



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

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

4

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19 **ABSTRACT**

20

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

## 37 **1. Introduction**

38

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

61 colonization of microbial surfaces by seaweeds (Feldmann and McKenzie, 1998) to the  
62 disruption of originally laminated structures by bioturbation or diagenesis (e.g. Chafetz,  
63 1973; Hofmann, 1973; Walter and Heys, 1985; Tarhan et al., 2013; Bernhard et al.,  
64 2013).

65 Viewed broadly, the carbonate record suggests that metazoans and microbial mat  
66 communities are antagonistic, with mat colonization reduced through time by metazoan  
67 grazing and competition for space on the shallow seafloor (e.g., Awramik, 1971; Garrett,  
68 1970). Yet, the co-occurrence of microbialites and carbonate skeletons through some fifty  
69 million years of early Paleozoic history suggests a richer array of ecological interactions.  
70 In western Newfoundland, a well-preserved Cambrian to Lower Ordovician carbonate  
71 succession contains both microbialites and animal fossils, providing an opportunity to  
72 evaluate the spatial relationships between animals and microbial communities during the  
73 time when both populated coastal oceans. In this succession, we demonstrate that while  
74 animal trace fossils and microbialites only rarely have overlapping facies distributions,  
75 supporting the hypothesis of antagonism, skeletons of benthic invertebrates commonly  
76 co-vary positively with thrombolites, indicating biological facilitation between microbial  
77 bioherms and at least some animals.

78

## 79 **2. Geologic setting**

80

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

85 Point (James and Stevens, 1982; Levesque, 1977). Depositional ages are constrained  
86 primarily by means of biostratigraphy, particularly trilobite zones (Westrop, 1992);  
87 identification of the SPICE carbon isotope excursion corroborates biostratigraphic  
88 placement (Saltzman et al., 2004; Hurtgen et al., 2009). The uppermost Cambrian Series  
89 3 and Furongian (traditionally, upper Middle and Upper Cambrian) Port au Port Group  
90 consists from stratigraphically lowest to highest of the March Point, Petit Jardin and  
91 Berry Head formations, a mixed carbonate-siliciclastic succession deposited in shallow  
92 subtidal to peritidal settings. Carbonates include abundant oolite, thin-bedded limestone  
93 with desiccation or diastasis cracks (Cowan and James, 1992), microbial limestone and  
94 dolostone, and lenses of flat-pebble conglomerate, with lesser amounts of shale and  
95 siltstone. The overlying St. George Group, deposited during Early Ordovician time,  
96 consists, from lowest to highest, of the Watts Bight, Boat Harbour, Catoche, and  
97 Aguathuna formations (e.g., Knight and James, 1987). These units are predominantly  
98 carbonate, and facies record deposition in peritidal to shallow subtidal settings. As in the  
99 underlying units, microbial build-ups are common (Knight and James, 1987; Pratt, 1980).  
100 Carbonate facies include fine-grained bioturbated limestone, mudcracked, thinly-bedded  
101 limestone and microbial laminite. Some reef complexes are large in comparison to  
102 Cambrian build ups, particularly the sponge-microbial reef at Green Head in the Watts  
103 Bight Formation (Pratt, 1980; Pratt and James, 1982). The Green Head reef represents the  
104 lowermost microbial-metazoan complex preserved in these Cambro-Ordovician strata;  
105 despite the presence of sponges, however, reef fabrics are still predominantly microbial.

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

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

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

126

### 127 **3. Boat Harbour parasequences**

128

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

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

134 Individual parasequences show some general trends. Laminated calcilutite  
135 commonly characterizes flooding surfaces and is commonly the initial surface on which  
136 microbial mounds develop. Within the basal 4 m of this section, each microbial unit  
137 consists of domal stromatolites overlain by blunt stromatolitic columns that more or less  
138 retain the overall domical shape of the build-ups (Fig. 2, PAR 1-2). Mounds are about 10  
139 cm thick, with a synoptic relief of no more than a few cm. Microbial units begin to  
140 increase in thickness above the 4 meter mark, even though fabrics remain similar (PAR  
141 3-5). In these lower parasequences, stromatolitic mounds are commonly overlain by fine-  
142 grained limestones that preserve desiccation cracks. The columnar stromatolites in the  
143 upper part of build-ups are commonly brecciated, complementing desiccation cracks in  
144 documenting upward shallowing to exposure at the tops of parasequences.

145 Parasequences that conform to this general pattern continue to thicken upward; at  
146 5.75 m above the base of the succession, there is a pronounced increase in both the  
147 abundance and dimensions of domal stromatolites (PAR 6). In this parasequence,  
148 microbial domes are continuous through about .7 m of strata; although synoptic relief was  
149 likely not more than 10 cm. Intraclasts occur in the troughs between domes, and the  
150 upper 10 cm of the build ups exhibit a pseudocolumnar morphology. The largest  
151 stromatolitic mounds occur at ~7.0 m, where a discontinuous series of 3-m wide mounds  
152 can be seen (PAR 8). This is also the horizon where thrombolites first occur as  
153 conspicuous components of the succession.

