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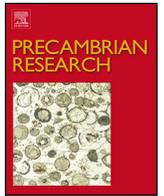
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Early non-marine life: Evaluating the biogenicity of Mesoproterozoic fluvial-lacustrine stromatolites



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ABSTRACT

The record of life on land or in non-marine environments during the Precambrian is sparse, limiting our ability to understand life outside of marine settings before the advent of animals. Stromatolites from such environments are known, but demonstrating stromatolite biogenicity remains difficult, as stromatolite growth can be controlled by a spectrum of biologic, chemical, and biologically-mediated processes. Stromatolites from the Mesoproterozoic (1.09 Ga) Copper Harbor Conglomerate, an alluvial fan, fluvial, and lacustrine deposit, offer an interesting test for the presence and nature of microbial life in shallow, Mesoproterozoic non-marine settings.

Stromatolites from a siltstone facies are interpreted as biogenic, as they contain detrital-rich laminae, likely indicative of trapping and binding by microbes and fenestral fabrics suggestive of desiccation or lift-off structures in mats via the presence of gas (perhaps O₂ from photosynthesis or other gases from mat decay). The stromatolites formed as microbial mats grew over a mudflat or sandflat with carbonate filled desiccation cracks on an erosive topography, and thus provide evidence for life in a very shallow, predominantly desiccated environment. Stromatolites from a conglomerate facies are microdigitate and record both isopachous laminae with radial-fibrous calcite fans and botryoids, typically considered abiogenic in origin, as well as wavy, conical laminations likely indicative of the former presence of microbial mats. The conglomerate-facies stromatolites are interpreted to have formed in a flooded braidplain setting with restricted circulation. This study supports the suggestion that microbial communities were abundant in non-marine environments in the Midcontinent Rift during the Mesoproterozoic. It also highlights how variable environmental factors can influence stromatolite growth, even in similar depositional settings and with a consistent microbial presence.

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1. Introduction

Precambrian fossil evidence for non-marine microbial life is rare compared to that for marine microbial life. As a result, microbial colonization of terrestrial environments is poorly understood and the timing is not well constrained. Microbes have been recognized in subaerial environments for at least ~2.7 billion years based on organic matter in paleosols from South Africa (Watanabe et al., 2000). The oldest microfossil evidence of life on land is from a 1.2 Ga paleokarst in Arizona (Horodyski and Knauth, 1994). However, much of the Precambrian evidence for non-marine life is found in

geochemical proxies (e.g. Ohmoto, 1996; Stüeken et al., 2012) or from aquatic terrestrial settings (e.g. Battison and Braiser, 2012; Schopf and Walter, 1983).

There are few examples of the paleoenvironments in which Precambrian non-marine microbes lived and how they were adapted to various environmental conditions. For example, little is known about how such microbes evolved to handle UV radiation, desiccating environments, changes in alkalinity, and variable discharge. Furthermore, the presence of Precambrian non-marine life is largely inferred from stromatolites, whose growth is controlled by an assortment of biologic, chemical, and biologically-mediated processes (e.g. Buck, 1980; Buick, 1992; Elmore, 1983). It is therefore important to investigate the biogenicity and depositional context of Precambrian non-marine stromatolites before making interpretations about the possible microbes that formed them.

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Microbially induced sedimentary structures (MISS) and carbonate stromatolites found within the Mesoproterozoic (1.09 Ga) Copper Harbor Conglomerate of northern Michigan have been interpreted as evidence for fluvial-lacustrine microbial communities that colonized the failed Midcontinent Rift System (Elmore, 1983; Wilmett et al., 2014). There are other signs of microbial activity in the Midcontinent Rift System during the Mesoproterozoic as well. The Nonesuch Shale, which directly overlies and interfingers with the Copper Harbor Conglomerate, contains abundant organic carbon and microfossils (Elmore et al., 1989; Pratt et al., 1991; Wellman and Strother, 2015). Additionally, paleosols containing organic matter have been described within interflow deposits of the Portage Lake Lava Series, which interfingers with the Copper Harbor Conglomerate (Mitchell and Sheldon, 2009, 2010; Sheldon, 2012).

While the Copper Harbor stromatolites were initially interpreted as purely biogenic constructions, some of the stromatolites from the Copper Harbor Conglomerate exhibit characteristics of abiogenic formation (Elmore, 1983). These characteristics include radial-fibrous calcite fans that are commonly thought to form through the direct inorganic precipitation of calcite as opposed to microbially induced formation (e.g. Corsetti and Storie-Lombardi, 2003; Grotzinger, 1989; Grotzinger and Knoll, 1999; Pope et al., 2000). As is common with Precambrian stromatolites, there is a lack of conclusive microfossil evidence in the Copper Harbor stromatolites (Elmore, 1983). These stromatolites developed in a depositional setting that includes evidence for alluvial fan, fluvial, and lacustrine sedimentation. If shown to be biogenic in origin, these stromatolites offer an opportunity to understand the microbial communities responsible for their formation and to characterize the environment in which they formed. In the absence of microfossil evidence, there is no single method that can be used to determine stromatolite biogenicity. Therefore, this study utilizes a suite of evidence to test the hypothesis that the Copper Harbor Conglomerate stromatolites formed primarily through biogenic processes.

2. Stromatolite biogenicity

A non-genetic stromatolite definition that is suitable to this study is “an attached, laminated, lithified sedimentary growth structure, accretionary away from a point or limited surface of initiation” (Semikhatov et al., 1979). Precambrian stromatolites have been used extensively as evidence for some of the earliest life on Earth, as well as indicators of geochemical and other paleoenvironmental conditions (Bosak et al., 2013; Grotzinger and Knoll, 1999). Microbial trapping and binding of sediment dominates classic models of stromatolite formation and is common in modern marine examples (e.g. Gebelein, 1969; Reid et al., 2000). However, there is also evidence that encrusting cements are capable of forming stromatolites and associated morphologies without a clear biogenic component (e.g. Grotzinger and Knoll, 1999; Grotzinger and Rothman, 1996; Knoll and Semikhatov, 1998). Grotzinger and Rothman (1996) used the Kadar-Parisi-Zhang (KPZ) equation to demonstrate that some stromatolite forms (such as domal morphologies) can be created abiogenically. Additionally, a diffusion limited aggregation (DLA) model in which particles (sediment, ions, and nutrients) arrive at an aggregate through a path similar to Brownian motion (diffusion) can be coupled with episodic sedimentation to create columnar branching stromatolite morphologies (Grotzinger and Knoll, 1999; Verrecchia, 1996). The morphology and microstructure of stromatolites has also changed through geologic time (e.g. Grotzinger and Knoll, 1999; Riding, 2011), and thus it is likely that the various processes that interact to form stromatolites have likewise changed through time

(Bosak et al., 2013). For these reasons, macroscopic stromatolite morphologies, with the possible exception of some conical morphologies (e.g. Batchelor et al., 2004), alone are not very useful in determining biogenicity. However, there are a number of features, as well as combinations of these features, that are unlikely to have been formed by purely abiotic processes (Awramik and Grey, 2005). Therefore, each structure must be evaluated individually using multiple lines of evidence at multiple scales to test where it falls within a spectrum of biogenicity, with the understanding that some stromatolites may lack sufficient evidence to make a clear determination.

A number of attempts have been made to establish comprehensive criteria for determining stromatolite biogenicity (e.g. Buick et al., 1981; Hofmann et al., 1999; Walter, 1983), although none of them have become definitive (Awramik and Grey, 2005). In the absence of organic matter or microfossils, evidence of biogenic structures commonly includes wavy or crinkled detritus-rich laminations with grains trapped beyond the angle of repose (e.g. Buick et al., 1981). This suggests that the blockage of grain movement (baffling) or adhesion to the extracellular polymeric substance (EPS) produced by microbial communities, as well as microbial binding, played a role in forming the stromatolites (e.g. Riding, 2000). Microbial mat baffling, trapping, and binding may also result in biostabilization of the substrate, in which sediment may experience flexible deformation (e.g. Noffke et al., 2003). Evidence of phototropism, in which stromatolites are inclined towards the direction of maximum insolation, may also be used as evidence for stromatolite biogenicity (e.g. Awramik and Vanyo, 1986; Petryshyn and Corsetti, 2011). Additionally, the photosynthetic production of O₂ and other gases originating from mat decay can build-up under a microbial mat and contribute to the creation of conical stromatolite morphologies that contain fenestrae or lift-off structures between laminations (Bosak et al., 2009, 2010).

Indirect evidence of abiogenic precipitation may include oscillating Ca/Mg ratios between laminae and compositional differences between stromatolites and the surrounding sediment (Frantz et al., 2014; Grotzinger and Knoll, 1999). For example, when entirely calcareous stromatolites are surrounded by siliciclastic sediment it suggests that trapping and binding were not involved in stromatolite formation (Grotzinger and Knoll, 1999). In addition, isopachous laminae and a number of cement textures within stromatolites have been recognized by most authors as indicators of direct precipitation. These include textures such as radial-fibrous, herringbone calcite, radiaxial-fibrous, and fascicular-optic calcite or dolomite (e.g. Grotzinger and Knoll, 1999; Pope et al., 2000; Sumner and Grotzinger, 1996). Isopachous laminae with radial-fibrous fans or botryoids are highly uniform and exhibit a high degree of inheritance. This is inconsistent with accretion in which crystal nucleation and growth is controlled by microbial mats that exhibit spatial heterogeneity (e.g. Bartley et al., 2000; Grotzinger and Knoll, 1999; Knoll and Semikhatov, 1998; Pope et al., 2000).

