Environmental Covariation of Metazoans and Microbialites in the Lower Ordovician Boat Harbour Formation, Newfoundland

Citation

Pruss, Sara B., and Andrew H. Knoll. 2017. Environmental Covariation of Metazoans and Microbialites in the Lower Ordovician Boat Harbour Formation, Newfoundland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 485 (November): 917-929.

Permanent link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:41291562>

Terms of Use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Open Access Policy Articles, as set forth at <http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#OAP>

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. [Submit a story](#).

[Accessibility](#)

1 Environmental Covariation of Metazoans and Microbialites
2 in the Lower Ordovician Boat Harbour Formation,
3 Newfoundland
4

5 Sara B. Pruss^{a,*} and Andrew H. Knoll^b

6 ^aDepartment of Geosciences, Smith College, Northampton, Massachusetts 01063, USA,

7 ^bDepartment of Organismic and Evolutionary Biology, Harvard University, Cambridge,
8 MA 02138, USA
9

10

11

12

13

14

15

16

17 *Corresponding author. Tel.: +1 413 585 3948

18 *Email Address: spruss@smith.edu*

ABSTRACT

An antagonistic view of the relationship between microbialites and metazoans has long been inferred, in part because of the large scale anticorrelation of these two groups through geologic time. The nexus of this relationship occurs in the Early Paleozoic Era: stromatolites declined in abundance as complex animals and algae diversified, but thrombolites, a type of microbialite little known before the Proterozoic-Cambrian boundary, proliferated for the first time. Well-preserved parasequences in the basal portion of the Lower Ordovician Boat Harbour Formation, western Newfoundland, contain a succession of stromatolites and thrombolites that permit an investigation into the role metazoans played in shaping the nature and abundance of microbialites in Early Paleozoic carbonate seas. Sessile benthic animals colonized thrombolite surfaces, but are nearly absent from stromatolites. Bioturbation rarely co-occurred with microbialites, but is widespread in clastic carbonates that lack microbialites. Our results, thus, support the hypothesis of ecological antagonism between microbial communities and motile benthic animals, but also demonstrate biological facilitation between thrombolites and both sessile benthic animals and nekton.

1. Introduction

Conventionally, the geologic record of carbonate rocks is parsed into a long pre-Cambrian interval rich in microbialites but lacking mineralized skeletons followed by a shorter Phanerozoic period in which skeletons dominate carbonate deposition (e.g., Zeebe and Westbroek, 2003). While this view is broadly correct, Ediacaran to Lower Ordovician carbonates show that the boundary between the two states was a corridor and not a door. Mineralized skeletons first appear during the last eight to nine million years of the Ediacaran Period (Grotzinger et al., 2005), but while skeletons are apparent in most Cambrian and Lower Ordovician carbonate successions, they commonly make only a limited contribution to carbonate sedimentation (Pruss et al., 2010; Pruss et al., 2012; Creveling et al., 2013). In contrast, while tabulations of stromatolite diversity suggest that these structures diminished in importance from the Proterozoic to the Phanerozoic (e.g. Awramik, 1971, 1992; Walter and Heys, 1985; Semikhatov and Raaben, 1996), microbialites are conspicuous features of Cambrian and Lower Ordovician sections worldwide (e.g. Riding, 2005; Peters et al., 2017). A unique aspect of Cambro-Ordovician microbialites is the abundance of thrombolites, microbial structures characterized by clotted rather than laminated textures (Aitken, 1967; Kennard and James, 1986). With limited exceptions (e.g., Aitken and Narbonne, 1989; Grotzinger et al., 2000; Harwood and Sumner, 2011), thrombolites are essentially unknown from Proterozoic successions. The global expansion of thrombolites during Cambro-Ordovician time has been noted previously (e.g. Kennard and James, 1986; Riding, 2000; Rowland and Shapiro, 2002; Shapiro and Awramik, 2006) and interpreted in terms that vary from a radiation of calcified cyanobacteria (Kennard and James, 1986) and the

colonization of microbial surfaces by seaweeds (Feldmann and McKenzie, 1998) to the disruption of originally laminated structures by bioturbation or diagenesis (e.g. Chafetz, 1973; Hofmann, 1973; Walter and Heys, 1985; Tarhan et al., 2013; Bernhard et al., 2013).

Viewed broadly, the carbonate record suggests that metazoans and microbial mat communities are antagonistic, with mat colonization reduced through time by metazoan grazing and competition for space on the shallow seafloor (e.g., Awramik, 1971; Garrett, 1970). Yet, the co-occurrence of microbialites and carbonate skeletons through some fifty million years of early Paleozoic history suggests a richer array of ecological interactions. In western Newfoundland, a well-preserved Cambrian to Lower Ordovician carbonate succession contains both microbialites and animal fossils, providing an opportunity to evaluate the spatial relationships between animals and microbial communities during the time when both populated coastal oceans. In this succession, we demonstrate that while animal trace fossils and microbialites only rarely have overlapping facies distributions, supporting the hypothesis of antagonism, skeletons of benthic invertebrates commonly co-vary positively with thrombolites, indicating biological facilitation between microbial bioherms and at least some animals.

2. Geologic setting

The Cambro-Ordovician Port au Port and St. George groups of western Newfoundland crop out in the study area (Fig. 1) in several well-exposed sea-cliffs along the south-facing shore of the Port au Port Peninsula. The stratigraphy is exposed across two arms of a broad gently-dipping anticline, the axis of which runs through Marches

Point (James and Stevens, 1982; Levesque, 1977). Depositional ages are constrained primarily by means of biostratigraphy, particularly trilobite zones (Westrop, 1992); identification of the SPICE carbon isotope excursion corroborates biostratigraphic placement (Saltzman et al., 2004; Hurtgen et al., 2009). The uppermost Cambrian Series 3 and Furongian (traditionally, upper Middle and Upper Cambrian) Port au Port Group consists from stratigraphically lowest to highest of the March Point, Petit Jardin and Berry Head formations, a mixed carbonate-siliciclastic succession deposited in shallow subtidal to peritidal settings. Carbonates include abundant oolite, thin-bedded limestone with desiccation or diastasis cracks (Cowan and James, 1992), microbial limestone and dolostone, and lenses of flat-pebble conglomerate, with lesser amounts of shale and siltstone. The overlying St. George Group, deposited during Early Ordovician time, consists, from lowest to highest, of the Watts Bight, Boat Harbour, Catoche, and Aguathuna formations (e.g., Knight and James, 1987). These units are predominantly carbonate, and facies record deposition in peritidal to shallow subtidal settings. As in the underlying units, microbial build-ups are common (Knight and James, 1987; Pratt, 1980). Carbonate facies include fine-grained bioturbated limestone, mudcracked, thinly-bedded limestone and microbial laminite. Some reef complexes are large in comparison to Cambrian build ups, particularly the sponge-microbial reef at Green Head in the Watts Bight Formation (Pratt, 1980; Pratt and James, 1982). The Green Head reef represents the lowermost microbial-metazoan complex preserved in these Cambro-Ordovician strata; despite the presence of sponges, however, reef fabrics are still predominantly microbial.

The Boat Harbour Formation, exposed near Isthmus Bay, overlies the Watts Bight Formation (Knight and James, 1987), the formational contact characterized by an erosional surface (Knight et al., 2008). Boat Harbour rocks record deposition in shallow

subtidal to supratidal environments, with evidence of episodic exposure. Carbonate lithologies include micrite, calcareous siltstone, microbialite, oolite, and rare skeletal grainstone. We begin by describing a ~12 m succession of exceptionally preserved stacked parasequences about 40 meters above the the base of the Boat Harbour Formation. We focus inititally on this unit because its abundant stromatolites, thrombolites, and metazoan traces and skeletons provide a framework for exploring relationships between microbialites and animals that can then be exported to consider coeval carbonates more generally.

