



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

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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 thombolitic 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 thombolites 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 Ω 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 Ω 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 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 Ω . 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

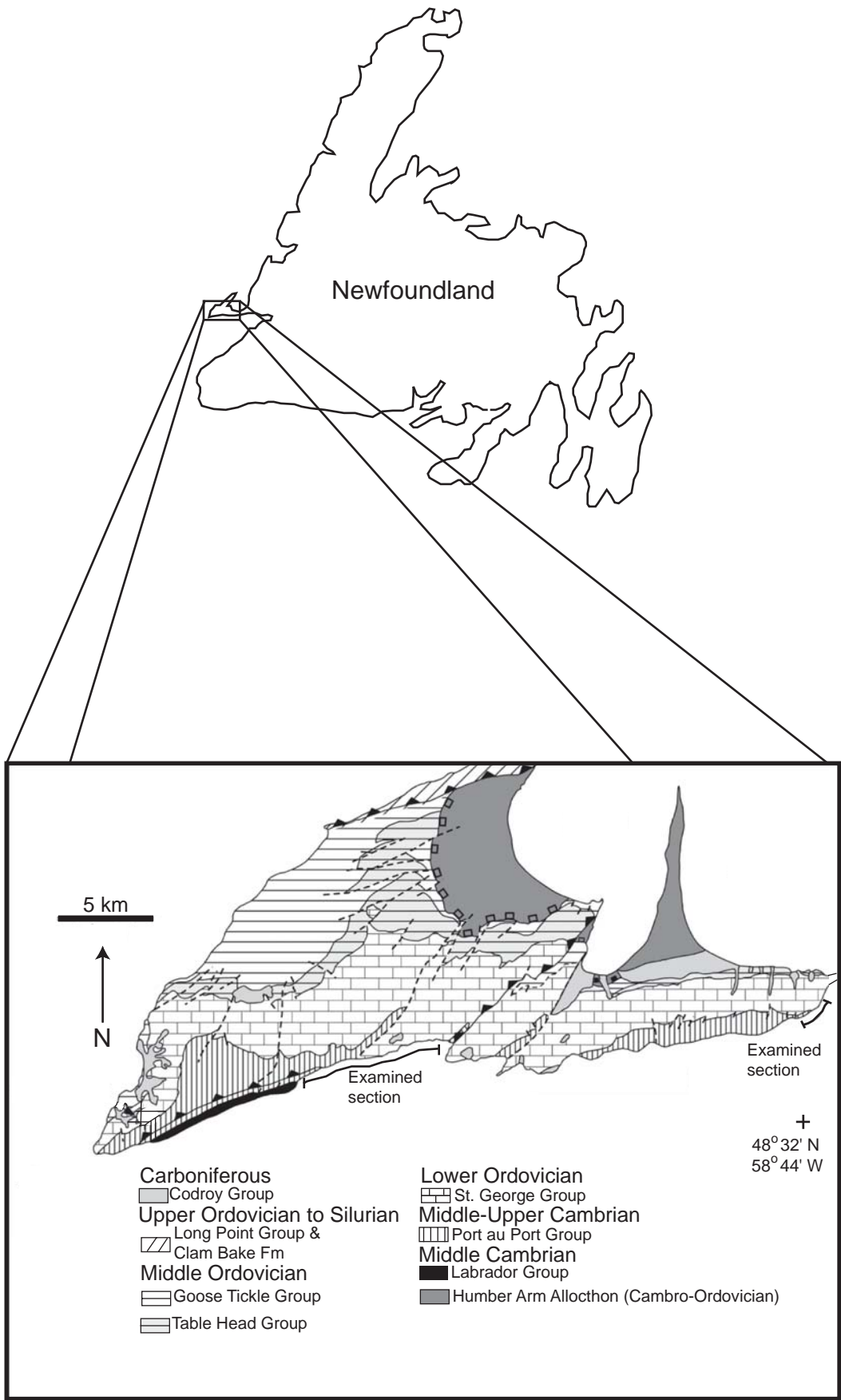


Fig. 1

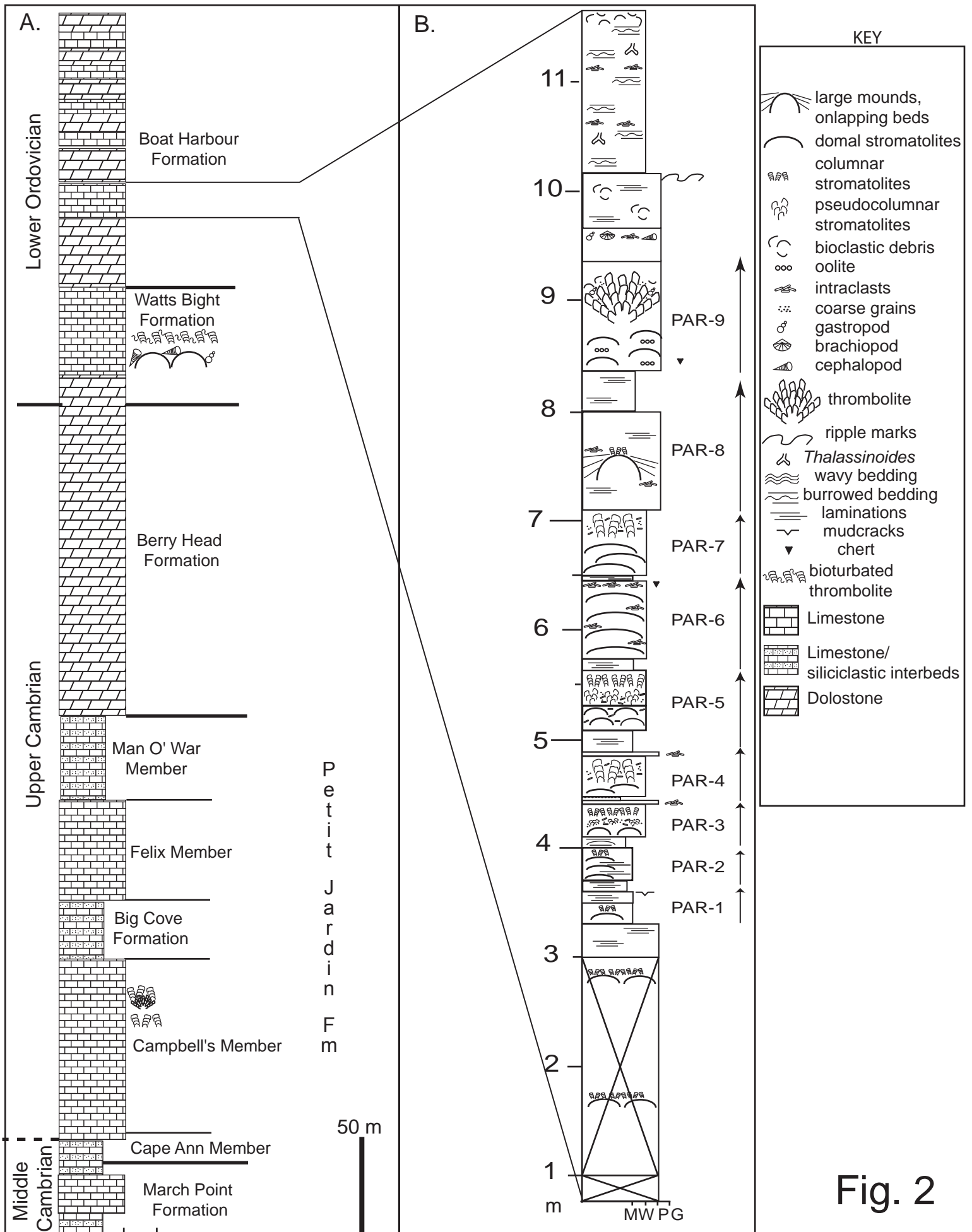


Fig. 2

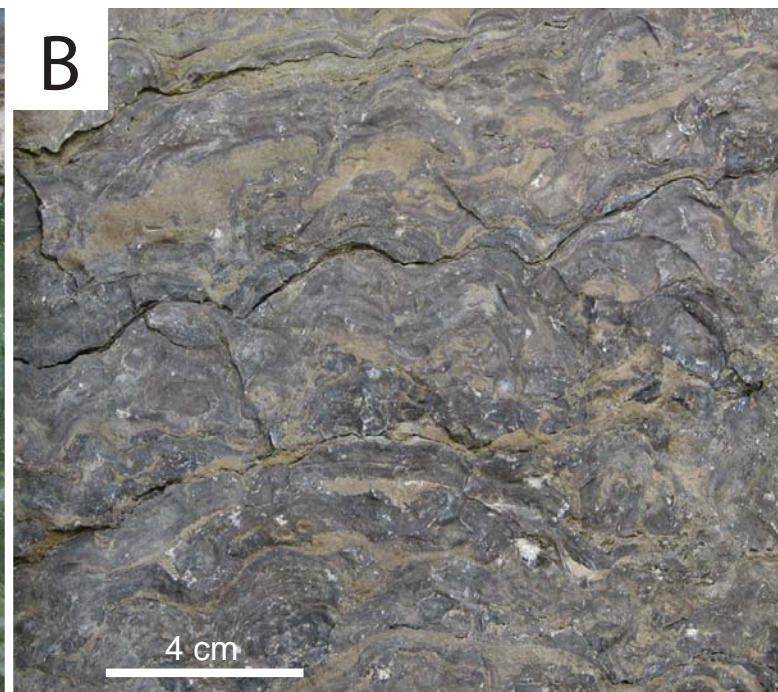
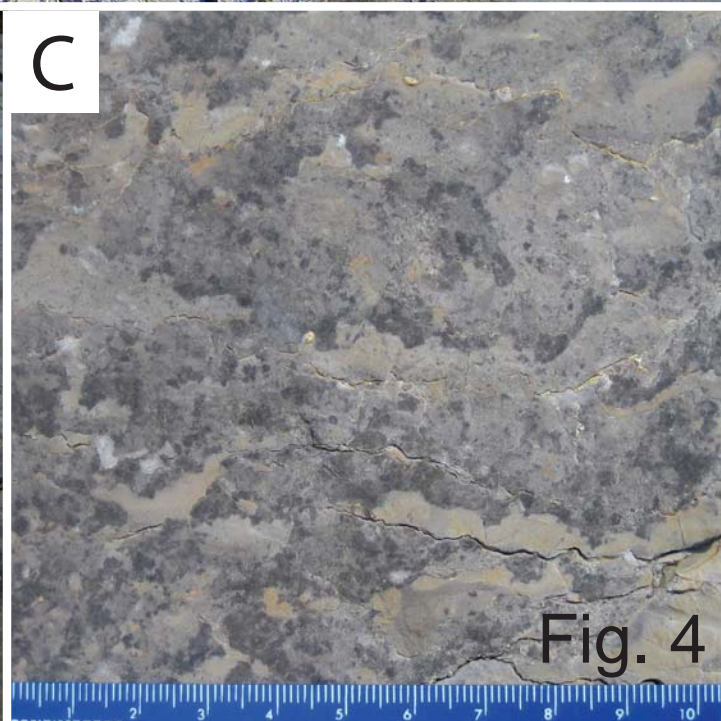
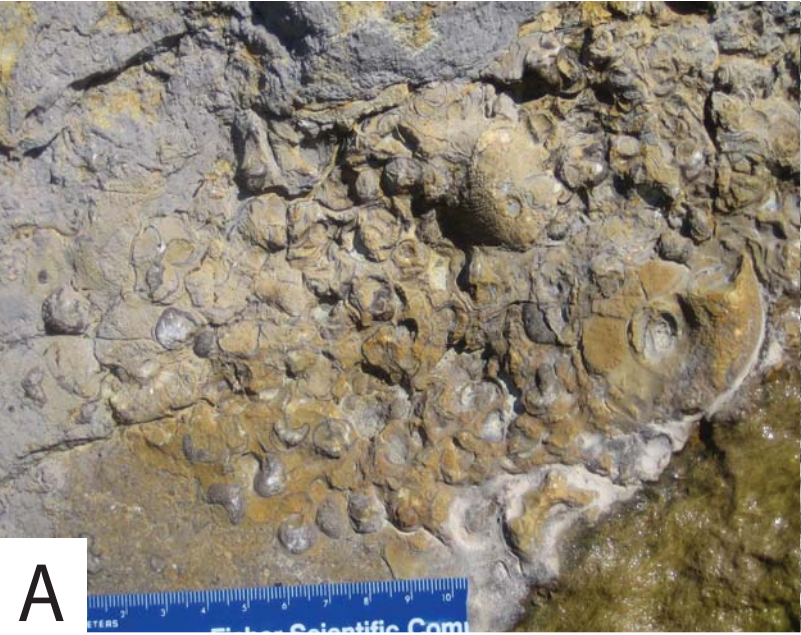