3. Geologic setting

3.1. Depositional setting and location

The Copper Harbor Conglomerate is a Mesoproterozoic (1.09 Ga) succession located within the upper peninsula of Michigan, northern Wisconsin, and on Isle Royale in Lake Superior. It is comprised of fluvial, lacustrine, and alluvial fan derived volcanoclastic sandstone, mudstone, and conglomerate that was infilling the Keweenaw Trough (Elmore, 1984). This basin is part of the Midcontinent Rift System, which extends from Canada to Kansas and, before failing, threatened to split the North American Craton (Van Schmus

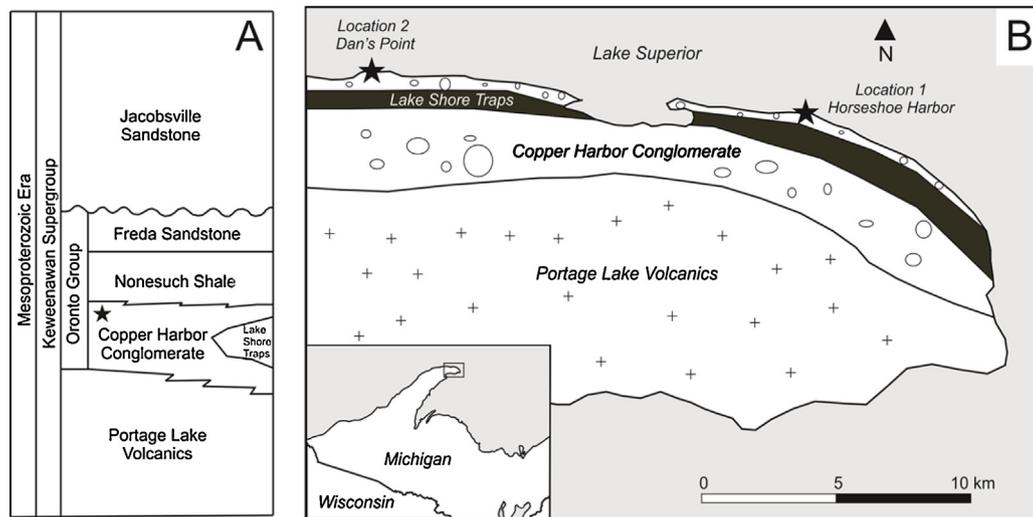


Fig. 1. (A) General stratigraphy of Midcontinent Rift System in Michigan. Location of Copper Harbor Conglomerate marked with star (after Schmidt and Williams, 2003). (B) Locality map of Keweenaw Peninsula in Upper Peninsula of Michigan (after Kulakov et al., 2013). Two study localities are marked as stars: Location 1 corresponds to Horseshoe Harbor and Location 2 corresponds to Dan's Point.

and Hinze, 1985). The Copper Harbor Conglomerate represents the base of the Mesoproterozoic (Middle and Upper Keweenaw) Oronto Group and the earliest infilling of the Keweenaw Trough after the cessation of volcanic activity (Fig. 1) (Dickas, 1986). Clast imbrications within the conglomerate suggest that sediment was being transported north, towards the center of the basin (Elmore, 1984).

The conglomerate interfingers with a series of lava flows known as the Lake Shore Traps. U–Pb dating of zircons within the Lake Shore Traps yields an age of 1087.2 ± 1.6 Ma (Davis and Paces, 1990), which constrains the age of sedimentation for the Copper Harbor Conglomerate. A paleomagnetic pole for the Lake Shore Traps (on the Keweenaw Peninsula) is reported at 23.1° N and 186.4° E (Kulakov et al., 2013).

The Copper Harbor Conglomerate is conformably overlain and interfingers with the siltstones and mudstones of the Nonesuch Shale, which is upper Keweenaw in age. These green and black siltstones and mudstones represent a perennial lacustrine environment (Paleo-lake Nonesuch) that was contemporaneous with deposition of the Copper Harbor Conglomerate (e.g. Cumming et al., 2013; Elmore et al., 1989). Although some authors (e.g. Hieshima and Pratt, 1991; Pratt et al., 1991) have argued for a marine influence in the Nonesuch Shale based on S/C ratios and biomarkers, most studies have interpreted it as a lacustrine environment based on facies analyses and paleogeographic reconstructions (e.g. Cumming et al., 2013; Elmore et al., 1989; Imbus et al., 1992; Ojakangas et al., 2001). The Nonesuch Shale also has Os isotopic values that reject marine influence and support interpretations of a rift lake setting (Cumming et al., 2013). The Nonesuch Shale is overlain by red sandstones and shale of the Freda Sandstone which represents the final stage of basin infilling (Elmore, 1984; Wolff and Huber, 1973).

This study focuses on two localities on the northeastern tip of the Keweenaw Peninsula that were described by Elmore (1983, 1984). These localities are approximately 13 km apart on the southern shore of Lake Superior near the town of Copper Harbor (Fig. 1). They correspond to two distinct facies where stromatolites occur within the Copper Harbor Conglomerate. The first locality is known as Horseshoe Harbor and is ~ 7 km east of the town Copper Harbor. The second locality is known as Dan's Point and is located ~ 6 km to the west of the town Copper Harbor.

3.2. Previous work on the Copper Harbor Conglomerate stromatolites

The Copper Harbor Conglomerate stromatolites have been described or mentioned numerous times (e.g. Elmore, 1983; Elmore, 1984; Elmore et al., 1989; Nishioka et al., 1984; Nordeng, 1963). However, the paucity of examples of Precambrian life in non-marine settings underscores the necessity for re-evaluating these stromatolites with regards to biogenicity, depositional setting, and what can be inferred about the interactions between microbes and their environments.

Elmore (1983) offered the most detailed description of the stromatolites as contorted beds in mudstone and as laterally linked hemispheroids that drape over cobbles. He interpreted the stromatolites to be biogenic in origin based on their general morphology and microfabrics. Elmore (1983) also mentions the possible abiogenic characteristics of some stromatolites such as radial-fibrous calcite fans superimposed on the stromatolite laminae. Nishioka et al. (1984) supported Elmore's (1983) claim of a biogenic origin based on observations of possible tubular microfossils within vugs, although identification of these microstructures was not definitive.

Elmore (1983, 1984) interpreted the stromatolites to have formed in ponded, abandoned fluvial channels within an arid alluvial fan system. Kalliokoski (1986) supported an arid or semi-arid climate based on caliche horizons within the Copper Harbor Conglomerate and a subtropical paleolatitude (confirmed by Kulakov et al., 2013). In order to explain standing water in abandoned channels, Elmore (1983, 1984) suggested that there were seasonal climate fluctuations that re-flooded abandoned channels and created the large standing ponds in which the stromatolites formed. Additionally, the nearby rift lake may have experienced an elevated water table and encroached on the distal alluvial fan, providing one method of re-filling the abandoned channels in an otherwise arid setting (Elmore, 1983).

The stromatolites in the Copper Harbor Conglomerate have been used as potential evidence for phototropism in stromatolites (Nordeng, 1963). The growth angle of the stromatolites was used to determine the angle of maximum solar insolation. Nordeng (1963) then used this angle to determine a paleopole for the Copper Harbor Conglomerate at 12° N and 144° E. However, the methodology for how oriented stromatolite growth angle measurements were collected by Nordeng (1963) is unclear. For example, the vertical

inclination of “colonies” is described. Whether a “colony” represents an individual stromatolite or a collection of stromatolites is unknown. Microdigitate stromatolite columns in the Copper Harbor Conglomerate nucleate on cobbles, not a flat substrate. Nordeng (1963) does not specify whether growth angles were measured only from columns that grew on the top of cobbles or if measurements were collected from the sides of cobbles and, if so, how this was corrected for. Additionally, a more current understanding of stromatolite formation predicts that a number of variables such as the current direction, sediment supply, and nutrient availability can also control the direction of growth. For these reasons, it is important to apply modern methodologies to re-evaluate whether there is indeed a phototropic response in the Copper Harbor Conglomerate stromatolites.

4. Methods

In the field, stratigraphic sections were measured and described at both the Horseshoe Harbor and Dan’s Point localities. Stromatolites and associated sedimentary features were placed in their depositional context at both locations and their macro-scale features were noted. Eleven large (10–15 kg) stromatolite samples were collected from the two localities for laboratory analyses. Six were collected from Horseshoe Harbor and 5 were collected from Dan’s Point. In the laboratory, stromatolite samples were serially sectioned into 30 slabs (~2 cm thick) and polished. Seven large (50 mm × 75 mm) petrographic thin sections, 4 from Horseshoe Harbor and 3 from Dan’s Point, were made from internal stromatolite slabs. These sections were used for standard petrographic analyses such as Alizarin Red-S staining and reflected light. Photomosaics of entire thin sections were also created in order to better visualize microfabrics. These photos allowed for the characterization of the gross morphology, microfabrics, and mineralogy of the stromatolites.

Petryshyn and Corsetti (2011) developed a method of evaluating for a phototropic response in stromatolites using growth angles of individual stromatolite columns (Fig. 2). They measured the growth angles of digitate cobble-draping columns in Walker Lake, Nevada to determine if a preferential growth direction towards sunlight occurred. This method is based on the assumption that stromatolite columns on all the sides of boulders will branch towards the direction of sunlight if a phototropic response existed. On the other hand, if non-phototropic or abiogenic processes (such as diffusion) dominate stromatolite growth, then stromatolite columns will accrete approximately surface normal (perpendicular to the sides of the boulder) (Petryshyn and Corsetti, 2011).

