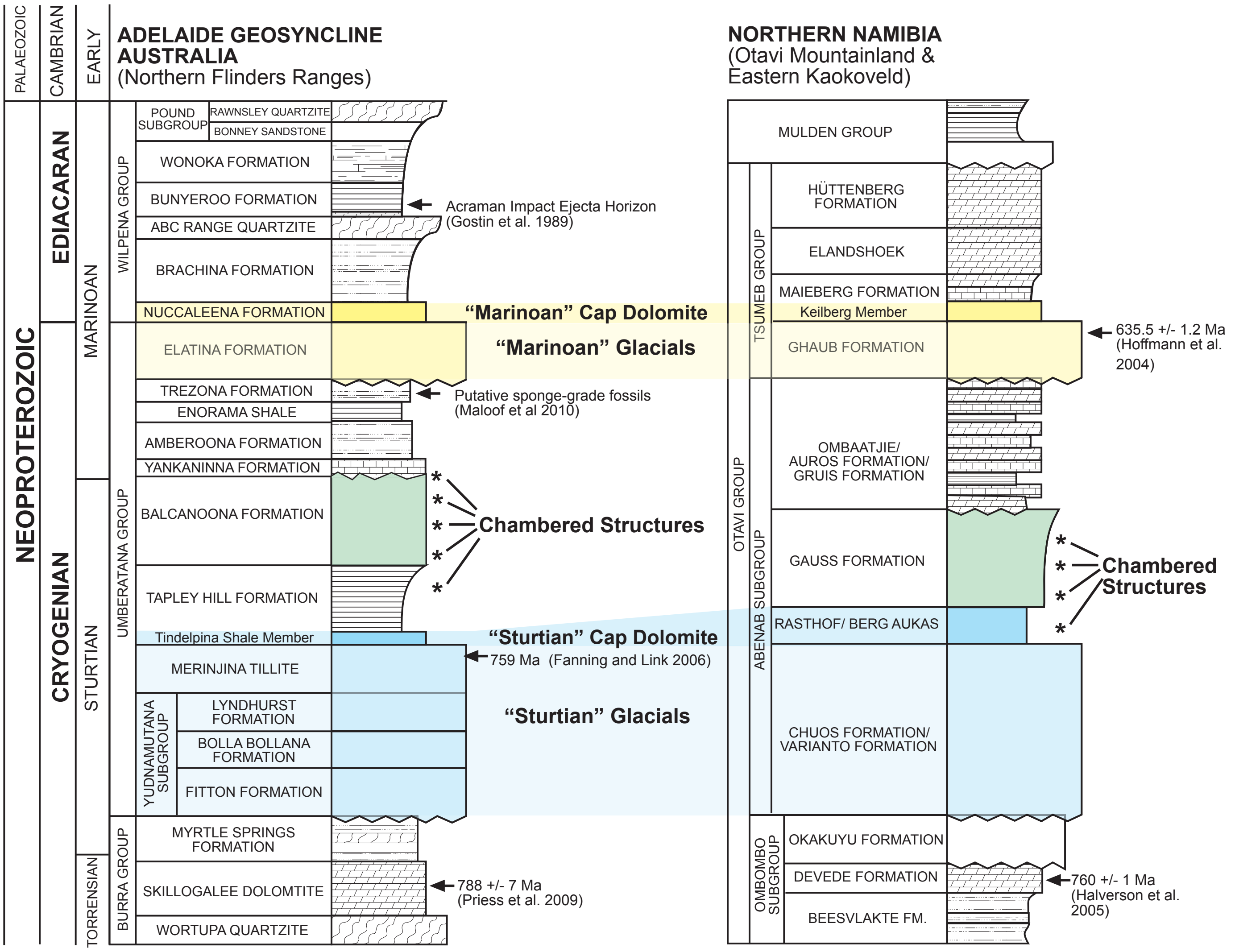


FIGURE 3

Figure 4

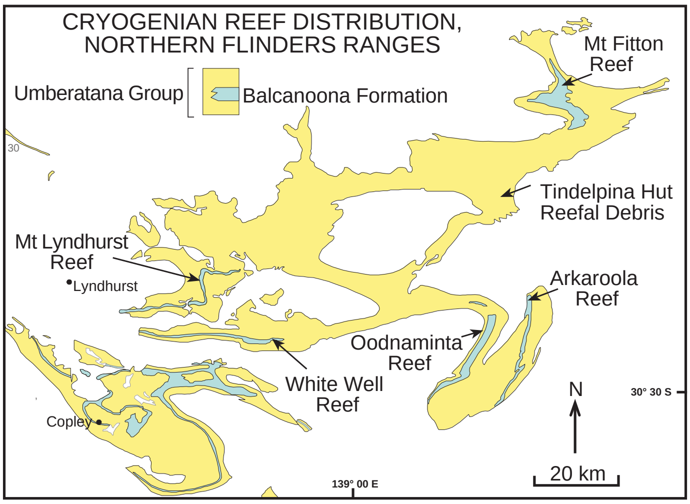