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

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

164

#### 165 **4. Environmental distributions of microbialites and metazoans**

166

167 As introduced above, small-scale sea-level changes are reflected in approximately  
168 ~12 m of shallow water carbonates that preserve abundant microbialites and sedimentary  
169 structures in the Boat Harbour Formation (Figs. 3-5). The preservation of microbial build  
170 ups within this series of well-exposed thickening upwards parasequences provides an  
171 opportunity to track how subtle changes in environment influenced microbialite form.  
172 Parasequences initially show an overall thickening, suggesting these are preserved as part  
173 of a larger transgressive sequence (Knight et al., 2008), represented in outcrop as a  
174 change in carbonates from abundant microbialites that exhibit evidence for exposure to  
175 skeletal packstones and grainstones and bioturbated limestones. The maximum depth  
176 reflected in these parasequences is likely represented by the large thrombolitic units  
177 flanked by skeletal limestones (Knight et al., 2008), which suggest local sediment  
178 starvation during sea-level rise.

179

180 *4.1. Peritidal facies*

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

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

200

201 *4.2. More persistently flooded platform environments*

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

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

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

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

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

230

## 231 **5. Controls on Boat Harbour microbialite distribution**

232

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

239           Parasequences generally shallow upward (Van Waggoner et al., 1988; 1990), and  
240 in Early Paleozoic microbialite-dominated successions, stromatolites tend to cap  
241 thrombolites (e.g., Kennard and James, 1986; Armella, 1994; Montanez and Osleger,  
242 1993), although this is not always the case. Much of what we observe in the Boat  
243 Harbour succession is consistent with the expectations of upward shallowing. In  
244 parasequence PAR 9, however, thrombolites conspicuously cap stromatolites. Deepening  
245 upward parasequences have been recorded in Cambro-Ordovician carbonates (e.g.,  
246 Kennard and James, 1986; Lukasik and James, 2003; Myrow et al., 2012); however, we  
247 suspect that another factor governs this pattern locally. On modern carbonate platforms,  
248 thrombolitic fabrics commonly develop where seaweeds (or animals) grow on  
249 microbialite surfaces; stromatolites persist where colonization by fleshy algae or animals  
250 is inhibited (Feldmann and Mackenzie, 1998; Andres and Reid, 2006). Inhibition of  
251 colonizing benthos can reflect elevated salinity or frequent exposure -- in general, the

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

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

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

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

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

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

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

324 where boxes were placed over coral reefs to exclude macroalgal grazers, fleshy algae  
325 commonly expanded dramatically, sharply reducing benthic invertebrate populations  
326 (e.g., Lewis, 1986; Vermeij et al., 2010). Grazer evolution, then, might well have  
327 influenced the distribution of skeletal animal benthos among thrombolites. [It is possible  
328 that macroalgal grazers existed among Cambrian mollusks, but the major groups of  
329 gastropods, echinoderms, vertebrates and arthropods that dominate macroalgal herbivory  
330 in modern oceans began to diversify only during the Ordovician radiation or later (Iken,  
331 2012; Zapata et al., 2014).]

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

339

## 340 **6. Stromatolites and thrombolites in space and time**

341

### 342 *6.1. Broader distribution in Cambro-Ordovician carbonates*

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

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

359           In units overlying the Green Head complex, a 3 m-thick limestone unit contains  
360 alternating beds of thrombolite and grainstone (Fig. 8B). The largely dolomitized  
361 thrombolite bioherm is similar in form to *Favosamaceria cooperi* (Shapiro and Awramik,  
362 2006), consisting of upward-oriented, occasionally anastomosing thrombolitic columns  
363 with abundant trace fossils in fine-grained limestone deposited between the columns (see  
364 Fig. 8B). Thrombolites are overlain by skeletal grainstones that contain abundant large  
365 cephalopods, and a ~0.5 m thrombolite-stromatolite bed caps this unit. Small stromatolite  
366 domes (5 cm in diameter) are exposed at the top of the section.

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

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

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

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

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

403

#### 404 *6.2. Stromatolites and thrombolites in time*

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

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

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

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

444 2017). Today, macroalgae occur abundantly in reef settings on hard substrates,  
445 particularly where grazers are limited (e.g., Lewis, 1986; Vermeij et al., 2010). Since  
446 these algae were radiating in Cambrian and Ordovician oceans, it is likely that they, too,  
447 colonized thrombolitic mounds, particularly before macroalgal grazers had attained their  
448 current ecological importance (Seilacher, 1999). Macroalgal growth, then, may have  
449 played a role in thrombolite fabric development, while providing nutrition for motile  
450 animals whose fossils indicate a preference for thrombolite environments. We note as  
451 well that meiofauna are common constituents of modern microbialites (Glud et al., 1995;  
452 Tarhan et al., 2013), although their role if any in thrombolitic fabric generation remains  
453 to be documented; small invertebrates also occur within microbial mats in restricted  
454 lagoonal and microbial marsh environments (e.g., Gomes et al., 2016).

455       Thrombolite abundances, morphologies, and fabrics vary in time and space within  
456 their Cambro-Ordovician acme, reflecting animal (the demise of archaeocyaths and  
457 expansion of other sponges) and algae (diversification of dasyclads) as well as changes  
458 in local physical and chemical environments (Rowland and Shapiro, 2002; Lee et al.,  
459 2015; Zhang et al., 2016; Theisen and Sumner 2016). Nonetheless, we believe that the  
460 interactions among physical environment, microbial communities, radiating animals, and  
461 macroalgae argued to govern relationships observed in Cambro-Ordovician strata of  
462 western Newfoundland have a more general application.