To complement petrographic data on three Boat Harbour microbialites, we quantified the composition of 22 additional thrombolites and stromatolites from the Furongian Cape Ann and Campbell's members of the Port au Port Formation, as well as the Jangle Member of the Series 3 (middle) Cambrian Carrara Formation exposed near Death Valley, California (Table 1; Adams and Grotzinger, 1996). Examination of thin sections in at least one area outside of Newfoundland permits some exploration of how generalizable our observations from the Port au Port and St. George groups are. Each thin section was point counted (*sensu* Flügel, 2004, Pruss and Clemente, 2011) and compared to the Boat Harbour microbialites.

3. Boat Harbour parasequences

A series of thickening-upward parasequences in the Lower Ordovician Boat Harbour Formation (Fig. 2) record repeated flooding and exposure in a clear water coastal setting. Parasequence boundaries are marked by flooding surfaces, lag deposits

and, in some cases, erosion (see Fig. 2). This thickening stack of parasequences indicates deepening during deposition, with the deepest facies near the top of the succession.

Individual parasequences show some general trends. Laminated calcilutite commonly characterizes flooding surfaces and is commonly the initial surface on which microbial mounds develop. Within the basal 4 m of this section, each microbial unit consists of domal stromatolites overlain by blunt stromatolitic columns that more or less retain the overall domical shape of the build-ups (Fig. 2, PAR 1-2). Mounds are about 10 cm thick, with a synoptic relief of no more than a few cm. Microbial units begin to increase in thickness above the 4 meter mark, even though fabrics remain similar (PAR 3-5). In these lower parasequences, stromatolitic mounds are commonly overlain by fine-grained limestones that preserve desiccation cracks. The columnar stromatolites in the upper part of build-ups are commonly brecciated, complementing desiccation cracks in documenting upward shallowing to exposure at the tops of parasequences.

Parasequences that conform to this general pattern continue to thicken upward; at 5.75 m above the base of the succession, there is a pronounced increase in both the abundance and dimensions of domal stromatolites (PAR 6). In this parasequence, microbial domes are continuous through about .7 m of strata; although synoptic relief was likely not more than 10 cm. Intraclasts occur in the troughs between domes, and the upper 10 cm of the build ups exhibit a pseudocolumnar morphology. The largest stromatolitic mounds occur at ~7.0 m, where a discontinuous series of 3-m wide mounds can be seen (PAR 8). This is also the horizon where thrombolites first occur as conspicuous components of the succession.

Within parasequence PAR 8, an increase in accommodation space is recorded in the large (meter-thick) microbial structures with synoptic relief of perhaps half a meter. In

the overlying parasequence (PAR 9), a 0.45-m thick oolitic horizon hosts large domal stromatolites; ooids surround, overlap, and occur within the laminae of the microbialites. Meter-scale thrombolite mounds cap the oolitic stromatolites. This horizon also contains the first significant contribution of bioclastic material, in beds that flank the thrombolites as well as within the thrombolite mounds themselves. Thrombolites, in turn, are overlain by ~0.5 m of intraclastic skeletal grainstone and then 2.5 m of moderately bioturbated calcisiltite (ichnofabric index of 3; Droser and Bottjer, 1986). No microbialites occur in these uppermost part of the succession.

4. Environmental distributions of microbialites and metazoans

As introduced above, small-scale sea-level changes are reflected in approximately ~12 m of shallow water carbonates that preserve abundant microbialites and sedimentary structures in the Boat Harbour Formation (Figs. 3-5). The preservation of microbial build ups within this series of well-exposed thickening upwards parasequences provides an opportunity to track how subtle changes in environment influenced microbialite form. Parasequences initially show an overall thickening, suggesting these are preserved as part of a larger transgressive sequence (Knight et al., 2008), represented in outcrop as a change in carbonates from abundant microbialites that exhibit evidence for exposure to skeletal packstones and grainstones and bioturbated limestones. The maximum depth reflected in these parasequences is likely represented by the large thrombolitic units flanked by skeletal limestones (Knight et al., 2008), which suggest local sediment starvation during sea-level rise.

4.1. *Peritidal facies*

Peritidal facies: low relief domal, columnar, and pseudocolumnar stromatolites (Fig. 3A, B) capped by desiccation cracks (Fig. 3C) and exposure surfaces are best developed in the lower parasequences (PAR 1-7 of Fig. 2). In this setting, low domal stromatolites are often the first microbial structures to accrete on calcilutite surfaces. Laminations are visible in hand sample, but are not always apparent in thin-section (Fig. 6); petrographic fabrics include peloids and renaloid-like mesoclots (Fig. 6B, C). In a few instances, wavy laminations pinch and swell laterally, suggesting microbial trapping and binding. Columnar and pseudocolumnar stromatolites (Fig. 3B, D) commonly occur at the tops of microbial mounds. Columns are internally brecciated, and the synoptic relief of individual columns is typically less than 10 cm. Columnar structure is occasionally complex, with a lower interval of irregular brecciated pseudocolumns capped by discrete, laterally linked columns. In thin section, columns exhibit a coarsely laminated peloidal fabric (Fig. 6B). In general, the spaces between columns are filled by coarse sediment, including intraclasts sourced from nearby mounds.

The microbialites are overlain by calcisiltites to lutites, with some terrigenous material and thin intraclast beds, likely representing flooding during deposition of overlying parasequences. The tops of parasequences often contain exposure surfaces marked by discontinuous silicification (Fig. 3F). Animal fossils are uncommon, but gastropods and trilobite debris occasionally occur in troughs between mounds.

4.2. *More persistently flooded platform environments*

The largest domal stromatolites in our succession occur in PAR 8-9, where they are capped by equally thick thrombolites (Fig 4A). Here, the domes reach nearly half a

meter in thickness, commonly with columns developing near their tops. The stromatolites are associated with ooid sands (Figs. 3E), with ooids commonly preserved within chert nodules in the troughs between columns. The thrombolite fabric directly overlies individual stromatolitic columns, suggesting essentially continuous deposition of this bioherm. In thin-section, oolitic stromatolites at the base of the complex exhibit a diffuse peloidal fabric with abundant recrystallized ooids preserved in some laminae. The ooids are occasionally truncated from partial dissolution (Fig. 6E); small intraclasts are also preserved between stromatolite columns.

Discrete 55 cm thick thrombolite mounds formed on top of the oolitic stromatolite horizon (Fig. 4). The thrombolites are 1 m wide and laterally continuous. In outcrop, their macrofabric consists of renaloid-like, sparry carbonate surrounded by skeletal material (Fig. 4C). Gastropods and disaggregated fossil material are preserved in the interstices of mesoclots (Fig. 6D, E). The skeletal material is coarse and is also preserved in beds that lap out against the sides of the mounds. Synoptic relief was likely about 20-50 cm. The thrombolitic fabric occurs in interstitial clasts but is generally overlain by coarse skeletal debris. The thrombolites themselves are draped by ~0.5 m of intraclastic skeletal grainstone. In thin section, thrombolite mounds contain a diffuse microbial fabric that also appears peloidal (Fig. 6D, E). Gastropods, trilobites, echinoderms, nautiloids and other fossil debris are visible in outcrop (Fig. 5A, B) and also occur within thin sections of the thrombolite mound. Samples taken from between mounds also contain fossil material, as do thrombolitic intraclasts. Skeletal material is most abundant within the thrombolite mounds and in beds flanking them (Fig 5A, B).

The uppermost portion of our Boat Harbour succession does not contain microbialites, but preserves abundant evidence of animal life. Cm-scale burrows occur

throughout the silty to fine sandy carbonates (Fig. 5C, D), and skeletons of gastropods, brachiopods, and trilobites are widely distributed (see Fig. 5A).

5. Controls on Boat Harbour microbialite distribution

In the Boat Harbour succession, then, we see a clear partitioning of microbialites among facies developed within and among parasequences. Stromatolites occur in restricted coastal facies marked by a low influx of mud and coarser clastic carbonates. Thrombolites occur in shallow subtidal facies where traction load sediments are sparse. And microbialites are absent off-shore, where bioturbated, fine-grained clastic carbonates predominate.