FIGURE 4

Figure 5

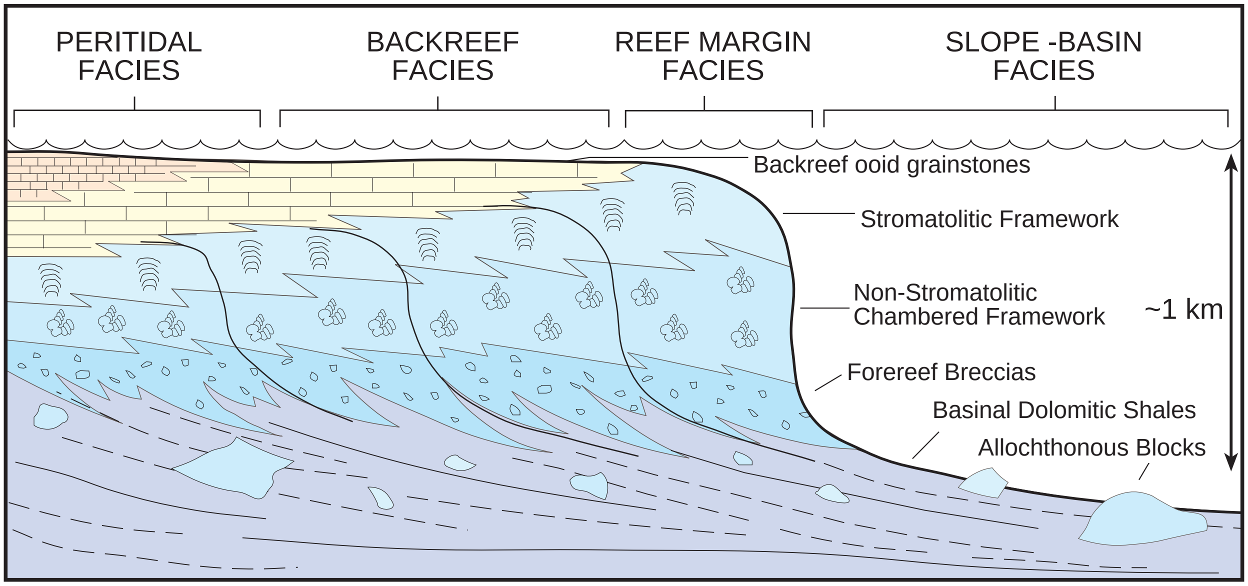