Fig. 3





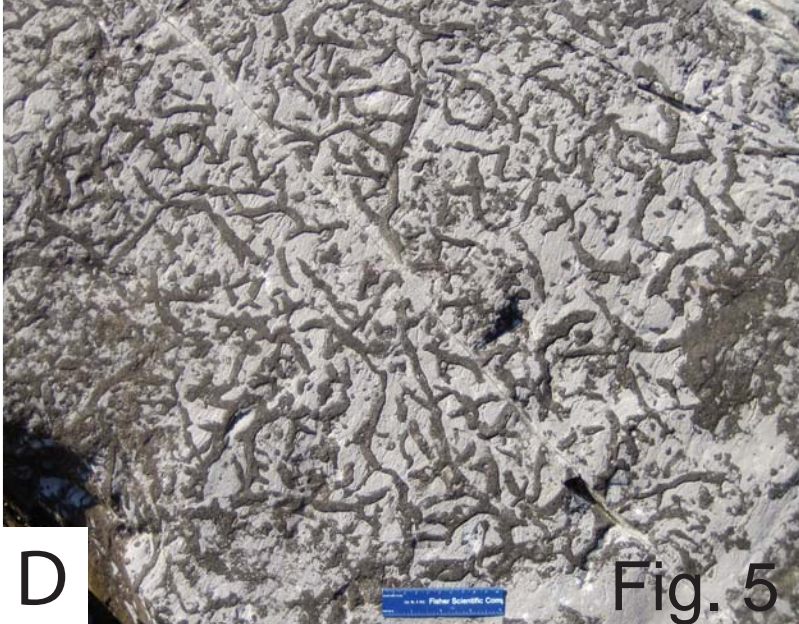
A



B



C



D

Fig. 5

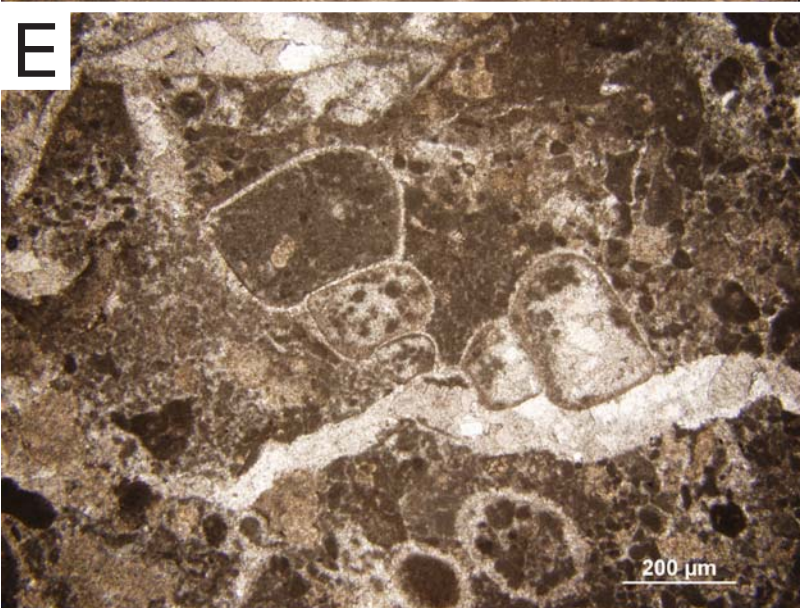
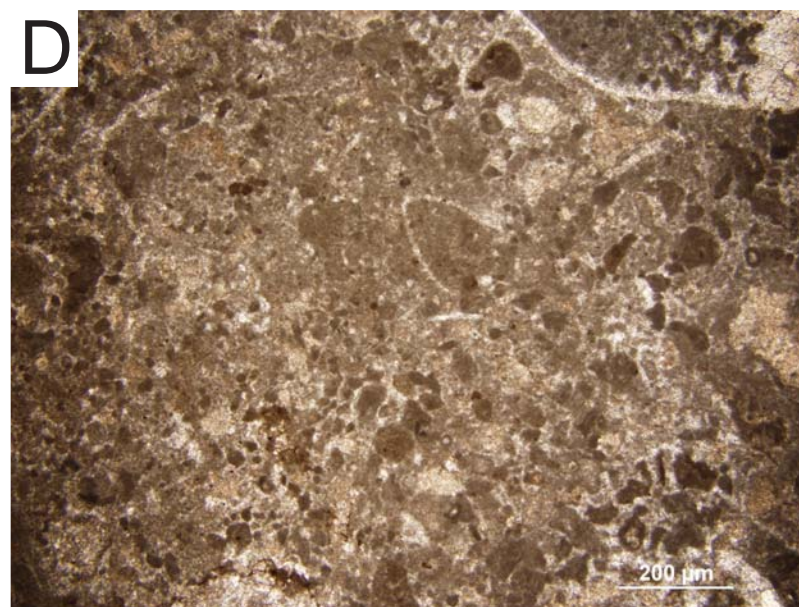