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

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

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

492 to the extent that  $p\text{CO}_2$  declined from the Cambrian through the Ordovician (Berner and  
493 Kothavala, 2011), increasing pH (Halevy and Bachan, 2017) and decreasing temperature  
494 (Trotter et al., 2008) would have increased supersaturation with respect to carbonate  
495 minerals. According to the Neritan ocean hypothesis (Zeebe and Westbroek, 2003),  
496  $\text{CaCO}_3$  biomineralization by animals could have kept surface water saturation levels  
497 below the threshold required for abiotic carbonate precipitation, so the Ordovician  
498 expansion of carbonate skeletons could have had at least a small influence on surface  
499 water  $\Omega$ . In any event, however, microbialite mineralization depends critically on the  
500 saturation levels of pore waters within mats, a parameter under strong control by  
501 heterotrophic metabolism (Dupraz et al., 2009). Thus, changes in seawater chemistry,  
502 either physically or biologically induced, probably played at best a subordinate role in the  
503 Ordovician decline of thrombolites. Animal competitors for space, grazers, and  
504 bioturbators are the most likely candidates for microbialite decline.

505

## 506 **7. Conclusions**

507

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

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

525

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530

531

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786

787 **Figures**

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

793

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

800

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 pseudo-columnar 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 renalcid 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)

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

826

827 Figure 7: Point counts of microbialites showing percent fossil material from the  
828 Cambrian Port au Port and Ordovician St. George groups, western Newfoundland, and  
829 the middle Cambrian Carrara Formation near Death Valley National Park, California.