FIGURE 5

Figure 6

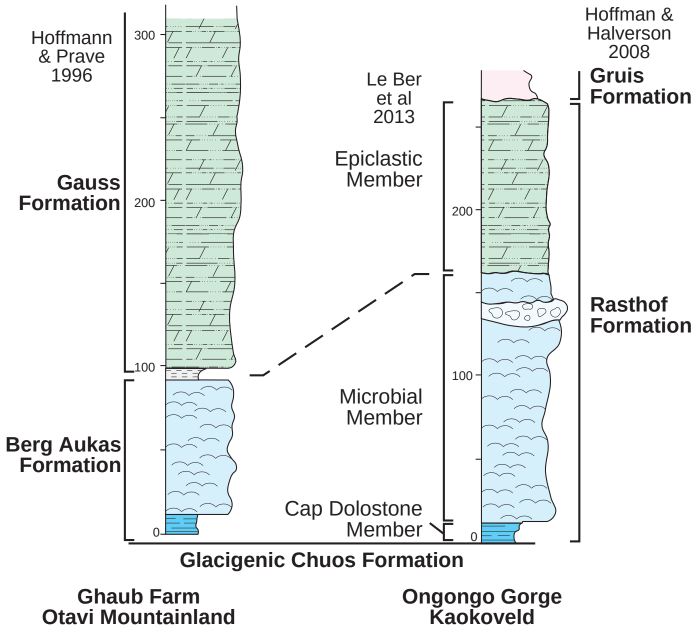


FIGURE 6

Figure 7