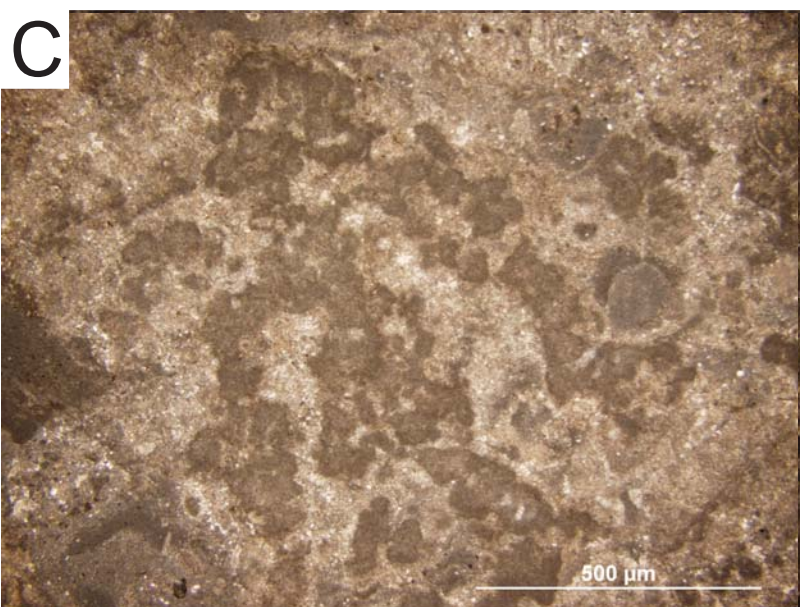
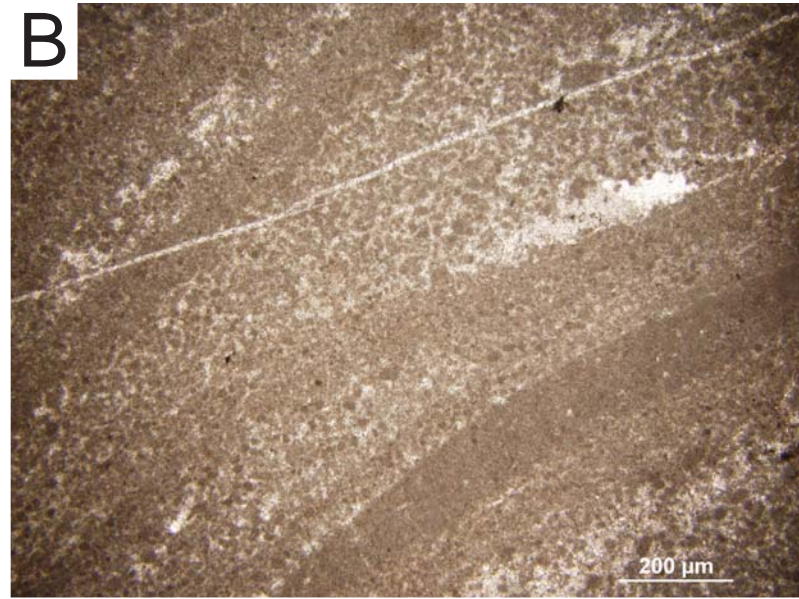
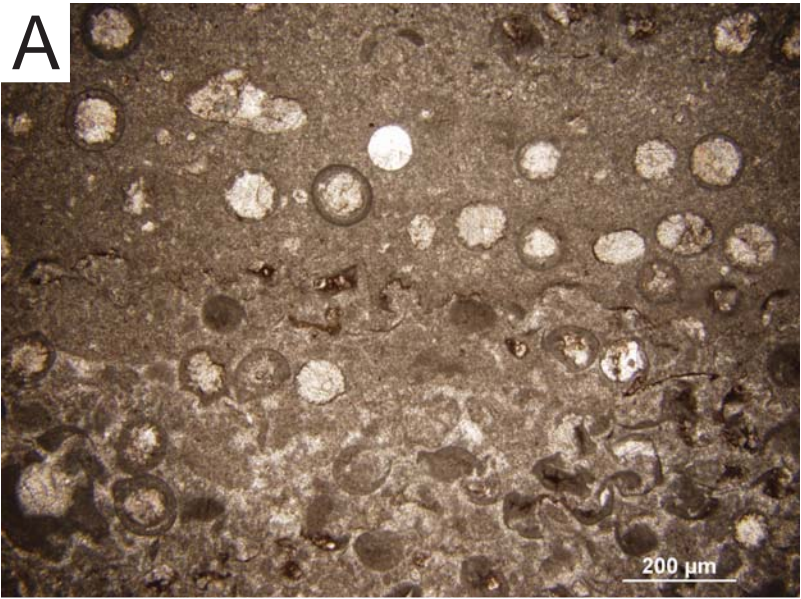