830 Circles indicate each slide counted, and diamonds show the average for each category.

831

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

838

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

844

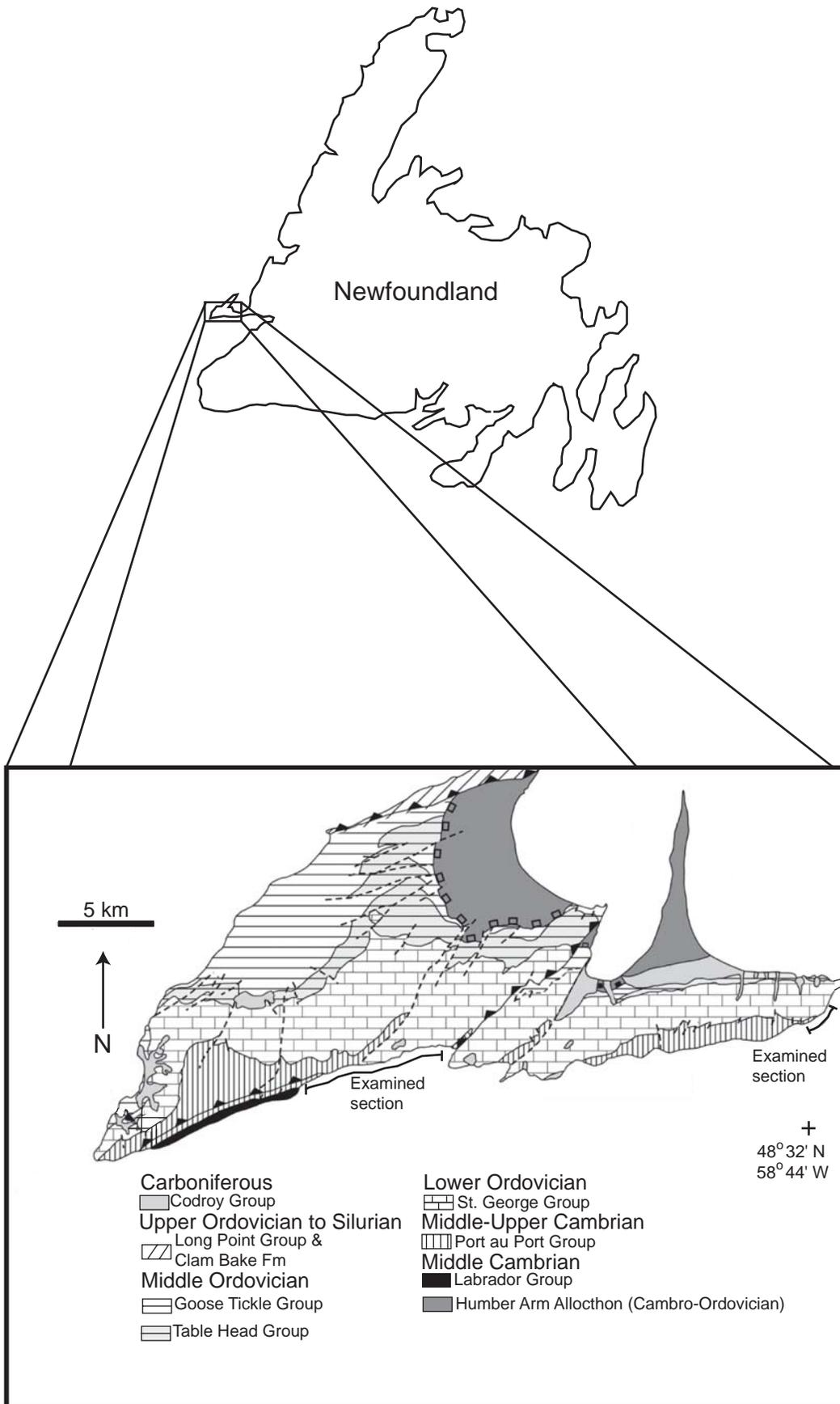


Fig. 1

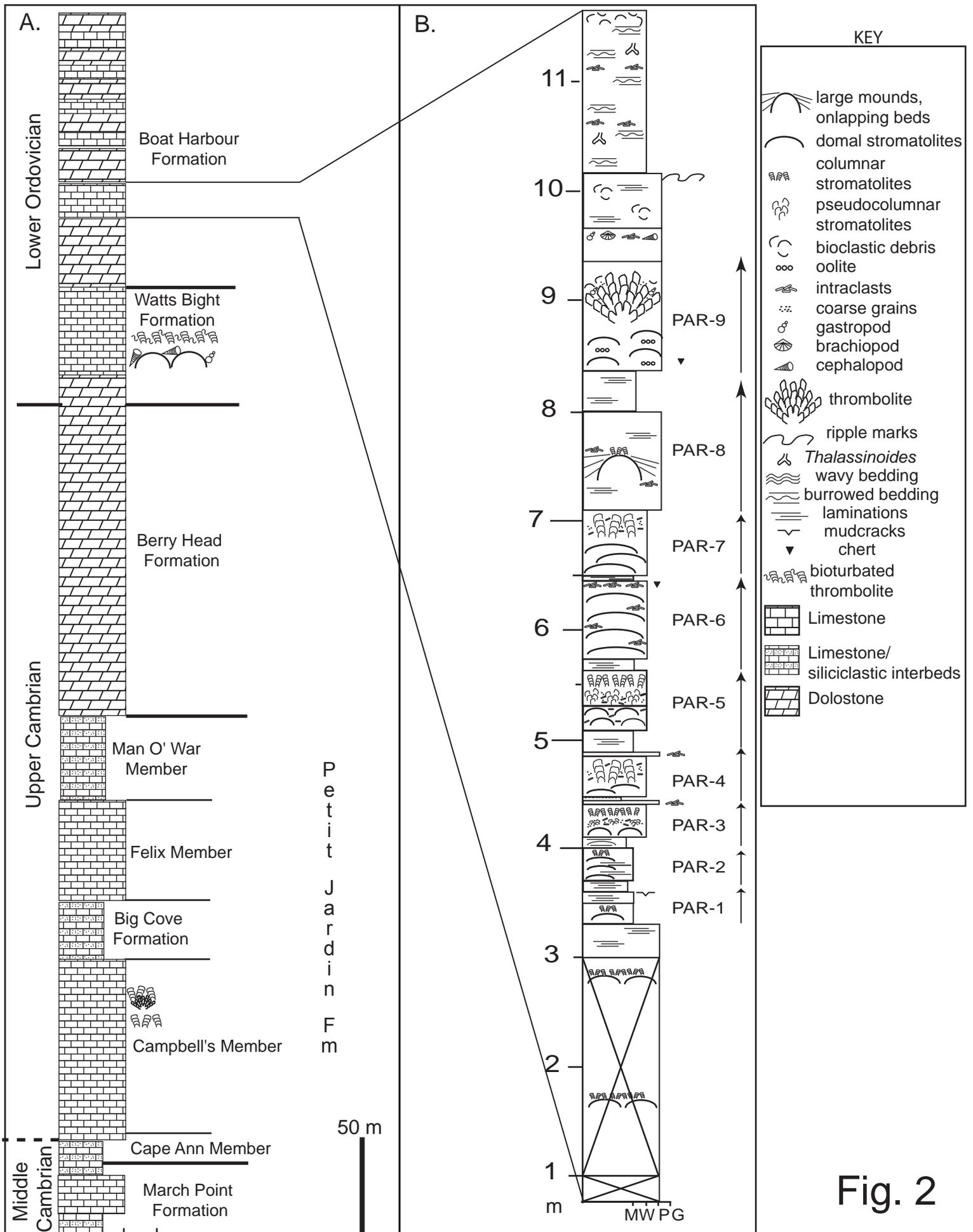


Fig. 2

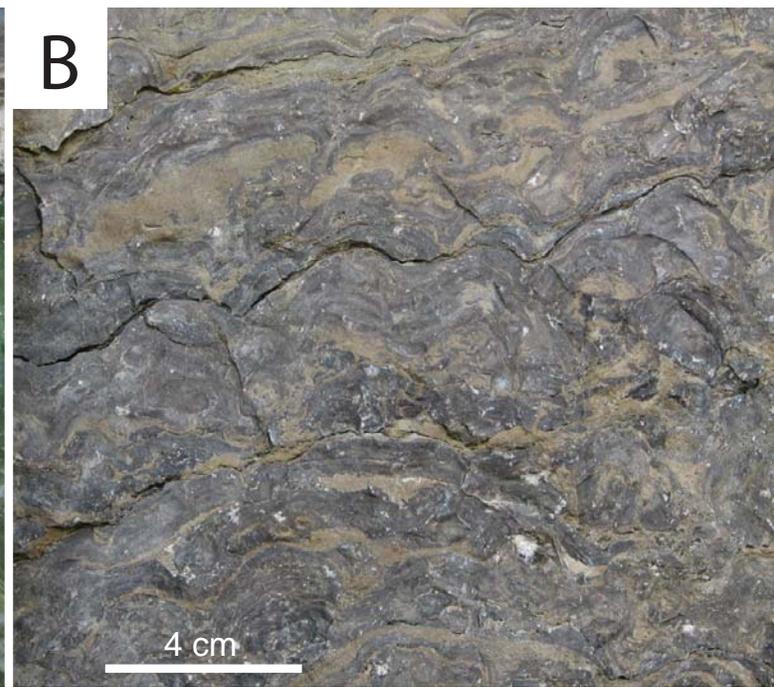
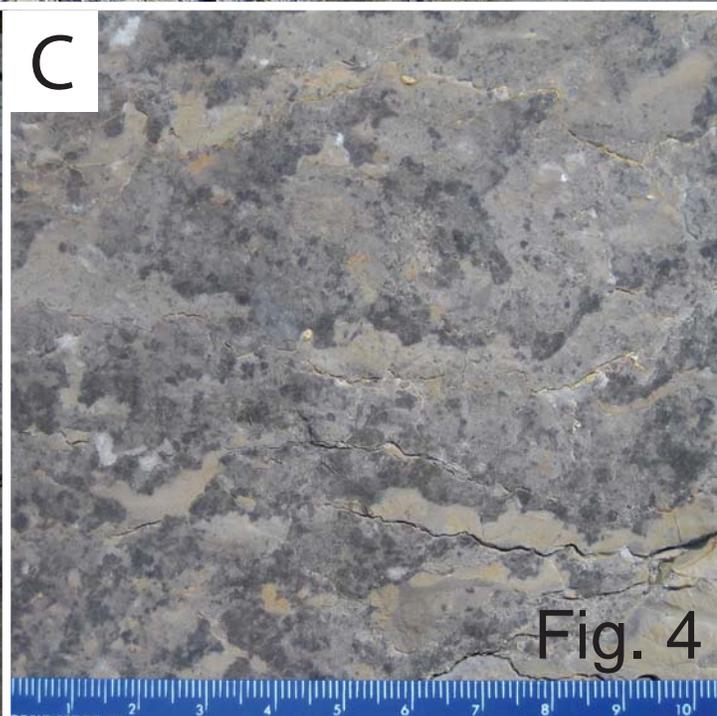
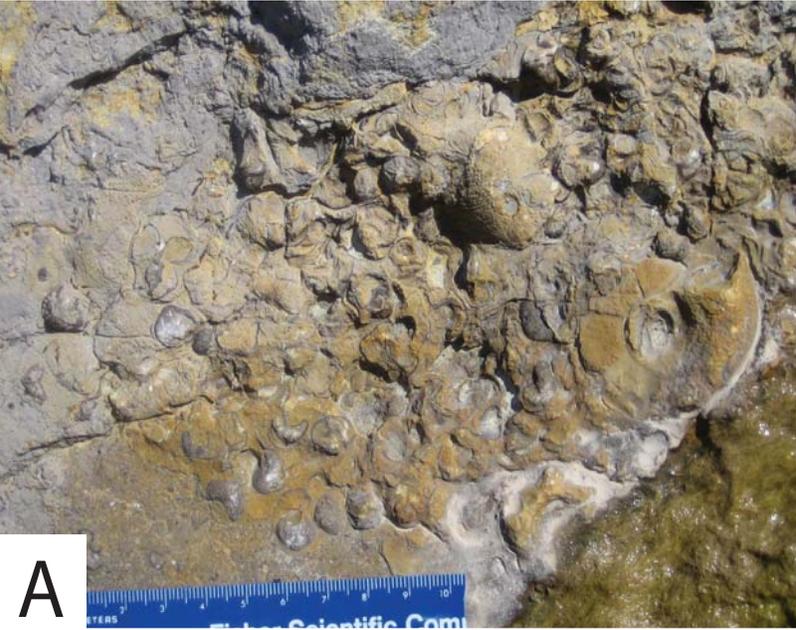