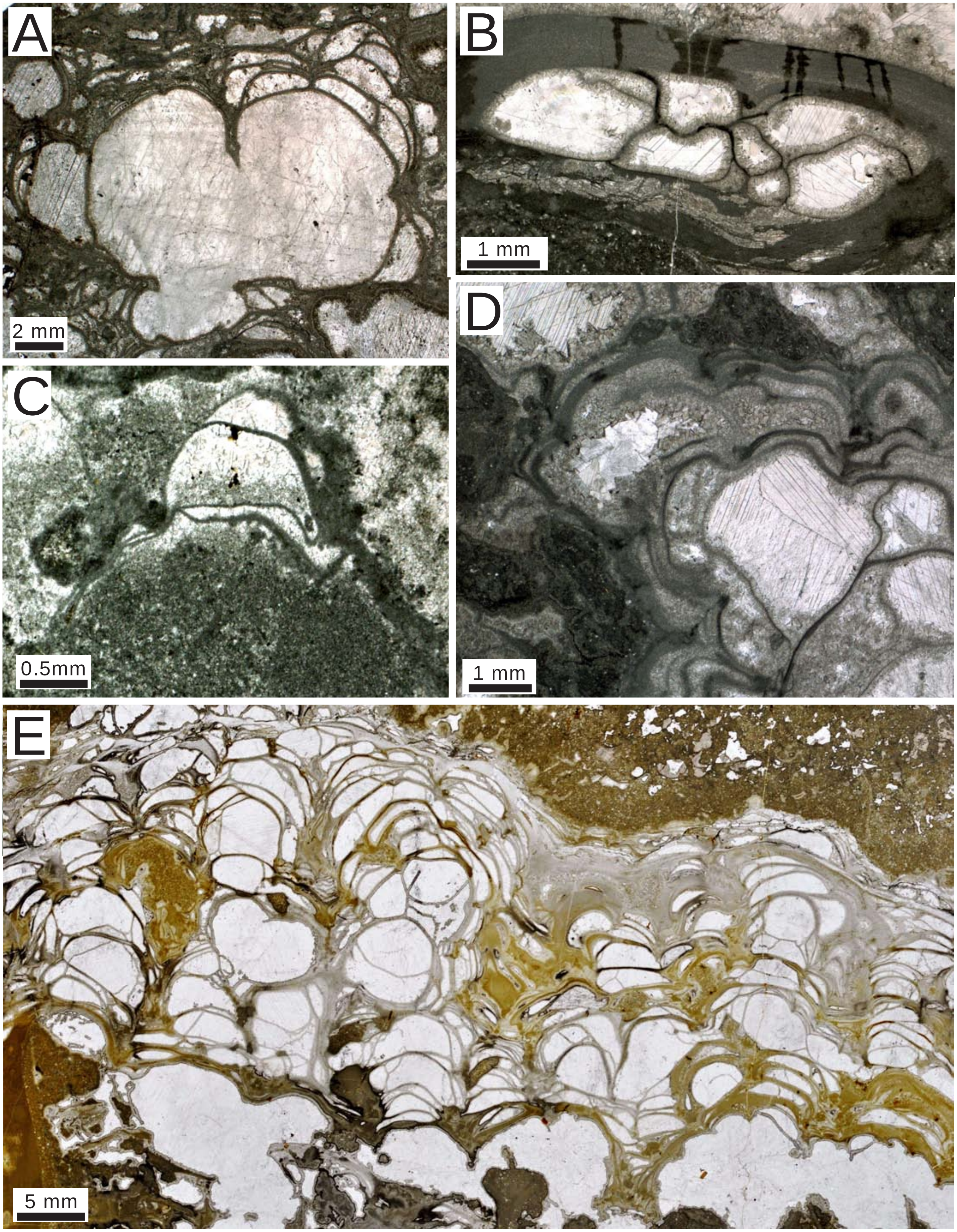
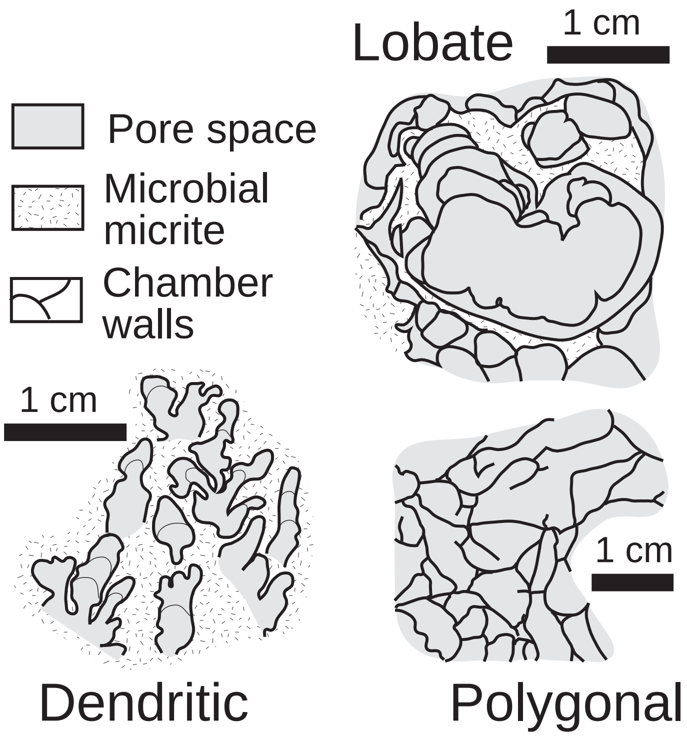