The lack of a phototropic response does not suggest stromatolite abiogenicity but it provides important evidence that variables besides the angle of maximum insolation are responsible for controlling the direction of growth. Since the test is only applicable to cobble or boulder draping stromatolites, it was only used on the Dan’s Point digitate cobble-draping stromatolite columns. The Horseshoe Harbor stromatolites are not cobble-draping, so this test could not be applied to them. To employ this method, 5 Dan’s Point cobble-draping stromatolite slabs with 46 individual digitate stromatolite columns (2 mm to 3 cm wide) were analyzed from 4 different encrusted cobbles. The growth angle of each stromatolite column was measured so that growth perpendicular to the initiation surface (surface normal) would measure at 90°. Stromatolites that branched upwards towards the top of the cobble or boulder would then measure less than 90°. Growth angles would only measure greater than 90° if the column branched downwards towards the substrate. The stromatolite growth angles were evaluated as a whole and also grouped according to the initial inclination of the growth surface to assure no bias.

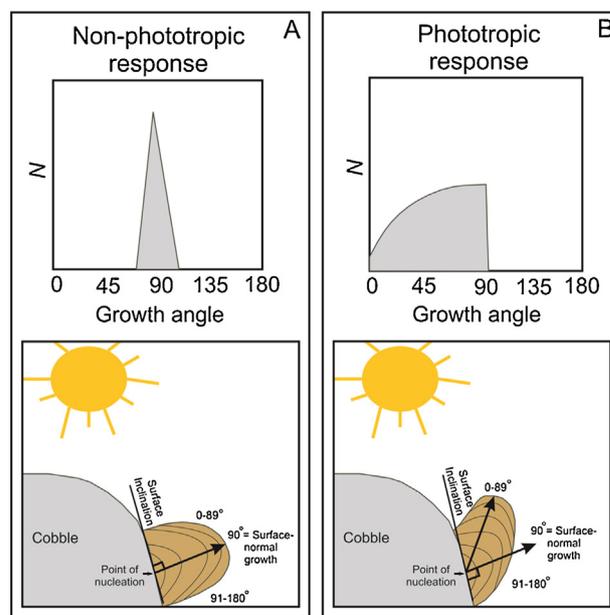


Fig. 2. Methodology used to test for phototropic response (after Petryshyn and Corsetti, 2011). (A) Hypothetical distribution of stromatolite growth angles centered around 90° that suggests non-phototropic response. (B) Surface normal growth (~90°) or downwards growth (>90°) is expected if there is not a phototropic response. (C) Hypothetical distribution of stromatolite growth angles <90° that suggests a phototropic response is present. (D) Stromatolites that grow upwards (<90°) towards maximum solar radiation would be expected if a phototropic response exists.

Awramik and Vanyo (1986) reported a phototropic response in stromatolites from Shark Bay, Western Australia (~26° S latitude). The stromatolite columns there branched at 21–33° N. Although these stromatolites are not cobble draping and likely formed under different conditions than those from the Copper Harbor Conglomerate, they demonstrate that stromatolites nucleating on a non-inclined substrate will grow towards the direction of maximum insolation (the equator) if a phototropic response exists. A paleomagnetic pole for the Lake Shore Traps, which interfinger with the Copper Harbor Conglomerate, has been reported at 23.1° N and 186.4° E (Kulakov et al., 2013). Therefore, we hypothesize that stromatolite columns that grew on the non-inclined top surfaces of cobbles in the Copper Harbor Conglomerate should branch at angles ~23° S if a phototropic response existed. Stromatolites nucleating on the sides of cobbles should branch upwards (less than 90°) towards the surface of the water, and maximum solar insolation, if a phototropic response existed (Fig. 2).

5. Results

5.1. Sedimentology and field observations

The Copper Harbor Conglomerate is comprised of volcanoclastic sediment that ranges from clay to boulder-sized (0.5 m) grains and contains a diagenetic calcite cement. There are three major facies that can be observed at both Horseshoe Harbor and Dan’s Point: a conglomerate facies, a siltstone facies, and a trough-cross stratified sandstone facies. Stromatolites are located within the siltstone facies at Horseshoe Harbor and overlying the conglomerate facies at Dan’s Point (Fig. 3).

5.1.1. Conglomerate Facies

The conglomerate facies is the most common facies at both localities. Beds range from approximately 3–20 m in thickness and have erosional lower contacts. The conglomerate is poorly sorted and

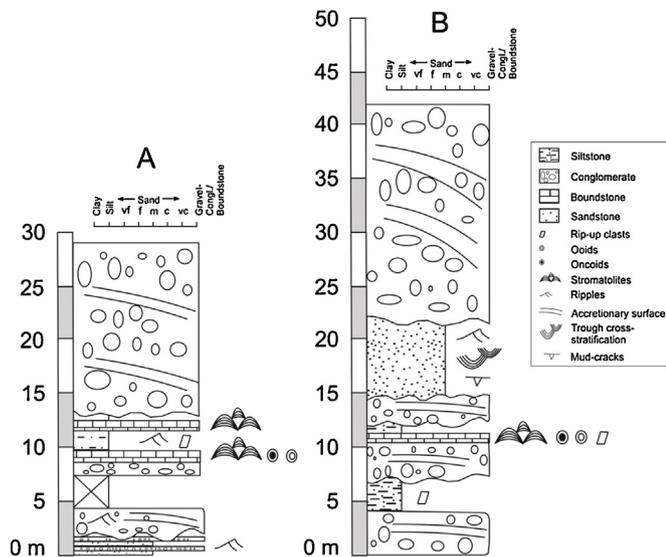


Fig. 3. Measured stratigraphic sections from Horseshoe Harbor (A) and Dan's Point (B) localities. Stromatolites occur above conglomerate facies and within siltstone facies.

contains well-rounded pebble to boulder sized clasts. The conglomerate matrix is a mixture of sand, silt, and clay sized grains and alternates between intervals of grain support and matrix support. The grain-supported conglomerate beds are often crudely graded and fine upwards. They contain cross-bedded sandy channel fills with lateral and downstream accretion. The channels are approximately 2–15 m in width and lenticular in form. Thin discontinuous (2–10 m long and <5 cm thick) carbonate crusts can be found within the conglomerate facies. The carbonate crusts are distinguishable from stromatolites in the conglomerate facies because they form around clasts instead of draping over the tops of clasts as the stromatolites do. These crusts have been interpreted as pedogenic caliche horizons by Kalliokoski (1986). Although their microfabrics are not described here, Kalliokoski (1986) observed sparry calcite cement filling in the voids between pebbles, carbonate-rimmed pebbles, pendulose calcite on the undersides of grains, and sand grains floating in a carbonate matrix.

Stromatolite mounds, comprised of multiple individual columns and domes, are found overlying the conglomerate facies at Dan's Point. The mounds drape over the top of cobbles as laterally linked hemispheroids and do not occur on the underside of clasts (Fig. 4). The stromatolite beds are ~0.3 m thick, laterally continuous, and are conformably overlain by a siltstone unit (Fig. 5). The

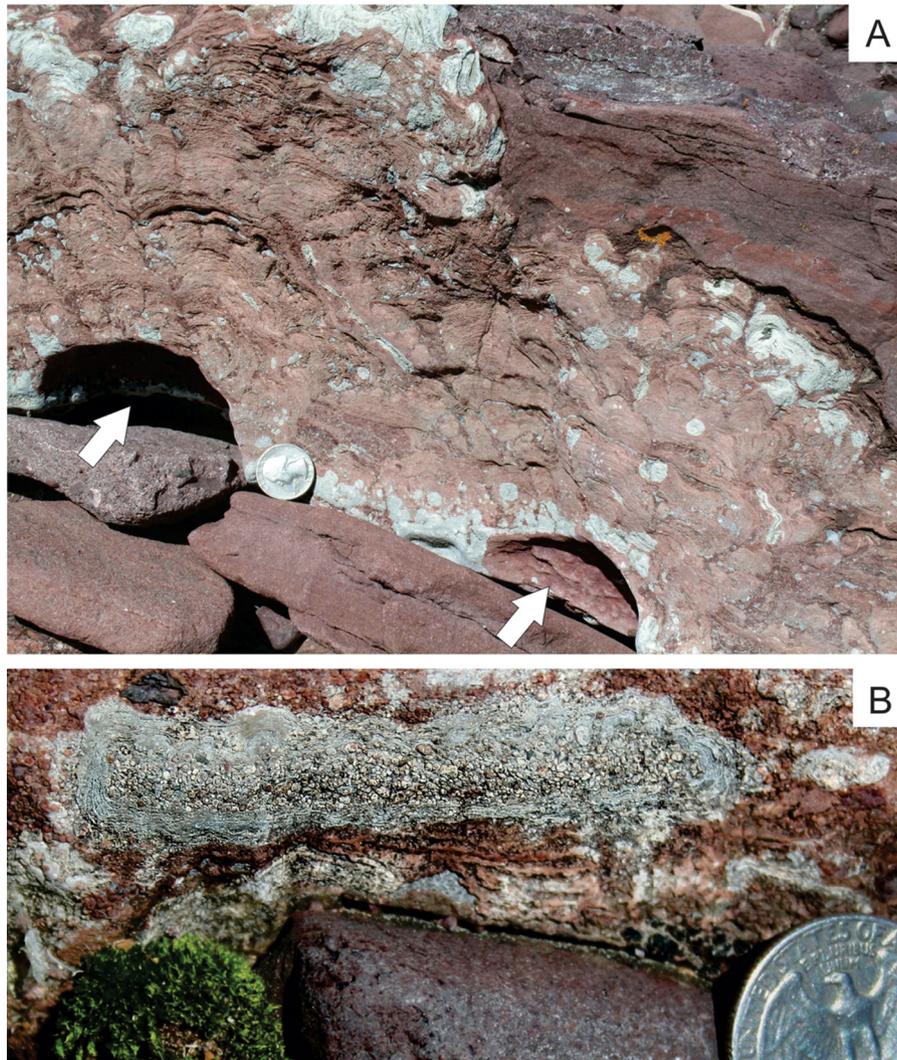


Fig. 4. (A) Example of multiple microdigitate stromatolite columns coating cobble-sized clasts from conglomerate facies to collectively form hemispheroidal stromatolite mounds. Void space where clasts previously rested distinguished by white arrows. (B) Collection of ooids cemented together and coated by calcite laminae to form botryoidal lump.