Parasequences generally shallow upward (Van Waggoner et al., 1988; 1990), and in Early Paleozoic microbialite-dominated successions, stromatolites tend to cap thrombolites (e.g., Kennard and James, 1986; Armella, 1994; Montanez and Osleger, 1993), although this is not always the case. Much of what we observe in the Boat Harbour succession is consistent with the expectations of upward shallowing. In parasequence PAR 9, however, thrombolites conspicuously cap stromatolites. Deepening upward parasequences have been recorded in Cambro-Ordovician carbonates (e.g., Kennard and James, 1986; Lukasik and James, 2003; Myrow et al., 2012); however, we suspect that another factor governs this pattern locally. On modern carbonate platforms, thrombotic fabrics commonly develop where seaweeds (or animals) grow on microbialite surfaces; stromatolites persist where colonization by fleshy algae or animals is inhibited (Feldmann and Mackenzie, 1998; Andres and Reid, 2006). Inhibition of colonizing benthos can reflect elevated salinity or frequent exposure -- in general, the

reasons why Cambro-Ordovician stromatolites most commonly accreted in restricted environments. Algal or animal colonization, however, can also be inhibited by physical factors, including constant scouring by ooids (for example, among the Exuma Cays in the Bahamas; McIntyre et al., 1996; Andres and Reid, 2006; Andres et al., 2009). Consistent with this hypothesis, the large subtidal stromatolites in PAR 9 developed in close association with ooids, and when ooid influx stopped, microbialite fabrics switched from lamination to thombolitic clots.

How are animals distributed along the same Boat Harbour gradient and how, in turn, does this reflect ecological relationships among microbial benthos, animals and macroalgae in Cambro-Ordovician seaways? Stromatolites accreted commonly in restricted environments along the margins of Proterozoic oceans and continued to do so through much of the Phanerozoic Eon. This pattern is consistent with antagonistic arguments about microbial mats and animals (Kepper, 1974): when and where animals were absent because of evolution (Proterozoic) or either physical or chemical environmental restriction (Phanerozoic), stromatolites accreted. In the Boat Harbour and other coeval successions, however, the reverse does not hold: the presence of animals does not neatly coincide with an absence of microbialites. In subtidal sands and muds, motile benthos is widely recorded by tracks and trails, and less so by skeletons. Such animals might have inhibited microbial mat development by disrupting sediments and grazing; however, a lack of firm substrates would also have imposed restrictions on mat development, as could persistent traction load movement. Consistent with this, in shallow environments where traction load was low, stromatolites *per se* did not form, but thombolites accreted widely. Sessile benthic animals, echinoderms locally, but sponges elsewhere (e.g., Pratt and James, 1982; Shapiro and Awramik, 2002; Lee et al., 2015;

Coulsen and Brand, 2016), colonized the hard substrates provided by accreting thrombolites. This bespeaks a more positive ecological relationship between mats and benthos – one of biological facilitation.

All thin sections, including those from the Cambrian and Ordovician of western Newfoundland and the Carrara Formation in the Death Valley region, preserve a general trend: stromatolites are more or less devoid of skeletal debris, with skeletons comprising only 4 points of the 2000 counted from stromatolitic thin sections (Fig. 7, Table 1). In contrast, thrombolites contain as much as 9% skeletal material in thin section. Furthermore, skeletons are present in 13 of the 15 thrombolitic thin sections examined. This suggests that skeletons are generally present in thrombolites but are only rarely preserved in stromatolites, corroborating outcrop level observations of Boat Harbour microbialites.

We believe that it is also important to consider a role for macroalgae in thrombolite fabric generation and invertebrate distribution. Seaweeds are not preserved within Boat Harbour carbonates, and so any discussion of their impact involves speculation. Nonetheless, there are at least three reasons for exploring the potential ecological and sedimentary importance of macroalgae along Cambro-Ordovician seacoasts. First, nektonic macroalgae are known to have existed on Cambrian and Early Ordovician seafloors (LoDuca et al., 2017). Second, a host of observations and experiments, some outlined below, document the roles played by macroalgae in the generation of thrombolitic fabrics and the distribution of reefs in modern marine environments. And third, sedimentary patterns that *are* recorded in the Boat Harbour succession are consistent with observations of macroalgae and their grazers in modern ecosystems. Thus, we believe that we ignore this fuller ecosystem framework at our peril.

On the modern Bahamian platform, clotted thrombolitic fabrics are associated with subtidal microbialites festooned with fleshy algae; algal holdfasts govern the observed discontinuous cementation pattern (Feldmann and McKenzie, 1998). Consistent with this, both sessile benthic animals (Erwin et al., 2011) and macroalgae (LoDuca et al., 2017) radiated within the same time frame that thrombolites expanded across shallow platforms. Thrombolite expansion also correlates in time with the expansion of animal bioturbation, but evidence for the disruption of hard substrates by burrowing metazoans is limited in Cambrian and Lower Ordovician carbonates (Buatois et al., 2016), and petrographic observations favor mm- to cm-scale spatial variations in precipitation as the source of thrombolitic fabric (Kennard and James, 1986). Theisen and Sumner (2016) noted the association of bioturbation with clotted diagenetic fabrics in Cambrian thrombolites from the Great Basin, but emphasized that the disrupted fabrics were themselves thrombolitic and not laminated. In general, bioturbation and other bioerosional processes can alter primary microbialite fabrics, but are not the source of them (Bernhard et al., 2013). And, importantly, the role of ooid sands in delimiting stromatolites vs. thrombolites cannot easily be ascribed to changes in seawater saturation with respect to carbonate minerals, but makes good sense in light of the colonization hypothesis. Thus, colonizing fleshy algae and invertebrates may explain both the thrombolite fabrics as well as their spatial association with sessile benthos such as stalked echinoderms.

While sessile invertebrates were present on thrombolitic surfaces, biomass was commonly low (Pruss et al., 2010; Creveling et al., 2013; Table 1). Macroalgae might have played a role here, too, by competing successfully for space on the firm thrombolite surface, thereby limiting colonization by sessile invertebrates. In ecological experiments

where boxes were placed over coral reefs to exclude macroalgal grazers, fleshy algae commonly expanded dramatically, sharply reducing benthic invertebrate populations (e.g., Lewis, 1986; Vermeij et al., 2010). Grazer evolution, then, might well have influenced the distribution of skeletal animal benthos among thrombolites. [It is possible that macroalgal grazers existed among Cambrian mollusks, but the major groups of gastropods, echinoderms, vertebrates and arthropods that dominate macroalgal herbivory in modern oceans began to diversify only during the Ordovician radiation or later (Iken, 2012; Zapata et al., 2014).]

At the same time, macroalgae would have provided a local source of nutrition for primary and secondary consumers, helping to explain the facies association between thrombolites and motile animals such as trilobites and nautiloids (Pratt and James, 1982). Elser et al. (2006) have argued that microbial mats provide a poor source of nutrition for metazoan grazers, and studies of modern environments where microbialites and animals co-occur demonstrate that grazing metazoans strongly favor macroalgae as a food source, feeding little if at all on microbial mat populations (Risworth et al., 2017).

6. Stromatolites and thrombolites in space and time

6.1. Broader distribution in Cambro-Ordovician carbonates

Microbial build ups broadly comparable to those of the Boat Harbour succession are conspicuous features of the Port au Port and St. George groups (Chow, 1985; Kennard, 1988; Kennard and James, 1986). Though common, microbial build ups are rarely >1 m in thickness, and many of the forms did not attain significant topographic relief above the seafloor.

The first conspicuous microbial build ups in Lower Ordovician strata on the Port au Port Peninsula are preserved in the Watts Bight Formation (Figs. 2, 8A), which underlies the Boat Harbour Formation. Approximately 25 meters above the base of the Watts Bight Formation, the Green Head complex is exposed (Pratt, 1980; Pratt and James, 1982). This reef consists of large coalescing thrombolitic mounds that are flanked by grainstones and preserve a complex architecture (Fig. 8A). The relationship between flanking beds and the thrombolite mounds suggests the reef may have attained meters of relief above the seafloor. Large cephalopod and gastropod fossils are preserved in the interstices of microbial mounds, and sponges possibly added to the framework of the reef (Pratt and James, 1982). This Lower Ordovician complex is laterally extensive (>10 meters) and contains relatively abundant fossil material.