FIGURE 7

Figure 8



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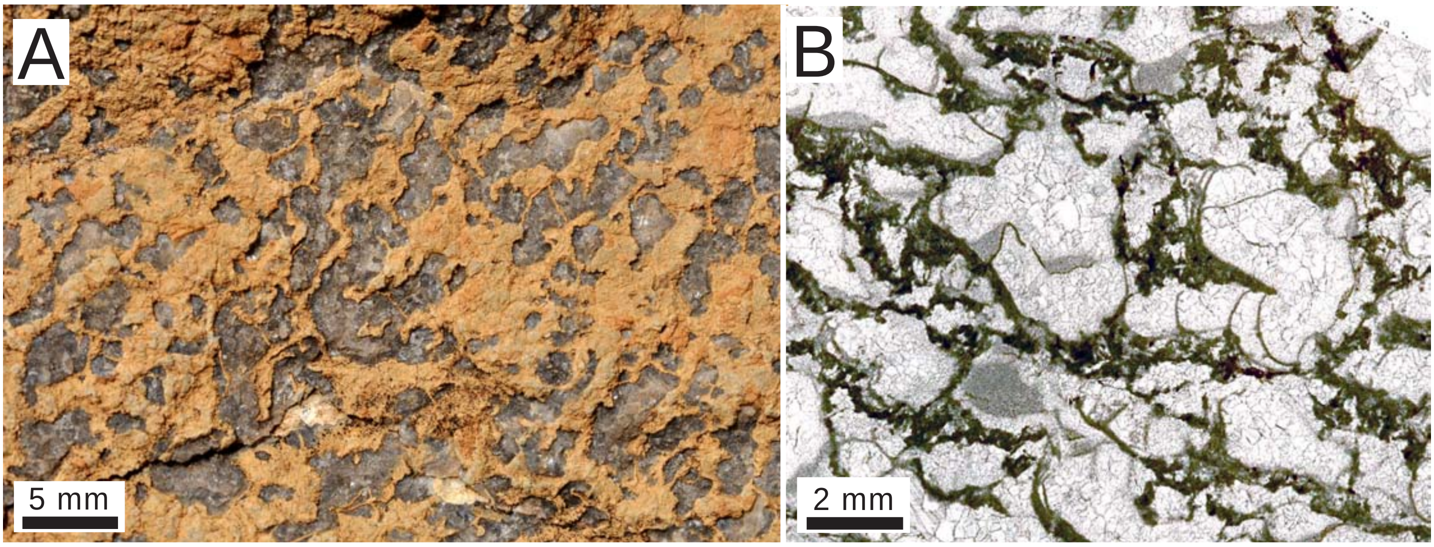