Fig. 3





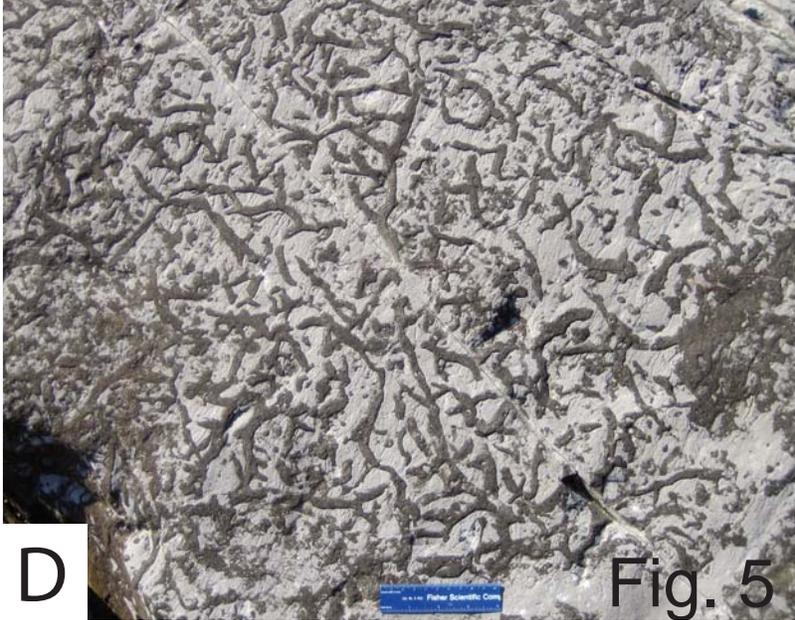
A



B



C



D

Fig. 5

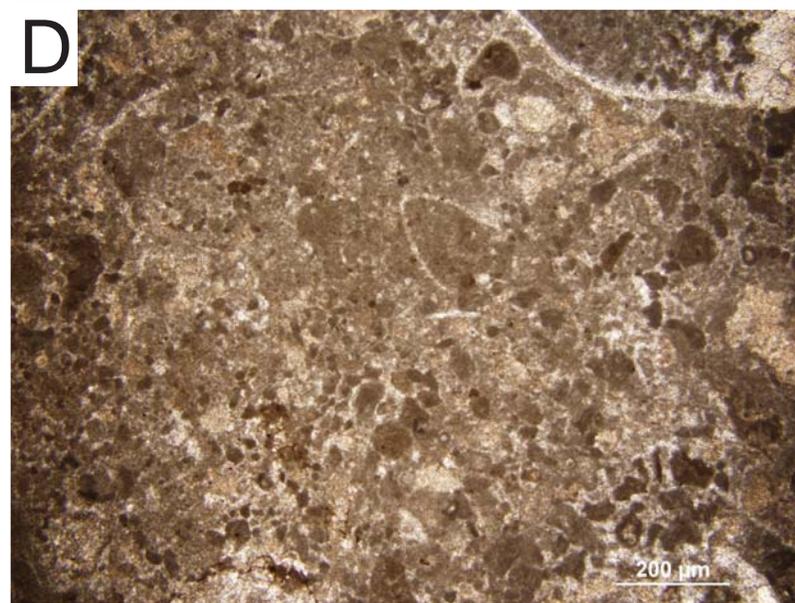
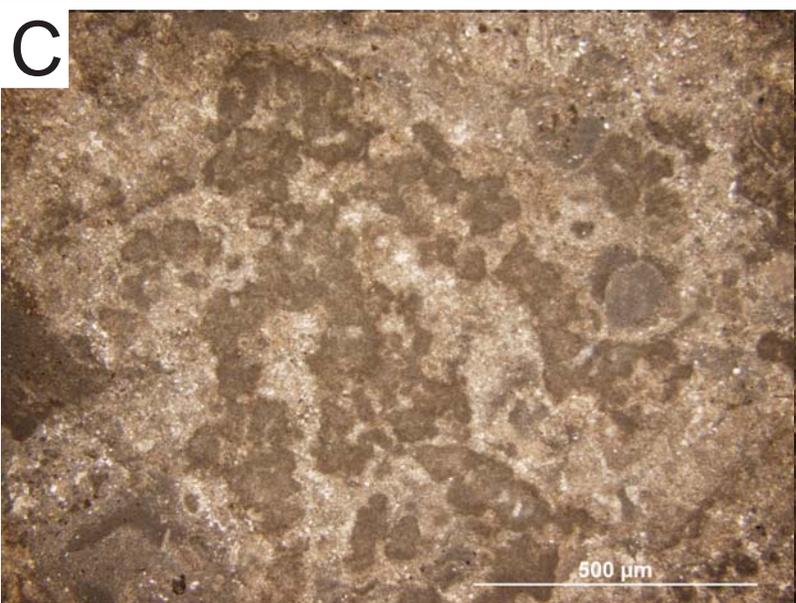
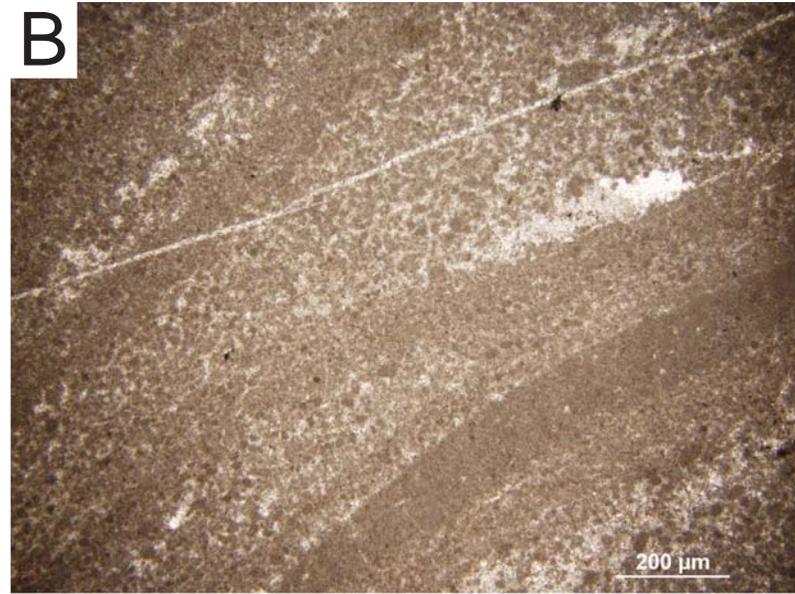
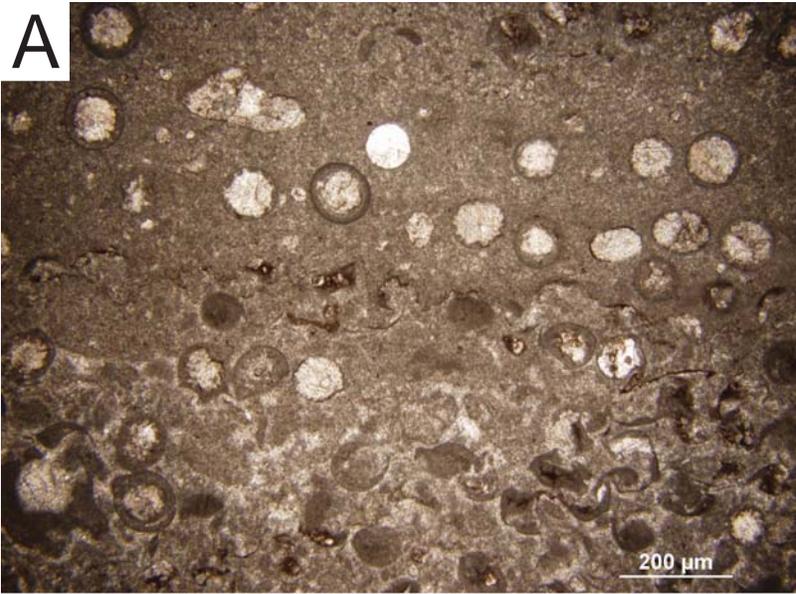