In units overlying the Green Head complex, a 3 m-thick limestone unit contains alternating beds of thrombolite and grainstone (Fig. 8B). The largely dolomitized thrombolite bioherm is similar in form to *Favosamaceria cooperi* (Shapiro and Awramik, 2006), consisting of upward-oriented, occasionally anastomosing thrombolitic columns with abundant trace fossils in fine-grained limestone deposited between the columns (see Fig. 8B). Thrombolites are overlain by skeletal grainstones that contain abundant large cephalopods, and a ~0.5 m thrombolite-stromatolite bed caps this unit. Small stromatolite domes (5 cm in diameter) are exposed at the top of the section.

Much like the Boat Harbour microbial units, skeletal material is a common constituent of thrombolitic mounds in the Green Head Complex, and stromatolitic fabrics tend to dominate in areas of higher traction load sedimentation. Gastropods, cephalopods and sponges lived on or near these microbial mounds as they accreted, and some probably influenced their development. Given an increase in accommodation space, large

bioherm complexes could develop. The abundance of skeletal material in these and other thrombolitic units also suggests that the presence of grazers such as gastropods did not interfere with microbial reef development.

In underlying Cambrian units, microbial mounds are also common (see Fig. 2), and these build ups again reflect environmental influences similar to those that shaped the Boat Harbour microbialites. For instance, the Furongian Cambrian Cape Ann and Campbell's members contain abundant microbial build ups that show evidence for *in situ* precipitation of carbonate (Fig. 8C—E); a few representative samples were examined in hand sample and point counted for comparison with the Boat Harbour microbialites. The Cape Ann and Campbell's thrombolites often preserve renalcid-like fabrics in slab view and in thin section, and nearly all of them preserve skeletons (Fig. 6F). Thrombolitic cores commonly have stromatolitic caps (Kennard and James, 1986; Kennard, 1988), likely representing small-scale shallowing-upward events in subtidal settings. The thrombolitic bases formed in deeper-water settings during sediment starvation, and the stromatolitic columns followed as traction load influx increased. In thin section, trilobites and echinoderms are the most common fossil constituents (Table 1, Fig. 6F), with much rarer contributions from brachiopods and molluscs.

In thrombolites and stromatolites of the Carrara Formation, California, a similar pattern emerges. These structures are most common in the carbonate-dominated Jangle Limestone Member of the Carrara Formation, and it should be noted that although oncoid-rich beds are also common in this unit (Adams and Grotzinger, 1996), they were excluded from this analysis. Fossils are rare in hand samples and thin sections of the Carrara stromatolites. In contrast, skeletons make up as much as 16% of points counted from the thrombolites, and they are present in all but one thin section. Renalcid fabric,

though visible in hand sample, is often not well preserve in thrombolite thin sections. Again, trilobites and echinoderms make up the vast majority of the skeletal material in thrombolites (Table 1). On the whole, stromatolites are less common in this unit than thrombolites; nonetheless, skeletal material is most abundant in Carrara thrombolites (Fig. 7), similar to the microbialites of Newfoundland. Indeed, such spatial relationships among microbialites and metazoans occur widely in Cambro-Ordovician platform carbonates observed globally (e.g., Lee et al., 2015).

6.2. *Stromatolites and thrombolites in time*

In Proterozoic oceans, stromatolites accreted from restricted coastal lagoons to the base of the photic zone (Grotzinger and Knoll, 1999). Stromatolite abundance appears to have decreased somewhat in Neoproterozoic oceans, perhaps in conjunction with the expansion of eukaryotic benthos (Monty, 1973; Knoll and Swett, 1990; Grotzinger and Knoll, 1999; Peters et al., 2017), but stromatolites remained principal features of carbonate stratigraphy until the end of the eon. Beginning in the Cambrian Period, stromatolites were increasingly confined to restricted coastal environments and subtidal settings characterized by shifting sands, as observed in the Boat Harbour succession. Thrombolites, however, emerged as important features of subtidal carbonates where traction load was limited (e.g., Riding, 2000; Rowland and Shapiro, 2002; Shapiro and Awramik, 2006; Bernhard et al., 2013; Lee et al., 2015). This stratigraphic pattern has been attributed to, among other things, the Paleozoic expansion of metazoans that grazed on microbialites or competed with them for space on the shallow seafloor; the radiation of macroalgae, which colonized microbialite surfaces, governing textural signatures; changing availability of hard grounds; and changing carbonate oversaturation in coastal

oceans. Thrombolites subsequently declined in distribution during the later Ordovician, as heavily skeletonized sessile benthic invertebrates radiated across shelves and platforms (Harper, 2006).

The facies distributions of animals and microbialites in the Boat Harbour succession and elsewhere indicate that ecological relationships between Cambrian Ordovician animals and microbial mat populations were diverse. As the Cambrian dawned, stromatolites became progressively restricted to environments where animals could not gain an ecological foothold, supporting the view that animal radiation influenced the spatial distribution of microbial mats. To a significant extent, however, subtidal stromatolites were supplanted not by animal reefs or shell beds, but by thrombotic microbialites. Thus, microbial mats continued to colonize broad areas of the subtidal photic zone where traction load sedimentation was low, and these mats continued to mineralize and build relief. Moreover, these build-ups actually facilitated populations of sessile benthic invertebrates and macroalgae that depend on firm substrates.

Hardgrounds are generally uncommon in Cambrian carbonate successions (Taylor and Wilson, 2003); thus, sessile benthos that require firm substrates may have thrived on subtidal thrombotic surfaces. (In principle, stromatolite surfaces would also have provided hard substrates for colonization; however, the dearth of evidence for macrobenthos in these structures suggests that other factors – for example exposure or salinity – restricted their abundance.) In addition to colonizing thrombolites, sessile Cambrian benthos requiring firm substrates grew epifaunally on animals and on their skeletal remains (Vinn, 2017); even in muddy environments like the Burgess Shale, articulate brachiopods found firm anchorage on other organisms and shells (Topper et al.,

2017). Today, macroalgae occur abundantly in reef settings on hard substrates, particularly where grazers are limited (e.g., Lewis, 1986; Vermeij et al., 2010). Since these algae were radiating in Cambrian and Ordovician oceans, it is likely that they, too, colonized thrombolitic mounds, particularly before macroalgal grazers had attained their current ecological importance (Seilacher, 1999). Macroalgal growth, then, may have played a role in thrombolite fabric development, while providing nutrition for motile animals whose fossils indicate a preference for thrombolite environments. We note as well that meiofauna are common constituents of modern microbialites (Glud et al., 1995; Tarhan et al., 2013), although their role if any in thrombolitic fabric generation remains to be documented; small invertebrates also occur within microbial mats in restricted lagoonal and microbial marsh environments (e.g., Gomes et al., 2016).

Thrombolite abundances, morphologies, and fabrics vary in time and space within their Cambro-Ordovician acme, reflecting animal (the demise of archaeocyaths and expansion of other sponges) and algae (diversification of dasyclads) as well as changes in local physical and chemical environments (Rowland and Shapiro, 2002; Lee et al., 2015; Zhang et al., 2016; Theisen and Sumner 2016). Nonetheless, we believe that the interactions among physical environment, microbial communities, radiating animals, and macroalgae argued to govern relationships observed in Cambro-Ordovician strata of western Newfoundland have a more general application.

What factors, then, might have contributed to the later Ordovician decline in thrombolite abundance? A full discussion of biological and physical changes underpinning Ordovician animal radiation (Algeo et al., 2016), is beyond the scope of this paper, but a few comments are in order. First, a significant increase in hardground distribution (Taylor and Wilson, 2003), perhaps in tandem with expanded grazing

pressure on macroalgae by an increasingly diverse and abundant marine fauna, may well have tipped the scales in favor of sessile benthic metazoan colonization of the shallow seafloor. Wright and Cherns (2016) attribute hardground expansion to an Ordovician increase in bioturbation depth – another, albeit indirect, ecosystem influence of animals, further restricting microbial communities while facilitating the radiation of heavily skeletonized, sessile invertebrates that require such hard substrates. We note, as well, that the Ordovician radiation, an event defined by an expansion of marine macrobenthos, also included a major increase in skeletonized macroalgae (Wray, 1977), supporting the idea of increased grazer pressure.