FIGURE 9

Figure 10

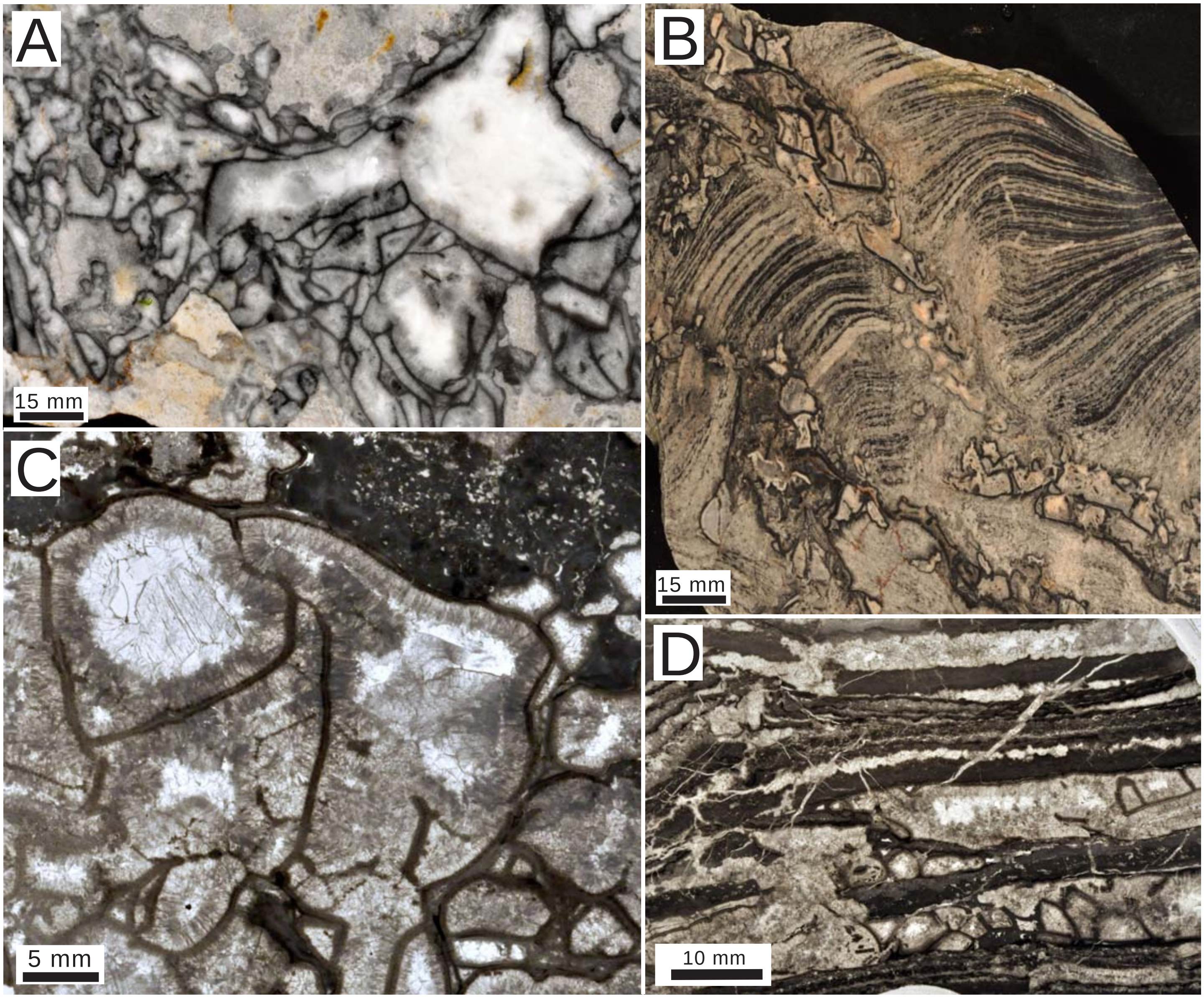
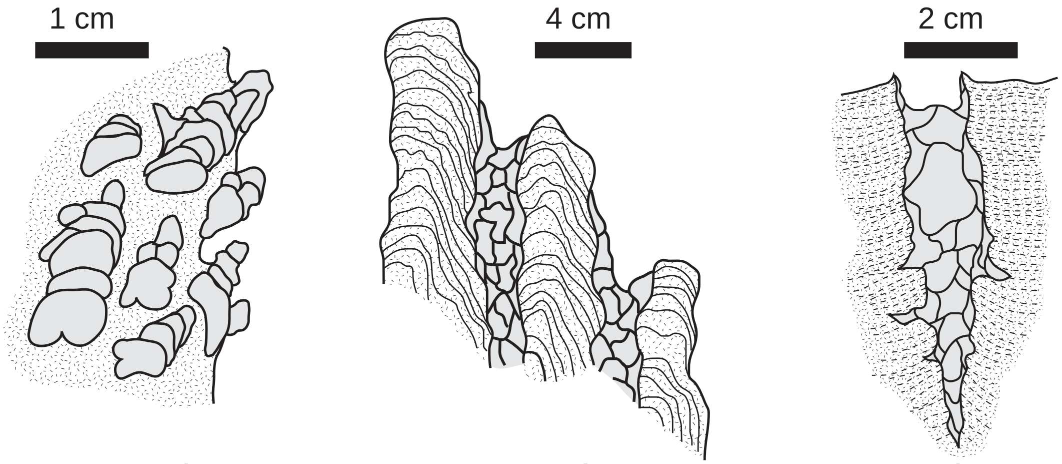