Fig. 6

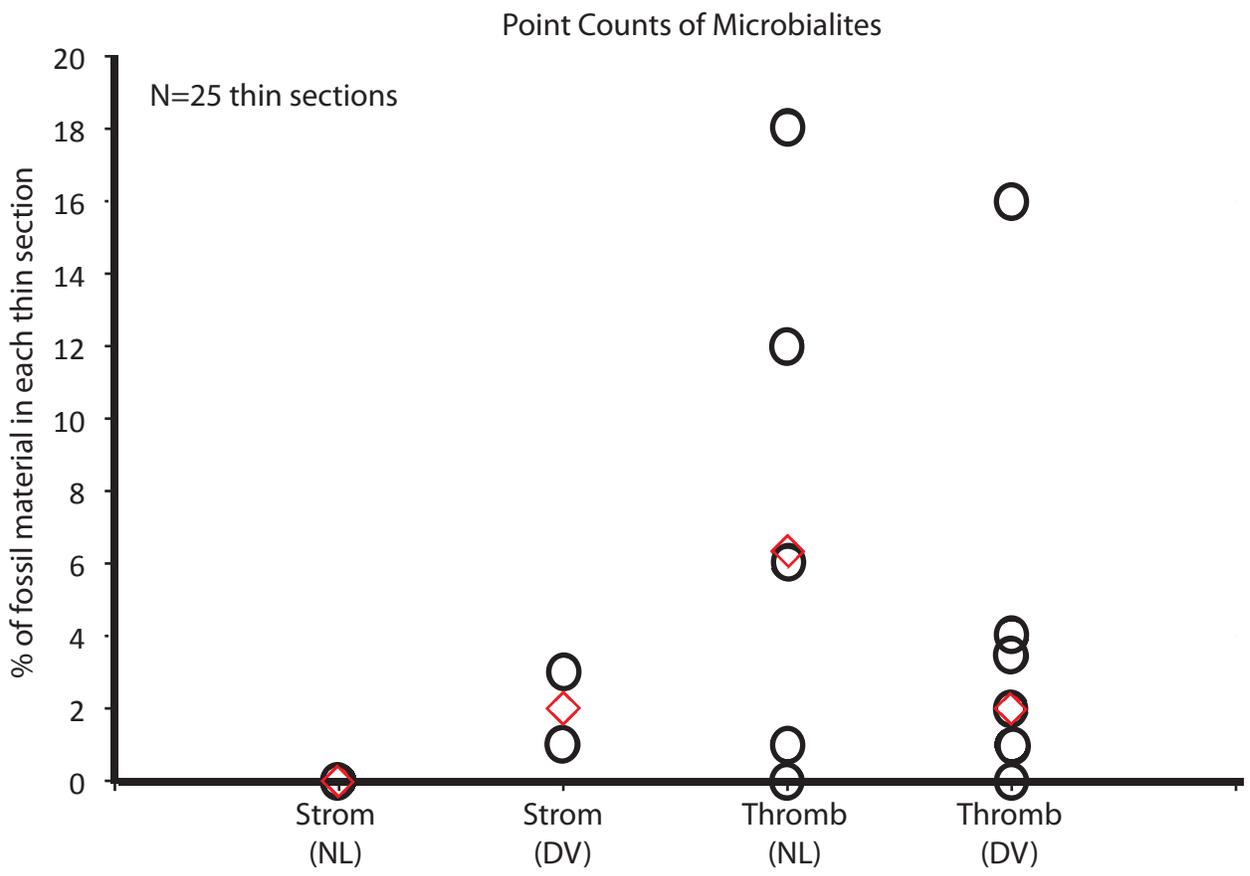


Fig. 7

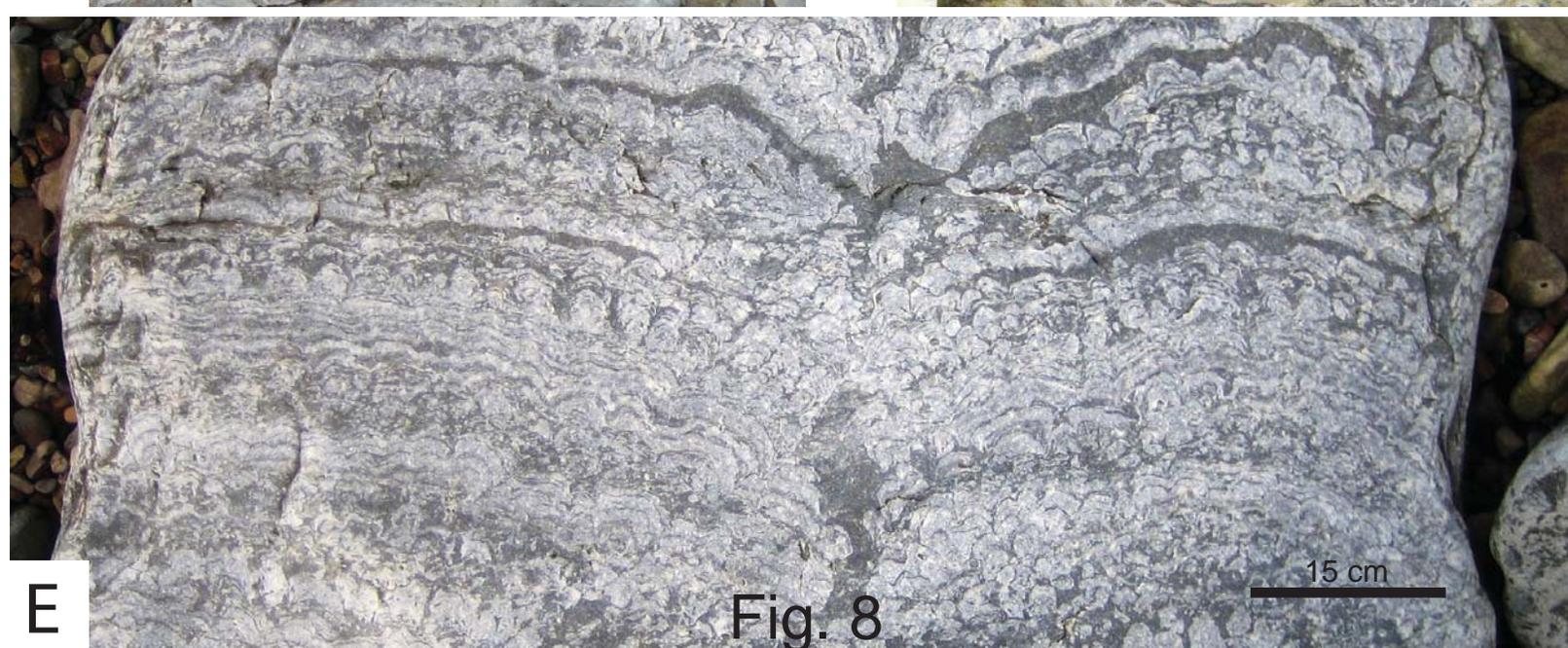
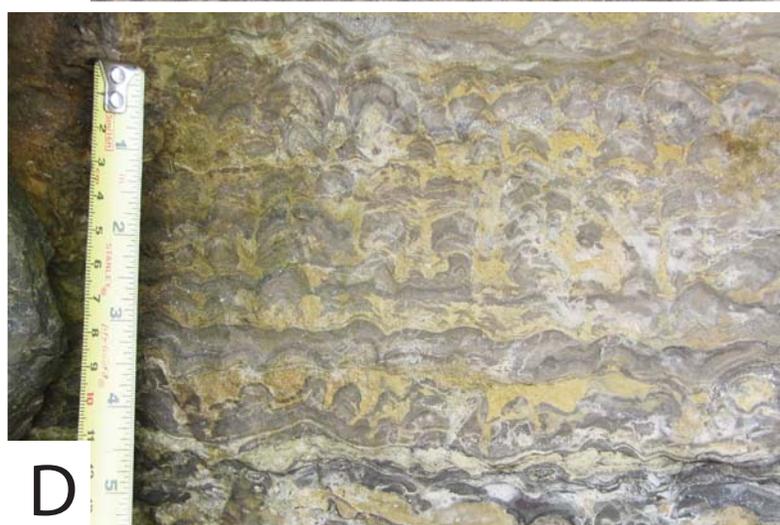