Microbially influenced sedimentary structures continued to form in siliciclastic environments, indicating that microbial mats were not banished completely from younger coastal environments; existing data, however, do not permit estimates of commonness for such features (Davies et al., 2016). Microbialites require both mat formation and mineralization. Riding (2000, 2005) proposed that Phanerozoic microbialite abundance reflects changing levels of seawater oversaturation with respect to calcite and aragonite, a view supported by Peters et al. (2017). Declining carbonate oversaturation could, in principle, have impeded microbialite mineralization, providing a physical influence on thrombolite decline. Estimating the saturation level of ancient oceans, however, is challenging, as illustrated by a comparison of Riding and Liang (2005) with Arvidson et al. (2013): Riding and Liang (2005) proposed that Ω was extremely high in early Paleozoic oceans and then declined through the remainder of the era; in contrast, Arvidson et al. (2013), who took changing pH into account, concluded that Ω increased through the era. Importantly, neither analysis indicated a major change in carbonate saturation levels during the Cambrian and Ordovician interval in question. Nonetheless,

to the extent that $p\text{CO}_2$ declined from the Cambrian through the Ordovician (Berner and Kothavala, 2011), increasing pH (Halevy and Bachan, 2017) and decreasing temperature (Trotter et al., 2008) would have increased supersaturation with respect to carbonate minerals. According to the Neritan ocean hypothesis (Zeebe and Westbroek, 2003), CaCO_3 biomineralization by animals could have kept surface water saturation levels below the threshold required for abiotic carbonate precipitation, so the Ordovician expansion of carbonate skeletons could have had at least a small influence on surface water Ω . In any event, however, microbialite mineralization depends critically on the saturation levels of pore waters within mats, a parameter under strong control by heterotrophic metabolism (Dupraz et al., 2009). Thus, changes in seawater chemistry, either physically or biologically induced, probably played at best a subordinate role in the Ordovician decline of thrombolites. Animal competitors for space, grazers, and bioturbators are the most likely candidates for microbialite decline.

7. Conclusions

The microbial build-ups preserved in an upward thickening succession of parasequences within the Lower Ordovician Boat Harbour Formation, western Newfoundland, provide insights into the development and distribution of distinct types of microbialites and animals. Microbialite distributions reflect interactions between Early Paleozoic environments and ecology. Many of the microbialites described here exhibit fabrics consistent with *in situ* microbially-mediated precipitation of carbonate. Stromatolites in these sections are typically devoid of fossils whereas thrombolites contain relatively abundant skeletal material, reflecting both hard substrates for sessile

organisms such as eocrinoids and local sources of food provided by macroalgae that also colonized thrombolitic surfaces. Cambro-Ordovician animals do not display a uniform relationship to microbialites because animals are not structurally, functionally or ecologically monolithic. In Cambrian and Early Ordovician oceans, motile benthic organisms contributed to the environmental restriction of microbial communities, but thrombolites facilitated sessile benthos and nekton. With the expansion of hardgrounds, the increased depth and environmental amplitude of bioturbation, and the concomitant diversification of biomineralized sessile benthic animals, microbial build ups largely disappeared from open marine environments.

Acknowledgments

AHK thanks the NASA Astrobiology Institute for support of this research. SBP acknowledges the Agouron Institute for the initial funding for this project, Smith College for subsequent support, and T. McGann for thin section analyses.

References

- Adams, R. D. and Grotzinger, J. P. 1996. Lateral continuity of facies and parasequences in Middle Cambrian platform carbonates, Carrara Formation, southeastern California, USA. *Journal of Sedimentary Research*, 66:1079-1090
- Aitken, J. D. 1967. Classification and environmental significance of cryptalgal limestones and dolomites, with illustrations from the Cambrian and Ordovician of southwestern Alberta. *Journal of Sedimentary Research*, 37: 1163-1178.

- 539 Aitken, J.D. and Narbonne, G.M. 1989. Two occurrences of Precambrian thrombolites
540 from the Mackenzie Mountains, Northwestern Canada. *Palaios* 4: 384-388.
- 541 Algeo, T.J., Marenco, P.J. and Saltzman, M.R. 2016. Co-evolution of oceans, climate,
542 and the biosphere during the 'Ordovician Revolution': A review.
543 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 458: 1-11.
- 544 Armella, C. 1994. Thrombolitic-stromatolitic cycles of the Cambro-Ordovician boundary
545 sequence, Precordillera Oriental Basin, western Argentina. In: *Phanerozoic*
546 *stromatolites II*, (Eds J. Bertran-Sarfati and C. Monty), Kluwer, Netherlands: 421-
547 441.
- 548 Arvidson, R.S., Mackenzie, F.T and Guidry, M.W. 2013. Geologic history of seawater: A
549 MAGic approach to carbon chemistry and ocean ventilation. *Chemical Geology*,
550 362: 287-304.
- 551 Andres, M. S. and Reid, R. P. 2006 Growth morphologies of modern marine
552 stromatolites: A case study from Highborne Cay, Bahamas. *Sedimentary Geology*,
553 185: 319-328.
- 554 Andres, M.S., Reid, R.P. and Bowlin, A.E. 2009. Microbes versus metazoans as
555 dominant reef builders: insights from modern marine environments in the Exuma
556 Cays, Bahamas. *International Association of Sedimentologists Special*
557 *Publication*, 41: 149-165
- 558 Awramik, S.M. 1971. Precambrian columnar stromatolite diversity; Reflection of
559 metazoan appearance. *Science*, 174: 825-827.
- 560 Awramik, S.M. 1992. The history and significance of stromatolites. In: *Early Organic*
561 *Evolution*, (Eds M. Schidlowski, S. Golubic, M. M. Kimberly, D. M. McKirdy,
562 and P. A., Trudinger), Springer, Berlin, pp 435-449.

- 563 Berner, R.A. and Kothavala, Z. 2001. GEOCARB III: a revised model of atmospheric
564 CO₂ over Phanerozoic time. *American Journal of Science*, 301: 182-204
- 565 Bernhard, J. M., Edgcomb, V. P. Visscher, P. T. McIntyre-Wressniga, A. Summons, R.
566 E., Bousseind, M. L. Louis, L. and Jeglinskia, M. 2013. Insights into
567 foraminiferal influences on microfabrics of microbialites at Highborne Cay,
568 Bahamas, *Proceedings of the National Academy of Sciences, USA* 24: 9830-4.
- 569 Buatois, L. A. Mángano, M. G. Olea, R. A. Wilson, M. A. 2016. Decoupled evolution of
570 soft and hard substrate communities during the Cambrian Explosion and Great
571 Ordovician Biodiversification Event, *Proceedings of the National Academy of*
572 *Sciences, USA*, 113, 6945-6948.
- 573 Chafetz, H.S. 1973. Morphological evolution of Cambrian algal mounds in response to a
574 change in depositional environment. *Journal of Sedimentary Petrology*, 43: 435-
575 446.
- 576 Chow, N. 1985. *Sedimentology and diagenesis of Middle and Upper Cambrian platform*
577 *carbonates and silticlastics, Port au Port Peninsula, western Newfoundland.*
578 PhD, Memorial University, St. John's, 458 pp.
- 579 Conliffe, J., Azmy, K., Knight, I., and Lavoie, D., 2009. Dolomitization of the Lower
580 Ordovician Watts Bight Formation of the St. George Group, western
581 Newfoundland: evidence of hydrothermal fluid alteration, *Canadian Journal of*
582 *Earth Sciences*, 46: 246-261.
- 583 Coulsen, K. P. and Brand, L. R. 2016. Lithistid sponge microbial reef-building
584 communities construct laminated, Upper Cambrian (Furongian) 'stromatolites'.
585 *Palaios*, 31: 358-370.