FIGURE 10

Figure 11



Framework Building

Stromatolite Intercolumnar

Cavity Filling

FIGURE 11

Figure 12

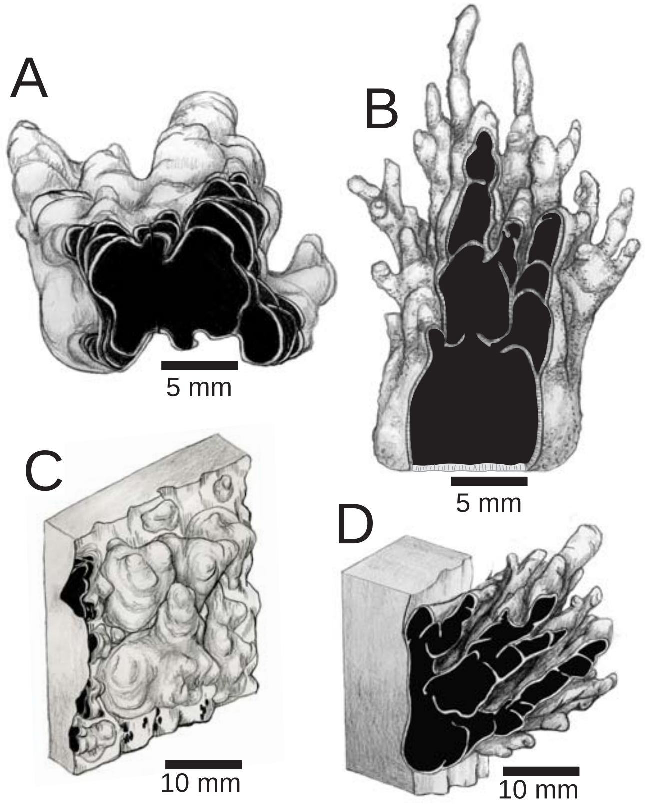