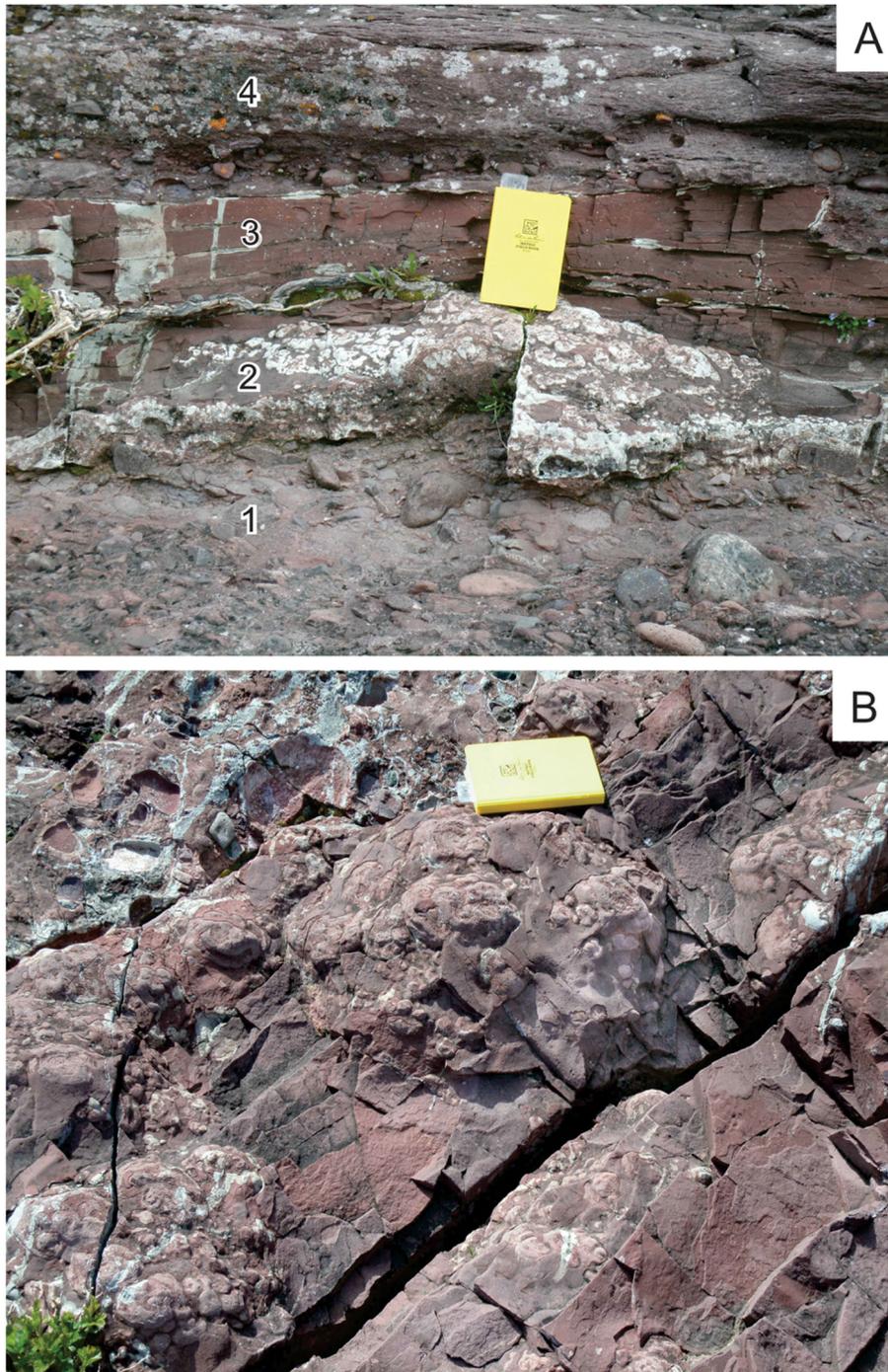


Fig. 5. (A) Carbonate stromatolite bed draping over conglomerate facies and overlain by siltstone facies: (1) conglomerate facies, (2) stromatolite bed, (3) siltstone facies, (4) conglomerate facies. (B) Large bulbous stromatolite mound with siltstone drapes. Field notebook is ~19 cm in length.

stromatolite mounds have a microdigitate structure (e.g. Grotzinger, 1989) in which each cobble-draping hemispheroid consists of multiple small (2 mm–3 cm wide) individual columns and domes (e.g. Hofmann, 1969). Together, the collection of individual stromatolite columns and domes gives each cobble-draping hemispheroid a bulbous cauliflower head appearance with individual mounds ranging from 0.1 to 1 m in diameter (Fig. 5). The stromatolite bearing carbonate bed also contains an abundance of ooids, oncoids, and aggregate grains. Oncoids consist of pebble and cobble-sized lithic clasts with thin (5–10 mm thick) laminated calcite coatings. Stromatolites extend over the top of conglomerate beds that contain these coated grains but grains are also observed

trapped within stromatolite laminae and in the spaces between individual stromatolite columns. Cemented collections of ooids (grapestone) are coated to form botryoidal lumps (Fig. 4).

5.1.2. Siltstone facies

The siltstone facies also contains stromatolites. This facies crops out at both the Horseshoe Harbor and Dan's Point localities but only contains stromatolites at Horseshoe Harbor. It primarily consists of silts but it also contains clay and fine sand that occurs in thin (cm-scale) horizontal beds. It has a conformable base and is observed draping onto the underlying conglomerate. Siltstone packages range from approximately 0.5 to 3 m in thickness.

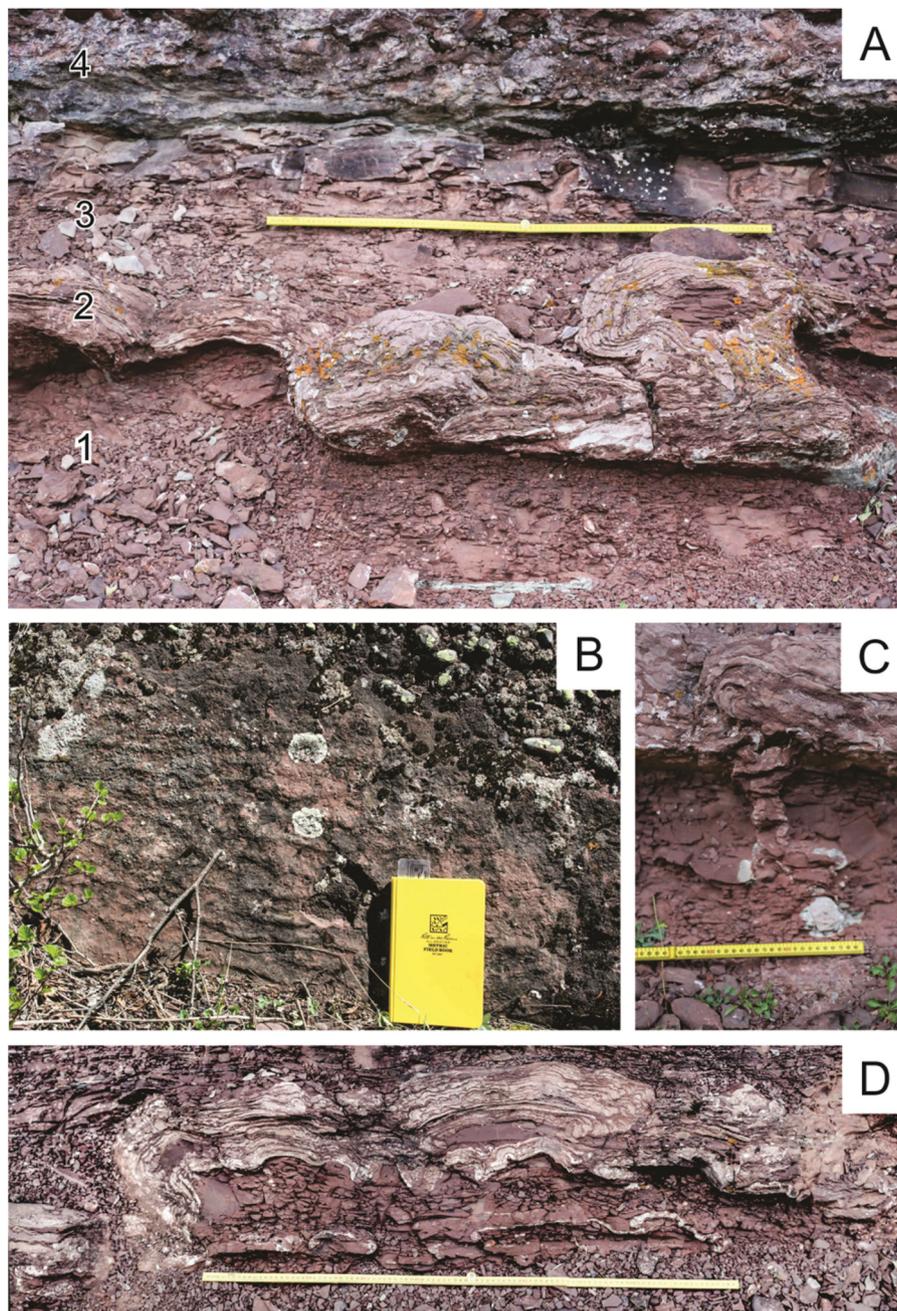


Fig. 6. Stromatolite bed and associated features from siltstone facies at Horseshoe Harbor ~12 m above base of measured section. (A) Location of stromatolite bed within siltstone facies: (1) siltstone facies, (2) stromatolite bed, (3) siltstone facies, (4) conglomerate facies. (B) Small wave ripples preserved in siltstone facies. Field notebook is ~19 cm in length. (C) Carbonate filled mud crack beneath stromatolite bed. (D) Contorted appearance of stromatolite bed as it grows over erosional surface. It is overlain and underlain by undeformed siltstone beds.