- 586 Cowan, C.A. and James, N.P. 1992. Diastasis cracks: mechanically generated synaeresis-
 587 like cracks in Upper Cambrian shallow water oolite and ribbon carbonates.
 588 *Sedimentology*, 39: 1101-1118.
- 589 Creveling, J. R. Fernández-Remolar, D. Rodríguez-Martínez, M. Menéndez, S.
 590 Bergmann, K. D. Gill, B. C. Abelson, J. Amils, R. Ehlmann, B. L. García-Bellido,
 591 D. C. Grotzinger, J. P. Hallman, C. Stack, K. M. and Knoll, A. H. 2013.
 592 Geobiology of a lower Cambrian carbonate platform, Pedroche Formation, Ossa
 593 Morena Zone, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 386:
 594 459-478.
- 595 Davies, N. S. Liu, A. G. Gibling, M. R. and Miller, R. F. 2016. Resolving MISS
 596 conceptions and misconceptions: A geological approach to sedimentary surface
 597 textures generated by microbial and abiotic processes. *Earth-Science Reviews*,
 598 154: 210-246.
- 599 Dupraz, C. Reid, R. P. Braissant, O. Decho, A. W. Norman, R. S. and Visscher, P. T.
 600 2009. Processes of carbonate precipitation in modern microbial mats, *Earth-*
 601 *Science Reviews*, 96: 141-162.
- 602 Droser, M.L. and Bottjer, D.J. 1986. A semiquantitative field classification of
 603 ichnofabric. *Journal of Sedimentary Petrology*, 56: 558-559.
- 604 Elser, J.J. Elser, Watts, J., Schampell, J.H. and Framer, J. 2006. Early Cambrian food
 605 webs on a trophic knife-edge? A hypothesis and preliminary data from a modern
 606 stromatolite-based ecosystem. *Ecology Letters*, 9: 295–303
- 607 Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D. and Peterson, K.J..
 608 2011. The Cambrian conundrum: early divergence and later ecological success in
 609 the early history of animals. *Science* 334: 1091--1097.

- 610 Feldmann, M. and McKenzie, J. 1998. Stromatolite thrombolite associations in a modern
611 environment, Lee Stocking Island, Bahamas. *Palaios*, 13:201–12.
- 612 Flügel, E. 2004. Microfacies of carbonate rocks: analysis, interpretation and application.
613 Springer, New York, 976 pp.
- 614 Garrett, P. 1970. Phanerozoic stromatolites: Noncompetitive ecologic restriction by
615 grazing and burrowing animals. *Science*, 169: 171-173.
- 616 Glud, R. N. Jensen, K. Revsbech, N. P. 1995. Diffusivity in surficial sediments and
617 benthic mats determined by use of a combined N₂O-O₂ microsensor, *Geochimica
618 et Cosmochimica Acta*, 59: 231-237.
- 619 Gomes, M., Lingappa, U. Metcalfe, K. O'Reilly, S. S. Riedman, L. A. Cantine, M.
620 Ireland, B. Philips, R. Stein, N. Orzechowski, E. A. Strauss, J. V. Grotzinger, H.
621 M. Quinn, D. P. Trower, L. Fischer, W. W. Grotzinger, J. P. Knoll, A. H. and
622 Fike, D. A. 2016. Linking the modern to the ancient with a comprehensive
623 geobiological understanding of biosignature preservation in microbial mats.
624 *American Geophysical Union, Fall Meeting*: B21E-0467.
- 625 Grotzinger, J.P. and Knoll, A.H. 1999. Proterozoic stromatolites: evolutionary mileposts
626 or environmental dipsticks? *Annual Review of Earth and Planetary Science*, 27:
627 313-358
- 628 Grotzinger, J.P., Watters, W.A. and Knoll, A.H. 2000. Calcified metazoans in
629 thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia.
630 *Paleobiology*, 26: 334-359.
- 631 Grotzinger, J.P., Adams, E.W., Schröder, S., 2005. Microbial–metazoan reefs of the
632 terminal Proterozoic Nama Group (c. 550–543 Ma), Namibia, *Geological
633 Magazine*, 142: 499-517.

- 634 Halevy, I. and Bachan, A. 2017. The geologic history of seawater pH. *Science*, 355:
635 1069-1071.
- 636 Harper, D.A.T. 2006. The Ordovician biodiversification: Setting an agenda for marine
637 life. *Palaeogeography Palaeoclimatology Palaeoecology*, 232: 148-166.
- 638 Harwood, C. L., and Sumner, D. Y., 2011, Microbialites of the Neoproterozoic Beck
639 Spring Dolomite, Southern California, *Sedimentology*, 58: 1648-1673.
- 640 Hofmann, H.J. 1973. Stromatolites: characteristics and utility. *Earth Science Reviews*, 9:
641 339-373.
- 642 Hurtgen, M.T. Pruss, S.B. and Knoll, A.H. 2009. Evaluating the relationship
643 between the carbon and sulfur cycles in the later Cambrian ocean: An example
644 from the Port au Port Group, western Newfoundland, Canada. *Earth and*
645 *Planetary Science letters*, 281: 288–297.
- 646 Iken, K. 2012. Grazers on benthic seaweeds. In: *Seaweed Biology: Novel Insights into*
647 *Ecophysiology, Ecology and Utilization* (Eds. C. Wiencke and K.Bischof),
648 Springer-Verlag, Heidelberg, pp. 157-176. James, N.P. and Stevens, R.K. 1982.
649 *Anatomy and evolution of a Lower Paleozoic continental margin, western*
650 *Newfoundland*. Field Excursion Guide Book. International Association of
651 Sedimentologists, Hamilton, 75 pp.
- 652 Kennard, J.M. 1988. *The structure and origin of Cambro-Ordovician thrombolites,*
653 *western Newfoundland*. PhD, Memorial University, St. John's, 600 pp.
- 654 Kennard, J.M. and James, N.P. 1986. Thrombolites and stromatolites; two distinct types
655 of microbial structures. *Palaios*, 1: 492-503.
- 656 Kepper, J.C., 1974. Antipathetic relation between Cambrian trilobites and stromatolites.
657 *Bulletin of the American Association of Petroleum Geologists*, 58: 141–143

- 658 Knight, I. and James, N.P. 1987. The Stratigraphy of the Lower Ordovician St-George
 659 Group, Western Newfoundland - the Interaction between Eustasy and Tectonics.
 660 *Canadian Journal of Earth Sciences*, 24: 1927-1951.
- 661 Knight, I. Azmy, K. Boyce, W.D. and Lavoie, D. 2008. Tremadocian carbonate rocks of
 662 the Lower St. George Group, Port au Port Peninsula, western Newfoundland:
 663 Lithostratigraphic setting of diagenetic, isotopic, and geochemistry studies,
 664 *Current Research of Newfoundland and Labrador Department of Natural*
 665 *Resources Geological Survey*, 08-1: 115-149.
- 666 Knoll, A. H. and Swett, K. 1990. Carbonate deposition during the late Proterozoic Era: an
 667 example from Spitsbergen. *American Journal of Science*, 290A: 104-132.
- 668 Lee, J.-H. Chen, J. and Chough, S. K. 2015. The middle-late Cambrian reef transition and
 669 related geological events: A review and new view. *Earth-Science Reviews*, 145:
 670 66-84.
- 671 Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef
 672 community, *Ecological Monographs*, 56: 183-200.
- 673 Levesque, R.J. 1977. *Stratigraphy and sedimentology of Middle Cambrian to Lower*
 674 *Ordovician shallow water carbonate rocks, western Newfoundland*. Masters
 675 thesis, Memorial University, St. John, 276 pp.
- 676 LoDuca, S.T., Bykova, N., Wu, M., Xiao S. and Zhao, Y. 2017. Seaweed morphology
 677 and ecology during the great animal diversification events of the early Paleozoic:
 678 A tale of two floras, *Geobiology* 15: 588–616.
- 679 Lukasik, J. J. and James, N. P. 2003. Deepening-upward subtidal cycles, Murray Basin,
 680 south Australia, *Journal of Sedimentary Research*, 73: 653-671.