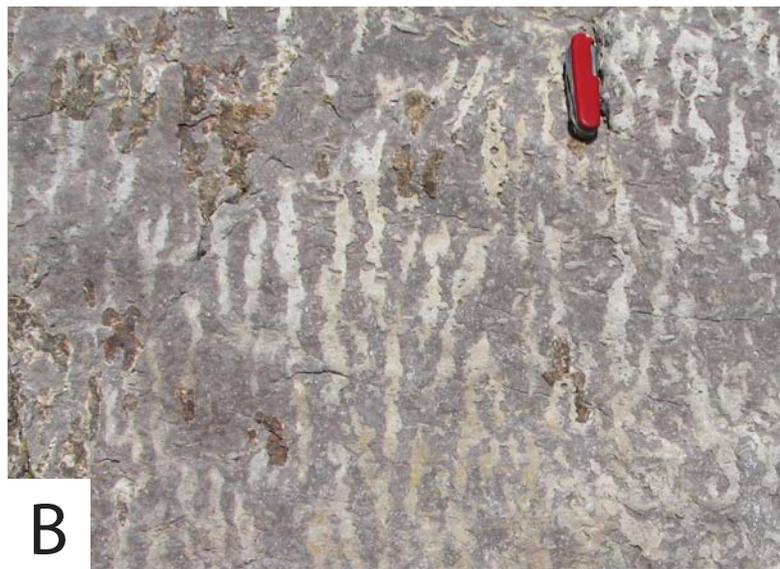


Fig. 8

	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	