The siltstone shows signs of subaerial exposure in the form of carbonate-filled desiccation cracks. Small bidirectional wave ripples can also be seen in some siltstone beds (Fig. 6). Elmore (1983) also reported rain drop impressions from within the mudstone beds of this facies. Rip-up clasts from the exposure cracks can be seen in overlying beds.

An undulose, laterally continuous, stromatolite bed is observed within the siltstone facies at the Horseshoe Harbor locality (Fig. 6). The bed is typically between 0.10 and 0.30 m in thickness. The stromatolites overlie an erosional topography within the siltstone unit that is associated with carbonate filled exposure cracks (Fig. 6). Stromatolite growth over the erosional surface likely

gives the stromatolite bed a contorted appearance, sometimes resulting in mushroom-shaped morphologies (Fig. 6). Hedlund (1953) interpreted these stromatolites as original growth forms that experienced slight deformation. Elmore (1983) thought they experienced deformation from either tectonic activity or loading. However, no evidence of deformation in the overlying and underlying siltstone beds was observed. Additionally, there are no detachment blocks of the stromatolite bed, which indicates that the contorted appearance does not reflect syndepositional slumping. Rip-up clasts of siltstone are sometimes found incorporated into the stromatolite laminae. Rip-up clasts of the stromatolite itself can also be seen floating in the overlying siltstone beds.

5.1.3. Trough-cross stratified sandstone facies

The trough-cross stratified sandstone facies does not contain stromatolites. It occurs only at the Dan's Point locality as a 9 m thick package of cross-bedded and trough-cross bedded sandstone that is found in between mass gravity flow conglomerate beds. It is comprised of medium sand with mud intraclasts and contains occasional mud drapes with polygonal desiccation cracks. It has an erosional base and contains small pebble sized lags within the sandstone. The trough-cross stratified sandstone facies contains both current ripples and wave ripples.

5.2. Stromatolite microfabrics

5.2.1. Horseshoe Harbor stromatolites

The stromatolites from Horseshoe Harbor consist of alternating dark (approximately 50 μm to 1 mm thick) and light laminae (approximately 0.5–3 mm thick), which are wavy and crinkled in

character (Fig. 7). The light laminae contain detrital fine sand, silt, and clay-sized grains, spar, and microspar, while the dark laminae are micrite and hematite-rich. The light laminae have more variable thicknesses than the dark laminae. They pinch and swell as detrital material from the light laminae fills in depressions in the underlying microtopography. The dark micritic layers have a clotted texture. They are opaque under plane and crossed polarized light. However, an abundance of hematite can clearly be seen under reflected light (Fig. 7). The entire outcrop is red-colored and hematite appears widespread throughout the stromatolites but is especially concentrated in the dark wavy laminae (Fig. 7). Alizarin Red-S staining shows that their laminae and cement is mostly comprised of CaCO_3 .

The stromatolites from Horseshoe Harbor also have an abundance of fenestral fabrics (Figs. 7 and 8). Fenestrae range in size from $\sim 100 \mu\text{m}$ to $\sim 5 \text{ mm}$ in diameter. They are larger than the grain-supported interstices and sometimes follow the orientation

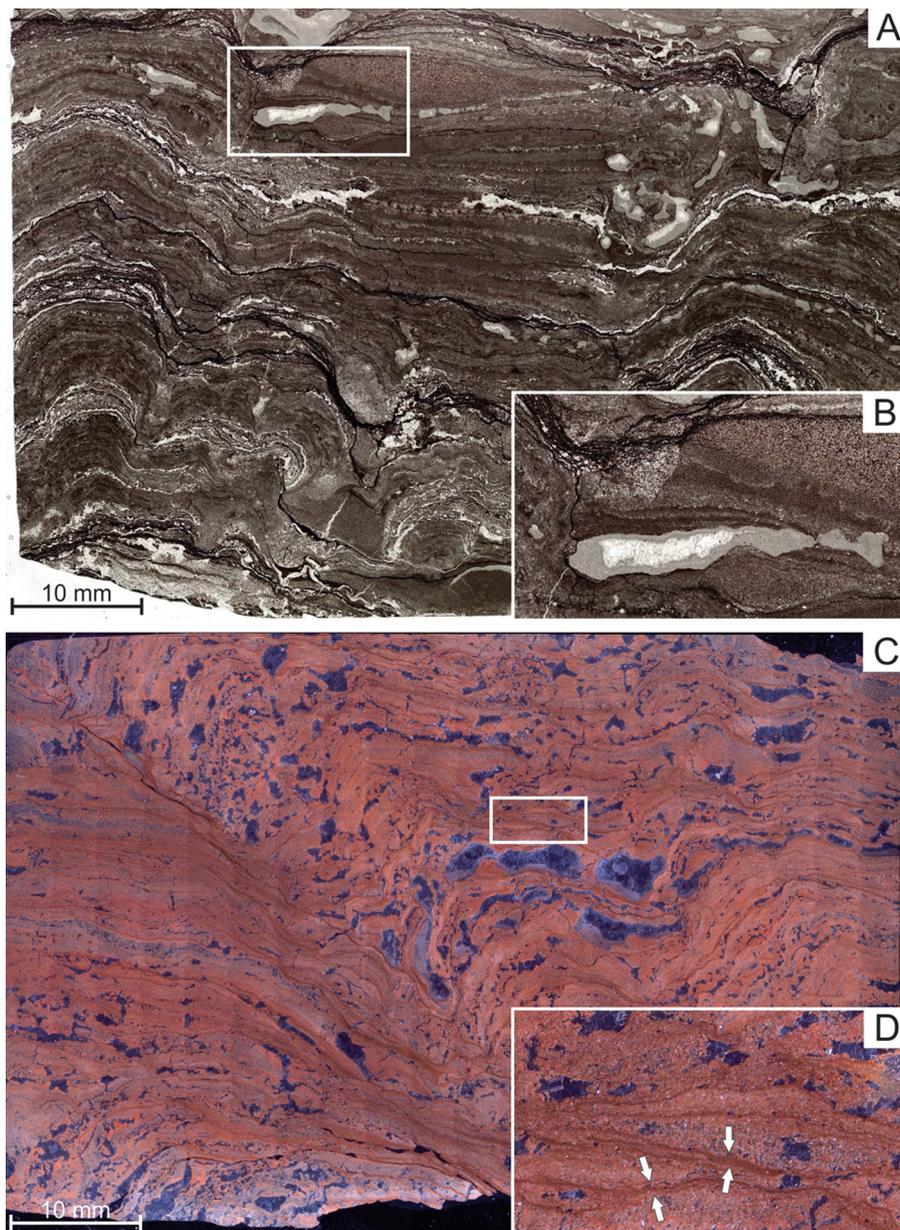


Fig. 7. Thin section photomosaics of Horseshoe Harbor-type stromatolite microfabrics. (A) Wavy and crinkled laminae and thin opaque laminae under plane polarized light. (B) Calcite filled fenestrae with two cement phases. (C) Photomosaic taken under reflected light showing abundance of hematite that gives orange-red color. (D) Opaque laminae under plane polarized light appear dark red and hematite-rich under reflected light (white arrows).

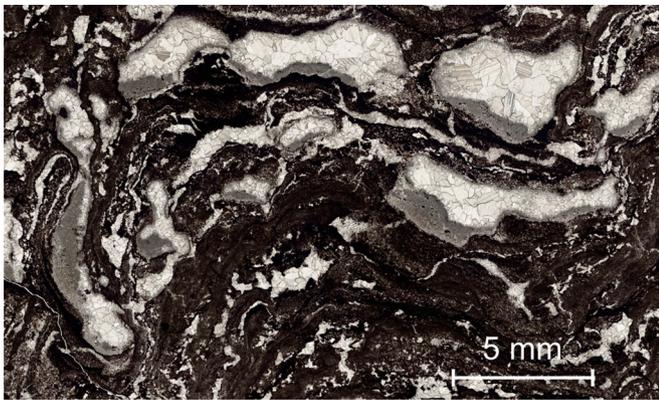


Fig. 8. Thin section photomosaic of fenestral fabrics within Horseshoe Harbor-type stromatolite. Micrite geopetals and two phases of inward-growing calcite cement are observed within fenestrae.

of underlying and overlying laminations. They occasionally have spherical and subspherical morphologies but mostly consist of irregular branching shapes. The fenestrae are filled with grey colored micrite that coats the rims of the voids. The micrite may represent calcite nucleation around microbes that lined the fenestrae. The micrite accumulations also act as geopetals, in which they are thickest on the bottom of the fenestrae, perhaps due to internal sediment or decayed organic material settling to the bottom of the void (Fig. 8). The fenestrae are also filled with two calcite cement phases (Fig. 8). The micrite coatings are overlain by a rim of dogtooth cement. This cement consists of elongated (<200 μm long) scalenohedral and rhombohedral crystals that grow normal to the surface they coat and extend towards the center of the fenestrae. The dogtooth cement is then overlain by drusy cement that is comprised of elongated subhedral crystals $\sim 200 \mu\text{m}$ to 1.3 mm in diameter. The size of the crystals increases towards the center of the void. The fact that the cements grow inwards (elongated in the direction of growth) from all directions, with crystals increasing in size towards the center of the void, suggests that the sediment overlying the fenestrae must have been present before the calcite grew inwards and that the void existed prior to lithification. Nishioka et al. (1984) reported putative algal filaments within the void spaces that they described as branching and tubular in morphology. We did not observe direct evidence for microfossils within the stromatolites from Horseshoe Harbor.