- 681 McIntyre, I. G. Reid, R. P. Steneck, R. S. 1996. Growth history of stromatolites in a
 682 Holocene fringing reef, Stocking Island, Bahamas. *Journal of Sedimentary*
 683 *Research*, 66: 231-242.
- 684 Montanez, I. P. and Osleger, D. A. 1993. Parasequence Stacking Patterns, Third-Order
 685 Accommodation Events, and Sequence Stratigraphy of Middle to Upper
 686 Cambrian Platform Carbonates, Bonanza King Formation, Southern Great Basin.
 687 In: *Carbonate Sequence Stratigraphy: Recent Developments and Applications*
 688 (Eds R. G. Loucks and J. F. Sarg), AAPG Memoir, pp. 305-326.
- 689 Monty C. L. V. 1973. Precambrian background and Phanerozoic history of stromatolitic
 690 communities, an overview. *Annales de la Société Géologique de Belgique*,
 691 96:585–624
- 692 Myrow, P. W. Taylor, J. F. Runkel, A. C. and Ripperdan, R. L. 2012. Mixed
 693 siliciclastic–carbonate upward-deepening cycles of the upper Cambrian inner
 694 detrital belt of Laurentia. *Journal of Sedimentary Research*, 82: 216-231.
- 695 Peters, S. E. Husson, J. M. and Wilcots, J. 2017. The rise and fall of stromatolites in
 696 shallow marine environments. *Geology*, doi:10.1130/G38931.1
- 697 Pratt, B.R. 1980. Algal-Metazoan Bioherms of Lower Ordovician Age - St-George
 698 Group, Western Newfoundland. *AAPG Bulletin-American Association of*
 699 *Petroleum Geologists*, 64: 767-768.
- 700 Pratt, B.R. and James, N.P. 1982. Cryptalgal-metazoan bioherms of Early Ordovician age
 701 in the St-George Group, western Newfoundland. *Sedimentology*, 29: 543-569.
- 702 Pruss, S. B., Finnegan, S., Fischer, W. W., and Knoll, A. H., 2010, Carbonates in
 703 skeleton-poor seas: New insights from Cambrian and Ordovician strata of
 704 Laurentia, *Palaaios*, 25: 73-84

- 705 Pruss, S. B., and Clemente, H., 2011. Assessing the role of skeletons in Early Paleozoic
 706 carbonate production: Insights from Cambro-Ordovician strata, western
 707 Newfoundland, *In: Quantifying the evolution of early life: Numerical and*
 708 *technological approaches to the study of fossils and ancient ecosystems*, (Eds
 709 Laflamme, M., Schiffbauer, J. D., and Dornbos, S. Q.), pp. 161-183, *Topics in*
 710 *Geobiology*, Springer, Berlin.
- 711 Pruss, S. B., Clemente, H., and Laflamme, M., 2012. Early Cambrian archaeocyathan
 712 reefs of the Forteau Formation, southern Labrador, as a locus for skeletal
 713 carbonate production, *Lethaia*, 45: 401-410.
- 714 Riding, R. 2000. Microbial carbonates; the geological record of calcified bacterial-algal
 715 mats and biofilms. *Sedimentology*, 47: 179-214.
- 716 Riding, R. 2005. Phanerozoic reefal microbial carbonate abundance: Comparisons with
 717 metazoan diversity, mass extinction events, and seawater saturation state. *Revista*
 718 *Española de Micropaleontología*, 37: 23-39.
- 719 Riding, R. and Liang, L. 2005. Geobiology of microbial carbonates: metazoan and
 720 seawater saturation state influences on secular trends during the Phanerozoic.
 721 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 219: 101-115.
- 722 Risworth, G. M. Perissinotti, R. Bird, M. S. Strydom, N. A. Peer, N. Miranda, N. A. F.
 723 Raw, J. L. 2017. Non-reliance of metazoans on stromatolite-forming microbial
 724 mats as a food resource. *Scientific Reports*, 7: 42614
- 725 Rowland, S.M. and Shapiro, R.S. 2002. Reef patterns and environmental influences in the
 726 Cambrian and earliest Ordovician. *In: Phanerozoic Reef Patterns* (Eds W.
 727 Kiessling, E. Flügel and J. Golonka). Society of Economic Paleontologists and
 728 Mineralogists Special Volume, Tulsa pp. 95-128.

- 729 Saltzman, M.R., Cowan, C.A., Runkel, A.C., Runnegar, B., Stewart, M.C. and Palmer,
 730 A.R. 2004. The Late Cambrian SPICE event and the Sauk II-Sauk III regression:
 731 New evidence from Laurentian basins in Utah, Iowa, and Newfoundland. *Journal*
 732 *of Sedimentary Research*, 74: 366-377.
- 733 Seilacher, A., 1999. Biomat-related lifestyles in the Precambrian, *Palaios*, 14: 86-93.
- 734 Semikhatov, M. A. and Raaben, M. E. 1996. Dynamics of the global diversity of
 735 Proterozoic stromatolites. Article II: Africa, Australia, North America, and
 736 general synthesis. *Stratigraphic Geologic Correlation*, 4: 26-55.
- 737 Shapiro, R.S. and Awramik, S.M. 2006. *Favosamaceria cooperi* new group and form: A
 738 widelydispersed, time-restricted thrombolite. *Journal of Paleontology*, 80: 411-
 739 422.
- 740 Shapiro, R.S. and Rigby, J.K. 2004. First occurrence of an *in situ* anthaspidellid sponge
 741 in a dendrolite mound (Upper Cambrian; Great Basin, USA). *Journal of*
 742 *Paleontology*, 78: 645-650.
- 743 Tarhan, L. G., Planavsky, N. J., Laumer, C. E., Stolz, J. F., Reid, R. P., 2013. Microbial
 744 mat controls on infaunal abundance and diversity in modern marine microbialites,
 745 *Geobiology*, 11: p. 485-497.
- 746 Taylor, P. D. and Wilson, M. A. 2003. Paleoecology and evolution of marine hard
 747 substrate communities. *Earth-Science Reviews*, 62: 1-103.
- 748 Theisen, C.H. and Sumner, D.Y. 2016. Thombolite facies and fabrics:Influences of
 749 diverse mcorbial and metazoan processes on Cambrian thrombolite variability in
 750 the Great Basin, California and Nevada. *Sedimentology* 63: 2217-2252.
- 751 Topper, T.P., Strotz, L.C., Skovsted, C.B. and Holmer, L.E. 2017. Do brachiopods show
 752 substrate-related phenotypic variation? A case study from the Burgess Shale.

- 753 *Palaeontology*, 60: 269–279.
- 754 Trotter, J.A., Williams, I.S., Barnes, C.R., Lecuyer, C. and Nicoll, R.S. 2008. Did cooling
 755 oceans trigger Ordovician biodiversification? Evidence from conodont
 756 thermometry. *Science*, 321: 550-554.
- 757 Van Wagoner J.C., Posamentier, H. W., Mitchum, R.M., Vail, P. R., Sarg, J. F., Loutit, T.
 758 S., and Hardenbol, J., 1988, An overview of the fundamentals of sequence
 759 stratigraphy and key definitions, In *Sea-Level Changes: An Integrated Approach*
 760 (eds. Wilgns, C.K. Hastings, B.S., Kendall, C.G.St.C. Posamentier, H.W. Ross,
 761 C.A., and Van Wagoner, J.C.). SEPM Special Publication 42: 9-45.
- 762 Van Wagoner J.C., Mitchum, R.M., Campion, K.M., Rahmanian V.D., 1990, Siliciclastic
 763 Sequence Stratigraphy in Well Logs, Cores and Outcrops: American Association
 764 of Petroleum Geologists, *Methods in Exploration Series 7*: 55 pp.
- 765 Vermeij, M. J. A. Mooreselaar, I., v. Engelhard, S. Hörnlein, C. Vonk, S. M. Visser, P.
 766 M. 2010. The effects of nutrient enrichment and herbivore abundance on the
 767 ability of turf algae to overgrow coral in the Caribbean. *PLoS ONE*: 5: e14312.
- 768 Vinn, O. 2017. Early symbiotic interactions in the Cambrian. *Palaaios*, 32: 213-237.
- 769 Walter, M.R. and Heys, G.R. 1985. Links between the rise of the Metazoa and the decline
 770 of stromatolites. *Precambrian Research*, 29: 149-174.
- 771 Westrop, S.R. 1992. Upper Cambrian (Marjuman-Steptoean) Trilobites from the Port Au
 772 Port Group, Western Newfoundland. *Journal of Paleontology*, 66: 228-255.
- 773 Wray J.J. 1977. Calcareous Algae. Elsevier, Amsterdam, 185 pp.
- 774 Wright, P. V. and Cherns, L. 2016. How far did feedback between biodiversity and early
 775 diagenesis affect the nature of Early Palaeozoic sea floors. 753-765.
 776 *Palaeontology*, 59: 753-765.