Fig. 6

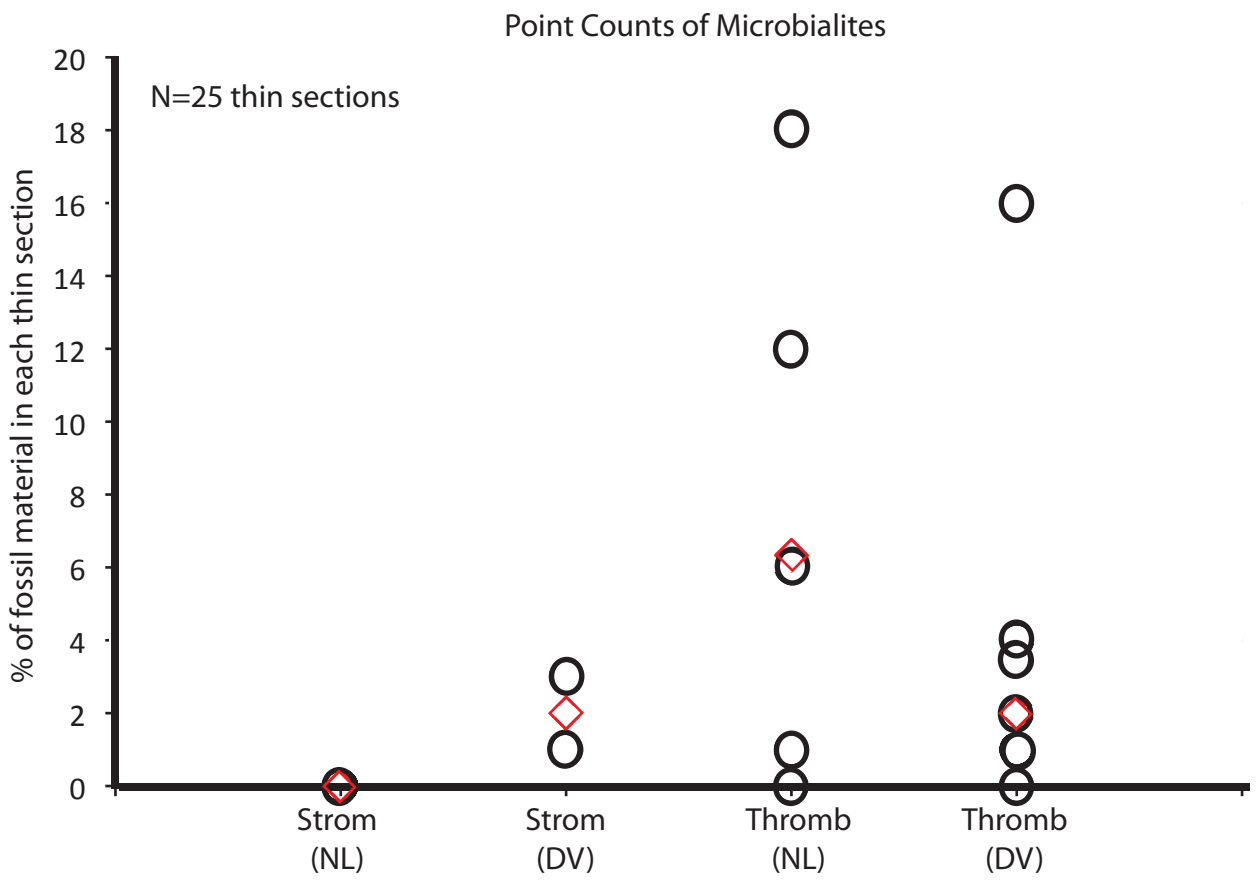


Fig. 7

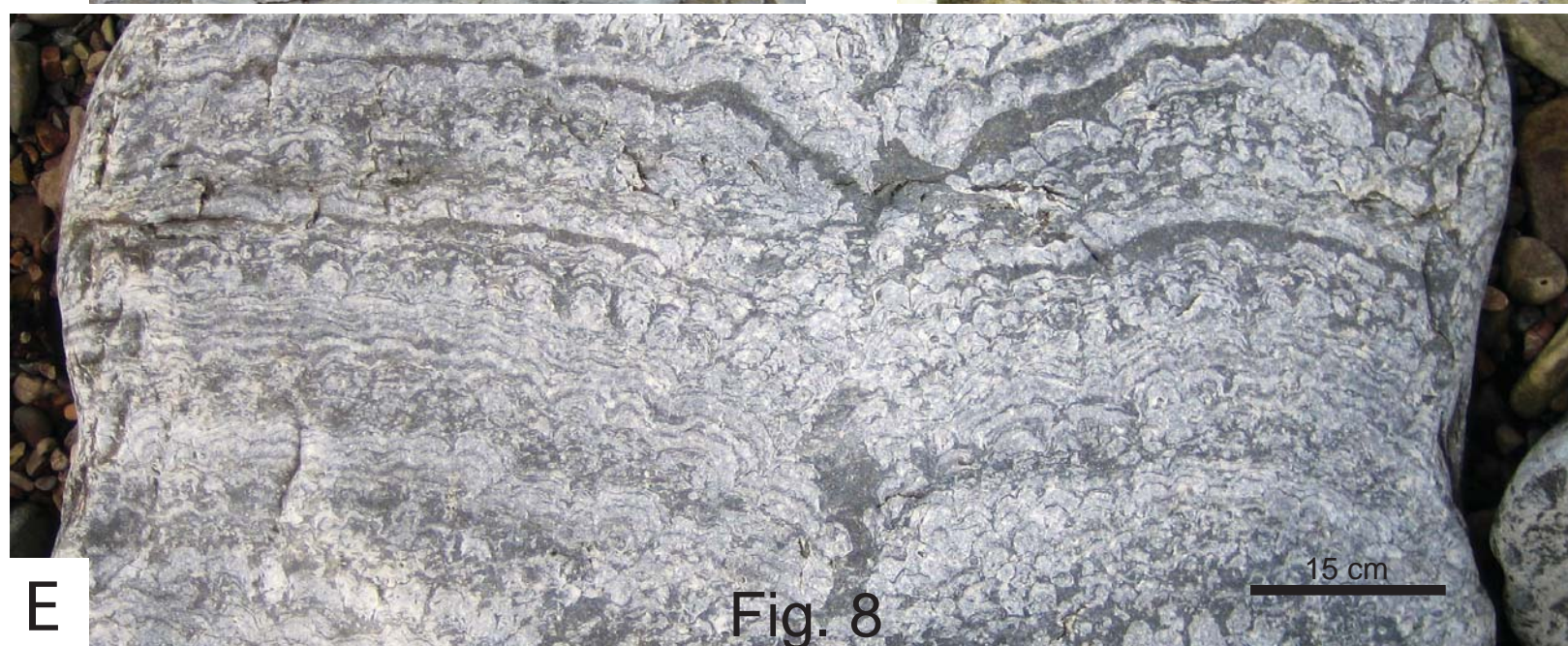


Fig. 8

	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	