5.2.2. Dan's Point stromatolites

The stromatolites from Dan's Point have some distinctly different microfabrics than those at Horseshoe Harbor. The stromatolites drape over conglomerate beds that contain ooids, oncoids or large clasts. Ooids and oncoids are often incorporated into the stromatolite laminae or are located in between individual stromatolite columns. The stromatolites themselves are either small domes or branching columns (e.g. Hofmann, 1969) that have collectively been described as microstromatolites (e.g. Raaben, 2006) or microdigitate stromatolites (e.g. Grotzinger, 1989; Knoll and Semikhatov, 1998; Petryshyn and Corsetti, 2011; Riding, 2008). The laminations of these stromatolites alternate between radial-fibrous and non-radial fibrous laminae (Fig. 9) so that they appear similar to hybrid sparry fine-grained crusts described by Riding (2008). Individual stromatolite domes and columns range from 2 mm to 3 cm in width (Fig. 10a and b). The laminae are isopachous, between 20 and 200 μm thick, and sometimes alternate between dark and light. The dark laminae are comprised of clotted micrite while the light laminae are mostly comprised of microspar. Very fine sand, silt and clay sized detritus is dispersed evenly across both light and dark laminae. Trapped grains are observed on the high angle sides

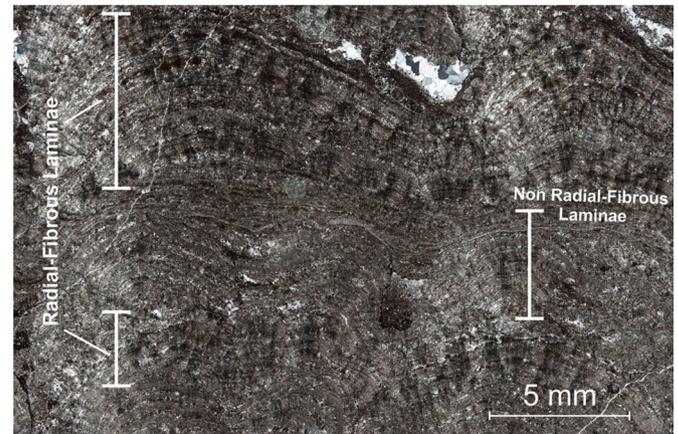


Fig. 9. Thin section photomosaic of Dan's Point-type stromatolite with alternating radial-fibrous and non radial-fibrous laminae.

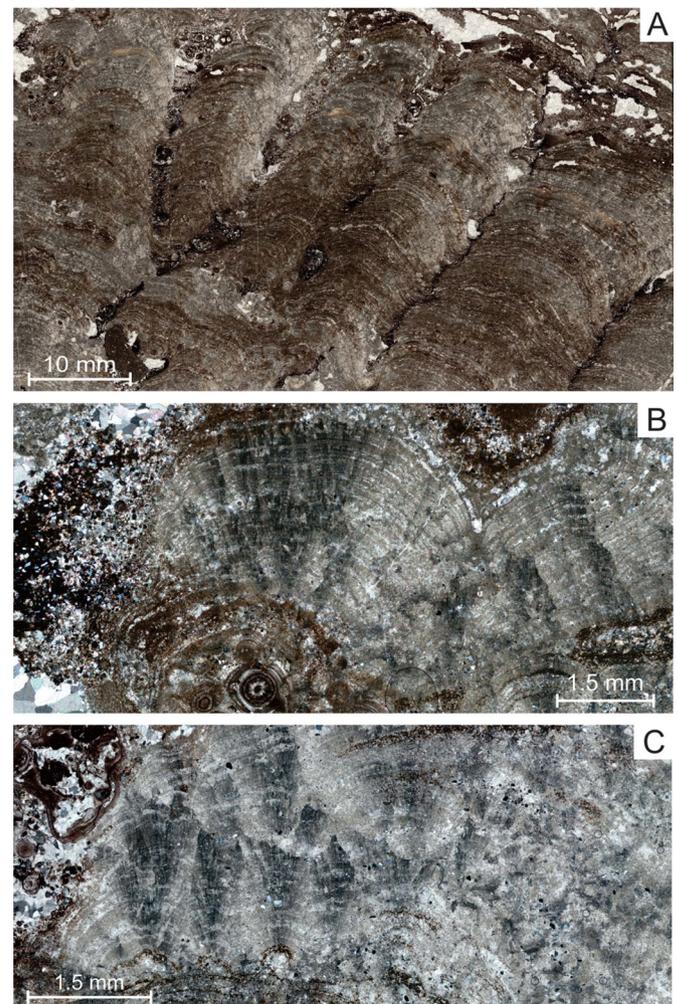


Fig. 10. Thin section photomosaics of Dan's Point-type stromatolite microfabrics. (A) Microdigitate stromatolites which consists of individual small columns. (B) Stromatolite domes under cross-polarized light exhibiting interference growth with radial fibrous calcite fans superimposed across laminae. (C) Radial-fibrous botryoids with discontinuity surfaces under cross-polarized light within Dan's Point-type stromatolite.

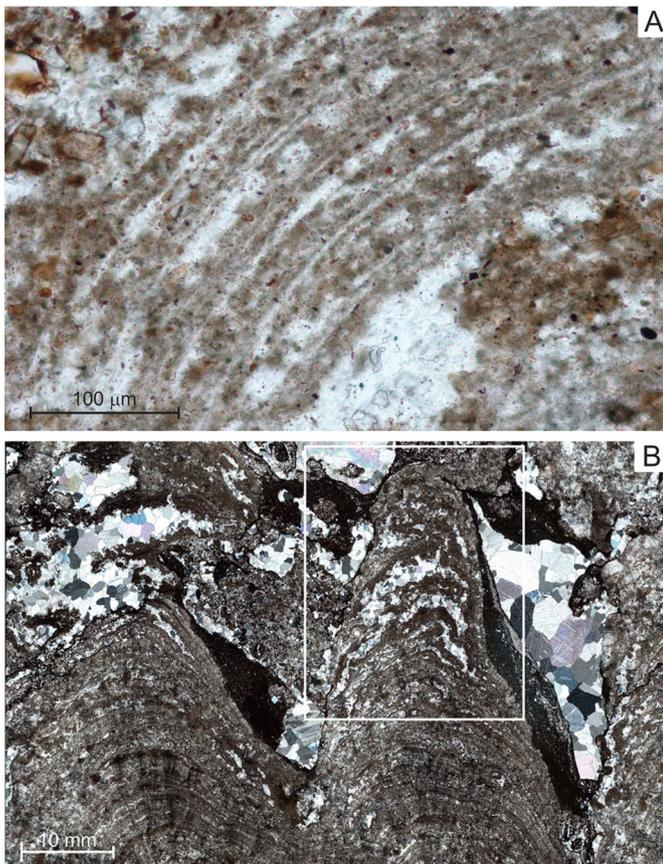


Fig. 11. Thin section photomosaics of Dan's Point-type stromatolite microfabrics. (A) Detrital grains trapped within laminae on high angle sides of individual stromatolite dome. (B) Mixed biogenicity stromatolite dome under cross-polarized light. Note transition from isopachous laminae with radial fibrous fans at base to conical morphology with wavy laminae separated by fenestrae at top (within boxed area).

of some stromatolite domes or columns (Fig. 11a). The light laminae observed here contain more microspar and have significantly less detrital material than the light laminae in stromatolites from Horseshoe Harbor, which have laminae composed almost entirely of detrital grains. The dark micritic laminae at Dan's Point have a similar clotted, hematite-rich texture to the dark laminae at Horseshoe Harbor. However, most of the dark laminae at Dan's Point are not wavy and crinkled like those at Horseshoe Harbor.

Radial-fibrous calcite fans (typically <1 mm wide) are superimposed across multiple isopachous laminae and oriented perpendicular to the laminae in the stromatolites from Dan's Point (Fig. 10b). These fans consist of needle-like individual crystals that are ~1–2 mm in length and ~20 μm in width. The crystals have clear terminations and exhibit sweeping extinction under crossed polars. Radial-fibrous botryoids (~1–2 mm in length and width) (Fig. 10c) also have needle-like individual crystals with sweeping extinction and appear similar to the radial-fibrous fans. However, they can be distinguished from the radial-fibrous fans because they are typically larger, they consist of both individual and coalescent dome-shaped hemispheroids, and they are sometimes separated by discontinuity surfaces. In contrast, the fans are smaller, do not have discontinuity surfaces and only occur superimposed across isopachous laminae. The radial-fibrous fans and botryoids sometimes occur within discrete intervals of stromatolite columns (Fig. 9) but also constitute the primary fabric of other columns or domes (Figs. 10b and c). The columns or domes comprised of radial-fibrous fans and botryoids exhibit interference growth in which they grow into each other but do not join together and become laterally linked

so that laminae cannot be traced from one stromatolite to the adjoining stromatolite (Fig. 10c).