FIGURE 12

Figure 13

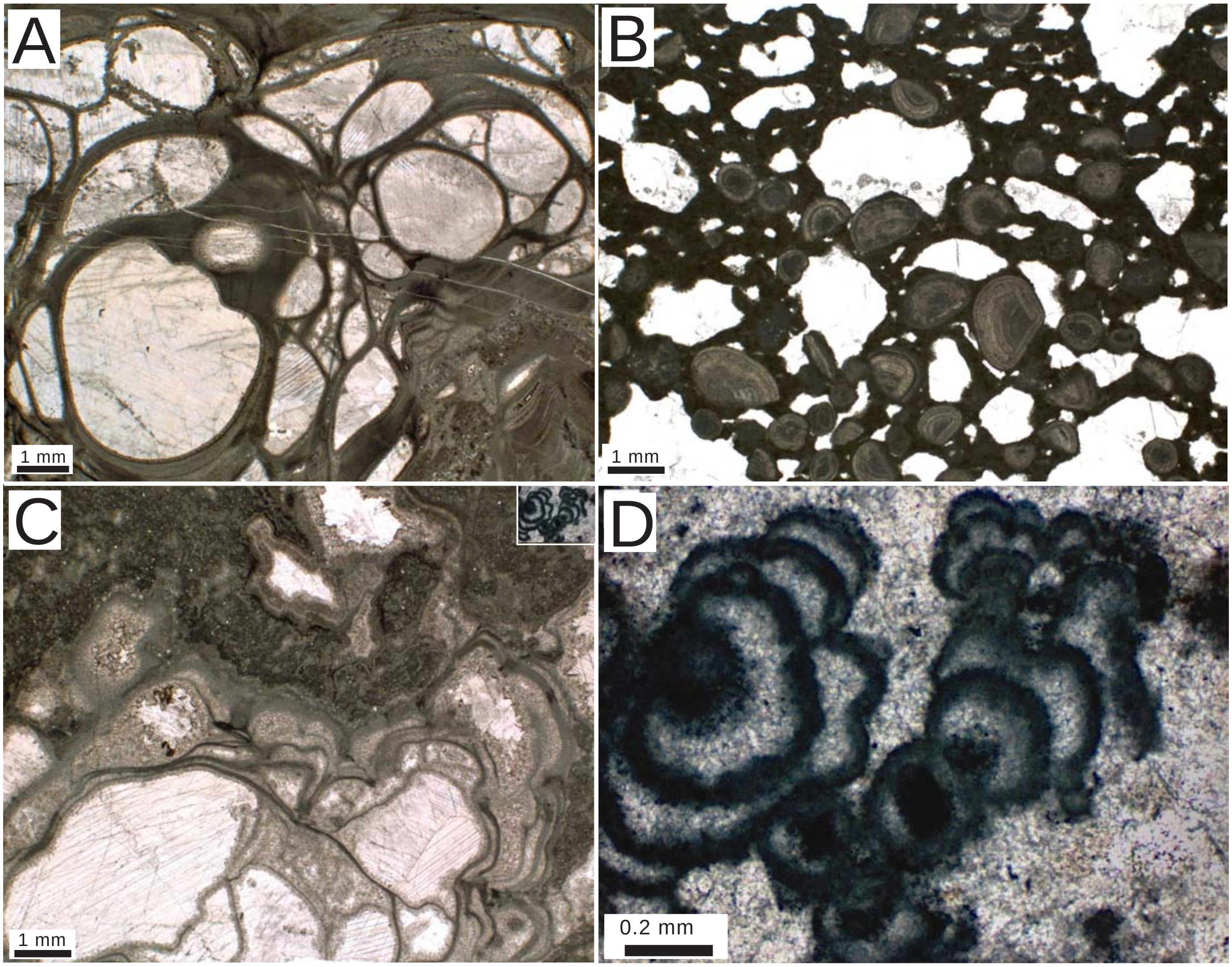


FIGURE 13

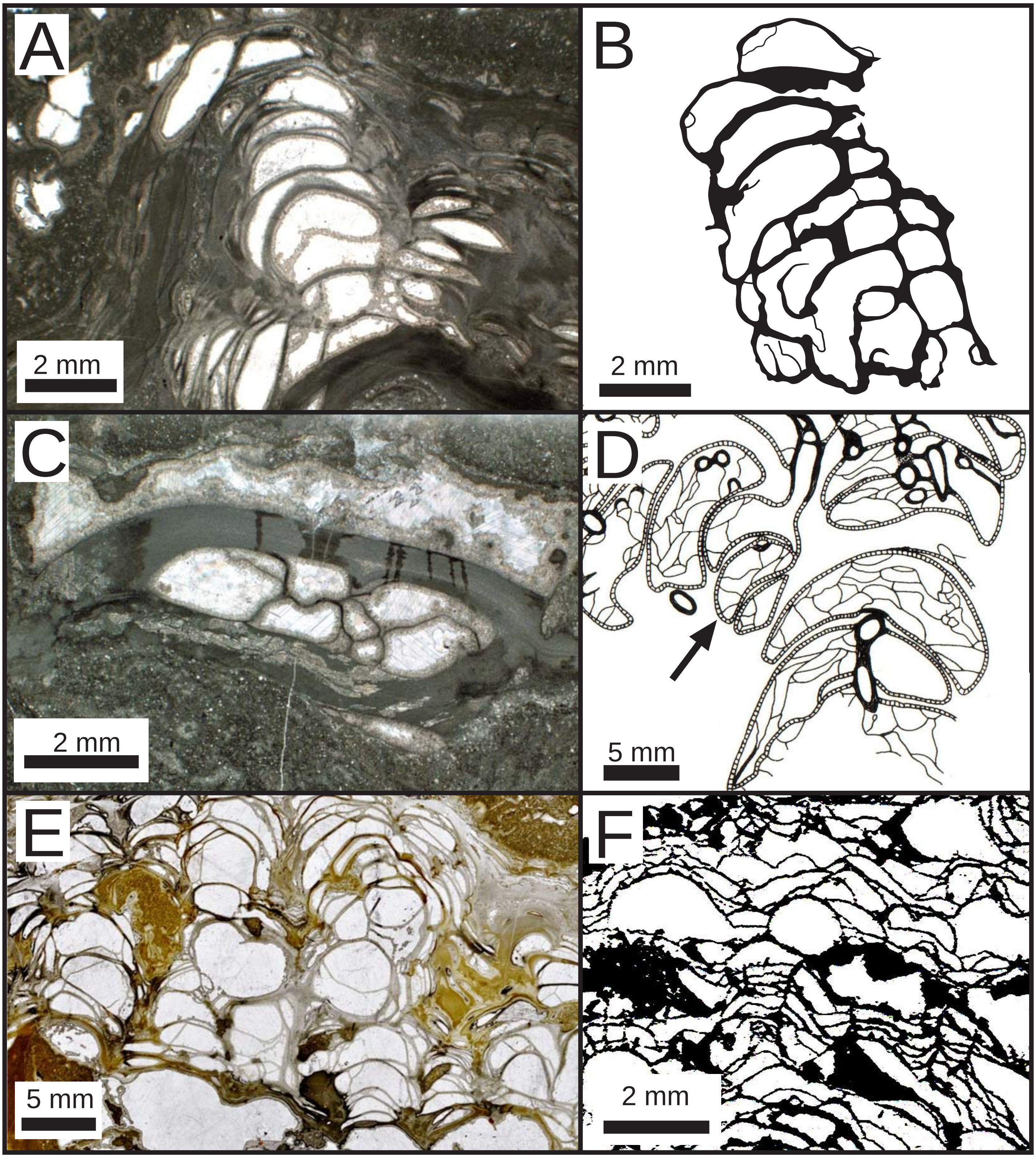


FIGURE 14