- Zapata, F., Wilson, N.G., Howison, M., Andrade, S.C.S., Jörger, K.M. et al. 2014.
Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda.
Proceedings of the Royal Society B 281, 20141739.
- Zhang, Y., Li, Q., Li, Y., Kiessling, W. and Wang, J. 2016. Cambrian to Lower
Ordovician reefs on the Yangtze Platform, South China, and their controlling
factors. *Facies* 62: doi: 10.1007/s10347-016-0466-8.
- Zeebe, R. E., and Westbroek, P., 2003, A simple model for the CaCO₃ saturation state of
the ocean: The "Strangelove", the "Neritan", and the "Cretan" ocean:
Geochemistry, Geophysics, Geosystems, 4: 1-26

Figures

Figure 1: Locality map showing the Port au Port Peninsula in southwestern
Newfoundland, Canada. The Boat Harbour Formation crops out along the eastern part of
the south-facing shore of the peninsula. Cambro-Ordovician strata extend along two arms
of an anticline on this southern shore, and examined sections are noted. Geologic map
modified from Conliffe et al., (2009).

Figure 2: A) Stratigraphic column of the Port au Port and St. George groups. Note
microbial build-ups in the Upper Cambrian Campbell's Member and Lower Ordovician
Watts Bight Formation. B) Detailed stratigraphy of the ~12-m succession of stacked
parasequences preserved in the Boat Harbour Formation. Basal portion of the section was
covered, and only ~2 m of the 2.5 m-thick bioturbated bed are shown at the top. Arrows
indicate thickening-upward parasequences that contain microbial build ups.

801 Figure 3: Stromatolites and associated bedding features from the Boat Harbour
 802 Formation. A) Low relief domal stromatolites in the lowermost parasequences (note
 803 hammer for scale). B) Columnar and pseduocolumnar stromatolites in peritidal facies in
 804 lower half of the section; C) Mudcracks; D) Columnar stromatolites accreting on a
 805 surface of thinly bedded micrite. Note orange pods of chert. E) Pink, lightly silicified
 806 ooids associated with stromatolites that directly underlie the thrombolite mounds; F)
 807 Chert-rich horizon marking exposure surface.

808

809 Figure 4: Boat Harbour thrombolites. A) Large domal stromatolites and overlying
 810 thrombolites of PAR 9; B) Thrombolite mound. Note discrete edges of mound and
 811 distinct renaloid fabric within mound. Lower third of photo shows oolitic stromatolites
 812 below thrombolite. Measuring tape shows 30 cm. C) Close up image of thrombolite
 813 showing clotted fabric.

814

815 Figure 5: Metazoan records in upper parasequences. A) Skeletal material in beds
 816 overlying thrombolite mounds. Gastropods and brachiopods are shown, among other
 817 invertebrate shell hash. 10 cm scale bar; B, D) Bedding plane showing *Thalassinoides*
 818 traces; gastropods visible in B. C) Bioturbated laminated beds in uppermost part of
 819 measured section. 10 cm scale bar.

820

821 Figure 6: Petrographic images of selected facies, Boat Harbour Formation (A-E) and
 822 Campbell's Member (F). A) Silicified and partially dissolved ooids from the stromatolitic
 823 horizon below the thrombolites; B) Peloidal laminations preserved in a stromatolite; C)

Clotted, renalcid fabric in a thrombolite; D) and E) Peloidal fabric and skeletal material in thrombolites; F) Echinoderm plates in a dendrolitic thrombolite.

Figure 7: Point counts of microbialites showing percent fossil material from the Cambrian Port au Port and Ordovician St. George groups, western Newfoundland, and the middle Cambrian Carrara Formation near Death Valley National Park, California. Circles indicate each slide counted, and diamonds show the average for each category.

Figure 8: Other Cambrian and Lower Ordovician microbial build ups from the Port au Port and St. George groups. A) Green Head reef complex, Lower Ordovician Watts Bight Formation; B) *Favosamaceria cooperi* from the Watts Bight Formation; C) Dendrolitic thrombolite from the Furongian (upper) Cambrian Campbells' Member; D) and E) Laterally-linked columnar stromatolites from the Campbell's Member. Scale is 15 cm in E.

Table 1: Points counted for all thin sections examined from the Cambrian Port au Port and Ordovician St. George groups, Newfoundland and middle Cambrian Carrara Formation, California. The following abbreviations are used: microbial is microbial carbonate, trilo is trilobite, brach is brachiopod, unID fossils is unidentified fossils, and echino is echinoderm.

Fig. 1

Fig. 2

A **B** **C** **D** **E** **F**

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Fig. 8

	micrite	microbial	ooid	ostracod	mollusc	trilo	brach	unID fossil	echino	other	TOTAL
NL strom CMCC-20	66	119	0	0	0	0	0	0	0	15	200
NL strom MF-41-THB	105	90	0	0	0	0	0	0	0	5	200
NL strom MF-42-TH	93	101	0	0	0	0	0	0	0	6	200
NL strom BH-MI-5	24	155	0	0	0	0	0	0	0	21	200
NL strom BH-MI-4B	43	136	0	0	0	0	0	0	0	21	200
NL strom MF-48	132	50	4	0	0	0	0	0	0	14	200
NL strom BH-120A	101	75	16	0	0	0	0	0	0	8	200
NL strom CM-30	39	123	1	0	0	0	0	0	0	37	200
NL Thromb CMCC-18	0	156	0	0	0	0	0	0	0	44	200
NL Thromb MF-41-TH	87	100	0	0	0	0	1	0	0	12	200
NL Thromb BH08-64-B2	126	58	0	0	1	0	0	0	0	15	200
NL Thromb CMCC-5	151	23	0	0	0	6	0	0	0	20	200
NL Thromb CMCC-13	126	36	4	0	0	0	0	4	14	16	200
NL Thromb CM-28-MI3	139	39	0	0	0	7	0	1	4	10	200
	106	69	0	0	0	0	0	1	0	24	200

DV strom EM01 49- 3A											
DV strom EM01 49- 3B	69	104	0	1	0	0	0	2	0	24	200
DV thromb EM01 TB-A	106	77	0	0	0	1	0	0	0	16	200
DV thromb EM01 TB-B	99	77	0	0	0	0	0	0	0	24	200
DV thromb EP01 ST-BB	63	126	0	0	0	1	0	0	0	10	200
DV thromb EP01 ST-CB	74	107	1	0	0	3	0	1	0	14	200
DV thromb EP01 ST-CD	73	101	0	0	0	1	0	0	1	24	200
DV thromb EP01 ST-AA	89	93	1	0	0	2	0	0	2	13	200
DV thromb EP01 ST-FB	78	97	0	0	0	0	0	0	1	24	200
DV thromb EP01 ST-G	100	86	0	0	0	0	0	0	2	12	200
DV thromb EP01 ST-HA	104	69	0	0	0	16	0	0	0	11	200