Towards the top of some stromatolite columns, the laminae transition from sparry and isopachous with calcite fans to more micritic, wavy, and variable in thickness. Individual stromatolite columns decrease in width, laminae in the apical zone thicken, and the columns have flanks over-steepened in excess of 80° relative to the surface they nucleate on (Fig. 11b). Even within these over-steepened flanks, detrital grains can be observed trapped in both the light and dark laminae. These small stromatolites contain irregular-shaped spar-filled fenestrae (>3 mm) that follow the orientation of overlying and underlying laminae but appear thickest at the crest. The dark micrite laminae also thicken at the apical zone where they are cross-cut by the fenestrae. The fenestrae contain two calcite cement phases (drusy and dogtooth) that grow inwards towards the center of the void, just like those within the stromatolites from Horseshoe Harbor. These small (mm scale) stromatolites appear similar to those described by Bosak et al. (2009, 2012, 2013) as coniform, in which the fenestral fabrics are attributed to gas bubbles.

5.3. Growth angle analysis

Using the methodology described in Fig. 2, the growth angles of individual stromatolite columns (2 mm to 3 cm wide) were measured from the points of nucleation to the crests of the columns. For the growth angle analysis, 46 cobble-draping stromatolite samples from Dan's Point were binned according to three groups (0–20°, 20–50° and 50–90°) based on the inclination of the surface they grew on. Nineteen samples were analyzed that grew on an initial inclination between 0 and 20°. These samples had a mean growth direction of 87.9° with a standard deviation (2σ) of $\pm 14.5^\circ$ (Fig. 12). Eighteen samples were measured that initiated on surfaces inclined between 20 and 50°. Samples in this bin exhibited a mean growth direction of $87.8 \pm 8.1^\circ$. Nine samples were measured that nucleated on substrates with an inclination between 50 and 90°. These yielded a mean growth direction of $86.7 \pm 11.4^\circ$. Finally, a total growth angle analysis of all 46 samples yielded a mean growth direction of $87.6 \pm 11.5^\circ$ (Fig. 12).

6. Discussion

6.1. Depositional setting of stromatolites

The alteration between grain-support and matrix-support conglomerates indicates shifts between fluvial, sheet flow, and mass-gravity flow deposition on an alluvial fan. The massive, matrix-supported beds are the result of mass-gravity flows. The grain-supported conglomerate beds often contain crudely graded beds that fine upward, indicating waning flow during channelized and sheet-flow sedimentation. Mass-gravity flow conglomerate beds that are matrix supported are commonly seen on alluvial fans that lack vegetation, dip steeply, and have subaqueous terminations (e.g. Bull, 1977; Nemeč and Steel, 1984). The siltstone facies is both overlain and underlain by the conglomerate facies. It is interpreted as a mudflat or sandflat setting located along the margin of Lake Nonesuch.

At both localities, the Copper Harbor Conglomerate stromatolites occur on the top of the conglomerate facies, overlain by siltstone, or within the siltstone facies itself. This suggests that the stromatolites formed along the lake margin during times when subsidence outpaced sedimentation and/or the water level was elevated in the rift basin. This study does not rule out Elmore's (1983) suggestion that wetter conditions in the rift basin may have

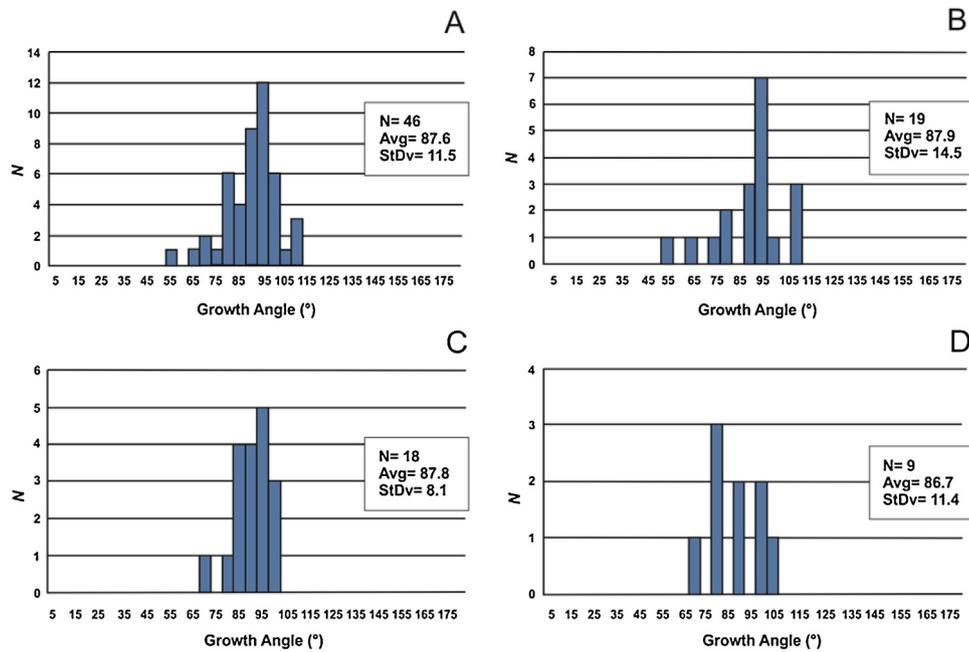


Fig. 12. Distribution of total stromatolite growth angles grouped according to angle of accretion surface. (A) Growth angle distribution of all stromatolite samples analyzed. (B) Growth angle distribution of stromatolites nucleated on surfaces inclined between 0 and 20°. (C) Growth angle distribution of stromatolites nucleated on surfaces inclined between 20 and 50°. (D) Growth angle distribution of stromatolites nucleated on surfaces inclined between 50 and 90°.

elevated the water table at times when the stromatolites were being formed.

The Horseshoe Harbor stromatolites likely formed on a shallow mudflat or sandflat. The stromatolites grew over an erosive topography underlain by calcite filled desiccation cracks, giving them a contorted appearance. They contain siltstone rip-up clasts trapped within their laminae and there are rip-up clasts of stromatolite laminae in the overlying siltstone beds. This suggests that erosion of the substrate was ongoing as the stromatolites formed. Additionally, rain drop impressions reported by Elmore (1983), bidirectional wave ripples, and calcite-filled cracks within the siltstone beds imply that these stromatolites were formed in a shallow desiccating setting. Although rare, Precambrian non-marine stromatolites have been reported from similar shallow desiccating lacustrine environments (e.g. Awramik and Buchheim, 2009; Buck, 1980).

In contrast, we hypothesize that the Dan's Point cobble-draping stromatolites formed on a shallow flooded braidplain where the lake had transgressed over a back-stepping fan lobe. Elmore (1983) thought that the cobble-draping stromatolites likely formed in abandoned fluvial channels that were re-flooded seasonally. Similar living stromatolites have been shown to form in the evaporative ephemeral streams of Anza-Borrego Desert State Park (Buchheim, 1995). However, we do not see evidence of the stromatolites forming within channel bodies. The stromatolite beds at both localities appear as laterally continuous carbonate beds whereas the channels located within the conglomerate facies are seen as lenticular sand and gravel bodies that range from 2 to 15 m in width. The presence of ooids, oncoids, and coated grains suggests a setting that would require substantial wave activity, which would not exist in small abandoned channels. Finally, the lack of significant detrital laminae within the stromatolite bed from Dan's Point indicates an extended period with low sedimentation rates. Based on this evidence, the cobble-draping stromatolites likely formed along the shallow shoreline of the lake itself. One hypothesis, similar to those of Elmore (1983), is that the flooded braidplain setting may have contained isolated pools along the shoreline that were periodically re-filled. This setting would have restricted circulation and increased alkalinity, contributing to the growth of the

cobble-draping stromatolites over top of the ooid and oncoid-rich conglomerate bed. Buck (1980) describes Precambrian stromatolites from a similar fluvial-lacustrine setting and interprets them as having formed in pools on an alluvial plain during intervals between major fluvial discharges. A modern analog for stromatolites forming in this setting is an arid, high-altitude saline lake in Argentina (Gomez et al., 2014). The mixing of hypersaline lake water and more dilute groundwater in pools along the lake margin was cited as a critical variable in forming these strikingly similar living stromatolites (Gomez et al., 2014).

6.2. Stromatolite biogenicity

6.2.1. Horseshoe Harbor stromatolites

The Horseshoe Harbor stromatolites are interpreted to have formed on a shallow, desiccating mudflat or sandflat. The microfabrics of the Horseshoe Harbor stromatolites strongly suggest a biogenic origin. Alternating layers of micrite, microspar, and detrital material is consistent with trapping and binding activity by microbes in a mudflat or sandflat setting that experienced episodic deposition. Some of the fenestrae within these stromatolites follow the overlying and underlying laminae, contain micrite geopetal fills, and have inward growing calcite cement fill. This demonstrates that the fenestral fabrics are primary and that they existed prior to lithification. Fenestral fabrics that occur elongated along stromatolite laminations have been interpreted as the result of desiccation that shrinks and lifts microbial mats along laminae, producing primary voids (e.g. Davies, 1970; Hardie and Ginsburg, 1977; Logan et al., 1974). Along with the siltstone rip-up clasts incorporated into the laminae and the rip-up clasts of stromatolite laminae in the overlying siltstone, this is congruent with a microbial mat that experienced repeated subaerial exposure. Primary fenestrae are also consistent with gas (CO, CO₂, H₂, H₂S, CH₄) build-up due to the decomposition of organic material within a microbial mat (e.g. Gerdes, 2007; Gerdes et al., 2000; Schieber et al., 2007; Shin, 1968). Additionally, millimeter scale, oxygen-rich bubbles produced during photosynthesis have been shown in laboratory experiments to exist for weeks within a mat before their shape is preserved

by early lithification of stromatolite laminae (Bosak et al., 2010). The spherical and subspherical morphologies of some fenestrae, as well as the fact that many do not extend horizontally along laminae, suggests that desiccation is not responsible for creating all of the fenestrae observed. Thus, it seems likely that some fenestrae are the products of gas bubbles within a microbial mat. A shallow flooded mudflat or sandflat setting that experienced frequent sub-aerial exposure offers ideal conditions for the formation of complex layered microbial mats such as those preserved in the Horseshoe Harbor locality.

6.2.2. Dan's Point stromatolites

The stromatolites from Dan's Point are interpreted to have formed in a flooded braidplain or fan delta setting through a mix of both microbial and abiogenic chemical processes. The stromatolites have a microdigitate morphology which is commonly associated with abiotic carbonate crusts that form from direct precipitation at the sediment-water interface (e.g. Bartley et al., 2000; Knoll and Semikhatov, 1998; Pope and Grotzinger, 2000; Riding, 2008). The small columnar and domal stromatolites do not have laminae comprised of predominately detrital clastic grains as would be found in a stromatolites (like those from Horseshoe Harbor) formed by trapping and binding. Instead, they have isopachous laminae with radial-fibrous calcite fans and botryoids, which are all considered to be strong indicators of abiogenic chemical precipitation (e.g. Bartley et al., 2000; Kah and Knoll, 1996; Grotzinger and Knoll, 1999). The regularity and high degree of inheritance observed in isopachous laminae suggest that microbes are not controlling crystal nucleation and growth (e.g. Gomez et al., 2014; Knoll and Semikhatov, 1998; Pope et al., 2000). Similar isopachous laminae with radial-fibrous fans superimposed across them have been described as amalgamated precipitate layers or sparry crusts (e.g. Knoll and Semikhatov, 1998; Riding, 2008). The individual stromatolites columns and domes also show evidence of interference growth in which they grow into each other but do not become laterally linked as is common in microbial mat growth (Corsetti and Storie-Lombardi, 2003; Grotzinger and Knoll, 1999).

These cobble and boulder draping stromatolites also demonstrate surface-normal growth and they lack evidence of a phototropic response to incident light as suggested by Nordeng (1963). Stromatolites on the tops of cobbles are not inclined towards $\sim 23^\circ$ as would be expected based on their paleolatitude if a phototrophic response existed. Surface-normal growth is commonly associated with in situ mineral precipitation and abiogenic structures (e.g. Pope et al., 2000; Pope and Grotzinger, 2000). However, it may simply imply that sunlight was abundant in a shallow reflective setting or that space was a greater limiting factor in determining stromatolite growth direction than sunlight. It may also indicate that the stromatolites were dominated by heterotrophic microbial communities instead of photosynthetic cyanobacteria. However, this growth angle data combined with the microfabric evidence makes a strong argument that growth was driven, at least in large part, by abiogenic chemical processes.

There is also evidence that there was a microbial component in the formation of the Dan's Point stromatolites. Some of the stromatolite columns and domes show a transition from isopachous laminae with radial-fibrous fans to cone-shaped morphologies with wavy micritic laminae and trapped grains, which are common features of biogenic structures (e.g. Bosak et al., 2009; Petroff et al., 2010). The micritic laminae of these structures thicken in the apical zone, a feature suggestive of biogenicity in conical stromatolites where the crests grew faster than the flanks due to preferential photosynthesis (e.g. Batchelor et al., 2004). Grains trapped along the flanks at angles greater than 80° relative to the nucleation surface also implies that trapping and binding of grains by microbes helped create these laminae. Fenestrae between laminae in these cones

contain calcite cements that grow inwards towards the center of the voids, implying that the voids are primary features. Fenestrae are also thickest at the apex of the structure where they cross-cut the micritic laminae, leaving them with a contorted appearance. These fenestrae are similar features to lift-off structures described by Bosak et al. (2009) that formed when gas builds up within the crest of conical stromatolites, lifting and breaking through the overlying laminae. The cross-cutting fenestrae observed here are also consistent with small diapirs described by Bosak et al. (2009) that formed where gas built up enough pressure to pierce the overlying laminae. Like the fenestrae from Horseshoe Harbor, the gas responsible for their formation could have originated from mat decay or photosynthesis (e.g. Gerdes, 2007; Gerdes et al., 2000; Bosak et al., 2010; Schieber et al., 2007).

It is not uncommon for microbial communities to colonize abiogenic stromatolites. Allwood et al. (2009) describe Archean stromatolites from Western Australia that have similar laminae characteristic of both biogenic and abiogenic growth. More similar to the Copper Harbor Conglomerate stromatolites, Frantz et al. (2014) report lacustrine stromatolites from the Eocene Green River Formation that alternate between a biogenic micritic fabric and abiogenic sparry calcite fans and correlate the alternation to changes in lake level/chemistry. They relate the changes between microbial dominated growth and in situ abiogenic precipitation to shifting environmental conditions. Additionally, examples of similar living stromatolites have been described from Anza-Borrego Desert State Park in California and a high-altitude saline lake in Argentina (Buchheim, 1995; Gomez et al., 2014). Stromatolites in both studies have a similar microdigitate cobble-draping morphology. These stromatolites formed in similar terrestrial depositional settings and under similar arid conditions to the Copper Harbor stromatolites. They have alternating detrital/micritic and sparry laminae (with radial-fibrous fans and botryoids) which the authors relate to changing environmental conditions (i.e. hydrologic conditions, temperature, and saturation with respect to carbonate minerals) under a consistent microbial presence (Buchheim, 1995; Gomez et al., 2014). The Dan's Point stromatolites apparently formed through a combination of chemical precipitation and microbially influenced growth in a shallow and possibly more restricted setting than those at Horseshoe Harbor.

7. Implications for early non-marine life

The Copper Harbor Conglomerate stromatolites provide evidence of microbes stabilizing an erosive, frequently subaerially exposed, substrate along the margin of an ancient rift lake. Precambrian non-marine stromatolites or MISS have been described from similar shallow depositional environments (e.g. Awramik and Buchheim, 2009; Buck, 1980; Prave, 2002) but the abundance of sedimentologic evidence (i.e. bidirectional wave ripples, rip-up clasts of stromatolites laminae, rip-up clasts within stromatolites, rain-drop impressions, mud cracks) for a shallow desiccating environment is rare. There is evidence of life in paleokarst or paleosols during the Precambrian (e.g. Horodyski and Knauth, 1994; Watanabe et al., 2000) but it remains difficult to prove that subaerial life was extensive and long-lived on the Precambrian landscape. This study supports the suggestion that that microbial life was well-suited to handling desiccating environments and exposure to UV radiation in shallow non-marine setting. This may also support models demonstrating that DNA-weighted UV irradiance had decreased to levels similar to the present day by the beginning of the Proterozoic (Cockell and Horneck, 2001). The alteration between in situ chemical-dominant growth and more microbially mediated growth within the stromatolites from Dan's Point may also imply that these microbes could adapt to frequent changes in

alkalinity, often forming in conjunction with abiotic structures. In the case of the Copper Harbor Conglomerate stromatolites, there are distinctly different stromatolite morphologies and microfabrics between Dan's Point and Horseshoe Harbor even though these two localities are established to be from roughly the same time and similar depositional settings. This implies that the different characteristics of these particular stromatolites were likely the result of variable environmental conditions (i.e. possibly a restrictive setting or groundwater mixing). These conditions likely influenced their formation directly as well as indirectly by controlling the microbial communities responsible for their formation.

8. Conclusions

The Copper Harbor Conglomerate stromatolites provide insight into the interactions between microbes and their environments as well as the nature of non-marine microbial life during the Precambrian. They also fit within a broader story of Proterozoic microbial life in the Midcontinent Rift System (e.g. Mitchell and Sheldon, 2009, 2010; Sheldon, 2012; Wellman and Strother, 2015; Wilmeth et al., 2014). The results suggest that the stromatolites formed in two different terrestrial environments. A siltstone facies corresponds to a shallow mudflat or sandflat that experienced subaerial exposure and flooding. The conglomerate facies represents a shallow flooded braidplain with conditions that sometimes favored inorganic carbonate precipitation. Stromatolite bed geometries, an elevated water level, and interpretations of wave energy all suggest that both of these environments occurred along the shoreline of an ancient rift lake.

Stromatolites from the Horseshoe Harbor locality have characteristics of microbial mats that stabilized an erosive substrate, providing evidence for microbial life in a shallow and frequently subaerially exposed setting. These stromatolites contain fenestral fabrics that may be indicative of desiccation and gas bubbles from photosynthesis or mat decay. The laminae of these stromatolites were formed by the trapping and binding of sediment during episodic sedimentation and the precipitation of calcite, either chemically or biologically derived.

The stromatolites from Dan's Point are different from those at Horseshoe Harbor. The microfabrics and growth angles suggest that abiogenic chemical growth was an important factor in the formative architecture of these stromatolites. This may be related to these stromatolites forming in a setting more saturated with respect to calcium carbonate compared to that in which the Horseshoe Harbor stromatolites formed. Most of the laminae in these stromatolites are not comprised of detrital grains. This suggests that the Dan's Point stromatolites did not form primarily from the trapping and binding of episodic sedimentation. There is some evidence that the growth of these stromatolites was occasionally influenced by microbial activity and that these microbial communities may have been episodically responsible for controlling growth patterns.

The fact that the same fluvial-lacustrine depositional environment facilitated the growth of distinctly different types of stromatolites has implications for understanding the controls on stromatolite biogenicity during the Precambrian. The Copper Harbor Conglomerate stromatolites illustrate how minor environmental influences may favor either biogenic or abiogenic growth, even with a consistent microbial presence and a similar depositional setting. This study demonstrates the utility of examining the Copper Harbor stromatolites for improved understanding of early life in non-marine settings.

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